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Triassic Foraminifera from the Great Bank of Guizhou, Nanpanjiang Basin, south China: taxonomic account, biostratigraphy, and implications for recovery from end-Permian mass extinction

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Abstract.—Foraminifera are important components of tropical marine benthic ecosystems and their recovery pattern from the end-Permian mass extinction can yield insights into the Mesozoic history of this group. Here we report the calcareous and agglutinated foraminifera recovered from five measured stratigraphic sections on the Great Bank of Guizhou, an uppermost Permian to Upper Triassic isolated carbonate platform in the Nanpanjiang Basin, south China. The material contains >100 Triassic species, including three that are newly described (*Arenovidalina weii* n. sp., *Meandrospira*? *enosi* n. sp., and *Spinoendotebanella lehrmanni* n. gen., n. sp.), ranging from Griesbachian (Induan) to Cordevolian (Carnian) age. The species belong to the classes Miliolata, Textulariata, Fusulinata, Nodosariata, and to an unknown class housing all aragonitic forms of the orders Involutinida and Robertinida. Based on previously established conodont zones and carbon isotope chemostratigraphy, the Griesbachian (early Induan) through Illyrian (late Anisian) interval has been subdivided into 12 foraminiferal zones and two unnamed intervals devoid of foraminifera. Following the extinction at the Permian-Triassic boundary, habitable ecological niches of Griesbachian age were invaded by disaster taxa that subsequently became extinct during the Dienerian (late Induan) and left no younger descendants. The disaster taxa were replaced by Lazarus taxa with Permian origins, which were then decimated by the Smithian-Spathian (mid-Olenekian) boundary crisis. The tempo of recovery appears to have been modulated by environmental changes during the Griesbachian through Smithian that involved both climate change and expansion of anoxic ocean bottom waters. Uninterrupted and lasting recovery of benthic foraminifera did not begin until the Spathian.

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Introduction

The events at the Permian-Triassic boundary profoundly changed the evolutionary history of Earth's biota (Sepkoski, 1981; Erwin, 1994). Foraminifera were among the major faunal groups severely affected by these events, and several distinct Permian foraminiferal assemblages became extinct at the end of the Permian Period. Following this end-Permian mass extinction, the largest biotic and ecological crisis of the Phanerozoic (Raup and Sepkoski, 1982; Bambach, 2006; Payne and Clapham, 2012), recovery of foraminifera and other benthic marine organisms was delayed and interrupted by ongoing adverse environmental conditions as well as several distinct environmental crises (Payne et al., 2004; Lau et al., 2016; Zhang et al., 2018). Due to the complexity of environmental change and biological response during the extended recovery interval, which lasted into the Middle Triassic (Hallam, 1991; Payne et al., 2011; Chen and Benton, 2012), detailed taxonomic study and fine-scale time resolution are required to establish the pattern of recovery and its relationship to environmental change.

Foraminifera are well suited to the study of recovery dynamics due to their diversity and abundance in Lower and Middle Triassic carbonates. The Triassic foraminiferal fauna of the Great Bank of Guizhou, an isolated carbonate platform of latest Permian to Late Triassic age within the Nanpanjiang Basin of south China, are particularly advantageous for this purpose. Foraminifera are abundant in many samples, distributed throughout stratigraphic sections exceeding 2000 m in thickness, and preserved in depositional environments from platform interior to basin margin (Payne et al., 2006, 2011; Song et al., 2011a).

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The Great Bank of Guizhou, studied in five different measured sections, namely Dawen (PDW), Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PDG), and Upper Guandao (PUG), contains well-diversified Early to early Late Triassic benthic foraminifera assemblages. Under the Phylum Foraminifera, the studied foraminifera assemblages belong to classes Miliolata, Textulariata, Fusulinata, Nodosariata, and to an uncertain class housing the involutinid- and robertinid-type foraminifera.

During the second half of the last century, several authors described and documented Early to Middle Triassic foraminiferal taxa (Ho, 1959; Luperto, 1965; Pantić, 1965; Kochansky-Devidé and Pantić, 1966; Koehn-Zaninetti, 1969; Baud et al., 1971, 1974; Premoli Silva, 1971; Brönnimann and Zaninetti, 1972; Brönnimann et al., 1972a, b, 1973a, b, c, 1974; Zaninetti et al., 1972a, b, c, 1978, 1994; Efimova, 1974; Gazdzicki et al., 1975; Stampfli et al., 1976; Zaninetti, 1976; Gazdzicki and Smit, 1977; Dağer, 1978a; Trifonova, 1978a, b, c, 1992, 1993, 1994; Čatalov and Trifonova, 1979; Altıner and Zaninetti, 1981; Salaj et al., 1983; He, 1984, 1988, 1993; Orovecz-Scheffer, 1987; Benjamini, 1988; He and Wang, 1990; He and Cai, 1991; Altıner and Koçyiğit, 1993; Rettori et al., 1994; Rettori, 1995). Some selected genera directly from the late Paleozoic in the definition of their new taxa, such as *Rectocornuspira* (now *Postcladella*), *Cornuspira* (previously described as *Cyclogyra*), *Permodiscus*, *Endothyra*, and *Earlandia*, therefore studies relating Early Triassic foraminiferal taxa to the Permian-Triassic mass extinction event were carried out only rarely prior to the end of the last century (Nakazawa et al., 1975; Altıner et al., 1980; Taraz et al., 1981; Sheng et al., 1984; Neri and Pasini, 1985; Pasini, 1985; Broglio Loriga et al., 1988; Cirilli et al., 1998).

As the importance of the Permian-Triassic boundary mass extinction within the evolution of Phanerozoic marine ecosystems became clear (Sepkoski, 1981; Raup and Sepkoski, 1982; Wignall and Hallam, 1992; Erwin, 1993), research into the causes and mechanisms of the mass extinction and controls on subsequent biotic recovery accelerated (Erwin, 1994, 2007; Rampino and Adler, 1998; Jin et al., 2000; Tong and Shi, 2000; Leven and Korchagin, 2001; Wignall and Newton, 2003; Altıner et al., 2005; Groves and Altıner, 2005; Kaiho et al., 2006; Song et al., 2007, 2011a, 2013; Yin et al., 2007; Algeo et al., 2011; Payne et al., 2011; Rego et al., 2012). As part of this previous research, the evolution of foraminifera in the Lower to Middle Triassic stratigraphy has been studied to understand extinction and recovery dynamics. Foraminiferal paleontologists and stratigraphers started to trace and document foraminifera along measured sections encompassing the Permian-Triassic boundary and to include data from other disciplines in order to improve their foraminifera-based chronology (Broglio Loriga and Cassinis, 2003; Ünal et al., 2003; Altıner et al., 2005; Groves et al., 2005, 2007; Mohtat-Aghai and Vachard, 2005; Angiolini et al., 2007; Théry et al., 2007; Vuks, 2007; Galfetti et al., 2008; Maurer et al., 2008; Korchagin, 2011; Krainer and Vachard, 2011; Nestell et al., 2011; Song et al., 2011b, 2015, 2016, 2018; Lehrmann et al., 2015).

The purpose of this study is to give a comprehensive taxonomic account of the Early to Middle Triassic foraminifera from the Great Bank of Guizhou, including descriptions of one new genus and three new species recovered. In addition, the occurrence patterns of the taxa along measured stratigraphic sections are used to develop a foraminiferal biostratigraphic framework for the Lower Triassic through Anisian interval. This biostratigraphic study excludes the Ladinian and Carnian stages of the measured sections because the foraminiferal data recovered from these stages are more fragmentary due to a combination of unfavorable facies and poor preservation in collected samples. The occurrence patterns are further used to assess the recovery of foraminifera following the end-Permian mass extinction within an Early to Middle Triassic timescale calibrated by conodonts.

Geological setting and studied stratigraphic sections

The foraminiferal study is based on samples from five stratigraphic sections measured on outcrops of the Great Bank of Guizhou (GBG), an isolated carbonate platform of latest Permian to earliest Late Triassic age located in the Nanpanjiang Basin of the Yangtze Block, southern China (Fig. 1). The Nanpanjiang Basin was a deep-marine embayment in the southern margin of the south China tectonic block and is bordered by the Yangtze Platform, a vast shallow-marine carbonate platform that stretched across south China. The GBG initiated in the latest Permian during a relative rise in sea level that drowned much of the Yangtze Platform (Fig. 1.1; Lehrmann, 1993; Lehrmann et al., 1998, 2005, 2007, 2015; Payne et al., 2004, 2006). Uppermost Permian skeletal carbonates of the Wujiaping Formation underlie the platform interior, whereas fine-grained siliciclastics of the uppermost Permian Dalong Formation underlie the Permian/Triassic transition beneath Lower Triassic slope facies. During the Early Triassic, the depositional setting of the GBG was a low-relief bank with oolite shoals developed at the margin, a shallow subtidal to peritidal interior, and slopes dominated by hemipelagic carbonate mud intercalated with thin carbonate turbidites and debris flows shed from the margin (Lehrmann et al., 1998, 2005). Recently, reconstruction of the GBG in the latest Permian to Early Triassic interval has been partly revised by Kelley et al. (2020), who defined three stages of development. These authors considered the latest Permian–Smithian interval as the initiation and low-relief bank stages, and the Smithian to late Spathian interval as the aggrading and steepening stage. The Lower Triassic platform interior consists of shallow-marine carbonates of the Daye Formation overlain by dolomitized shallow-marine carbonates of the Anshun Formation. The Lower Triassic shales, micritic carbonates, carbonate turbidites, and allodapic breccias of the slope belong to the Luolou Formation. In the Middle Triassic, Anisian *Tubiphytes* reefs rimmed the outer margin and slope of the GBG while peritidal conditions continued in the interior (Fig. 1.2). The platform subsequently developed a high-relief escarpment during Ladinian. The escarpment profile continued until the early Carnian, when the GBG drowned due to accelerated tectonic subsidence and was subsequently buried by siliciclastic turbidites (Lehrmann et al., 1998, 2005). The Middle Triassic shallow-marine carbonates of the platform interior belong to the Yangliujing Formation, and the Middle Triassic slope carbonates belong to the Xinyang Formation. The Upper Triassic siliciclastic turbidites of the Bianyang Formation filled the remaining accommodation in the basin and, ultimately, buried the platform top.

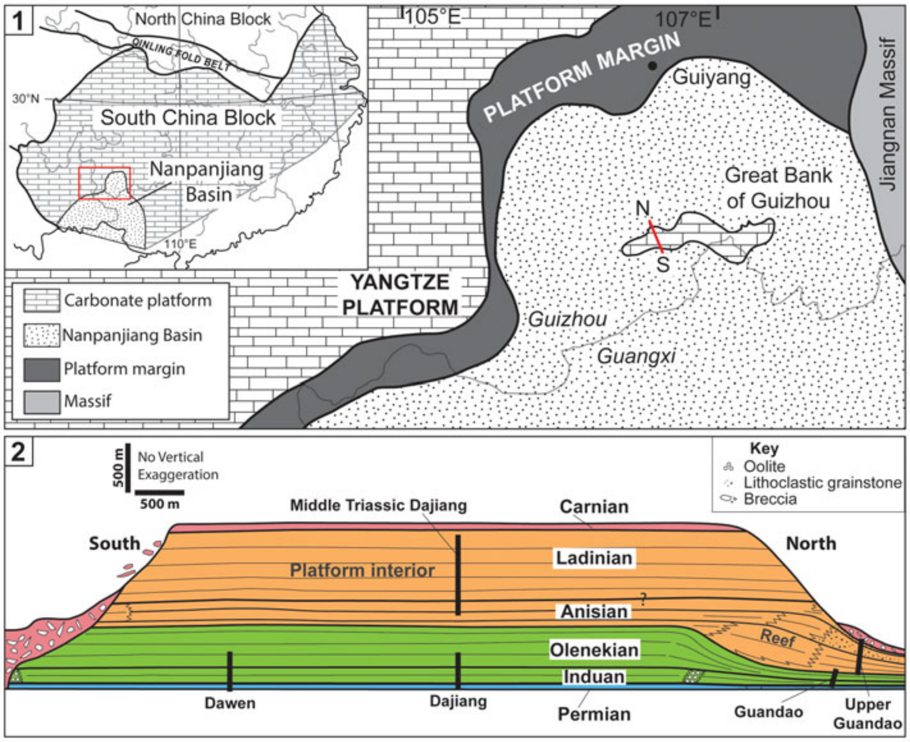


Figure 1. (**1**) Early Triassic paleogeographic map (Lehrmann et al., 1998; Payne et al., 2004). Hash pattern indicates the Nanpanjiang Basin and brick pattern indicates the Yangtze Platform and GBG. (**2**) Schematic cross section of the Great Bank of the Guizhou, illustrating the locations of Dawen, Dajiang, Middle Triassic Dajiang, Guandao, and Upper Guandao sections within the platform architecture.

The studied stratigraphic sections span a range of depositional environments. Three of the studied sections—the Dawen, Dajiang, and Middle Triassic Dajiang sections—are located in the platform interior (Fig. 1.2). Both the Dawen and Dajiang sections cover the stratigraphic interval from Griesbachian to Smithian. The Middle Triassic Dajiang section consists of four short sections (~20 m) measured at intervals through a part of the thick carbonate platform spanning from the Pelsonian (mid Anisian) to Ladinian. The Guandao and Upper Guandao sections, representing the slope and basin-margin environments, cover the entire Griesbachian–lower Carnian interval (Fig. 2).

Materials

From the stratigraphic sections measured in the Great Bank of Guizhou, we collected a total of 1106 samples for lithostratigraphy, facies analysis, isotope stratigraphy, conodont and foraminiferal taxonomy, and biostratigraphy. From the samples displaying fossil fragments and suitable carbonate facies, 598 thin sections were prepared for the foraminifera, 246 of which contained at least one foraminifer. The total number of foraminifera specimens is >2500, of which 351 were illustrated in the figures of this paper.

Foraminifera recovered from the samples were first used in a genus-level study by Payne et al. (2011). These authors carried out a study on the Early–Middle Triassic trends in diversity, evenness, and size of the foraminifers to investigate the tempo and mode of biotic recovery. The current study concentrates, with a different scope and resolution, on species-level taxonomic description with many illustrations, construction of a new biostratigraphic scheme calibrated by conodonts, and a discussion of species-level recovery of Early–Middle Triassic foraminifera, with attention to phyletic relationships.

Repositories and institutional abbreviations.—Types, figures, and other specimens examined in this study are deposited in the thin section laboratory of the Department of Geological Sciences, Stanford University, with the following catalog abbreviations: Dawen (PDW), Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PGD) and upper Guandao (PUG) sections.

Systematic paleontology

Demir Altıner and Jonathan L. Payne

As indicated by Vachard (2016, 2018) the current classification of foraminifera based on wall microstructure disagrees with the results of molecular phylogenetic studies of extant species (e.g., Pawlowski et al., 2013). However, molecular results remain difficult to reconcile with the Paleozoic–Mesozoic fossil record. In this study, the Triassic foraminifera of the Great Bank of Guizhou have been classified at first in distinct populations at species rank, and then placed into reasonable categories at the genus level based on wall structure and composition and other morphological characters. Despite uncertainties in higher taxonomic ranks, we consider most of the families used in the Triassic foraminiferal paleontology to be adequate for recognized genera

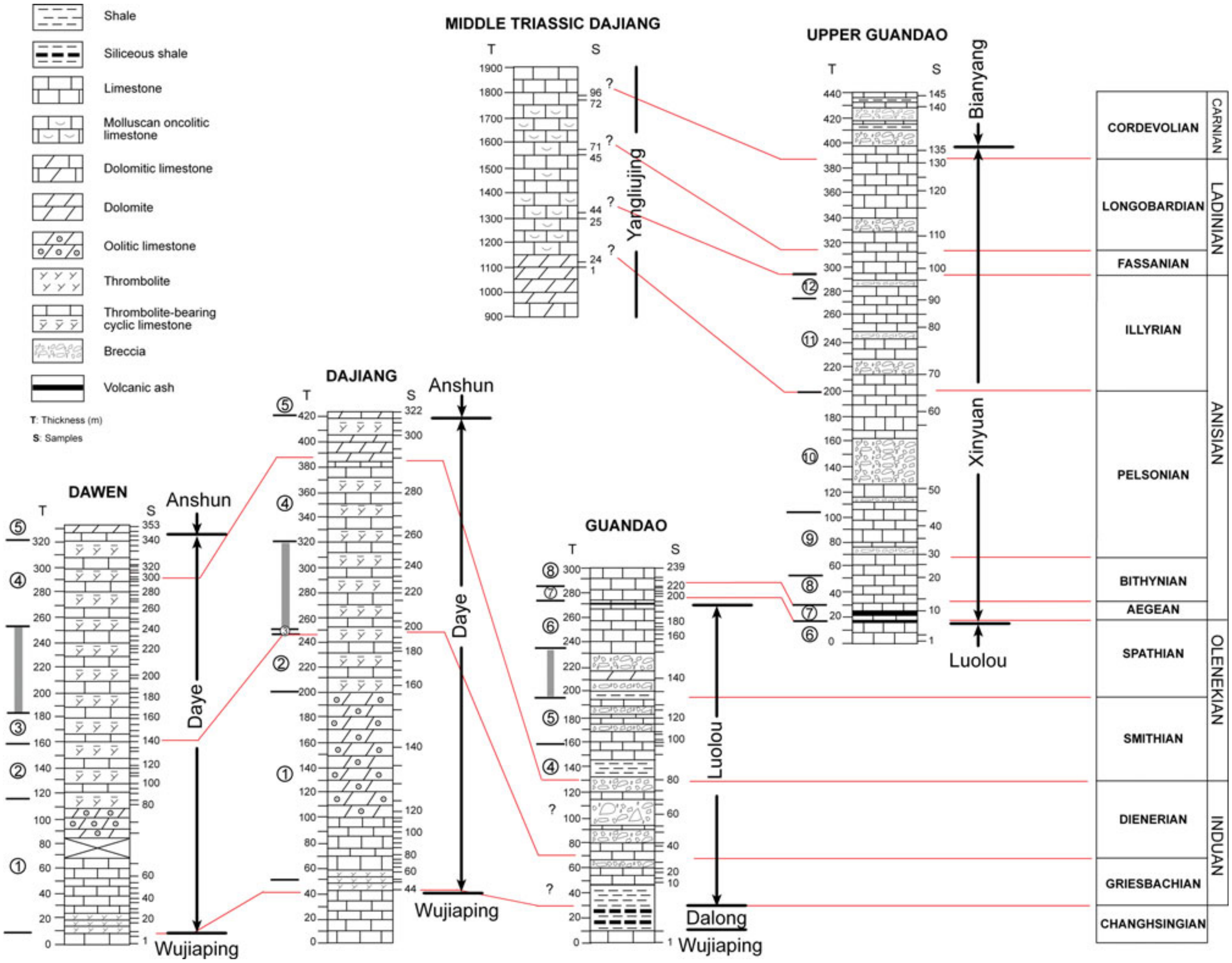


Figure 2. Stratigraphic columns of measured sections. Timescale is constrained by conodont occurrence data and physical stratigraphic and carbon isotope correlations between the basin margin and the platform interior (Payne et al., 2004; Lehrmann et al., 2015; Kelley et al., 2020). 1–12 = Biozones of foraminifera (for biozone names see Fig. 21). Gray vertical bar indicates intervals devoid of foraminifera.

and species. However, intermediate taxonomic ranks, including superfamily, suborder, and order, are less stable in their use across studies and have not been used in this study. For the largest groups of foraminifera, classified based on wall microstructure and assigned class rank, we have largely followed Vachard (2016, 2018) and Cavalier-Smith (2002, 2003), the latter of whom demonstrated that foraminifera constitute a phylum or subphylum.

Class Miliolata Saidova, 1981

Remarks.—One of the dominant groups of Early–Middle Triassic foraminifera on the Great Bank of Guizhou is the bilocular Miliolata, consisting of Cornuspiridae, Arenovidalinidae, Meandrospiridae, Hoyenellidae, and Agathamminidae and the primitive multilocular miliolid families Ophthalmiidae, Quinquelloculinidae, and Galeanellidae.

Family Cornuspiridae Schultze, 1854
Subfamily Cornuspirinae Schultze, 1854

Genus *Postcladella* Krainer and Vachard, 2011
Postcladella kalhori (Brönnimann, Zaninetti, and Bozorgnia, 1972a)
Figure 3.1–3.26

Remarks.—There is currently disagreement regarding the taxonomy of Early Triassic cornuspirin taxa, which is one of the most common foraminiferal groups in basal Triassic strata. Two of the frequently cited taxa, *Rectocornuspira kalhori* and *Cyclogyra*? *mahajeri*, were described by Brönnimann et al. (1972a). The primary difference between these two taxa, commonly encountered in axial sections, is that the lumen of the final whorl of *C*.? *mahajeri* overlaps laterally onto the previous coil. Brönnimann et al. (1972a) added that this character distinguishes this species from the axially slender and strongly biumbilicate planispiral stage of *R*. *kalhori*. This approach was altered by Gaillot and Vachard (2007, p. 84), who considered Early Triassic *Rectocornuspira* as an uncoiled *Cornuspira* and stated that '*Rectocornuspira* would correspond to *Cornuspira* with a morphological adaptation, more or less developed, depending on the local or regional

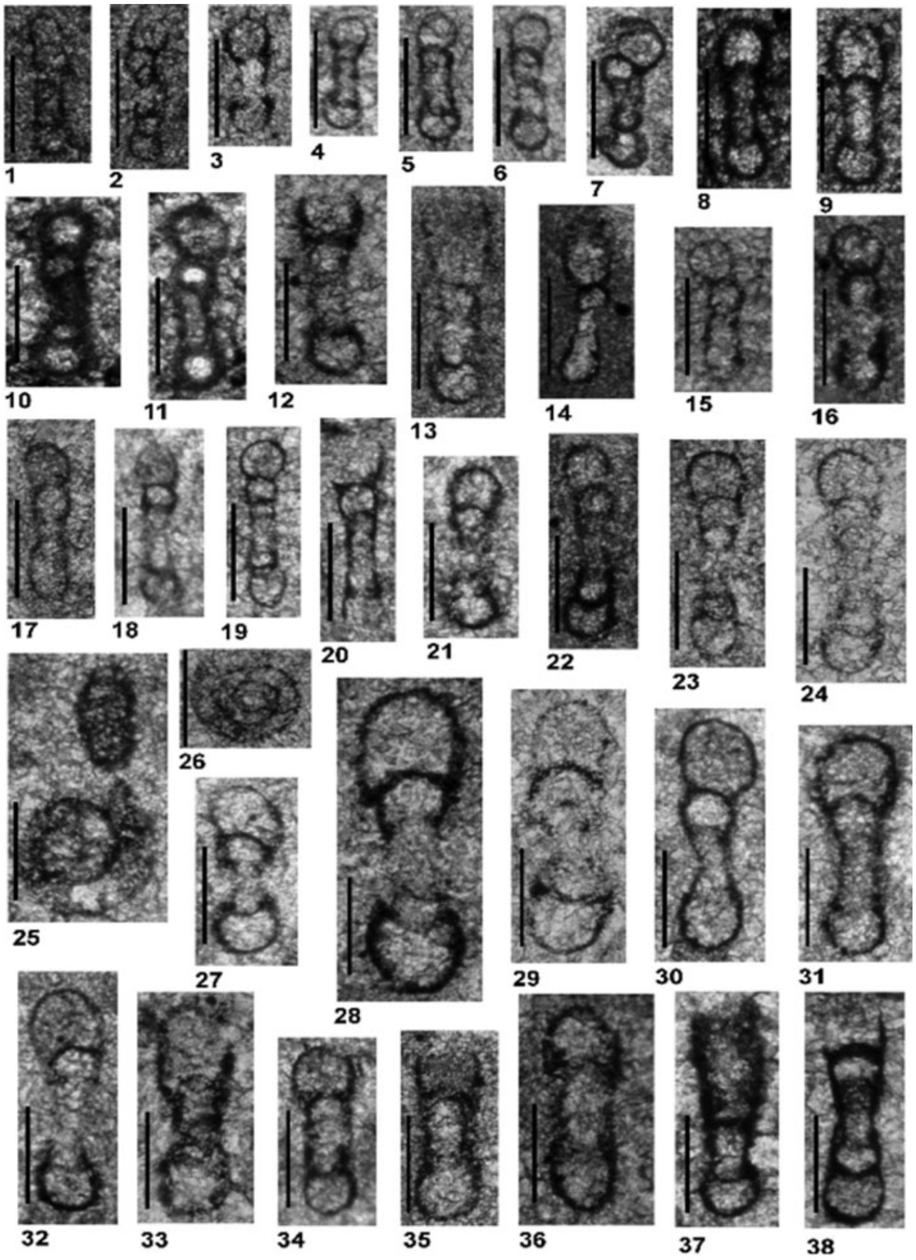


Figure 3. All specimens are from Dawen (PDW) and Dajiang (PDJ) sections. (**1–26**) *Postcladella kalhori* (Brönnimann, Zaninetti, and Bozorgnia, 1972a); (**27–38**) *Postcladella grandis* (Altıner and Zaninetti, 1981). (**1, 2, 22**) PDW-011; (**3**) PDJ-164; (**4, 7, 18–21, 25, 27, 30–32, 34**) PDJ-174; (**5**) PDJ-178; (**6, 17, 23, 24, 29**) PDW-108; (**8, 9**) PDJ-157; (**10, 11**) PDW-099; (**12, 28, 33, 36**) PDW-118; (**13**) PDJ-162; (**14**) PDJ-200; (**15**) PDW-087; (**16**) PDJ-161; (**26**) PDW-123; (**35**) PDJ-170; (**37**) PDJ-158; (**38**) PDW-126. Scale bars = 100 μm.

ecological parameters.' This interpretation did not take into account the morphological difference between the *kalhori* and *mahajeri* populations.

Although the reasons given by Krainer and Vachard (2011) were correct for the creation of their new genus *Postcladella* for the *kalhori* population, these authors did not consider the morphological difference between *kalhori* and *mahajeri* populations as a valid criterion for distinguishing between the species, and therefore synonymized these two taxa under *Postcladella*. More recently, Nestell et al. (2011), describing the foraminifera from the Permian–Triassic transition in Slovenia, rejected *Postcladella* of Krainer and Vachard (2011), illustrated all *P. kalhori* populations as '*Cornuspira*' *mahajeri*, and considered *Postcladella* (given as '*Rectocornuspira*') to be a teratologic form of *Cornuspira*, following Gaillot and Vachard (2007). In Nestell et al. (2015), the *kalhori* population took priority over the *mahajeri* population, and was illustrated and described under the agglutinated genus *Ammodiscus*. The basis of this taxonomic reassignment was explained as the absence of calcium carbonate and the presence of a significant amount of elemental carbon, along with oxygen and silica in the walls of *kalhori* specimens. In our view, however, these authors did not sufficiently discuss the diagenetic processes that could have affected the tests of the *kalhori* specimens. Specifically, it is possible that the specimens illustrated from the washed conodont residues do not display the originally preserved wall. Therefore, in this study, we consider *Postcladella* as a valid genus and *Postcladella kalhori* as a porcelaneous form belonging to the Class Miliolata.

Cornuspirins recognized in the Chinese samples consist of three species within the studied interval. Among these taxa, the individuals assigned to the *Postcladella kalhori* population (Fig. 3.1–3.26) are nearly identical to types described under the genus *Rectocornuspira* by Brönnimann et al. (1972a); however, the size variation in the Chinese forms is much greater. The diameter of the coiled portion reaches up to 160 µm, as noted previously in Altıner and Zaninetti (1981). The number of whorls, reaching to 2.5 or 3 in some specimens, is also greater than in the type specimens, which display 1.5–2 whorls. Previously, *P. kalhori* was generally reported from the microbialite-bearing successions from the base of the Triassic (Zaninetti, 1976; Rettori, 1995 and the references therein). In the more recent literature, *P. kalhori* has been reported as *Cornuspira mahajeri* from the Griesbachian of Antalya Nappes, Turkey (Angiolini et al., 2007); Alborz Mountains, Iran (Angiolini et al., 2010); western Slovenia (Nestell et al., 2011); the Dead Sea region, Jordan (Powell et al., 2016); and from the Nanpanjiang basin, south China (Bagherpour et al., 2017). Hips (1996) reported *P. kalhori* from the Spathian of northern Hungary, but did not satisfactorily illustrate these forms. The associated forms illustrated as *Cyclogyra mahajeri* were misidentified and belong to *Pseudoammodiscus* (formerly known as *Ammodiscus*). The same problem has also occurred in the description of material from Israel. Korngreen et al. (2013) mentioned the presence of *P. kalhori* in strata of later Early Triassic age, but these forms were not illustrated in their study. *Postcladella* also has been partly misidentified in Rossignol et al. (2018) from northern Vietnam. Their figure 11C and 11E illustrated specimens that are *Glomospirella vulgaris* Ho, 1959, not *Postcladella* (Rossignol et al., 2018, fig. 11E is associated with *Arenovidalina* sp.).

In both the Dawen and Daijiang sections, *P. kalhori* ranges from the base of Griesbachian to the lowermost Dienerian (Figs. 5, 6). The stratigraphic range in the Chinese sections is indistinguishable from the range given in Rettori (1995). In several recent studies, including Crasquin-Soleau et al. (2002, 2004) from the Antalya Nappes, Turkey, Song et al. (2009, 2016), Yang et al. (2011), and Dai et al. (2018) from south China, and Kolar-Jurkovšek et al. (2018) from western Slovenia, the stratigraphic range of *P. kalhori* has been partially studied in stratigraphic sections covering only a few meters of the base of Triassic and reported as Griesbachian based on conodont zones. Galfetti et al. (2008) reported the full range as Griesbachian to Dienerian from the Nanpanjiang Basin, similar to the range given in this study. Some authors reported this interval simply as Induan (Insalaco et al., 2006 from southern Iran; Powell et al., 2019 from Jordan). Krainer and Vachard (2011) reported the stratigraphic distribution of *P. kalhori* from the Werfen Formation (southern Austria) also as Induan, based on Broglio Loriga et al. (1990), and added that this species also could be present in the Olenekian. However, neither in Krainer and Vachard (2011) nor other studies have properly illustrated the *kalhori* population from well-dated Olenekian strata.

Postcladella grandis (Altıner and Zaninetti, 1981)
Figures 3.27–3.38, 4.1–4.16

Remarks.—The other species that we recognize in the Chinese material also belongs to the genus *Postcladella*. Introduced by Altıner and Zaninetti (1981) from Turkey, *R. kalhori* f. *grandis* was raised by Lehrmann et al. (2015) to a species rank under the genus *Postcladella*. *Cyclogyra* nov. sp.? of Resch (1979) and *Rectocornuspira reschi* of Orovecz-Scheffer (1983) were considered as synonyms of *Postcladella grandis* (Figs. 3.27–3.38, 4.1–4.16). Although Rettori (1995) considered *Postcladella grandis* to be a synonym of *P. kalhori*, the former species is easily distinguished from the latter by the larger size of the tubular chamber, which is nearly twice that of *P. kalhori* in every step of its ontogeny, and the larger diameter of the coiled portion of the test. In addition, the first appearance of *P. grandis* always postdates that of *P. kalhori* in south China, Turkey, and the Transdanubian Range of Hungary (Altıner and Zaninetti, 1981; Orovecz-Scheffer, 1987; Lehrmann et al., 2015). *Postcladella grandis* was also illustrated or described from other studies in the Tethyan belt. For example, the specimens illustrated as *R. kalhori* in Brönnimann et al. (1972a, pl. 4, fig. 15) and *Cyclogyra*? *mahajeri* in Brönnimann et al. (1972a, pl. 4, fig. 18) should be assigned to *P. grandis*. Forms from Austria illustrated by Krainer and Vachard (2011, pl. 5, figs. 9, 10, 14) are referable to *P. grandis*. *Cyclogyra*? *mahajeri* illustrated from the Alborz Mountains, Iran by Stampfli et al. (1976) is *P. grandis*. In addition, *P. grandis* has been illustrated as both *C.*? *mahajeri* and *R. kalhori* in Orovecz-Scheffer (1987).

The stratigraphic range of *P. grandis* is much shorter than the range of *P. kalhori* (Figs. 5, 6). The first occurrence of *P. grandis* is higher in the Griesbachian in China than in Turkey (Altıner and Zaninetti, 1981), and its last occurrence is just below the Griesbachian-Dienerian boundary in the Dawen and Daijiang sections. The stratigraphic range of *C. mahajeri*? is similar to that of *P. kalhori*, as stated by Rettori (1995). Forms close to this species are present both in Dawen and Dajiang sections, within the interval corresponding to the stratigraphic range of *P. grandis*.

Genus *Cornuspira* Schultz, 1854
Cornuspira mahajeri? (Brönnimann, Zaninetti, and Bozorgnia, 1972a)
Figure 4.15

Remarks.—Rarely recorded forms assigned to *Cornuspira mahajeri*? (Fig. 4.15) in this study differ from the types (given as *Cyclogyra*? *mahajeri* by Brönnimann et al., 1972a) in having slightly larger dimensions of the test and the lumen of the final whorl covering the previous whorl in a less-pronounced way.

Subfamily Calcivertellinae Loeblich and Tappan, 1964
Genus *Planiinvoluta* Leischner, 1961
Planiinvoluta? *mesotriasica* Baud, Zaninetti, and Brönnimann, 1971
Figure 7.1–7.7

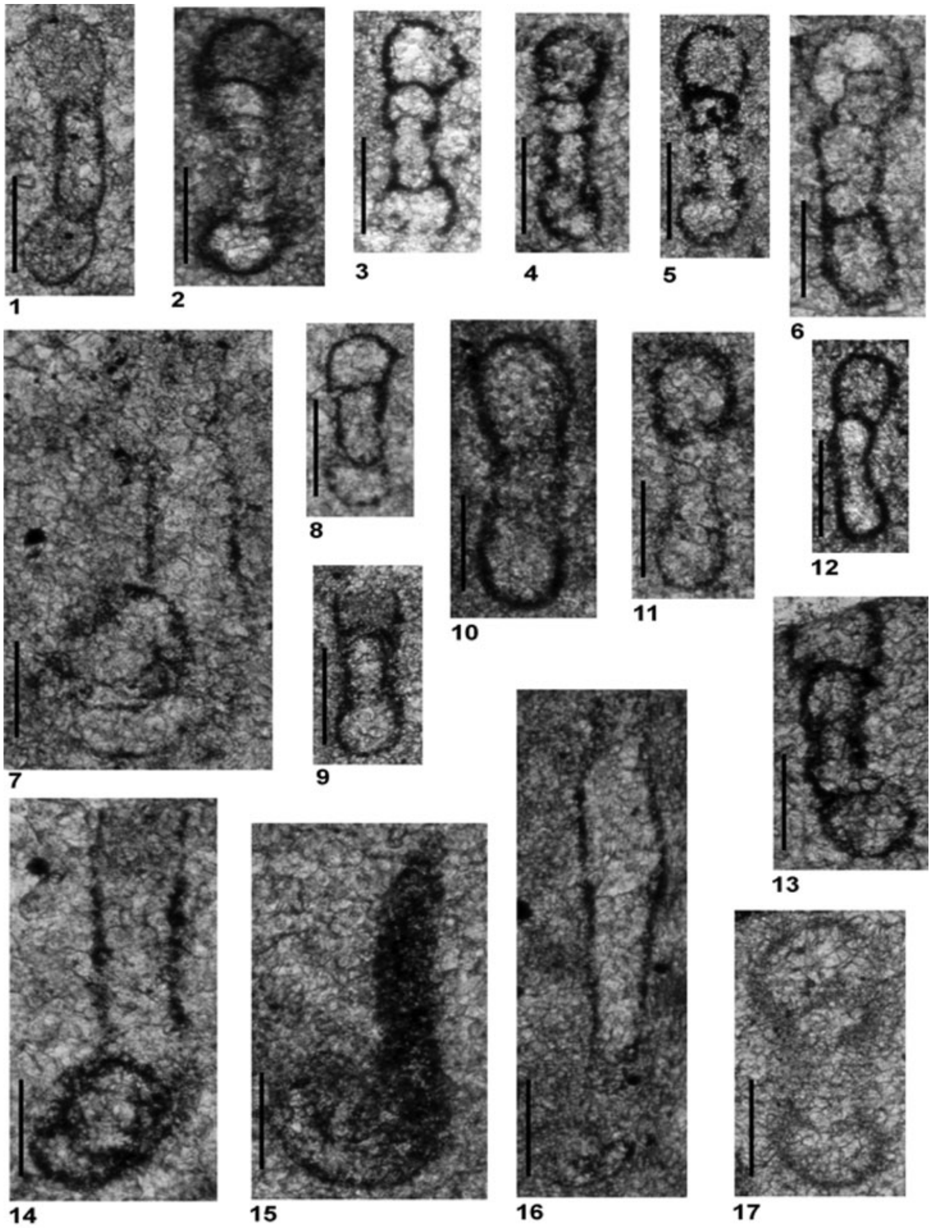


Figure 4. All specimens are from Dawen (PDW) and Dajiang (PDJ) sections. (**1–16**) *Postcladella grandis* (Altıner and Zaninetti, 1981); (**17**) *Cornuspira mahajeri*? (Brönnimann, Zaninetti, and Bozorgnia, 1972a). (**1, 17**) PDW-108; (**2**) PDJ-178; (**3**) PDW-102; (**4, 6**) PDW-096; (**5**) PDJ-164; (**7, 10, 11, 13–15**) PDW-118; (**8, 16**) PDW-123; (**9**) PDJ-158; (**12**) PDJ-157. Scale bars = 100 µm.

Remarks.—The subfamily Calcivertellinae, a group of tubular, porcelaneous foraminifera, is represented only by *Planiinvoluta*? *mesotriasica* (Fig. 7.1–7.7) in the studied material. The size of the proloculus, diameter of the tubular chamber, and the test are similar to those of the types originally described by Baud et al. (1971). However, the genus attribution remains unclear because the individuals belonging to this species never display a proper planispirally enrolled second chamber as described by Leischner (1961). In the recent literature, *P.*? *mesotriasica* has been clearly illustrated in Altıner and Koçyiğit (1993) and Okay et al. (2015) from the Anisian of central and northern Anatolia (Turkey), and in Fugagnoli and Posenato (2004) from northern Italy. The specimens illustrated as *Meandrospira*? sp. from western Kyushu, Japan, by Kobayashi et al. (2005) are most probably sections of *P.*? *mesotriasica*. The stratigraphic range of *P.*? *mesotriasica* is from Bithynian to Illyrian in the Upper Guandao section and Illyrian in the Middle Triassic Dajiang section (Figs. 8–10).

Family Arenovidalinidae Zaninetti and Rettori in Zaninetti et al., 1991
Subfamily Arenovidalininae Zaninetti and Rettori in Zaninetti et al., 1991
Genus *Arenovidalina* Ho, 1959

Type species.—*Arenovidalina chialingchiangensis* Ho, 1959, from the Triassic Chialingkiang Limestone of South Szechuan, China.

Arenovidalina abriolense (Luperto, 1965)
Figure 7.14, 7.15

Remarks.—Two species from the subfamily Arenovidalininae, *Arenovidalina abriolense* (Luperto, 1965) (Fig. 7.14, 7.15) and *Arenovidalina weii* n. sp. (Fig. 7.8–7.13), are present in the Chinese sections. *Arenovidalina abriolense*, previously defined as a Permian form and thus placed under the genus *Hemigordius* by Luperto (1965), was later placed in the genus *Ophthalmidum* by Ciarapica et al. (1990). Consisting of a proloculus followed by an undivided second chamber, the *abriolense* population does not carry the primitively developed multilocular character of the genus *Ophthalmidium*, and is therefore placed under the genus *Arenovidalina* in this study. *Arenovidalina abriolense* differs from the two other, similar-looking species of *Arenovidalina*, *A. chialingchiangensis* Ho, 1959 and *A. amylovoluta* Ho, 1959 (Ho, 1959; Zaninetti, 1976; Okay et al., 2015) in having a more tightly enrolled and slowly growing second chamber. In Senowbari-Daryan et al. (1993), *Ophthalmidium* (=*Arenovidalina*) *chialingchiangensis* illustrated from the Anisian of the northern Dolomites, Italy, belongs to *A. abriolense*. Some specimens illustrated as *Ophthalmidium* spp. from the Anisian of western Kyushu, Japan, are referable to *A. abriolense* (Kobayashi et al., 2005). *Ophthalmidium abriolense* illustrated in Velledits et al. (2011) from NE Hungary is *Eoophthalmidium tricki* Langer, 1968. The stratigraphic range of *A. abriolense* is Anisian (Aegean) to Carnian (Cordevolian) in the Upper Guandao section (Figs. 8, 9). The description of the other *Arenovidalina* species, *A. weii* n. sp., is given below.

Arenovidalina weii new species
Figure 7.8–7.13

?1990 *Arenovidalina amylovoluta* Ho; Baroz et al., pl. 4, figs. 8, 9.

Holotype.—PGD-112 (Fig. 7.9).

Diagnosis.—A laterally compressed *Arenovidalina* species with a maximum of four whorls, becoming evolute in the late stage of the ontogeny.

Occurrence.—Smithian, Guandao section of the Great Bank of Guizhou, Nanpanjiang Basin, south China, Sample PGD-112 (Figs. 2, 11).

Description.—Test is laterally compressed and consists of a relatively large proloculus and a maximum number of four planispiral whorls rapidly increasing in height. The coiling, involute in the earlier 2.5 whorls, becomes evolute in the last 1.5 whorls (Fig. 7.9). A possible dimorphism is present in the population (Fig. 7.10). In microspheric forms, the number of whorls increases to five and the test displays a slight deviation in the axis of coiling in the initial 1–2 whorls. The wall is originally porcelaneous and appears slightly granular due to recrystallization. It is relatively thicker when compared with the volume of the test.

Etymology.—This new species is dedicated to Dr. Jiayong Wei of the Guizhou Geological Survey, China, who made great contributions to the understanding of the geology of the Nanpanjiang Basin.

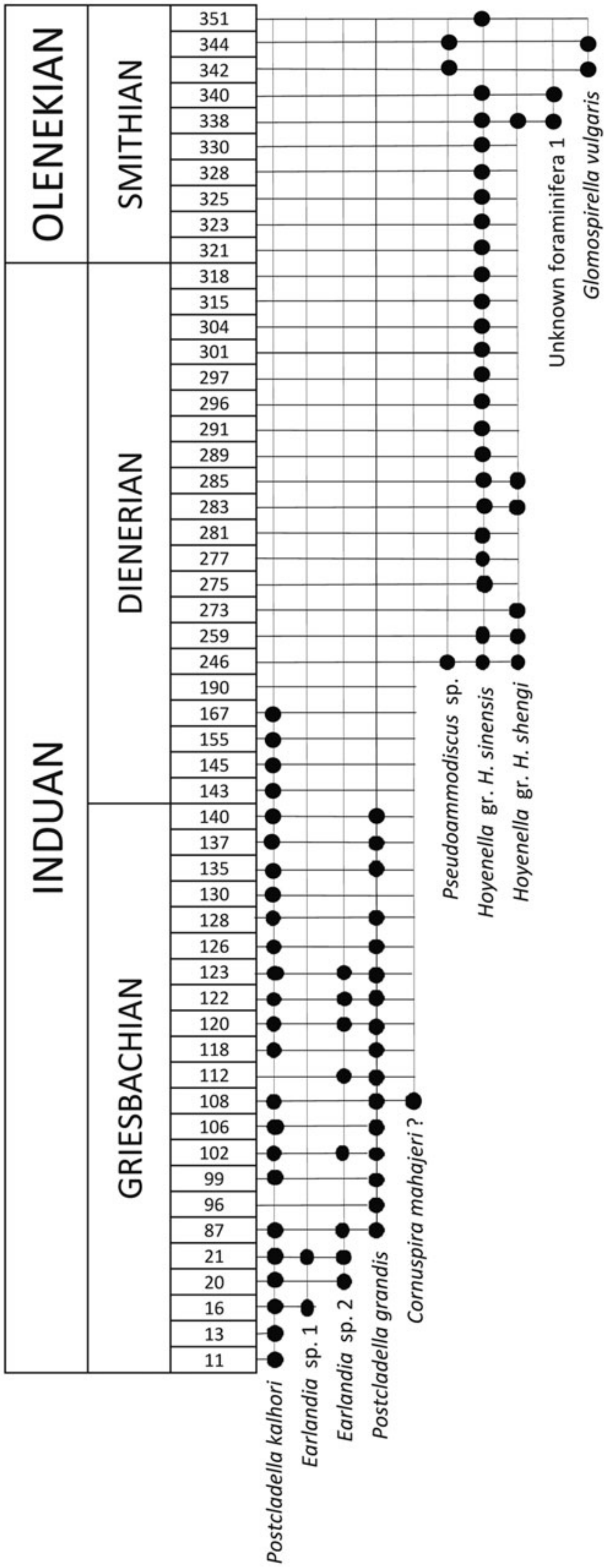


Figure 5. Stratigraphic occurrences of foraminiferal taxa at Dawen measured section (barren samples not shown). Because the goal of the figure is to illustrate the occurrences and co-occurrences of species for the purpose of chronostratigraphy, only fossiliferous samples are included along with sample numbers. For stratigraphic positions of illustrated samples, we refer readers to Figure 2.

Materials.—Samples PGD-96, 109, 111, 112, 131 (Smithian). More than 20 specimens. Six of these specimens, including the holotype, are illustrated in Figure 7.8–7.13.

Microfossil association.—In the samples collected from the Smithian, *Arenovidalina weii* n. sp. is associated with *Hoyenella* gr. *H. sinensis*, *H.* gr. *H. shengi*, *Glomospirella vulgaris*, *Pseudoammodiscus* sp., *Praetriadodiscus zaninettiae* Altıner and Payne, 2017, and *P. tappanae* Altıner and Payne, 2017.

Dimensions.—Diameter of proloculus: 50–55 µm. Diameter of test: 360–420 µm. Width of test: 100–115 µm. W/D ratio: 0.24–0.32. Height of last whorl (only lumen): 55–60 µm. Thickness of wall: 10–14 µm.

Remarks.—*Arenovidalina weii* n. sp. is probably the oldest *Arenovidalina* species known in the Triassic stratigraphy. It differs from the two other well-known species, *A. chialingchiangensis* and *A. amylovoluta*, in having a nearly parallel-sided, compressed test and few whorls, which increase rapidly in height and become evolute toward the end of the ontogeny. The specimens illustrated as *Arenovidalina amylovoluta* by Baroz et al. (1990) from Greece probably belong to our *A. weii* n. sp. population. These forms are similar to *A. weii* n. sp. in having highly compressed axial profiles and evolute last whorls, but they contain more whorls and a smaller proloculus. *Arenovidalina* sp. illustrated by Kobayashi (1996) from the Anisian of the Kanto Mountains, Japan, is also characterized by involute earlier whorls and evolute later whorls. However, the D/W ratio is greater in the Japanese forms. Finally, the microfacies photographs illustrated by Song et al. (2016, fig. 9c) from the Smithian of south China contain sections of *A. weii* n. sp.

Family Meandrospiridae Saidova, 1981 emend. Zaninetti et al., 1987a

Subfamily Meandrospirinae Saidova, 1981 emend. Zaninetti et al., 1987a

Remarks.—Meandrospirin foraminifera of the Great Bank of Guizhou are classified under two genera, *Meandrospira* and *Meandrospiranella*. The validity of the former genus in the Triassic stratigraphy has been questioned recently by Ueno et al. (2018), who suggested the replacement of *Meandrospira* with *Citaella*, which was originally described by Premoli Silva (1964). These authors concluded that *Citaella*, *Meandrospira*, and *Streblospira* are meandrospiral homeomorphs that appeared independently at different times in the evolutionary history of the class Miliolata. In contrast, we argue that Triassic *Meandrospira* was derived as a Lazarus taxon from Permian *Streblospira*, as argued by Groves and Altıner (2005) and Altıner et al. (2005). Recently, *Streblospira* (*S. minima*) Kotljar et al., 1984 has been illustrated from the Changhsingian of western Slovenia by Kolar-Jurkovšek et al. (2018). Previous findings of *Streblospira* within middle and upper Permian strata (Kotljar et al., 1984; Şahin et al., 2012) demonstrate that the genus was not confined to lower Permian strata, as was supposed by Ueno et al. (2018). Furthermore, we consider that the 'absence' of *Meandrospira* in post-Anisian to Jurassic rocks may not indicate the 'phylogenetical isolation' of '*Citaella*' in the Early to Middle Triassic. Tubular foraminifera might survive as rare members of communities, confined to narrow ecological and/or environmental niches before becoming more common again in a much younger time interval, as in *Meandrospira* (Charollais et al., 1966; Altıner, 1991; Ivanova and Kołodziej, 2010). Because the ancestor of Cretaceous *Meandrospira* is not known from the Cretaceous, we take the more conservative route and continue to use *Meandrospira* in Triassic foraminiferal taxonomy.

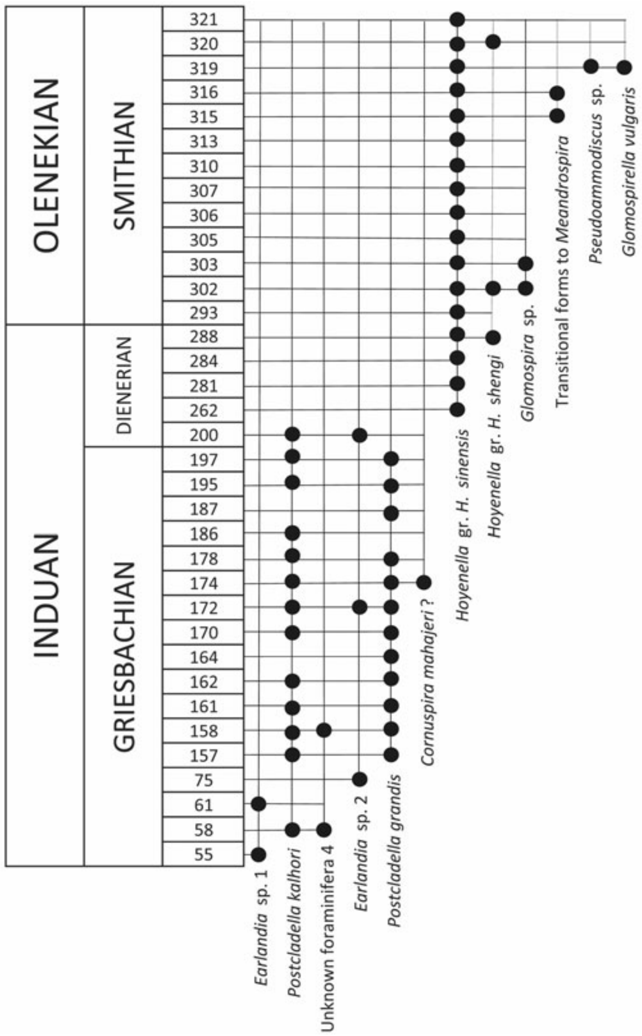


Figure 6. Stratigraphic occurrences of foraminiferal taxa at Dajiang measured section (barren samples not shown). In this section, samples numbered less than 44 were collected from the Permian strata and are not considered in this study.

Genus *Meandrospira* Loeblich and Tappan, 1946

Type species.—*Meandrospira washitensis* Loeblich and Tappan, 1946, from the Lower Cretaceous Washita Group of southern Oklahoma and northern Texas, USA.

Meandrospira pusilla (Ho, 1959)
Figure 7.16–7.20

Remarks.—From the *Meandrospira* population in the Chinese material, the well-known species *M. pusilla* (Ho, 1959)

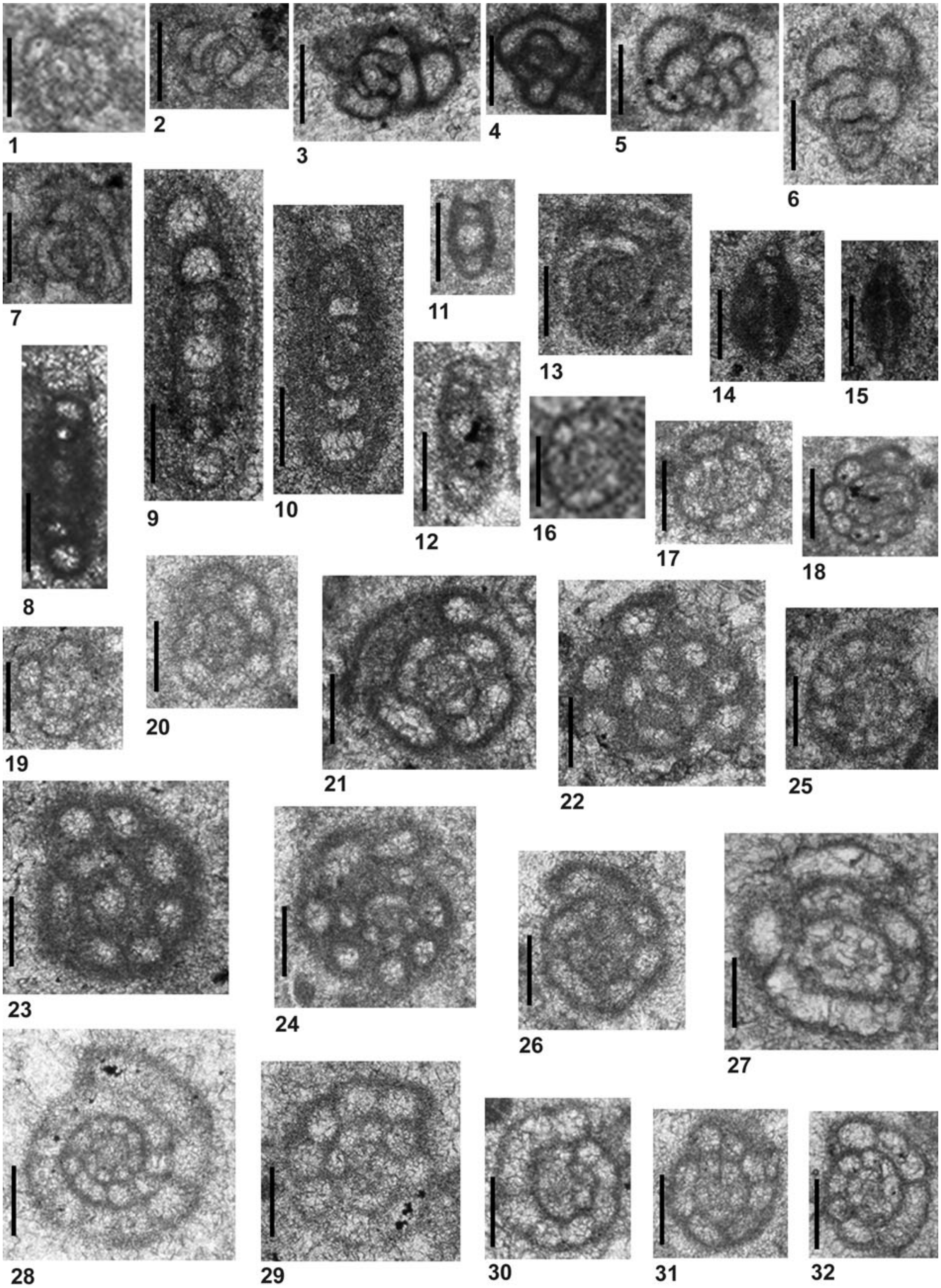


Figure 7. All specimens are from Guandao (PGD), Upper Guandao (PUG) and Middle Triassic Dajiang (MDJ) sections. (**1–7**) *Planiinvoluta*? *mesotriasica* Baud, Zaninetti, and Brönnimann, 1971; (**8–13**) *Arenovidalina weii* n. sp.; (**14, 15**) *Arenovidalina abriolense* (Luperto, 1965); (**16–20**) *Meandrospira pusilla* (Ho, 1959); (**21–24, 26**) *Meandrospira cheni* (Ho, 1959); (**25, 27–32**) *Meandrospira dinarica* Kochansky-Devidé and Pantić, 1966. (**1**) MDJ-025; (**2**) PUG-065; (**3, 5**) PUG-085; (**4**) MDJ-039; (**6, 32**) PUG-054; (**7**) MDJ-035; (**8**) PGD-131; (**9**) PGD-112 (holotype); (**10**) PGD-111; (**11**) PGD-109; (**12, 13**) PGD-096; (**14**) PUG-051; (**15**) PUG-089; (**16**) MDJ-007; (**17, 19**) PGD-174; (**18**) PUG-012; (**20, 31**) PUG-009; (**21**) PGD-151; (**22**) PGD-168; (**23**) PGD-154; (**24, 26**) PGD-157; (**25**) PGD-226; (**27**) MDJ-019; (**28**) PUG-027; (**29**) PGD-215; (**30**) PUG-023. Scale bars = 100 μm.

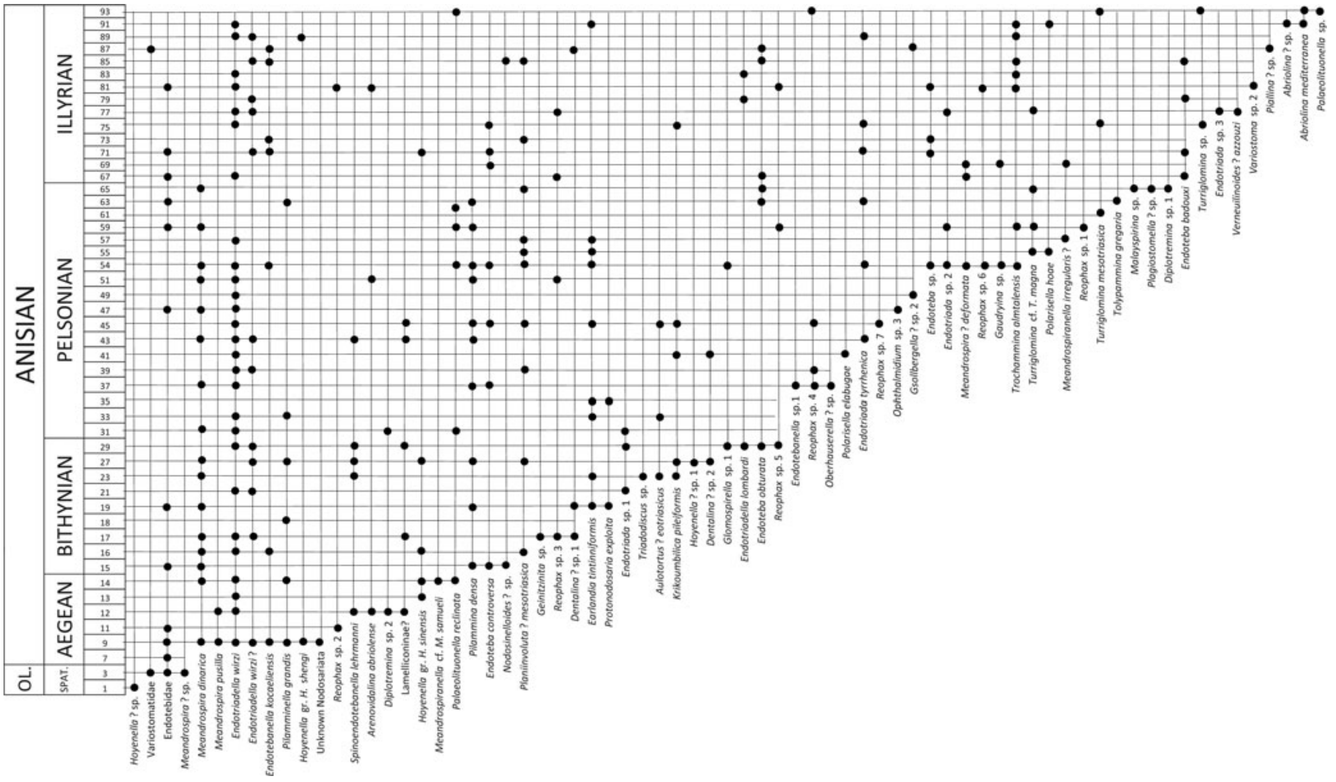


Figure 8. Stratigraphic occurrences of foraminiferal taxa in the lower part of Upper Guandao section (barren samples not shown). OL.: Olenekian; Spat.: Spathian.

(Fig. 7.16–7.20), characterized by 1.5–2 whorls and a tightly coiled spire consisting of 8–9 sections of the zig-zag bends of the meandering second tubular chamber in the last whorl, is nearly identical to the holotype described by Ho (1959). *Meandrospira pusilla* was extensively reported from the whole Tethyan Belt (Zaninetti, 1976; Rettori, 1995). More recently, it has been reported from southern Austria by Krainer and Vachard (2011) and from Jordan by Powell et al. (2016). Some of the specimens illustrated as *M. pusilla* from the Qingyan section of south China by Song et al. (2015) belong to *M. dinarica* Kochansky-Devidé and Pantić, 1966.

Meandrospira pusilla ranges from the Spathian to the Bithynian in the Guandao and Upper Guandao sections (Figs. 8, 11). It is also present in the Pelsonian of the Middle Triassic Dajiang section (Fig. 10). In the Smithian of the Daijiang section (Fig. 6), forms identified as 'transitional to *Meandrospira*' could also be included in the population of *M. pusilla*. *Meandrospira cheni* is strictly confined to the Spathian in the Guandao section (Fig. 11). *Meandrospira*? *deformata* has been recognized from the Pelsonian to lower Illyrian of the Upper Guandao section (Fig. 8).

Meandrospira cheni (Ho, 1959)
Figure 7.21–7.24, 7.26

Remarks.—*Meandrospira cheni* (Ho, 1959) (Fig. 7.21–7.24, 7.26), a similarly coiled but larger form than *M. pusilla*, differs from *M. pusilla* in having fewer (6–8) zig-zag bends of the meandering second tubular chamber. Our specimens are nearly identical to forms illustrated as the *cheni* population in Ho (1959) and He (1993) from China. Some of the *M. pusilla* sections illustrated from Julfa, northwestern Iran, by Baud et al. (1974) belong to *M. cheni*. The specimen illustrated from Hydra (Greece) by Rettori et al. (1994) is probably an *Endoteba* section. *Meandrospira cheni* also has been reported from the Spathian of Israel (Korngreen et al., 2013) and the northern Arab Emirates (Maurer et al., 2008).

Meandrospira dinarica Kochansky-Devidé and Pantić, 1966
Figures 7.25, 7.27–7.32, 12.1–12.4

Remarks.—The other well-established species of *Meandrospira*, *M. dinarica* (Figs. 7.25, 7.27–7.32, 12.1–12.4), consisting of 8–10 sections of the second tubular chamber in the last whorl, is characterized by rectangular outlines of the sections of the tubular chamber in the equatorial plane. *Meandrospira dinarica* is one of the most widely cited Anisian species in the Tethyan Belt (Zaninetti, 1976; Rettori, 1995). In more recent literature, it has been reported from the Anisian of Japan (Kobayashi, 1996; Kobayashi et al., 2005), Thailand (Kobayashi et al., 2006), Laos (Miyahigashi et al., 2017), Vietnam (Martini et al., 1998), northern Italy (Fugagnoli and Posenato, 2004; Berra et al., 2005), and Hungary (Velledits et al., 2011). Korchagin (2008) identified *M. dinarica* as *M. cheni* from Pamirs. Tian et al. (2014), based on Song et al. (2011a), reported earliest *M. dinarica* from the Smithian–Spathian interval of south China. This unusual report is probably the result of a taxonomic misidentification. Both *M. pusilla* and *M. cheni* might have been misidentified as *M. dinarica* (see also Song et al., 2015).

Meandrospira dinarica, whose first appearance nearly coincides with the Olenekian-Anisian boundary, extends from the Aegean to the Pelsonian in the Guandao and Upper Guandao sections (Figs. 8, 11). It also occurs in the Pelsonian of the

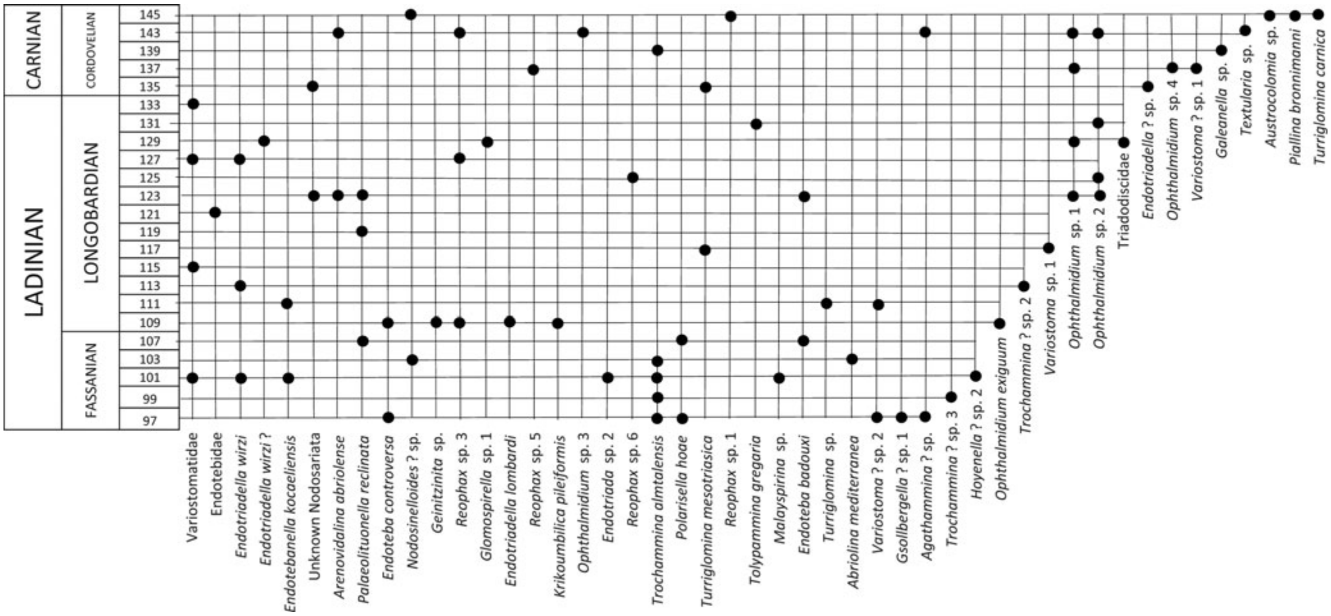


Figure 9. Stratigraphic occurrences of foraminiferal taxa in the upper part of Upper Guandao section (barren samples not shown).

Middle Triassic Dajiang section (Fig. 10). From the *Meandrospiranella* side, *M*. cf. *M*. *samueli* is found in the uppermost Aegean, whereas *M*. *irregularis*? occurs in the Pelsonian to lowermost Illyrian of the Upper Guandao section (Fig. 8).

Meandrospira? *deformata* Salaj in Salaj et al., 1967
Figures 12.14, 13.1–13.4

Remarks.—*Meandrospira*? *deformata* Salaj in Salaj et al., 1967 (Figs. 12.14, 13.1–13.4), a doubtful member of the genus *Meandrospira*, is characterized by an irregularly coiled meandering second chamber throughout its ontogeny. After the type description of Salaj et al. (1967), *M*.? *deformata* has been reported from the Anisian of Slovenia (Flügel et al., 1994), Japan (Kobayashi, 1996), Pamirs (Korchagin, 2008), and more recently from Laos (Miyahigashi et al., 2017) as *Citaella*? *deformata*.

Meandrospira? *enosi* new species
Figure 12.5–12.13

Holotype.—PGD-176 (Fig. 12.5).

Diagnosis.—A meandrospirin species characterized by an initial *Meandrospira* stage followed by oscillating whorls, but not zig-zag bends, of the tubular chamber.

Occurrence.—Spathian, Guandao section of the Great Bank of Guizhou, Nanpanjiang Basin, south China, PGD-176 (Figs. 2, 11).

Description.—Following a globular and small proloculus, the initial stage of the new species is typically coiled like a *Meandrospira* with three whorls. The height of the tubular chamber increases rather rapidly in the final whorl of this stage and, generally, seven sections of zig-zag bends of the second tubular chamber are present in the last whorl. Later in the ontogeny, coiling changes its style and direction. This stage is characterized by 1.5 oscillating whorls, generally arranged perpendicular to the axis of coiling of the *Meandrospira* stage. The wall is porcelaneous, similar to the other *Meandrospira* species in this study.

Etymology.—This new species is dedicated to Prof. Dr. Paul Enos from the University of Kansas, USA, for his contributions to the Permian–Triassic carbonates in China.

Materials.—Samples PGD-171, 176, 178, 181 (Spathian). More than 20 specimens. Nine of these specimens are illustrated in Figure 12.5–12.13.

Microfossil association.—In the Spathian samples, the new species co-occurs with *Hoyenella* gr. *H*. *sinensis*, *Meandrospira pusilla*, *Meandrospira cheni*, *Trochammina* sp. 1, *Verneuilinoides*? *azzouzi* (Salaj, 1978), *Endoteba bithynica* Vachard et al., 1994, *Endotebanella kocaeliensis* (Dağer, 1978b), *Krikoumbilica pileiformis* He, 1984, *Variostoma* sp. 2, and *Diplotremina* sp. 2.

Dimensions.—Diameter of proloculus: 36–50 µm. Diameter of test: 280–340 µm. Height of the last whorl (only lumen): 36–40 µm. Thickness of wall: 15–18 µm.

Remarks.—*Meandrospira*? *enosi* n. sp., probably derived from *M*. *cheni*, is easily distinguished from the other *Meandrospira* species of the Lower–Middle Triassic by the coiling in the second stage of its ontogeny, characterized by oscillating whorls of the second tubular chamber arranged perpendicular to the coiling axis of the *Meandrospira* stage. The genus *Meandrovoluta*, described by Fugagnoli et al. (2003) from the Liassic of the southern Alps, Italy, is morphologically close to *M*.? *enosi* n. sp. The coiling style of our new species differs from *Meandrovoluta* in two ways: (1) *Meandrovoluta* is characterized by a more irregularly coiled, widely meandering

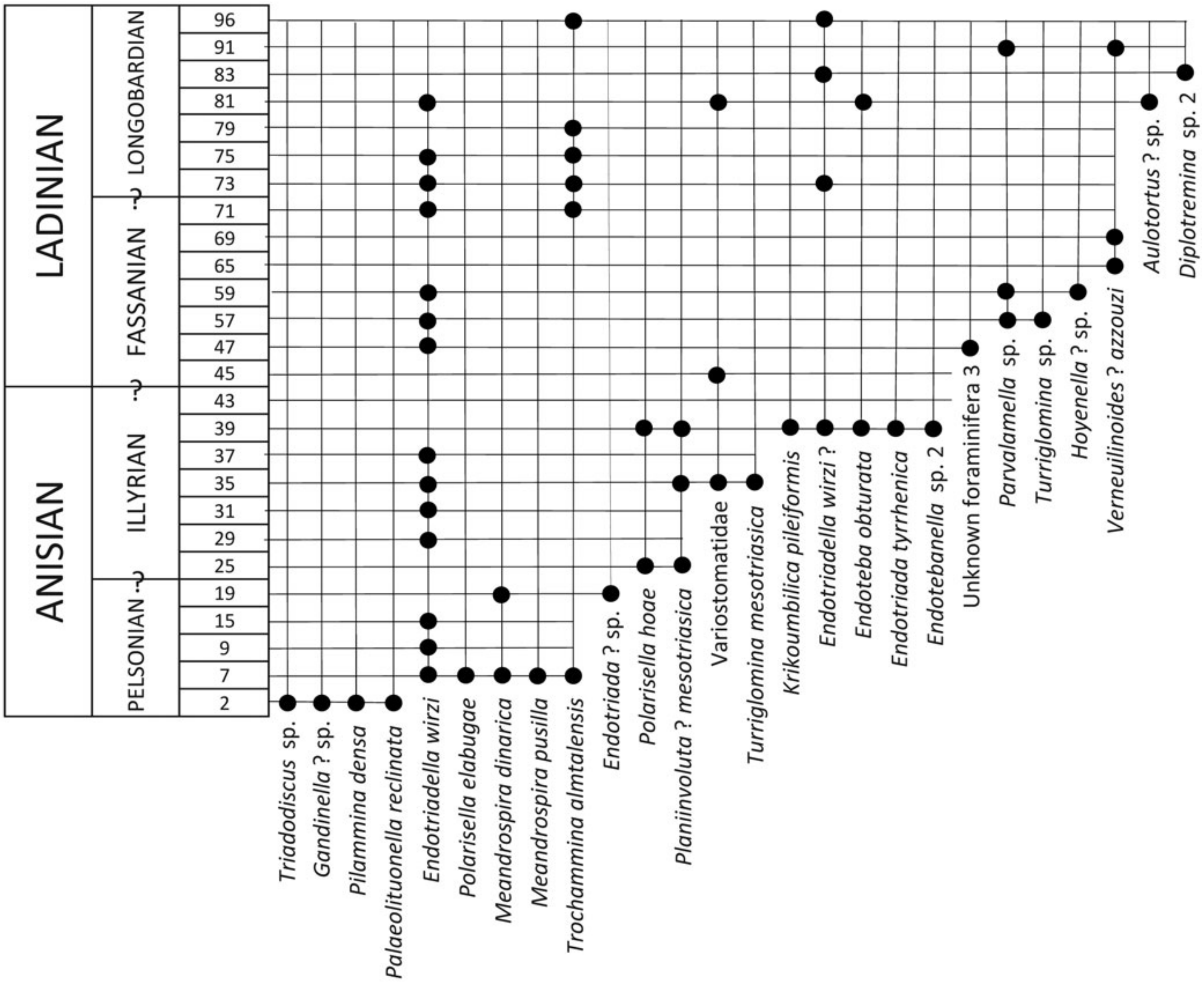


Figure 10. Stratigraphic occurrences of foraminiferal taxa at Middle Triassic Dajiang measured section (barren samples not shown).

tubular chamber in the second stage of its morphology, whereas *M.*? *enosi* n. sp. is characterized by a tubular chamber coiled simply in oscillating whorls; and (2) the *Meandrospira*-like stage is irregular and complicated in the holotype of *Meandrovoluta*, whereas this stage is more *Meandrospira*-like in the *M.*? *enosi* n. sp. population, even morphologically close to *M. cheni*. We remain uncertain whether a new genus should be created to house forms such as the *enosi* population within meandrospirin foraminifera.

Genus *Meandrospiranella* Salaj in Salaj et al., 1967
Meandrospiranella cf. *M. samueli* Salaj in Salaj et al., 1967
Figure 13.5

Remarks.—Species doubtfully attributed to *Meandrospiranella* are rare and sporadic in the Chinese material. *Meandrospiranella* cf. *M. samueli* Salaj in Salaj et al., 1967 (Fig. 13.5) is an incomplete specimen lacking the uncoiled portion. Flügel et al. (1994) illustrated a form similar to ours from the Pelsonian of Slovenia. Zaninetti et al. (1972c), from Switzerland, and Baroz et al. (1990), from Greece, illustrated specimens very similar to the holotype. *Meandrospiranella samueli* illustrated by Velledits et al. (2011) from the Anisian of Hungary probably belongs neither to the genus nor to the species of this form. The illustrated specimen is characterized by a granular wall, biserial chambers in the uncoiled portion, and an unrecognizable coiled portion. *Meandrospiranella irregularis*? Salaj in Salaj et al., 1967 (Fig. 13.6) is characterized by a well-defined, broadly meandering, uncoiled portion that has not been illustrated in the holotype (Salaj in Salaj et al., 1967).

Subfamily Turriglomininae Zaninetti in Limogni et al., 1987
Genus *Turriglomina* Zaninetti in Limogni et al., 1987

Remarks.—Characterized by an initial meandrospiroid or glomospiroid stage followed by a tightly coiled helicoidal stage consisting of numerous whorls, the genus *Turriglomina* is composed of three species in the Triassic of the Great Bank of Guizhou. *Turriglomina mesotriasica* (Koehn-Zaninetti, 1968) (Fig. 13.7–13.9), as described by Koehn-Zaninetti (1969), consists of a slender test with up to 14 tightly coiled whorls. *Turriglomina mesotriasica* has been extensively

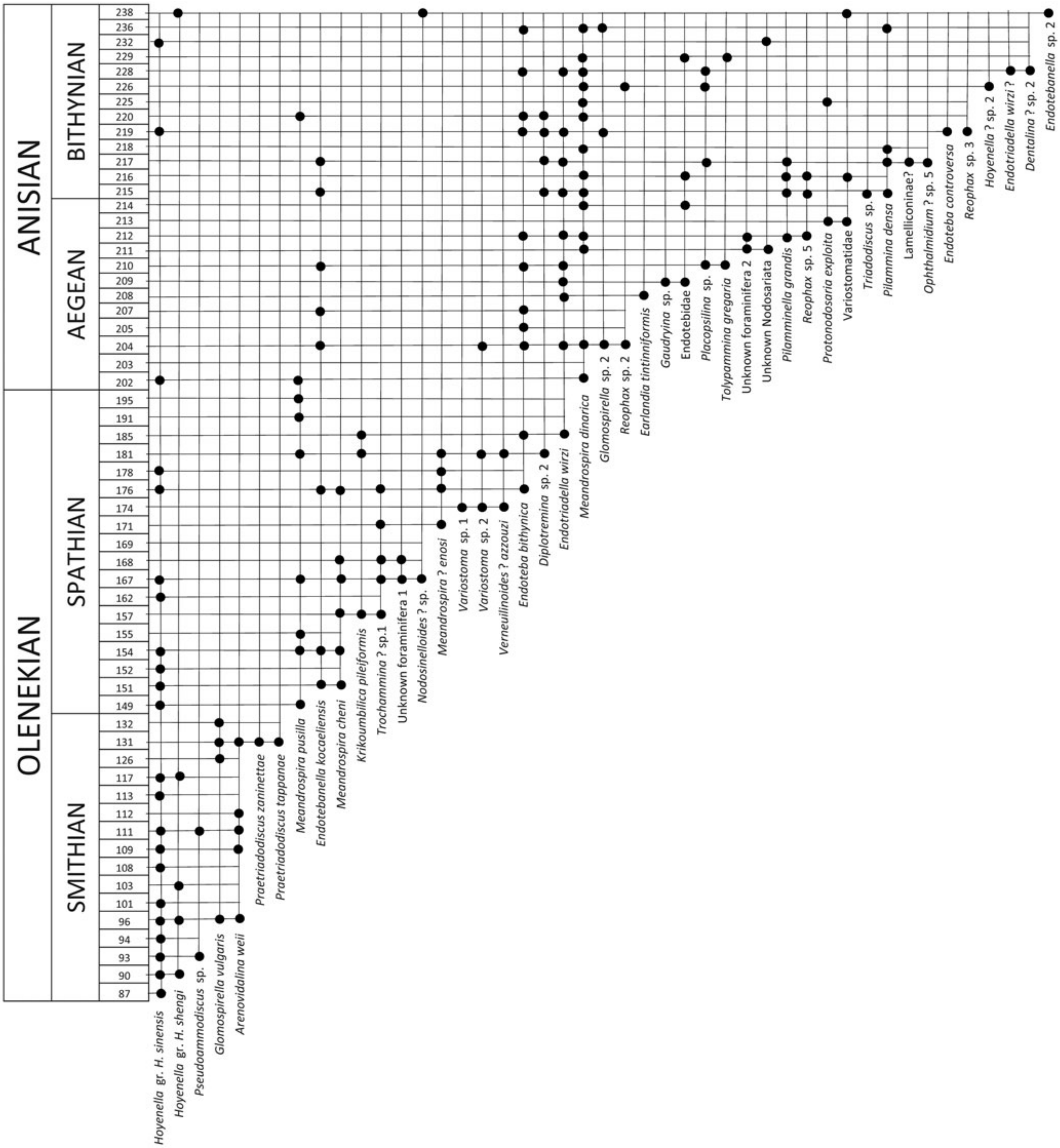


Figure 11. Stratigraphic occurrences of foraminiferal taxa at Guandao measured section (barren samples not shown).

reported from the Triassic deposits of the Tethyan Belt (Zaninetti, 1976; Rettori, 1995). In more recent literature, Emmerich et al. (2005) reported this form from the Illyrian to Ladinian of the Latemar (Dolomites, Italy). Song et al. (2015) illustrated this species (given as *Turritellella mesotriasica*) from the Qingyan section of south China. However, the form illustrated by Song et al. (2015) does not display the slender aspect of *T. mesotriasica* and should be corrected as *T. conica* He, 1984 from Guizhou, south China. *Turriglomina* cf. *T. magna* (Urošević, 1977) (Fig. 13.10–13.13), a relatively larger form, is always found as incomplete oblique sections. Here we note that *T. guangxiensis* described by He and Cai (1991) from the Middle Triassic of Guangxi, China, is a synonym of *T. magna*. *Turriglomina carnica* Dağer, 1978b is very rare and recognized in oblique sections with spiny extensions from the periphery of the test (Fig. 13.14).

Turriglomina mesotriasica ranges from the upper Pelsonian to the base of the Carnian (Cordevolian) in the Upper Guandao section (Figs. 8, 9). It occurs also in the Illyrian of the

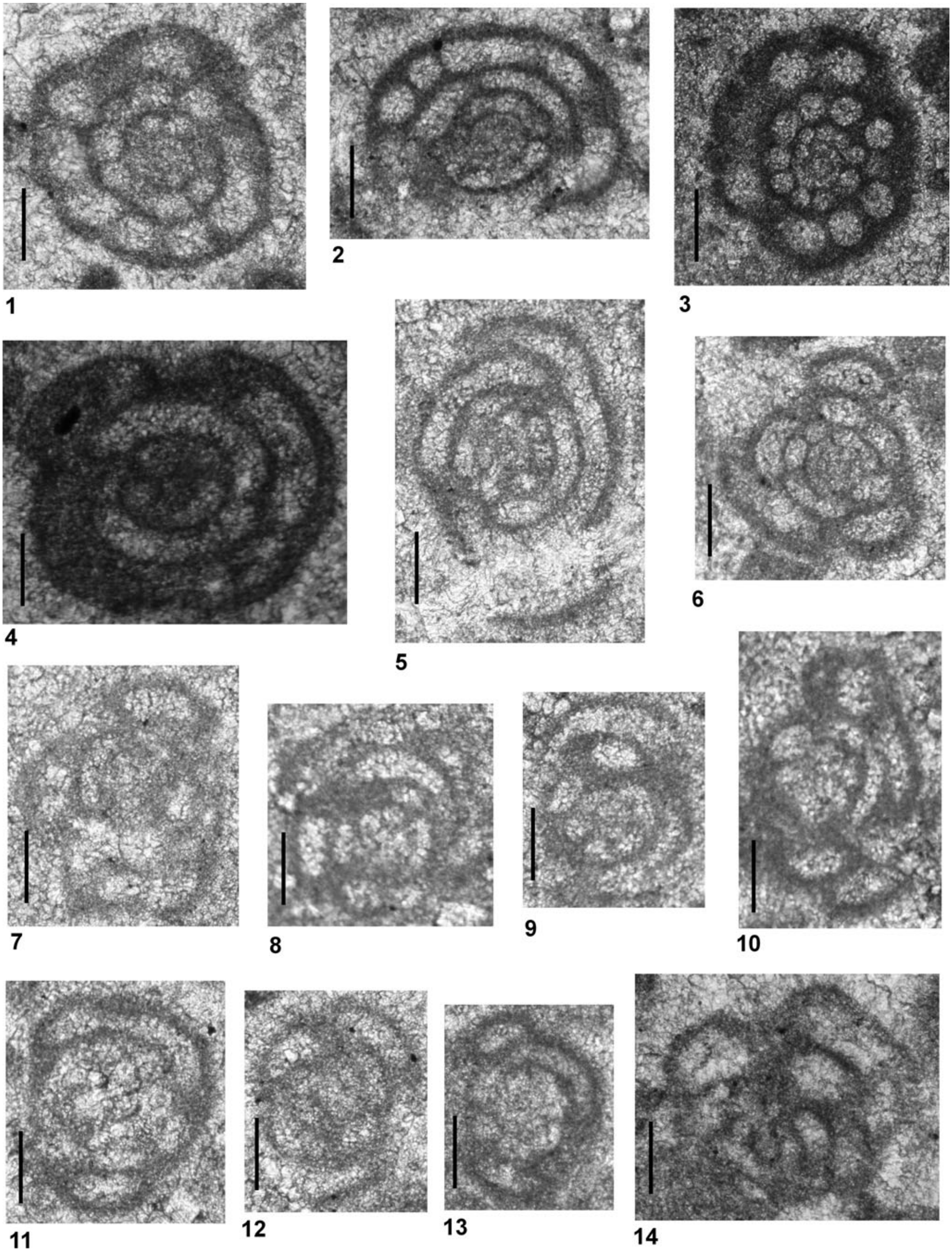
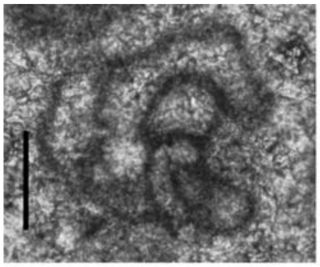


Figure 12. All specimens are from Guandao (PGD) and Upper Guandao (PUG) sections. (**1–4**) *Meandrospira dinarica* Kochansky-Devidé and Pantić, 1966 (**5–13**) *Meandrospira*? *enosi* n. sp.; (**14**) Meandrospira? *deformata* Salaj in Salaj et al., 1967. (**1**) PUG-037; (**2**) PUG-031; (**3**) PGD-212; (**4**) PUG-019; (**5–12**) PGD-176; (**13**) PGD-174; (**14**) PUG-054. Scale bars = 100 µm.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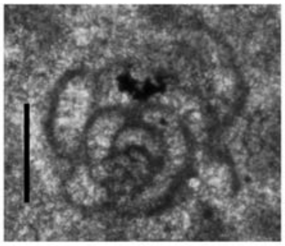
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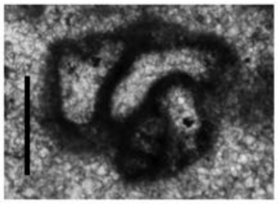
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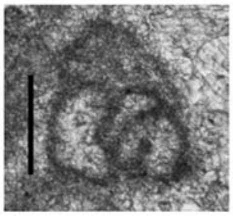
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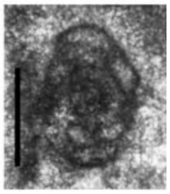
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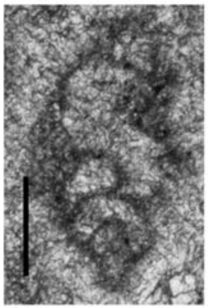
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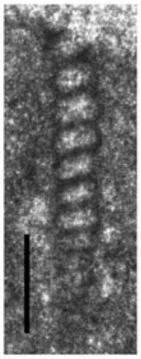
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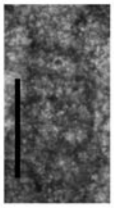
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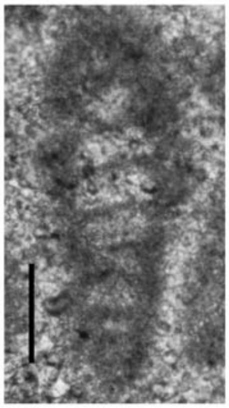
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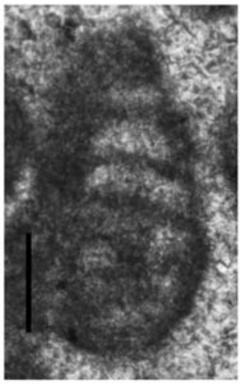
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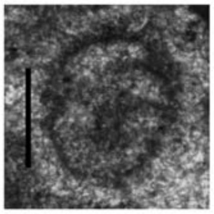
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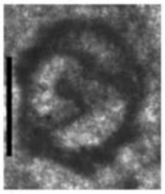
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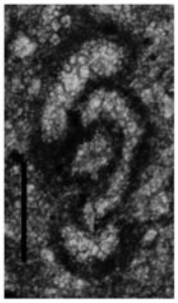
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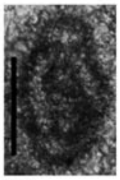
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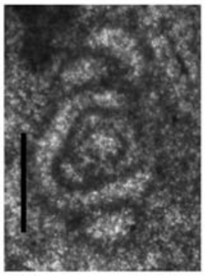
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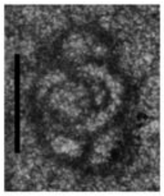
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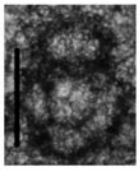
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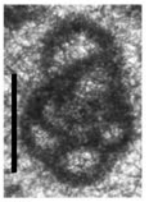
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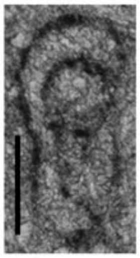
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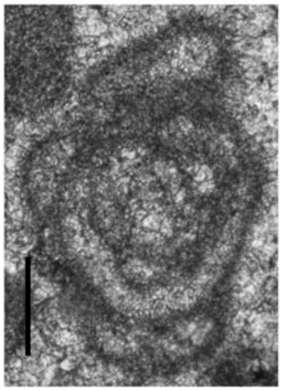
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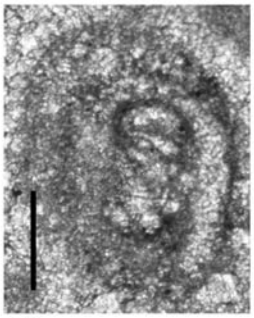
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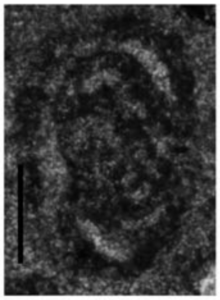
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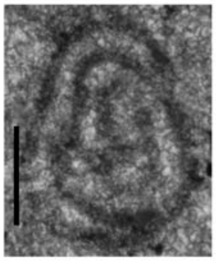
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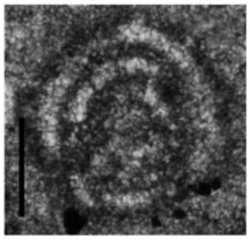
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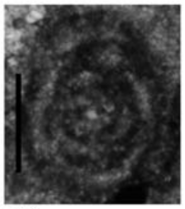
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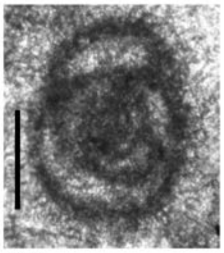
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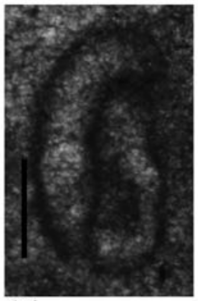
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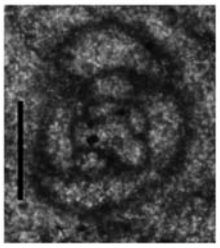
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Figure 13. All specimens are from Dawen (PDW), Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1–4**) Meandrospira? *deformata* Salaj in Salaj et al., 1967; (**5**) *Meandrospiranella* cf. *M. samueli* Salaj in Salaj et al., 1967; (**6**) *Meandrospiranella irregularis*? Salaj in Salaj et al., 1967; (**7–9**) *Turriglomina mesotriasica* (Koehn-Zaninetti, 1968); (**10–13**) *Turriglomina* cf. *T. magna* (Urošević, 1977); (**14**) *Turriglomina carnica* Dağer, 1978b; (**15–33**) *Hoyenella* gr. *H. sinensis* (Ho, 1959). (**1, 4**) PUG-067; (**2, 3**) PUG-069; (**5**) PUG-014; (**6**) PUG-057; (**7**) PUG-089; (**8**) PUG-091; (**9**) MDJ-35; (**10**) PUG-055; (**11**) PUG-077; (**12**) PUG-075; (**13**) PUG-085; (**14**) PUG-145; (**15, 33**) PDW-285; (**16**) PGD-101; (**17**) PGD-087; (**18**) PDW-281; (**19**) PDW-275; (**20, 30**) PGD-090; (**21**) PDW-259; (**22**) PGD-151; (**23**) PGD-176; (**24**) PDJ-302; (**25**) PDJ-313; (**26–28**) PDJ-303; (**29**) PDJ-281; (**31**) PDW-315; (**32**) PGD-168. Scale bars = 100μm.

Middle Triassic Dajiang section (Fig. 10). *Turriglomina* cf. *T. magna* has been recognized in the upper Pelsonian–Illyrian, whereas *T. carnica* occurs rarely in the Carnian of the Upper Guandao section (Figs. 8, 9)

Turriglomina mesotriasica (Koehn-Zaninetti, 1968)
Figure 13.7–13.9

Remarks.—Koehn-Zaninetti (1968) published a condensed version of Koehn-Zaninetti (1969) with the same title in which she reported the new taxa that she discovered in this paper. Although these taxa were also described as new in 1969 (her main work) we give priority to the 1968 publication. See additional remarks under Genus *Turriglomina*.

Turriglomina cf. *T. magna* (Urošević, 1977)
Figure 13.10–13.13

Remarks.—See Remarks under Genus *Turriglomina*.

Turriglomina carnica Dağer, 1978b
Figure 13.14

Remarks.—See Remarks under Genus *Turriglomina*.

Family Hoyenellidae Rettori, 1994
Genus *Hoyenella* Rettori, 1994

Remarks.—A variety of sections belonging to the genus *Hoyenella*, characterized by an ovoid to discoidal test with a large globular proloculus, an early stage coiled in several different planes, and a planispirally coiled later stage, have been grouped under two distinct and two questionable populations.

Hoyenella gr. *H. sinensis* (Ho, 1959)
Figures 13.15–13.33, 14.1

Remarks.—Although nearly all early hoyenellid forms of Early to Middle Triassic age (*Glomospirella sinensis* var. *rara* Ho, 1959, *Glomospirella facilis* Ho, 1959, and *Glomospirella shengi* Ho, 1959; *Glomospirella elbursorum* Brönnimann et al., 1972b and *Palaeonubecularia minuta* Brönnimann et al., 1972b; and *Calcitornella gebzensis* Dağer, 1978b) have been synonymized under *Hoyenella* gr. *H. sinensis* by Rettori (1994, 1995), we distinguish two main hoyenellid groups in the material of the Great Bank of Guizhou. *Hoyenella* gr. *H. sinensis* (Figs. 13.15–13.33, 14.1) differs from *H.* gr. *H. shengi* (Fig. 14.2–14.9) by its more voluminous irregularly coiled early stage, whereas in the *H.* gr. *H. shengi* population, planispiral coiling in the later stage is more prominent. In addition to taxa synonymized under *H.* gr. *H. sinensis* by Rettori (1995), we also consider *Glomospira roesingi* Blau et al., 1995, described from the Scythian–Anisian of Germany, as a synonym of *H.* gr. *H. sinensis* based on the similarity of the wall composition and the coiling of the tubular chamber.

In the Dajiang and Dawen sections (Figs. 5, 6), *H.* gr. *H. sinensis* and *H.* gr. *H. shengi* make their first appearances in the upper Dienerian strata. In the Guandao section these species range up to the Bithynian (Fig. 11), whereas in the Upper Guandao section they range into the Illyrian (Fig. 8). In Israel (Korngreen et al., 2013), Kashmir Valley, India (Baud and Bhat, 2014), and south China (Galfetti et al., 2008) the first appearance of *H.* gr. *H. sinensis* also has been reported as Dienerian in successions that are well dated by conodonts.

Hoyenella gr. *H. shengi* (Ho, 1959)
Figure 14.2–14.9

Remarks.—See Remarks under *Hoyenella* gr. *H. sinensis*.

Hoyenella? sp. 1
Figure 14.10

Remarks.—Two other, questionable hoyenellid species, *H.*? sp. 1 (Fig. 14.10) and *H.*? sp. 2 (Fig. 14.11, 14.12), characterized by more complicated coiling of the tubular chamber, are rare. *Hoyenella*? sp. 1 has been recorded from the uppermost Bithynian in the Upper Guandao section (Fig. 8).

Hoyenella? sp. 2
Figure 14.11, 14.12

Remarks.—See Remarks under *Hoyenella*? sp. 1. *Hoyenella*? sp. 2 ranges from the Bithynian to lower Ladinian (Fassanian) in the Guandao and Upper Guandao sections (Figs. 9, 11).

Family Agathamminidae Ciarapica, Cirilli, and Zaninetti in Ciarapica et al., 1987
Genus *Agathammina* Neumayr, 1887
Agathammina? sp.
Figure 14.13, 14.14

Remarks.—Oblique sections of some coiled bilocular forms with a probable *Quinqueloculina*-like arrangement of the tubular chamber are reported as *Agathammina*? sp. (Fig. 14.13, 14.14) from the Upper Guandao section. Such forms range from the Ladinian (Fassanian) to the Carnian (Cordevolian) (Fig. 9).

Family Ophthalmidiidae Wiesner, 1920
Genus *Ophthalmidium* Kübler and Zwingli, 1870
Ophthalmidium exiguum Koehn-Zaninetti, 1969
Figure 14.15

Remarks.—Identical to forms described by Koehn-Zaninetti (1969), *Ophthalmidium exiguum* is characterized by tests of small dimensions, thin wall, and chambers half-whorl long in the adult. It has been recorded from the Longobardian (Upper Ladinian) of the Upper Guandao section (Fig. 9). Typical sections of *O. exiguum* have been illustrated from the Ladinian to Carnian of Turkey (Altıner and Zaninetti, 1981) and China (He and Wang, 1990). Forms reported more recently from the Anisian of the southern Alps (Italy) by Faletti and Ivanova (2003) and the Qingyan section of south China by Song et al. (2015) do not belong to the population of *O. exiguum*. They should be attributed to the lineage of *Eoophthalmidium tricki*, described by Langer (1968; see also Zaninetti, 1976; Okay et al., 2015). The rest of the ophthalmidiid fauna consists of five different populations.

Ophthalmidium sp. 1
Figure 14.16–14.18

Remarks.—*Ophthalmidium* sp. 1 is recognized in robust axial sections, tends to uncoil toward the end of its ontogeny, and ranges from Longobardian (Ladinian) to Cordevolian (Carnian) in the Upper Guandao section (Fig. 9).

Ophthalmidium sp. 2
Figure 14.19–14.21

Remarks.—*Ophthalmidium* sp. 2, characterized by an elongate ellipsoidal test with narrow tubular chambers and a slightly sigmoidal coiling, also ranges from Longobardian to Cordevolian in the Upper Guandao section (Fig. 9).

Ophthalmidium sp. 3
Figure 14.22, 14.23

Remarks.—Small and slightly biumbilicate tests of *Ophthalmidium* sp. 3 have been recorded from the Pelsonian to Cordevolian interval of the Upper Guandao section (Figs. 8, 9).

Ophthalmidium sp. 4
Figure 14.25

Remarks.—*Ophthalmidium* sp. 4, with a losangic outline, is also found in the Cordevolian of the Upper Guandao section (Fig. 9).

Ophthalmidium? sp. 5
Figure 14.24

Remarks.—*Ophthalmidium*? sp. 5 (Fig. 14.24) is quite close to *Eoophthalmidium* of Langer (1968), with a cornuspirine tubular second chamber in early whorls and gradually shortened chambers in the adult similar to the illustrations given in Okay et al. (2015; see also Zaninetti and Brönnimann, 1969). This form occurs in the Bithynian of the Guandao section (Fig. 11).

Family Quinqueloculinidae Cushman, 1917
Genus *Gsollbergella* Zaninetti, 1979
Gsollbergella? sp. 1
Figure 14.26

Remarks.—Questionable forms assigned to *Gsollbergella*? sp. 1 (Fig. 14.26) and *G*.? sp. 2 (Fig. 14.27), characterized by incipient divisions in the tubular chamber, have been recognized in the Fassanian (lower Ladinian) and Pelsonian to Illyrian (Anisian), respectively, of the Upper Guandao section (Figs. 8, 9). However, transverse sections of such forms are not known, and only a quinqueloculine-type coiling would enable confident assignment to the genus *Gsollbergella*.

Gsollbergella? sp. 2
Figure 14.27

Remarks.—See Remarks under *Gsollbergella*? sp. 1.

Family Galeanellidae Zaninetti et al., 1982
Genus *Galeanella* Kristan, 1958
Galeanella sp.
Figure 14.28

Remarks.—A primitive form of the genus *Galeanella*, *G*. sp., characterized by a thick perforated wall and probably with a biloculine chamber arrangement, has been recorded in the Cordevolian (lower Carnian) strata of the Upper Guandao section (Fig. 9). According to Zaninetti, Martini, and Altıner (1992) and Zaninetti and Martini (1993), the earliest representatives of the genus *Galeanella* appeared early in the Carnian. This unusual *Galeanella* has also been illustrated by He and Wang (1990) from the Carnian of south China. The Chinese specimen could be considered as one of the earliest *Galeanella* populations.

Class Textulariata Mikhalevich, 1980

Remarks.—In the Great Bank of Guizhou, Textulariata is quite diverse and composed of the bilocular family Ammodiscidae and several multilocular families, namely Trochamminidae, Reophacidae, Spiroplectamminidae, Placopsilinidae, Verneulinidae, Cuneolinidae, Piallinidae, and Textulariidae.

Family Ammodiscidae Reuss, 1862
Subfamily Glomospirellinae Ciarapica and Zaninetti, 1985
Genus *Gandinella* Ciarapica and Zaninetti, 1985
Gandinella? sp.
Figure 15.12

Remarks.—In the subfamily Glomospirellinae, forms tending to display a sigmoidal coiling following a streptospiral early stage are reported as *Gandinella*? sp. Such forms have been discovered in the Pelsonian substage of the Middle Triassic Dajiang section (Fig. 10).

Genus *Glomospira* Rzehak, 1885
Glomospira sp.
Figure 15.10, 15.11

Remarks.—*Glomospira* sp., recorded from the Smithian of the Dajiang section (Fig. 6), is characterized by small, entirely streptospiral tests, nearly identical to forms illustrated as *G. regularis* by Ho (1959). Rettori (1995) placed such forms in synonymy under *Pilammina praedensa* Urošević, 1988.

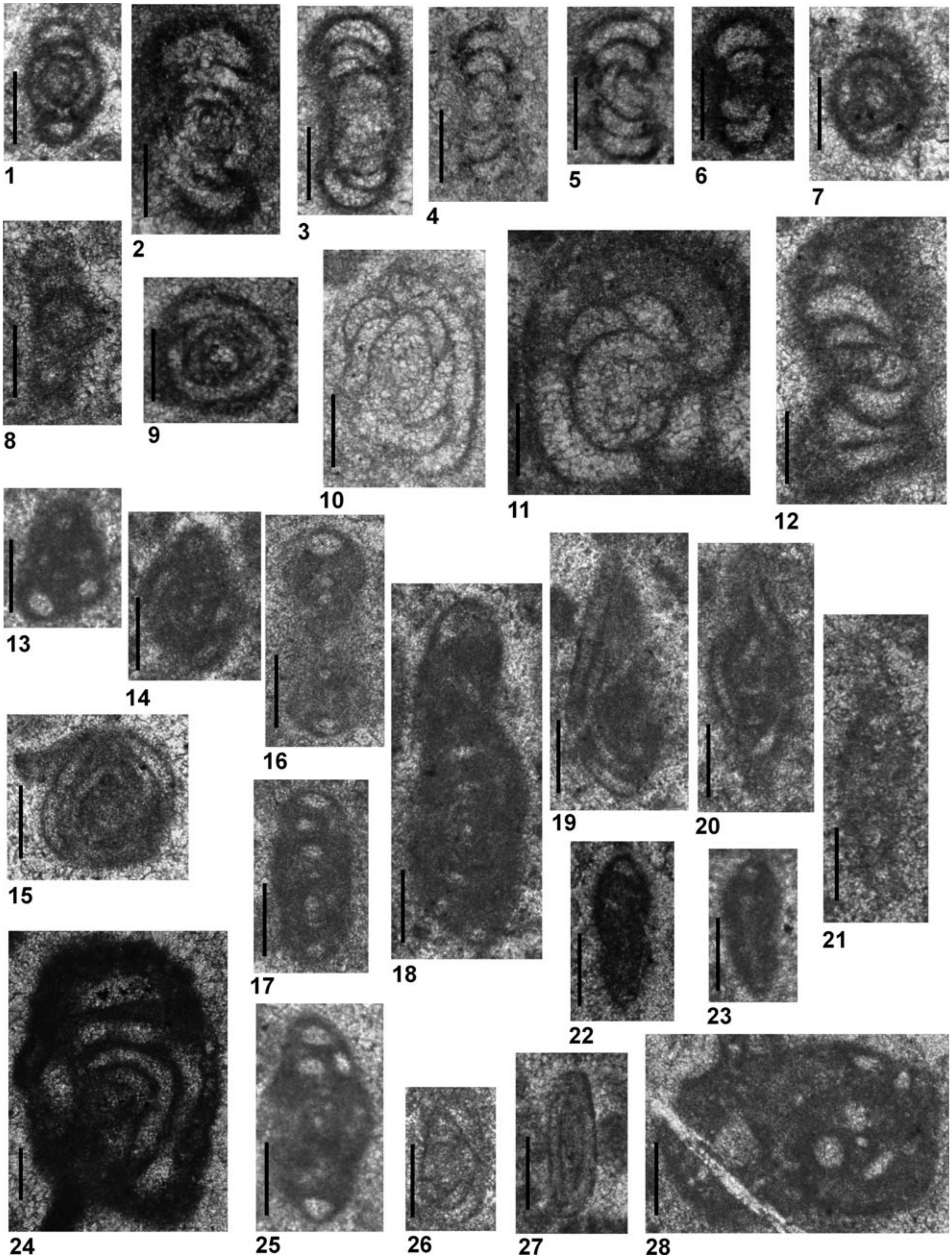


Figure 14. All specimens are from Dawen (PDW), Dajiang (PDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1**) *Hoyenella* gr. *H. sinensis* (Ho, 1959); (**2–9**) *Hoyenella* gr. *H. shengi* (Ho, 1959); (**10**) *Hoyenella*? sp. 1; (**11, 12**) *Hoyenella*? sp. 2; (**13, 14**) *Agathammina*? sp.; (**15**) *Ophthalmidium exiguum* Koehn-Zaninetti, 1969; (**16–18**) *Ophthalmidium* sp. 1; (**19–21**) *Ophthalmidium* sp. 2; (**22, 23**) *Ophthalmidium* sp. 3; (**24**) *Ophthalmidium*? sp. 5; (**25**) *Ophthalmidium* sp. 4; (**26**) *Gsollbergella*? sp.1; (**27**) *Gsollbergella*? sp. 2; (**28**) *Galeanella* sp. (**1, 7**) PGD-090; (**2, 6**) PDW-273; (**3**) PUG-009; (**4, 5**) PDW-259; (**8**) PGD-096; (**9**) PDJ-302; (**10**) PUG-027; (**11**) PGD-226; (**12**) PUG-101; (**13, 14, 17–20, 23**) PUG-143; (**15**) PUG-109; (**16, 25**) PUG-137; (**21**) PUG-131; (**22**) PUG-047; (**24**) PGD-217; (**26**) PUG-097; (**27**) PUG-087; (**28**) PUG-139. Scale bars = 100 µm.

Genus *Glomospirella* Plummer, 1945
Glomospirella vulgaris Ho, 1959
Figure 15.1–15.5

Remarks.—The genus *Glomospirella* is represented by three different populations. Among these, *G. vulgaris* consists of a deuteroloculus describing an initial streptospiral coiling with 3–5 whorls and then a planispiral coiling tending to become slightly sigmoidal in the adult. It has been recorded in the Smithian of the Dawen (Fig. 5), Dajiang (Fig. 6), and Guandao (Fig. 11) sections. In the recent literature, *Glomospirella* illustrated by Song et al. (2011b) from the Olenekian of the Yangtze Block is probably *G. vulgaris*. In addition, most of the forms illustrated as *Hoyenella* spp. by Song et al. (2016) in the facies photographs of the Olenekian of south China should also be referred to *G. vulgaris*. From the European side, *G. vulgaris* described from the Anisian of Poland and Slovakia by Rychliński et al. (2013) should be referred either to *Gandinella* or *Glomospirella*.

Glomospirella sp. 1
Figure 15.6, 15.7

Remarks.—*Glomospirella* sp. 1, recorded from the uppermost Bithynian to Longobardian interval of the Upper Guandao section (Figs. 8, 9), is characterized by a tightly coiled deuteroloculus with a smaller chamber height, similar to the morphology of *Glomospira tenuifistula* described by Ho (1959). However, this form has a *Glomospirella*-like planispiral stage and more compressed axial sections.

Glomospirella sp. 2
Figure 15.8, 15.9

Remarks.—The other *Glomospirella* population, *G.* sp. 2, is also distinct, with its pronounced streptospiral stage occupying more than half of the volume of the test and tightly coiled, oscillating to planispiral two or three whorls. *Glomospirella* sp. 2 is morphologically very close to *Glomospirella lampangensis* Kobayashi et al., 2006, which was described from northern Thailand. However, more material is required in order to decide on the degree of similarity in coiling between our *G.* sp. 2 and *G. lampangensis*. This form appears in the Aegean close to the Olenekian-Anisian boundary in the Guandao section and ranges into the Bithynian (Fig. 11).

Subfamily Pilammininae Martini, Vachard, and Zaninetti, 1995
Genus *Pilammina* Pantić, 1965
Pilammina densa Pantić, 1965
Figure 15.13–15.20

Remarks.—In the ammodiscid foraminiferal fauna, the main biostratigraphic markers in the Triassic stratigraphy belong to genera such as *Pilammina* and *Pilamminella*. *Pilammina densa* Pantić, 1965 has been reported from the Anisian by many authors (e.g., Baud et al., 1971; Premoli Silva, 1971; Brönnimann et al., 1973a, b; Gazdzicki et al., 1975; Zaninetti, 1976; Dağer, 1978a; Trifonova, 1978a; Salaj et al., 1983; He, 1984; He and Wang, 1990; Altıner and Koçyiğit, 1993; Rettori, 1995; Bucur et al., 1997; de Bono et al., 2001; Fugagnoli and Posenato, 2004; Berra et al., 2005; Kobayashi et al., 2005, 2006; Marquez, 2005; Payne et al., 2011; Velledits et al., 2011; Song et al., 2015; Lehrmann et al., 2015; Miyahigashi et al., 2017). It is mainly characterized by numerous streptospirally and tightly coiled whorls with planes of coiling changing slowly (Fig. 15.13–15.20).

In the Guandao and Upper Guandao sections (Figs. 8, 11), *P. densa* ranges from the Bithynian to the Pelsonian, as calibrated with conodonts (Lehrmann et al., 2015). It has been recorded in the Pelsonian of the Middle Triassic Dajiang section (Fig. 10). The first appearance of *P. densa* nearly coincides with the Aegean/Bithynian boundary, consistent with reporting by Song et al. (2015). Although the *P. densa* Zone has been assigned to the late Anisian in western Tethyan domains (See Rettori, 1995 and the references therein), this form has never been recorded from the upper Anisian (Illyrian) in the Chinese sections.

Pilammina densa? Pantić, 1965
Figure 15.21–15.24

Remarks.—Smaller forms with numerous whorls describing partly a sigmoidal coiling (Fig. 15.21, 15.22) and displaying a quadrangular profile (Fig. 15.23, 15.24) have been questionably assigned to *P. densa*. Similar forms were reported by Flügel et al. (1994) as *Glomospira*? sp. cf. *G.*? *micas* He and Yue, 1987 from the Pelsonian of Slovenia. *Pilammina densa*? of this study is also close to some specimens illustrated as *P. densa* from the Anisian of Malaysia by Gazdzicki and Smit (1977) and Greece by Rettori et al. (1994).

Genus *Pilamminella* Salaj, 1978
Pilamminella grandis Salaj in Salaj et al., 1967
Figure 15.25–15.27

Remarks.—The genus *Pilamminella* is represented by *P. grandis* in the Chinese material. This form is characterized by tests consisting of oscillating to planispiral whorls in the adult following a tightly coiled *Pilammina*-like stage. Rettori (1995) considered this form as a synonym of *P. semiplana*; however, *P. grandis* differs from this form in the absence of sigmoidal coiling in the initial stage and rather less tightly coiled whorls in the planispiral stage. Some sections of foraminifera illustrated as *Glomospira densa* or *Glomospira* sp. by Kobayashi (1996) from the Anisian of the Kanto Mountains, Japan, belong to *P. grandis*. Similarly, *P. grandis* has been reported from Japan as *Glomospirella irregularis* in Kobayashi et al. (2005). Bucur et al. (1997) extensively illustrated *P. grandis* from the Anisian of the southern Carpathians in Romania. In relatively recent literature, *P. grandis* has been reported as *P. semiplana*, following Rettori (1995), from the Anisian of northern Italy by Fugagnoli and Posenato (2004) and Berra et al. (2005). *Pilamminella grandis* ranges from Aegean to Pelsonian in the Upper Guandao section (Fig. 8) and Aegean to Bithynian in the Guandao section (Fig. 11).

Subfamily Tolypammininae Cushman, 1928
Genus *Tolypammina* Rhumbler, 1895
Tolypammina gregaria Wendt, 1969
Figure 16.1

Remarks.—Attached tests composed of an elongate, undivided, tubular chamber winding irregularly over the attachment surface are recognized as *Tolypammina gregaria* Wendt, 1969 in this study. This form has been reported from the Anisian to Carnian interval from several localities in the Triassic of Europe (Zaninetti, 1976). The specimens described and illustrated by Brönnimann and Zaninetti (1972) from the Muschelkalk of southern France as *Tolypammina*? aff. *gregaria* (Brönnimann and Zaninetti, 1972, pl. 9, Figs. 2, 5) are nearly identical to forms discovered from the Great Bank of Guizhou.

Family Reophacidae Cushman, 1927
Genus *Reophax* de Montfort, 1808
Reophax sp. 1
Figure 16.2, 16.3

Remarks.—In the studied Chinese stratigraphic sections, rectilinear uniserial tests of the genus *Reophax*, with a coarsely agglutinated wall and single, terminal and rounded aperture, appear at the base of the Anisian Stage. Seven different populations, reported with open nomenclature, have been recognized in the studied material. *Reophax* sp. 1, relatively smaller in size among the Chinese *Reophax* populations, consists of three or four chambers gradually increasing in width and height (Fig. 16.2, 16.3). In the Upper Guandao section it ranges from Pelsonian to Cordevolian (Carnian) (Figs. 8, 9).

Reophax sp. 2
Figure 16.4

Remarks.—*Reophax* sp. 2, again a small form, is characterized by a very narrow and tubular lumen in the two early chambers and the last chamber increasing rapidly in height (Fig. 16.4). It occurs from the Aegean to the Bithynian in the Guandao section (Fig. 11) and from the Aegean to the Illyrian in the Upper Guandao section (Fig. 8).

Reophax sp. 3
Figure 16.5, 16.6

Remarks.—*Reophax* sp. 3 consists of comparatively wider chambers than *Reophax* sp. 1 (Fig. 16.5, 16.6) and is present in the Bithynian of the Guandao section (Fig. 11) and the Bithynian to Cordevolian (Carnian) of the Upper Guandao section (Figs. 8, 9).

Reophax sp. 4
Figure 16.7, 16.8

Remarks.—*Reophax* sp. 4 is distinguished by a last chamber rapidly increasing in height (Fig. 16.7, 16.8). It occurs from the Pelsonian to the Illyrian in the Upper Guandao section (Fig. 8).

Reophax sp. 5
Figure 16.9, 16.10

Remarks.—*Reophax* sp. 5, a larger form, consists of a large proloculus and six succeeding chambers increasing very slowly in height and width (Fig. 16.9, 16.10). It occurs in Anisian to Carnian strata of the Guandao and Upper Guandao sections (Figs. 8, 9, 11). Flügel et al. (1994) reported this form as *Earlandinita elongata* Salaj et al., 1967 from the Pelsonian of Slovenia.

Reophax sp. 6
Figure 16.11

Remarks.—*Reophax* sp. 6, again a larger sized reophacid, is composed of three pyriform chambers rapidly growing in height with depressed sutures (Fig. 16.11). It has been recorded in the Pelsonian to Longobardian (Ladinian) interval of the Upper Guandao section (Figs. 8, 9).

Reophax sp. 7
Figure 16.12

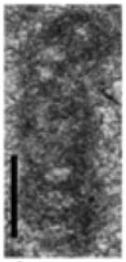
Remarks.—*Reophax* sp. 7, a long and arcuate reophacid, consists of eight chambers increasing slowly in size and becoming pyriform toward the end of ontogeny (Fig. 16.12). It has been recorded in the Pelsonian of the Upper Guandao section (Fig. 8).

Family Spiroplectamminidae Cushman, 1927
Subfamily Spiroplectammininae Cushman, 1927
Genus *Malayspirina* Vachard in Fontaine, Khoo, and Vachard, 1988
Malayspirina sp.
Figure 16.13, 16.14

Remarks.—The genus *Malayspirina* was placed in the Carboniferous family Forschiidae Dain in Dain and Grozdilova (1953) when it was created by Vachard (in Fontaine et al., 1988). Despite the morphological similarity with *Spiroplectammina*, *Malayspirina* differs from it by the irregularity of the coiled and uncoiled parts of the test (Fontaine et al., 1988) and the highly reduced coiled stage. Forms illustrated from the Kanto Mountains, Japan, by Kobayashi (1996) probably are not *Malayspirina*. Rather, they are sections of the uncoiled part of *Endotebanella*. In *Malayspirina* specimens of the Great Bank of Guizhou (Fig. 16.13, 16.14), the reduced coiled stage probably lies in a plane oblique to the axis of the biserial arrangement of chambers characterized by a highly thickened wall. *Malayspirina* sp. is found in the Illyrian (upper Anisian) to Fassanian (lower Ladinian) interval of the Upper Guandao section (Figs. 8, 9) and this range is definitely older than the upper Ladinian–Carnian range assigned to the type species, *Malayspirina fontainei* Vachard in Fontaine et al., 1988.

Family Placopsilinidae Rhumbler, 1913
Genus *Placopsilina* d'Orbigny, 1850
Placopsilina sp.
Figure 16.15–16.17

Remarks.—Attached to a substratum, coarsely agglutinated *Placopsilina* sp. specimens from China are characterized by a highly reduced coiled stage, 6–8 chambers in the uncoiled stage, and a single terminal aperture. In the uncoiled stage, the axis characteristically deviates 20–25° from the surface of attachment and chambers progressively grow in height. *Placopsilina* sp. differs from *P.*? *florae* and *P.*? *lacera* of Trifonova (1967) and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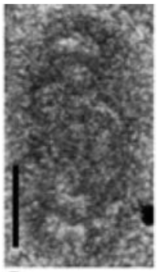
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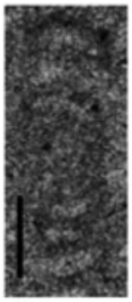
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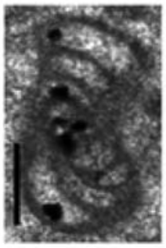
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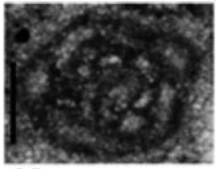
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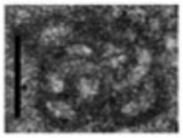
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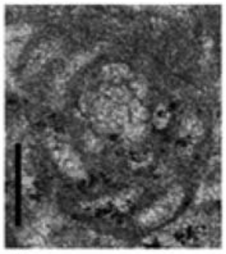
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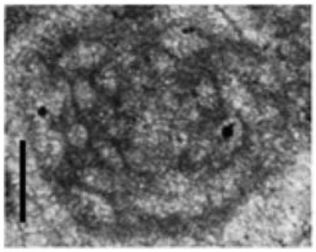
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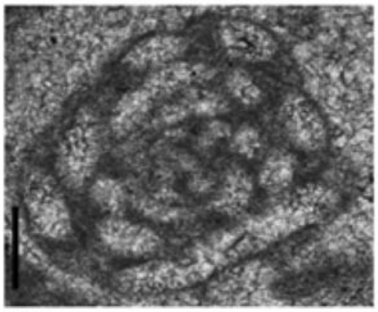
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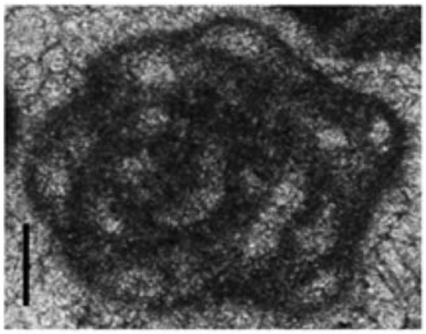
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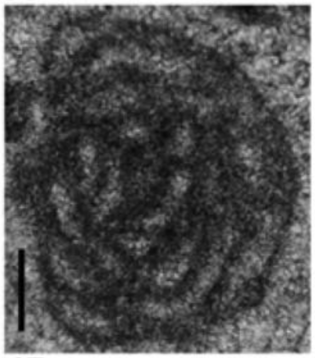
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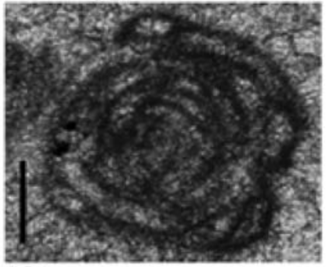
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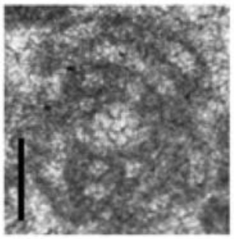
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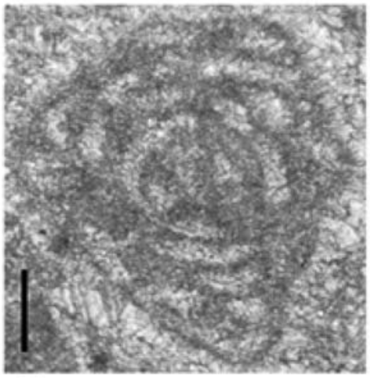
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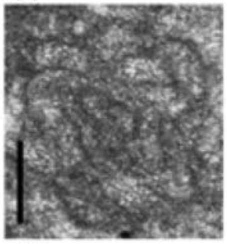
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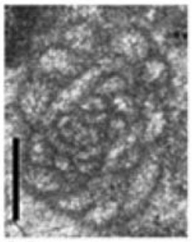
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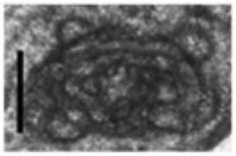
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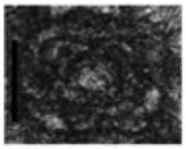
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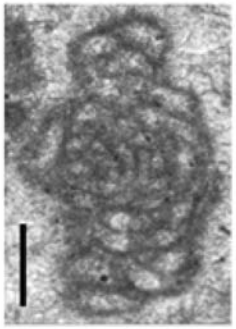
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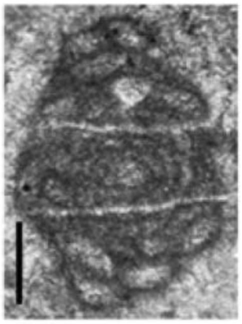
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Figure 15. All specimens are from Dawen (PDW), Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1–5**) *Glomospirella vulgaris* Ho, 1959; (**6, 7**) *Glomospirella* sp. 1; (**8, 9**) *Glomospirella* sp. 2 (*Glomospirella lampangensis*? Kobayashi et al., 2006); (**10, 11**) *Glomospira* sp. (*Pilammina praedensa*? Urošević, 1988); (**12**) *Gandinella*? sp.; (**13–20**) *Pilammina densa* Pantić, 1965; (**21–24**) *Pilammina densa*? Pantić, 1965; (**25–27**) *Pilamminella grandis* Salaj in Salaj et al., 1967. (**1, 2**) PDJ-319; (**3**) PGD-131; (**4**) PDW-342; (**5**) PGD-096; (**6, 19–22**) PUG-029; (**7**) PUG-054; (**8, 9**) PGD-236; (**10**) PDJ-302; (**11**) PDJ-303; (**12**) MDJ-02; (**13**) PUG-063; (**14**) PUG-059; (**15**) PUG-054; (**16**) PUG-045; (**17**) PUG-037; (**18**) PGD-217; (**23**) PUG-015; (**24**) PUG-051; (**25, 26**) PUG-027; (**27**) PUG-033. Scale bars = 100 µm.

P.? *hyerensis* of Brönnimann and Zaninetti (1972) by a much smaller coiled stage and a slender test containing more chambers in the uncoiled stage. *Placopsilina* sp. has been found in the Aegean–Bithynian of the Guandao section (Fig. 11).

Family Trochamminidae Schwager, 1877
Genus *Trochammina* Parker and Jones, 1859
Trochammina almtalensis Koehn-Zaninetti, 1968
Figure 16.18–16.23

Remarks.—Koehn-Zaninetti (1968) published a condensed version of Koehn-Zaninetti (1969) with the same title in which she reported the new taxa that she discovered in this paper. Although these taxa were also described as new in 1969 (her main work) we give priority to the 1968 publication. *Trochammina almtalensis* Koehn-Zaninetti, 1968 specimens of the Great Bank of Guizhou from south China are characterized by the small size and trochospirally coiled three or four whorls consisting of four chambers per whorl (Fig. 16.18–16.23). They are nearly identical to forms illustrated in the original description by Koehn-Zaninetti (1969). Typical specimens of *T. almtalensis* were illustrated from the Anisian of China by He and Wang (1990) and He and Cai (1991). Recently, Haig et al. (2007) considered the *almtalensis* population to be close to the genus *Siphovalvulina* Septfontaine, 1988. We disagree with this suggestion because *T. almtalensis* does not possess a central siphonal canal, as is characteristic of the type species of *Siphovalvulina*. According to Tian et al. (2014), *T. almtalensis* first appears in the Smithian of the Bianyang section of the Nanpanjiang Basin, south China. This report, not based on illustrated specimens, is probably an erroneous identification.

Trochammina? sp. 1
Figure 16.24, 16.25

Remarks.—In the absence of transverse sections, three other populations have been questionably assigned to the genus *Trochammina*. The small tests of *T.*? sp. 1 (Fig. 16.24, 16.25) are characteristically found in the Spathian of the Guandao section (Fig. 11).

Trochammina? sp. 2
Figure 16.26

Remarks.—Populations of *Trochammina*? sp. 2, characterized by very high trochospiral tests, are found in the Ladinian of the Upper Guandao section (Fig. 9).

Trochammina? sp. 3
Figure 16.27

Remarks.—Populations of *Trochammina*? sp. 3, characterized by very low trochospiral tests, are found in the Ladinian of the Upper Guandao section (Fig. 9).

Family Verneuilinidae Cushman, 1911
Subfamily Verneuilinoidinae Suleymanov, 1973
Genus *Verneuilinoides* Loeblich and Tappan, 1949
Verneuilinoides? *azzouzi* (Salaj, 1978)
Figure 16.30–16.32

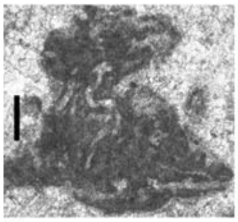
Remarks.—Following the original description from the Anisian to Carnian of the western Carpathians by Salaj (1978), *Verneuilinoides*? *azzouzi* has been reported several times as a species belonging to the genus *Valvulina* (Salaj et al., 1983; Michalík et al., 1993; Flügel et al., 1994; Korchagin, 2008; Ueno et al., 2012). However, this triserial form (Fig. 16.30–16.32) does not possess the canaliculate wall structure and valvular tooth covering the aperture, as given in the type description of the genus *Valvulina*. Following He and Wang (1990), we place this population questionably under the genus *Verneuilinoides* because the aperture is not clearly visible in our material. *Verneuilinoides*? *azzouzi* has been misidentified as *Gaudryina triadica* Kristan-Tollmann, 1964 from the Qingyan section of south China (Song et al., 2015; Figs. 5, 9). In the GBG material, this species is present in the Fassanian to Longobardian (Ladinian) of the Middle Triassic Dajiang section and in the Spathian and Illyrian of the Guandao and Upper Guandao sections (Figs. 8, 10, 11).

Subfamily Verneuilininae Cushman, 1911
Genus *Gaudryina* d'Orbigny, 1839
Gaudryina sp.
Figure 16.34, 16.35

Remarks.—*Gaudryina* sp., with a reduced triserial stage and a following biserial stage consisting of three or four rows, is found in the Pelsonian to Illyrian interval of the Upper Guandao section and in the Aegean of the Guandao section (Figs. 8, 11). Chinese specimens closely resemble *Gaudryina triadica* Kristan-Tollmann, 1964 from the Rhaetian Zlambach Marls of Austria and *G. triadica* specimens illustrated from the Anisian of Japan (Kobayashi et al., 2005) and Thailand (Kobayashi et al., 2006). It differs from two other Triassic species, *G. racema* Trifonova, 1961 and *G. triassica* Trifonova, 1961, in having less globular chambers and a wider frontal profile of the test, respectively.

Family Piallinidae Rettori and Zaninetti in Rettori et al., 1993
Genus *Piallina* Rettori and Zaninetti in Rettori et al., 1993
Piallina bronnimanni Martini, Rettori et al., 1995
Figure 16.28

Remarks.—Two specimens from the Chinese material have been assigned to the family Piallinidae (Rettori and Zaninetti in Rettori et al., 1993; Martini, Rettori et al., 1995). *Piallina bronnimanni* Martini, Rettori et al., 1995 (Fig. 16.28) is small,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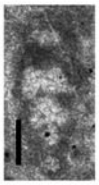
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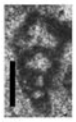
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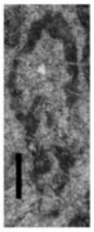
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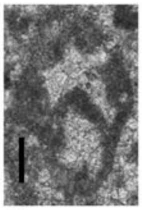
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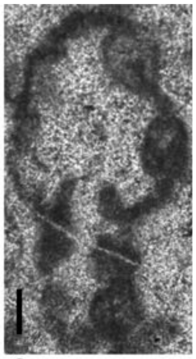
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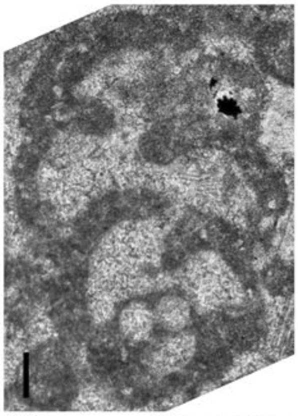
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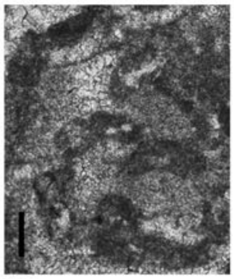
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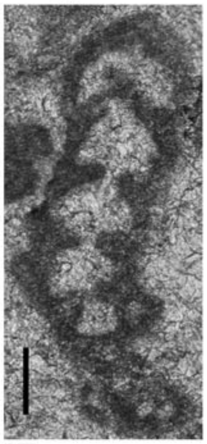
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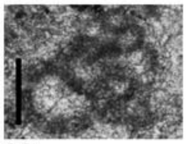
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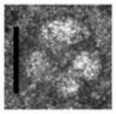
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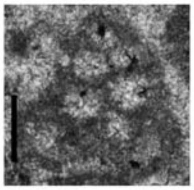
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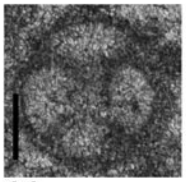
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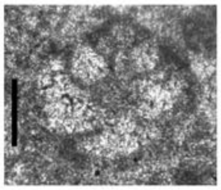
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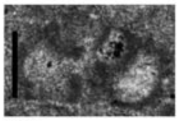
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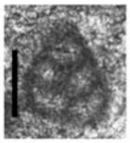
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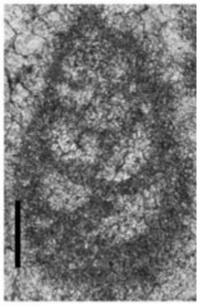
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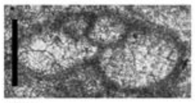
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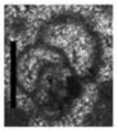
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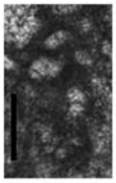
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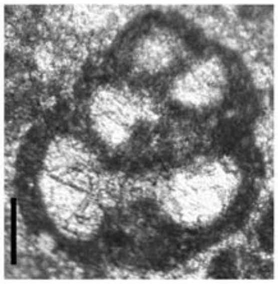
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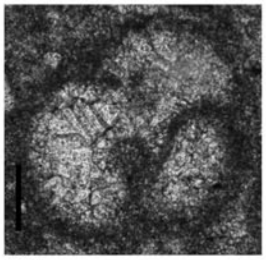
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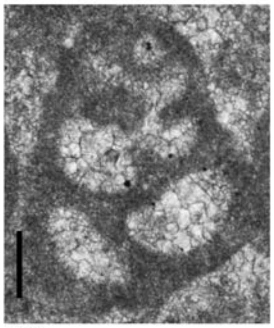
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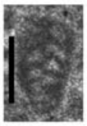
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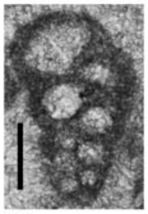
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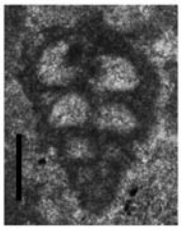
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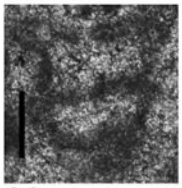
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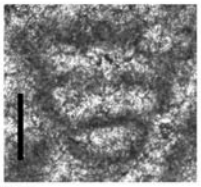
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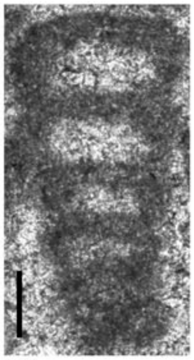
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Figure 16. All specimens are from Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1**) *Tolypammina gregaria* Wendt, 1969; (**2, 3**) *Reophax* sp. 1; (**4**) *Reophax* sp. 2; (**5, 6**) *Reophax* sp. 3; (**7, 8**) *Reophax* sp. 4; (**9, 10**) *Reophax* sp. 5; (**11**) *Reophax* sp. 6; (**12**) *Reophax* sp. 7; (**13, 14**) *Malayspirina* sp.; (**15–17**) *Placopsilina* sp.; (**18–23**) *Trochammina almtalensis* Koehn-Zaninetti, 1968; (**24, 25**) *Trochammina*? sp. 1; (**26**) *Trochammina*? sp. 2; (**27**) *Trochammina*? sp. 3; (**28**) *Piallina bronnimanni* Martini, Rettori et al., 1995; (**29**) *Piallina*? sp.; (**30–32**) *Verneuilinoides*? *azzouzi* (Salaj, 1978); (**33**) *Textularia* sp.1; (**34, 35**) *Gaudryina* sp. (*Gaudryina triadica*? Kristan-Tollmann, 1964); (**36–39**) *Palaeolituonella reclinata* He in He and Cai (1991); (**40**) *Palaeolituonella* sp. [*Palaeolituonella meridionalis*? (Luperto, 1965)]. (**1**) PUG-131; (**2, 23**) PUG-059; (**3, 28**) PUG-145; (**4, 9, 18**) PUG-081; (**5, 32**) PUG-077; (**6, 33**) PUG-143; (**7**) PUG-037; (**8, 37**) PUG-093; (**10**) PUG-137; (**11, 20, 34, 39**) PUG-054; (**12**) PUG-045; (**13, 14**) PUG-101; (**15**) PGD-126; (**16**) PGD-228; (**17**) PGD-210; (**19**) PUG-091; (**21**) MDJ-96; (**22**) PUG-097; (**24**) PGD-168; (**25**) PGD-167; (**26**) PUG-113; (**27**) PUG-099; (**29**) PUG-087; (**30**) MDJ-65; (**31**) PGD-181; (**35**) PUG-067; (**36**) PUG-123; (**38**) PUG-031; (**40**) PUG-093. Scale bars = 100 µm.

probably starting with a low trochospiral initial portion followed by a triserial stage composed of globular chambers. Very similar specimens of *P. bronnimanni* have been described by Rettori et al. (1998) from the lower Carnian of northeastern Italy. Both *Piallina bronnimanni* and *Piallina*? sp. occur in the Upper Guandao section (Figs. 8, 9). *Piallina bronnimanni* is from the Cordevolian (Carnian).

Piallina? sp.
Figure 16.29

Remarks.—The other form, assigned questionably to *Piallina*? sp., is again low trochospiral in the early portion; however, the chamber organization in the later stage of the ontogeny is not clearly visible. Both *Piallina bronnimanni* and *Piallina*? sp. occur in the Upper Guandao section (Figs. 8, 9). *Piallina*? sp. is older than *Piallina bronnimanni* and found in the Illyrian (Anisian).

Family Cuneolinidae Saidova, 1981
Subfamily Cuneolininae Saidova, 1981
Genus *Palaeolituonella* Bérczi-Makk, 1981
Palaeolituonella reclinata He in He and Cai, 1991
Figure 16.36–16.39

Remarks.—Two distinct populations of *Palaeolituonella* are present in the Chinese material. *Palaeolituonella reclinata* He in He and Cai, 1991 (Fig. 16.36–16.39) differs from the type species, *P. meridionalis* (Luperto, 1965), by its smaller and elongate bell-shaped test and thinner wall, and should not be synonymized under *P. meridionalis*, as was considered by Rettori (1995). Although poorly described, the other Chinese species, *P. minima* He and Wang, 1990, is a form close to *P. reclinata*, but differs from it by a less-pronounced uniserial stage and rapidly enlarging chambers in the initial stage. *Haplophragmium* sp., illustrated from the Lower Triassic to middle Anisian Karatash Group of Pamirs by Korchagin (2008), is probably an oblique section of *P. reclinata*. Gale et al. (2018) reported *P. reclinata* under the name of *P. meridionalis* from the lower Carnian of Slovenia.

Palaeolituonella reclinata is present in the Upper Guandao section from the uppermost Aegean (Anisian) to the Longobardian (Ladinian) (Figs. 8, 9). It has been also recorded from the Pelsonian of the Middle Triassic Dajiang section (Fig. 10).

Palaeolituonella sp.
Figure 16.40

Remarks.—Our second population in the Chinese material is characterized by a larger test and thicker wall. Despite the similarity to *P. meridionalis*, we classify such forms *Palaeolituonella* sp. (Fig. 16.40) in the absence of well-oriented sections. *Palaeolituonella* sp. has been found in the upper Illyrian (Anisian) of the Upper Guandao section (Fig. 8).

Family Textulariidae Ehrenberg, 1838
Genus *Textularia* de Blainville, 1824
Textularia sp.
Figure 16.33

Remarks.—Very rare, small, entirely biserial tests discovered in the Cordevolian (Carnian) of the Upper Guandao section (Fig. 9) have been classified as *Textularia* sp. (Fig. 16.33) in the Chinese material.

Class Fusulinata Gaillot and Vachard, 2007

Remarks.—The Class Fusulinata comprises four families in the material of the Great Bank of Guizhou. These are Earlandiidae, Pseudoammodiscidae, Endotebidae, and Endotriadidae.

Family Earlandiidae Cummings, 1955

Remarks.—See Remarks under Class Fusulinata Gaillot and Vachard, 2007.

Genus *Earlandia* Plummer, 1930

Remarks.—The genus *Earlandia*, well known from the Carboniferous and characterized by rectilinear, bilocular tests with micrognular walls, is also present in the uppermost Permian (Changhsingian) deposits of the Southern Biofacies Belt in Turkey (Altıner et al., 2000), as well as in several localities of the Middle East (Gaillot and Vachard, 2007). It is a Permian-Triassic boundary survivor (Groves and Altıner, 2005; Groves et al., 2005, 2007; Vachard et al., 2010; Krainer and Vachard, 2011), also appearing in the lowermost Triassic deposits of the Great Bank of Guizhou. Recently, Nestell et al. (2015) opposed the use of *Earlandia* in the Early Triassic and suggested classifying all *Earlandia*-like forms within the agglutinated genus *Hyperammina*. The walls of *Earlandia* specimens in our Chinese material are composed of microgranular calcite and are directly comparable with those of the other *Earlandia* populations from the Paleozoic (e.g., *Earlandia* gr. *E. elegans*, *E.* gr. *E. moderata*, *E.* gr. *E. minor*, etc.). We consider the specimens examined by Nestell et al. (2015) to be most probably diagenetically altered or totally replaced forms. Thus, we argue that the use of the genus *Hyperammina* is inadequate for the Early Triassic specimens.

The genus *Earlandia* consists of three distinct populations in the Chinese foraminiferal fauna: *Earlandia tintinniformis* (Misik, 1971), *E.* sp. 1, and *E.* sp. 2.

Earlandia tintinniformis (Misik, 1971)
Figure 17.5–17.7

Remarks.—*Earlandia tintinniformis* (Fig. 17.5–17.7), a conical tubular form nearly identical to specimens illustrated in Zaninetti et al. (1972c), differs from *Earlandia* sp. 1 and *E.* sp. 2 by the progressive increase of the diameter of the deuteroloculus during ontogeny. This form is found only in the Anisian Stage of the GBG. It is rare in the Aegean of the Guandao section (Fig. 11), but more common in the Bithynian to Illyrian deposits of the Upper Guandao section (Fig. 8). The specimen illustrated from the Aegean of the Qingyan section from south China by Song et al. (2015) is not *E. tintinniformis*. This form should be classified as an undeterminable *Earlandia* with a thick wall.

Earlandia sp. 1
Figure 17.1, 17.2

Remarks.—*Earlandia* sp. 1, characterized by a much smaller test (Fig. 17.1, 17.2) than *Earlandia* sp. 2 (Fig. 17.3, 17.4), is found only in the lowermost Griesbachian beds of the Dawen and Dajiang sections (Figs. 5, 6). *Earlandia tintinniformis* differs from *Earlandia* sp. 1 by the progressive increase of the diameter of the deuteroloculus during ontogeny. Nestell et al. (2011) illustrated this form as '*E.*' *gracilis* from the uppermost Permian of western Slovenia. *Earlandia* sp. described by Okuyucu et al. (2014) from the Induan of northwestern Turkey is also referable to our *E.* sp. 1.

Earlandia sp. 2
Figure 17.3, 17.4

Remarks.—*Earlandia* sp. 2 has a longer stratigraphic range, Griesbachian in the Dawen section (Fig. 5) and Griesbachian–lower Dienerian in the Dajiang section (Fig. 6). It has been reported as *Earlandia* sp. from the Griesbachian of China (Song et al., 2009, 2016), Slovenia (Nestell et al., 2011), and Turkey (Ünal et al., 2003). Angiolini et al. (2007) reported this form as *E. amplimuralis* from the Antalya Nappes, Turkey, whereas Krainer and Vachard (2011) preferred to name it as *E. dunningtoni* in the material of Austria. In a more recent study, Kolar-Jurkovšek et al. (2018) classified *E.* sp. 2 as *Hyperammina deformis* Bérczi-Makk, 1987 from the base of the Triassic, described as Permian-Triassic Boundary (PTB) transitional beds in Slovenia. *Earlandia tintinniformis* differs from *Earlandia* sp. 2 by the progressive increase of the diameter of the deuteroloculus during ontogeny.

Family Pseudoammodiscidae Conil and Lys in Conil and Pirlet, 1970

Remarks.—In his latest analysis on the macroevolutionary patterns of Paleozoic foraminifera, Vachard (2016, 2018) limited the stratigraphic range of Pseudoammodiscidae to the Serpukhovian Stage. However, as indicated by Altıner and Payne (2017), the pseudoammodiscid clade appears to have survived through the Permian as a sporadically occurring, 'hidden' taxon among the rapidly evolving fusulinoideans and other members of Fusulinata, Nodosariata, and Miliolata. Pseudoammodiscidae apparently survived the Permian-Triassic boundary crisis and appeared as a Lazarus taxon in the late Dienerian both in China and Turkey.

Genus *Pseudoammodiscus* Conil and Lys in Conil and Pirlet, 1970
Pseudoammodiscus sp.
Figures 17.8–17.14, 19.19

Remarks.—Specimens of *Pseudoammodiscus* sp. (Figs. 17.8–17.14, 19.19; Fig. 17.10 has been re-illustrated on Fig. 19.19 for comparison with *Praetriadodiscus*) discovered in the Lower Triassic deposits of the Great Bank of Guizhou from the Nanpanjiang Basin were previously reported and partly illustrated as an undetermined pseudoammodiscid ancestor by Altıner and Payne (2017). These authors considered the specimens that they illustrated to be identical to forms reported as *Ammodiscus parapriscus* Ho, 1959 from Turkey by Altıner and Zaninetti (1981). They stated that the true *parapriscus* population, as described by Ho (1959), is a taxon related to the evolution of porcelaneous hoyenellid foraminifera, and the specimens discovered both in China and Turkey belong to an undetermined pseudoammodiscid population, reported now as *Pseudoammodiscus* sp. in this study. *Pseudoammodiscus* sp. is present from the Dienerian to Smithian in the Dawen section (Fig. 5). It has been recorded in the Smithian of both Dajiang and Guandao sections (Figs. 6, 11).

Family Endotebidae Vachard et al., 1994

Remarks.—The family Endotebidae is diverse and common in the upper Spathian and Middle Triassic deposits of the Great Bank of Guizhou. It is represented by three genera: *Endoteba*, *Endotebanella*, and *Spinoendotebanella* n. gen. The description of the new genus *Spinoendotebanella* and its type species, *S. lehrmanni* n. gen., n. sp., is given below.

Genus *Endoteba* Vachard et al., 1994
Endoteba controversa Vachard and Razgallah, 1988
Figure 17.15–17.19

Remarks.—The type of the family, *Endoteba*, comprises five distinct populations. *Endoteba controversa*, the type species of the genus, is characterized by five chambers in the last whorl, a wall progressively increasing in thickness, and curved and cuneiform septa. The specimens illustrated as *Endoteba* ex gr. *controversa* by Chablais (2010) from the Upper Triassic atoll-like carbonates of Japan probably are not correct because these forms do not possess cuneiform septa and are characterized by a thinner wall. The holotype of *E. controversa* has been described from the Permian of Tunisia (Vachard and Razgallah, 1988), and the species survived the Permian-Triassic boundary. According to Rettori (1995; see also Vachard et al., 1994), the stratigraphic range of this form extends from the base of the

Triassic through the top of the Rhaetian; however, this range has not been confirmed by solid stratigraphic data. *Endoteba controversa* has been recorded from the Bithynian of the Guandao section (Fig. 11) and the Bithynian to lower Longobardian (Ladinian) of the Upper Guandao section (Figs. 8, 9).

Endoteba bithynica Vachard et al., 1994
Figure 17.20–17.23

Remarks.—Characterized by an irregular coiling, thick wall, and probably a longer spire, as indicated in the diagnosis by Vachard et al. (1994), *E. bithynica* has a stratigraphic range from the upper Spathian to Bithynian in the Guandao section (Fig. 11). Recently, specimens from northern Thailand that are similar to the GBG material were illustrated in Kobayashi et al. (2006).

Endoteba obturata (Brönnimann and Zaninetti, 1972)
Figure 17.24–17.26

Remarks.—Specimens belonging to *Endoteba obturata*, with its nautiloid profile, 4–5 chambers in the last whorl, and a thick wall, are nearly identical to forms illustrated in Brönnimann and Zaninetti (1972), Brönnimann et al. (1973a, b), Vachard et al. (1994), and Kobayashi et al. (2006). Haig et al. (2007) reported this form from the Carnian of East Timor. *Endoteba obturata* is present from the uppermost Bithynian to Illyrian in the Upper Guandao section (Fig. 8) and the Illyrian to Longobardian in the Middle Triassic Dajiang section (Fig. 10).

Endoteba badouxi (Zaninetti and Brönnimann in Zaninetti et al., 1972c)
Figure 17.28, 17.29

Remarks.—Larger *Endoteba* specimens with seven chambers in the last whorl are similar to forms described in Zaninetti et al. (1972c) from Switzerland, and reported in this study as *Endoteba badouxi*. The stratigraphic range of *E. badouxi* is reported as Anisian to Carnian in Rettori (1995). In the Chinese material, this form has been recorded from the Illyrian to the Longobardian in the Upper Guandao section (Figs. 8, 9). *Endoteba badouxi* was reported from the Middle Triassic of China (He and Wang, 1990), Illyrian–Ladinian of Italy (Emmerich et al., 2005), and Pelsonian–Carnian of Hungary (Velledits et al., 2011). The specimen illustrated from Pamirs by Korchagin (2008) is characterized by fewer chambers and is probably not *E. badouxi*.

Endoteba sp.
Figure 18.1, 18.2

Remarks.—Specimens with 4.5–5 globular chambers in the last whorl and a thin wall, from the Pelsonian–Illyrian in the Upper Guandao section (Fig. 8), are considered to be a distinct *Endoteba* population and named as *Endoteba* sp. (Fig. 18.1, 18.2).

Genus *Endotebanella* Vachard et al., 1994

Remarks.—The genus *Endotebanella* is composed of three morphologically distinct populations: *Endotebanella kocaeliensis*, *E.* sp. 1, and *E.* sp. 2.

Endotebanella kocaeliensis (Dağer, 1978b)
Figure 18.3–18.6

Remarks.—*Endotebanella kocaeliensis* consists of four or five chambers progressively growing in volume and a short, uncoiled stage with two or three chambers (Fig. 18.3–18.6). Chinese specimens are close to the holotype described by Dağer (1978a, b) and its emended definition given by Vachard et al. (1994). In Beccaletto et al. (2005), the specimen illustrated from an Upper Triassic block of northwestern Turkey does not belong to the *E. kocaeliensis* population. The coiled portion of this form differs from the *kocaeliensis* type by the presence of more chambers. The illustrated specimen might not even belong to the genus *Endotebanella* because the uncoiled portion appears to be biserial. *Endotebanella kocaeliensis* specimens illustrated from Upper Triassic atoll-like carbonates of Japan by Chablais (2010) are similarly not convincing. Coiled portions are not clearly visible in the illustrated specimens. Finally, in a more recent study, the specimen illustrated as *E. kocaeliensis* from the Qingyan section of south China by Song et al. (2015) is close to our *Endotebanella* sp. 2 (Fig. 18.11). *Endotebanella kocaeliensis* ranges from the Spathian to the Bithynian in the Guandao section (Fig. 11). It has been recorded from Aegean to lower Longobardian strata in the Upper Guandao section (Figs. 8, 9).

Endotebanella sp. 1
Figure 18.12

Remarks.—The other two populations of *Endotebanella*, *E.* sp. 1 (Fig. 18.12) and *E.* sp. 2 (Fig. 18.11), are characterized by a maximum of three chambers in the coiled stage and a slender test, respectively. Both forms are rare in the Bithynian and Pelsonian of the Guandao and Upper Guandao sections (Figs. 8, 11).

Endotebanella sp. 2
Figure 18.11

Remarks.—See Remarks under *Endotebanella* sp. 1.

Genus *Spinoendotebanella* new genus

Type species.—*Spinoendotebanella lehrmanni* new species.

Diagnosis.—A coiled–uncoiled endotebid genus with spinose projections at chamber corners in the coiled stage.

Etymology.—The prefix spino- in the name of the new genus has been used to refer the presence of spinose projections at chamber corners.

Remarks.—*Spinoendotebanella* n. gen. is the only representative of the Family Endotebidae exhibiting spinose projections at chamber corners of the coiled stage. It was most probably derived from the genus *Endotebanella*.

Spinoendotebanella lehrmanni new species
Figure 18.7–18.10


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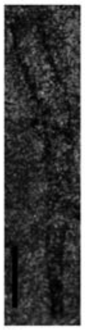
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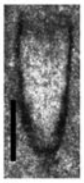
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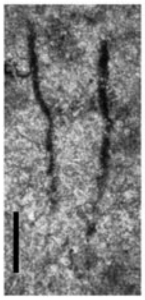
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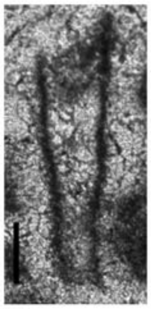
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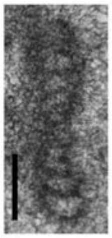
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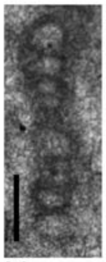
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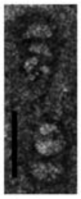
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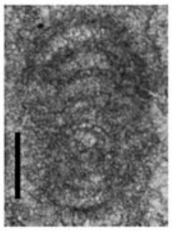
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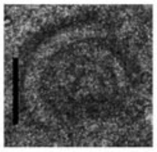
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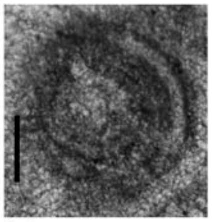
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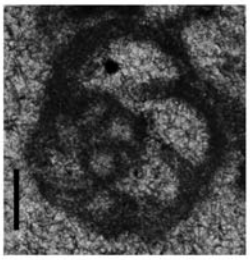
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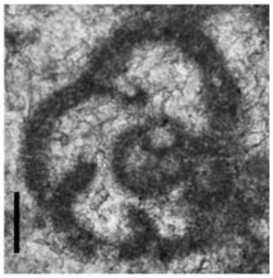
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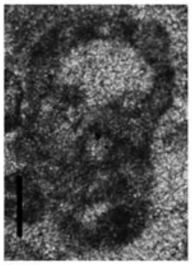
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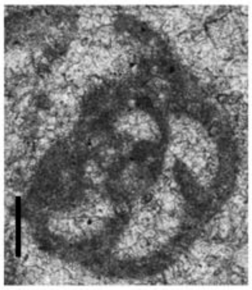
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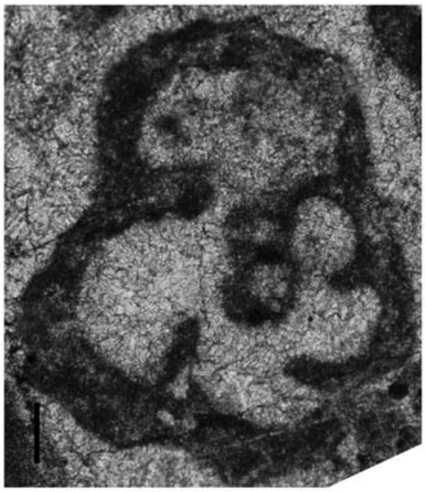
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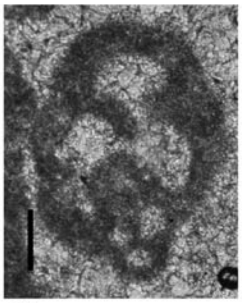
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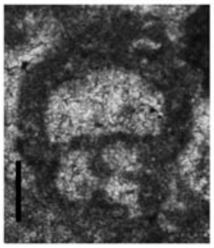
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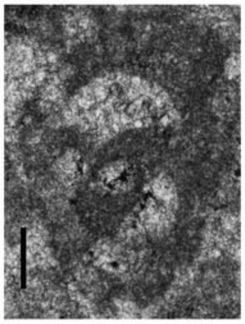
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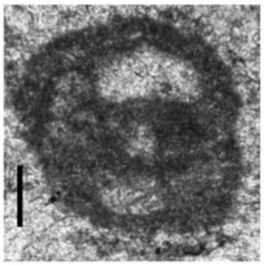
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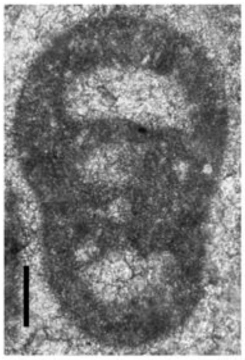
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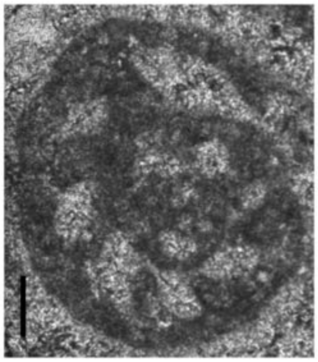
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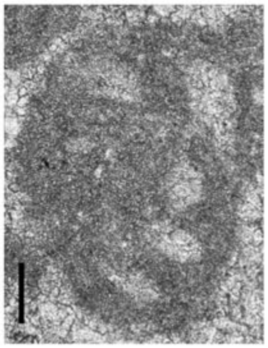
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Figure 17. All specimens are from Dawen (PDW), Dajiang (PDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1, 2**) *Earlandia* sp. 1; (**3, 4**) *Earlandia* sp. 2; (**5–7**) *Earlandia tintinniformis* (Misik, 1971); (**8–14**) *Pseudoammodiscus* sp.; (**15–19**) *Endoteba controversa* Vachard and Razgallah, 1988; (**20–23**) *Endoteba bithynica* Vachard et al., 1994; (**24–27**) *Endoteba obturata* (Brönnimann and Zaninetti, 1972); (**28, 29**) *Endoteba badouxi* (Zaninetti and Brönnimann in Zaninetti et al., 1972c). (**1, 2**) PDJ-055; (**3, 4**) PDJ-172; (**5**) PUG-091; (**6, 18**) PUG-054; (**7**) PUG-045; (**8–10, 12, 14**) PDJ-319; (**11**) PDW-344; (**13**) PDG-111; (**15**) PUG-037; (**16**) PUG-075; (**17, 20**) PGD-219; (**19**) PUG-069; (**21**) PGD-207; (**22**) PGD-220; (**23**) PGD-236; (**24**) PUG-085; (**25**) PUG-063; (**26**) PUG-029; (**27**) PUG-109; (**28**) PUG-123; (**29**) PUG-107. Scale bars = 100 µm.

Holotype.—The specimen comes from sample PUG-027 (Fig. 18.7), Upper Guandao section.

Diagnosis.—A species of *Spinoendotebanella* n. gen. with nearly two complete planispiral whorls, five or six chambers in the last whorl, and a test attaining 1 mm in length.

Occurrence.—Bithynian, Upper Guandao section of the Great Bank of Guizhou, Nanpanjiang Basin, south China, PUG-027.

Description.—Following a proloculus of medium size, the coiled portion of the test consists of two nearly planispiral whorls with 4–5 chambers in the last whorl. In the second whorl and uncoiled portion, chambers gradually increase in height. Chamber corners of the second whorl are generally ornamented with triangular spinose projections. When spinose projections are captured in the plane of equatorial section, chamber cavities also appear to be triangular in section. The uncoiled portion contains as many as five chambers. Wall is typically endotebid-type and the aperture system is as described in the definition of the genus.

Etymology.—The type species is dedicated to Prof. Dr. Daniel J. Lehrmann (Trinity University, USA) for his extensive and valuable contributions to the stratigraphy, sedimentology, and paleontology of the Nanpanjiang Basin, south China.

Materials.—Samples PUG-12, 23, 27, 29, 43 (Aegean to Pelsonian). More than 10 specimens, four of which are illustrated in Figure 18.7–18.10.

Microfossil association.—In the samples, the new species is accompanied by *Planiinvoluta*? *mesotriasica*, *Arenovidalina abriolense*, *Meandrospira pusilla*, *M. dinarica*, *Hoyenella* gr. *H. sinensis*, *Hoyenella* sp. 1, *Glomospirella* sp. 1, *Pilammina densa*, *Pilamminella grandis*, *Reophax* sp. 5, *Earlandia tintinniformis*, *Endoteba obturata*, *Endotriada tyrrhenica* Vachard et al., 1994, *Endotriada* sp. 1, *Endotriadella wirzi* (Koehn-Zaninetti, 1968), *Endotriadella wirzi*?, *E. lombardi* (Zaninetti and Brönnimann in Zaninetti et al., 1972c), *Triadodiscus* sp., *Aulotortus*? *eotriasicus* Zaninetti, Rettori, and Martini, 1994, Lamelliconinae?, *Krikoumbilica pileiformis*, *Diplotremina* sp. 2, and *Dentalina*? sp. 2.

Dimensions.—Diameter of proloculus: 52–60 µm (holotype: 52 µm). Diameter of coiled part: 360–400 µm (holotype: 380 µm). Maximum width of test: 380 µm. Maximum length of test: 955 µm (holotype: 720 µm). Thickness of wall 35–45 µm (holotype: 35 µm).

Remarks.—*Spinoendotebanella lehrmanni* n. gen. n. sp. is the only endotebid population ornamented with spines at chamber corners of the second whorl of its spire. It is very probable that the morphologically close *Endotebanella kocaeliensis* is the ancestor of this form.

Family Endotriadidae Vachard et al., 1994

Remarks.—The other *Endothyra*-like group in the Triassic of the GBG is the family Endotriadidae, which differs from Endotebidae primarily in having a thin and uniform, microgranular wall. The type-genus, *Endotriada*, consists of four different populations.

Genus *Endotriada* Vachard et al., 1994
Endotriada tyrrhenica Vachard et al., 1994
Figure 18.13–18.17

Remarks.—The type-species, *E. tyrrhenica*, is present in the GBG and characterized by a small test with depressed sutures, 6–7 chambers in the last whorl, and a highly compressed profile in the axial section. The forms illustrated (Fig. 18.13–18.17) are nearly identical to forms described by Vachard et al. (1994). Although *E. tyrrhenica* is a well-established species, several sections attributed to the *tyrrhenica* population from the Upper Triassic of Slovenia (Gale et al., 2012), Turkey (Beccaletto et al., 2005), Thailand (Ueno et al., 2012), and Japan (Chablais, 2010) and the Middle Triassic of Indonesia (Rossignol et al., 2018) are problematic either because of incomplete illustrations or incorrect interpretation of the wall structure and the test morphology. *Endotriada tyrrhenica* has been found in the Pelsonian to Illyrian strata of the Upper Guandao section (Fig. 8).

Endotriada sp. 1
Figure 18.20, 18.21

Remarks.—Three populations of *Endotriada* are left in open nomenclature. *Endotriada* sp. 1 is characterized by lenticular tests, always with an initial skewed coiling. *Endotriada* sp. 1 has been recorded from the Bithynian to Pelsonian (Figs. 8, 9).

Endotriada sp. 2
Figure 18.22–18.24

Remarks.—*Endotriada* sp. 2 is characterized by nautiloid tests, always with an initial skewed coiling. *Endotriada* sp. 2 has been recorded from the Pelsonian to Fassanian interval (Figs. 8, 9).

Endotriada sp. 3
Figure 18.18, 18.19

Remarks.—*Endotriada* sp. 3 is characterized by biumbilicate tests, always with an initial skewed coiling. *Endotriada* sp. 3 has been recorded very rarely from the Illyrian of the Upper Guandao section (Figs. 8, 9).

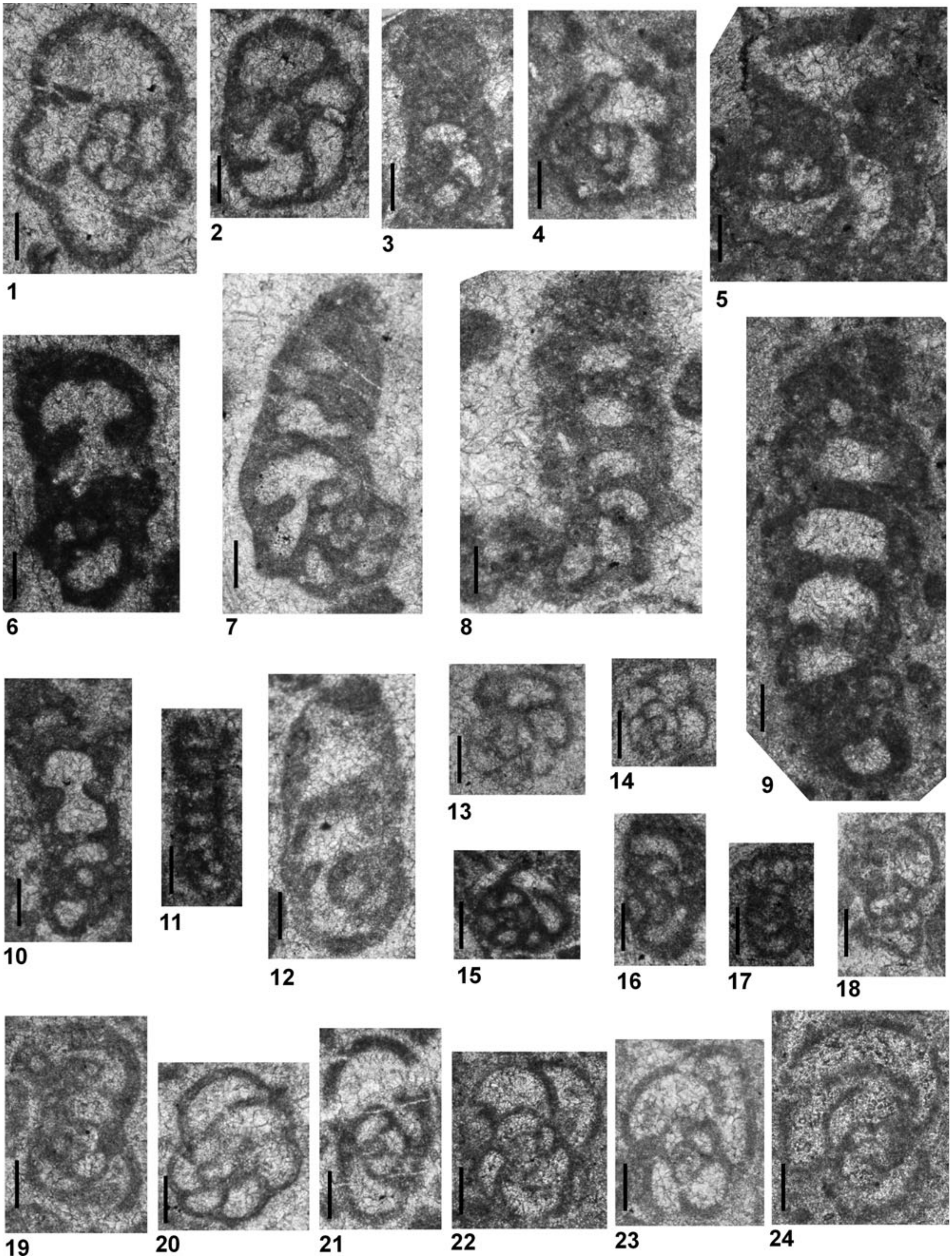


Figure 18. All specimens are from Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1, 2**) *Endoteba* sp.; (**3–6**) *Endotebanella kocaeliensis* (Dağer, 1978b); (**7–10**) *Spinoendotebanella lehrmanni* n. gen., n. sp.; (**11**) *Endotebanella* sp. 2; (**12**) *Endotebanella* sp. 1; (**13–17**) *Endotriada tyrrhenica* Vachard et al., 1994; (**18, 19**) *Endotriada* sp. 3; (**20, 21**) *Endotriada* sp. 1; (**22–24**) *Endotriada* sp. 2. (**1, 2**) PUG-081; (**3**) PUG-101; (**4**) PUG-009; (**5**) PUG-087; (**6**) PGD-217; (**7**) PUG-027; (**8, 20**) PUG-029; (**9**) PUG-012; (**10**) MDJ-39; (**11**) PGD-238; (**12**) PUG-037; (**13**) PUG-043; (**14**) PUG-054; (**15**) PUG-071; (**16**) PUG-063; (**17**) PUG-089; (**18, 19, 23**) PUG-077; (**21**) PUG-031; (**22, 24**) PUG-099. Scale bars = 100 μm.

Genus *Endotriadella* Vachard et al., 1994
Endotriadella wirzi (Koehn-Zaninetti, 1968)
Figure 19.1–19.14

Remarks.—The other member of the family Endotriadidae, *Endotriadella*, contains two distinct species. The *E. wirzi* population, quite frequent in the Triassic of the GBG, is nearly identical to specimens described as *Ammobaculites wirzi* by Koehn-Zaninetti (1968, 1969) and Zaninetti et al. (1972c), with a spiral portion of the test composed of 1.5–2 whorls and an uncoiled, rectilinear part consisting of 6–8 wide and globular chambers. Koehn-Zaninetti (1968) published a condensed version of Koehn-Zaninetti (1969) with the same title in which she reported the new taxa that she discovered in this paper. Although these taxa were also described as new in 1969 (her main work) we give priority to the 1968 publication.

Endotriadella wirzi has been found in the uppermost Spathian–Bithynian in the Guandao section (Fig. 11), the Aegean–Longobardian of the Upper Guandao section (Figs. 8, 9), and the Pelsonian–Longobardian of the Middle Triassic Dajiang section (Fig. 10). *Endotriadella wirzi* has been reported extensively from the Middle Triassic of Europe (Zaninetti, 1976; Rettori, 1995). In more recent literature, Emmerich et al. (2005) reported *E. wirzi* from the Illyrian to Ladinian of the Latemar platform (Dolomites, Italy). Apthorpe (2003) described a terminal opening with possible radiating slits in the free specimens of *E. wirzi* extracted from the Locker Shale, Western Australia. In Song et al. (2015), the first appearance of *E. wirzi* was reported from the uppermost Smithian of south China. Sections of *Diplosphaerina inaequalis* Derville, 1931, reported from the Anisian by these authors, are probably the oblique sections cutting through the uncoiled portion of *E. wirzi*.

Endotriadella wirzi?
Figure 19.15, 19.16

Remarks.—*Endotriadella wirzi*?, with a much larger test and wider chambers in the uncoiled part, has a similar stratigraphic range to that of *E. wirzi*. Flügel et al. (1994) reported forms similar to our *E. wirzi*? as *Earlandinita grandis* Salaj, 1978 from the Pelsonian of Slovenia. Specimens in Rettori et al. (1994) from Hydra (Greece), illustrated as *E. wirzi*, are nearly identical to the uncoiled portion of our *E. wirzi*?.

Endotriadella lombardi (Zaninetti and Brönnimann in Zaninetti et al., 1972c)
Figure 19.17, 19.18

Remarks.—Another distinct species, *E. lombardi* (Fig. 19.17, 19.18), is characterized by tests with a shorter uncoiled portion and a more prominent initial spiral part when compared with *E. wirzi* (Zaninetti et al., 1972c). This form is present in the Pelsonian to Longobardian strata of the Upper Guandao section (Figs. 8, 9).

Class uncertain

Remarks.—This uncertain class includes all Triassic aragonite-walled foraminifera belonging to orders Involutinida and Robertinida. In the latest classification based on molecular phylogenetic studies, Pawlowski et al. (2013) suggested that Order Involutinida could be assigned to their Class Tubothalamea, which contains both agglutinated and calcareous (calcitic and aragonitic) taxa. They suggested that Order Robertinida falls within their Class Globothalamea, consisting of several multi-chambered groups (except the orders Lagenida and Fusulinida) with agglutinated and calcareous walls. In this study, our taxonomic classification requires wall composition and structure to be used in our taxonomic hierarchy, including the class rank. The study of Pawlowski et al. (2013) could be a meaningful agglomeration of different taxonomic groups. However, the taxonomic rank that they suggest should not be considered in class rank; instead, it may be a higher position in the hierarchical classification of foraminifera.

Order Involutinida Hohenegger and Piller, 1977
Family Triadodiscidae Zaninetti, 1984 emend. Altıner and Payne, 2017
Subfamily Triadodiscinae Zaninetti, 1984
Genus *Praetriadodiscus* Altıner and Payne, 2017

Remarks.—The family Triadodiscidae was introduced by Zaninetti (1984) for the planispirally coiled, lenticular, and trochospirally coiled conic forms, with aragonitic walls and a coiling mode consisting of one lamella for one complete whorl of the deuteroloculus. It recently has been emended by Altıner and Payne (2017) and a new genus, *Praetriadodiscus*, was created in the subfamily Triadodiscinae for lenticular and planispiral forms characterized by a double-layered, inner microgranular and outer hyaline and aragonitic wall structure.

Praetriadodiscus zaninettiae Altıner and Payne, 2017
Figure 19.20, 19.22

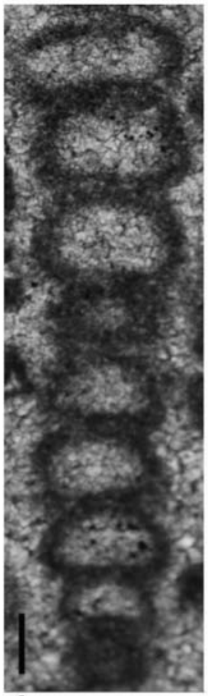
Remarks.—*Praetriadodiscus zaninettiae* differs from its congener, *P. tappanae*, in having a smaller form ratio (D/W), and thus a more inflated test in axial section. Both of these species evolved from a *Pseudoammodiscus* ancestor (Fig. 19.19) and the transition from the ancestor to *Praetriadodiscus* has been clearly illustrated in Altıner and Payne (2017). Two distinct populations, *P. zaninettiae* and *P. tappanae*, come from the Smithian of the Guandao section (Fig. 11) and are partly illustrated in this study, in addition to the specimens illustrated in Altıner and Payne (2017).

Praetriadodiscus tappanae Altıner and Payne, 2017
Figure 19.20, 19.22

Remarks.—See Remarks under *Praetriadodiscus zaninettiae*.

Praetriadodiscus? sp.
Figure 19.24

Remarks.—*Praetriadodiscus*? sp. is a form characterized by deviations of the axis of coiling as seen in the axial profile and a less-developed outer hyaline layer.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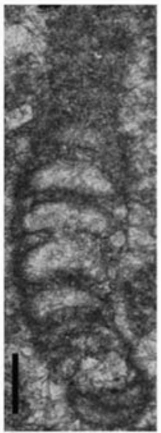
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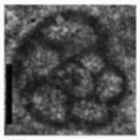
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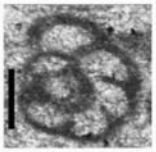
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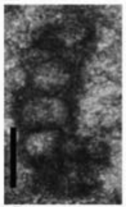
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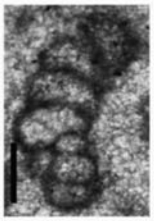
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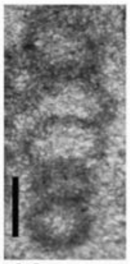
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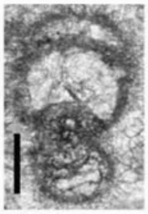
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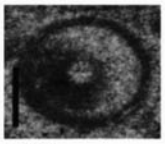
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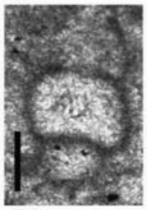
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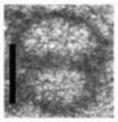
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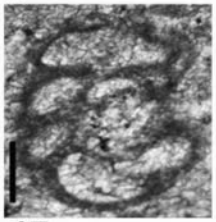
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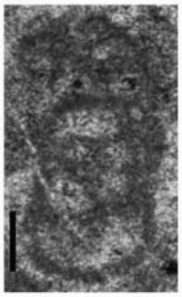
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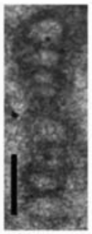
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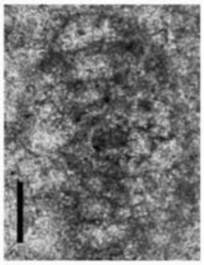
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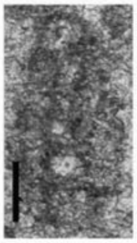
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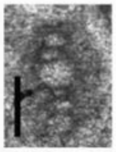
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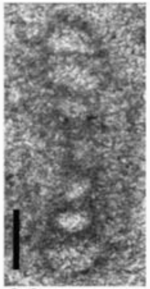
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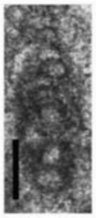
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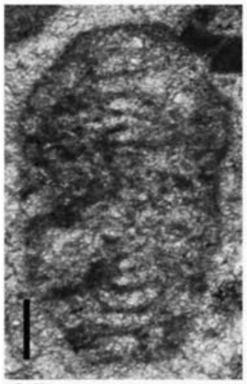
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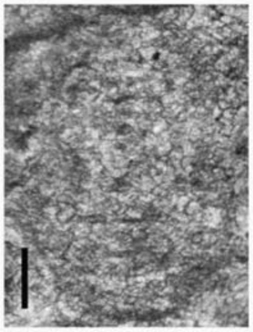
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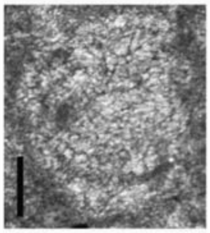
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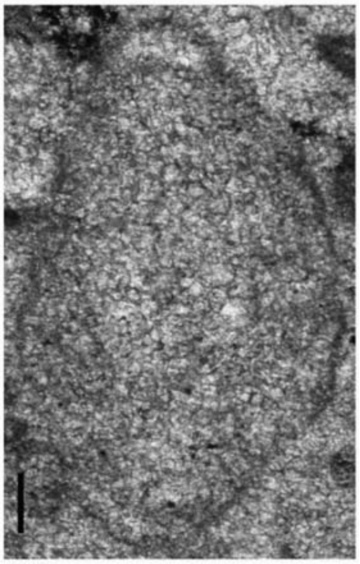
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Figure 19. All specimens are from Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1–14**) *Endotriadella wirzi* (Koehn-Zaninetti, 1968); (**15, 16**) *Endotriadella wirzi*? (Koehn-Zaninetti, 1968); (**17, 18**) *Endotriadella lombardi* (Zaninetti and Brönnimann in Zaninetti et al., 1972c); (**19**) *Pseudoammodiscus* sp.; (**20, 22**) *Praetriadodiscus zaninettiae* Altıner and Payne, 2017; (**21, 23**) *Praetriadodiscus tappanae* Altıner and Payne, 2017; (**24**) *Praetriadodiscus* ? sp.; (**25–27**) *Triadodiscus* sp.; (**28**) *Parvalamella* sp.; (**29, 30**) *Aulotortus*? *eotriasicus* Zaninetti, Rettori, and Martini, 1994. (**1, 15**) PUG-043; (**2**) MDJ-09; (**3**) PUG-016; (**4**) PUG-037; (**5**) PUG-045; (**6**) PUG-067; (**7, 17**) PUG-029; (**8**) MDJ-39; (**9**) PUG-017; (**10**) PUG-054; (**11**) PUG-014; (**12**) PUG-089; (**13**) PUG-091; (**14, 28**) MDJ-57; (**16**) MDJ-15; (**18**) PUG-083; (**19**) PDJ-319; (**20–24**) PGD-131; (**25–27**) PUG-023; (**29**) PUG-045; (**30**) PUG-023. Scale bars = 100 µm.

Genus *Triadodiscus* Piller, 1983
Triadodiscus sp.
Figure 19.25–19.27

Remarks.—Forms illustrated as *Triadodiscus* sp. differ from the type of *Triadodiscus*, *T. eomesozoicus*, in having more robust tests with a less angular periphery and more densely coiled deuteroloculus with a low chamber height. A very similar population to our *Triadodiscus* sp. has been illustrated as *Arenovidalina amylovoluta* by Kobayashi (1996) from the Kanto Mountains, Japan. In Kobayashi et al. (2005), similar forms have been reported as *T. eomesozoicus* from the Anisian of western Kyushu, Japan. *Triadodiscus* sp. has been recovered from the Bithynian of the Guandao and Upper Guandao sections (Figs. 8, 11) and the Pelsonian of the Middle Triassic Dajiang section (Fig. 10). Involutinid forms reported from south China as '*Triadodiscus eomesozoicus*' (Oberhauser, 1957) and '*Aulotortus*? *bakonyensis*' Blau, 1989 by Song et al. (2016) may have been misclassified. These specimens were first reported by Song et al. (2011a) from the upper Smithian in association with species such as *Meandrospira dinarica* and *Pilammina densa*, which are typical markers of the Anisian.

Subfamily Lamelliconinae Zaninetti et al., 1987b?
Lamelliconinae?
Figure 20.1–20.5

Remarks.—Trochospirally coiled, conical forms with five or six whorls and aragonitic walls from the Aegean–Pelsonian of the Upper Guandao section and the Bithynian of the Guandao section (Figs. 8, 11) are reported as Lamelliconinae? In this study. These forms are probably the oldest records of the trochospiral involutinid foraminifera. Some Anisian forms similar to our Chinese specimens have been described in previous studies (e.g., Zaninetti et al., 1972c; Zaninetti, 1976) as populations belonging to the genus *Turrispirillina* (Spirillinidae). We strongly question the validity of this taxonomy and argue that such forms, lacking a proper calcitic wall, should be classified under a taxon housing bilocular and trochospiral forms with aragonitic walls.

Family Aulotortidae Zaninetti, 1984
Subfamily Parvalamellinae Rigaud, Martini, and Rettori, 2012
Genus *Parvalamella* Rigaud, Martini, and Rettori, 2012
Parvalamella sp.
Figure 19.28

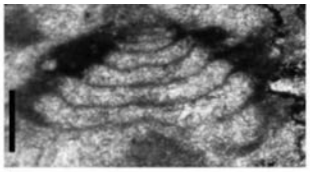
Remarks.—Following Rigaud et al. (2012), we assign our streptospirally coiled, recrystallized involutinid forms to *Parvalamella* sp. The Chinese forms are most likely closely related to the *Parvalamella praegaschei-friedli* group (*Parvalamella praegaschei* Koehn-Zaninetti, 1968 and *Parvalamella friedli* [Kristan-Tollmann, 1962]). However, we disagree with Rigaud et al. (2012) in the assignment of their newly created subfamily Parvalamellininae to the family Involutinidae. In our view, the presence of laterally more restricted L2 lamellae in the subfamily Parvalamellininae does not justify this distinction. The subfamily Aulotortinae is not composed only of planispiral forms, as Rigaud et al. (2012) have stated in comparison with Parvalamellininae. On the contrary, the presence of populations displaying an irregular coiling in Rigaud et al.'s (2012) ontogeny in Aulotortinae (ex., *Aulotortus* gr. *A. sinuosus* Weynschenk, 1956) is evidence for grouping Parvalamellininae and Aulotortinae under the family Aulotortidae. *Parvalamella* sp. has been recorded from Ladinian (Fassanian to Longobardian) of the Middle Triassic Dajiang section (Fig. 10).

Subfamily Aulotortinae Zaninetti, 1984
Genus *Aulotortus* Weynschenk, 1956
Aulotortus? *eotraisicus* Zaninetti, Rettori, and Martini, 1994
Figure 19.29, 19.30

Remarks.—We assign lenticular involutinid forms with a subangular periphery and a nearly planispiral coils whose diameters approach 1 mm to *Aulotortus*? *eotriasicus*, described by Zaninetti et al. (1994). This form was previously reported by Brönnimann et al. (1973a) as *Involutina sinuosa pragsoides* Oberhauser, 1964 and, as noted in Zaninetti et al. (1994), *A.*? *eotriasicus* differs from this latter form in having a narrower tubular chamber, a larger number of whorls, and a subangular periphery of the test. In more recent literature, *A.*? *eotriasicus* has been reported as *A.*? sp. from the Anisian of the Kanto Mountains, Japan (Kobayashi, 1996). Emmerich et al. (2005) reported typical specimens of *A.*? *eotriasicus* from the Anisian of the Latemar platform (Dolomites, Italy). Song et al. (2015) illustrated *A.*? *eotriasicus* as *A. sinuosus* from the Anisian of the Qingyan section of south China. *Aulotortus*? *eotriasicus* has been recorded from the uppermost Bithynian to Pelsonian in the Upper Guandao section (Fig. 8).

Order Robertinida Loeblich and Tappan, 1984
Family Variostomatidae Kristan-Tollmann, 1963

Remarks.—Variostomatidae is the oldest family in the Order Robertinida, which originated in the Early Triassic (Rigaud et al., 2015; Rigaud and Blau, 2016). As stated in Zaninetti (1976), it is difficult to study variostomatid taxa in thin section, even if sections of foraminifera are oriented. This difficulty arises because of the complexity of the apertural system of the group, which is a crucial morphological feature used in the distinction of genera. For this reason, with the exception of *Krikoumbilica pileiformis*, we have assigned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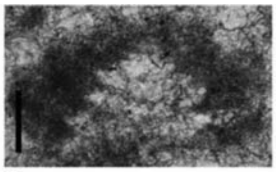
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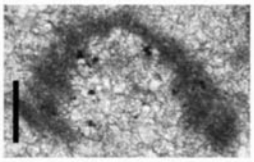
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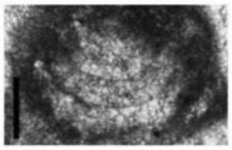
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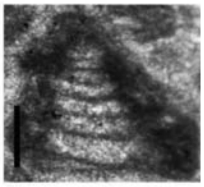
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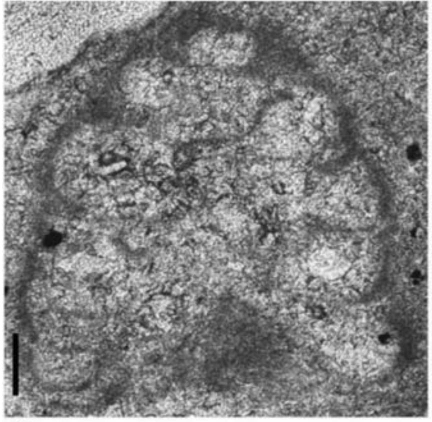
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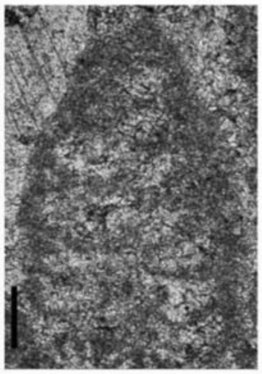
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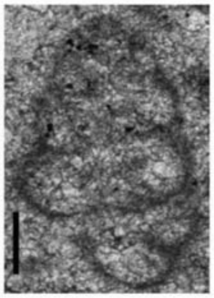
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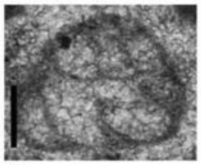
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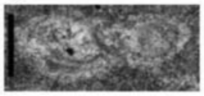
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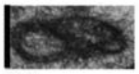
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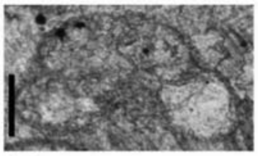
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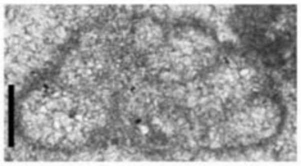
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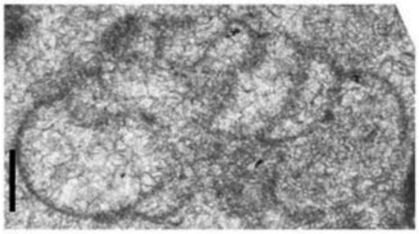
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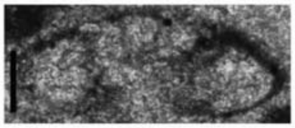
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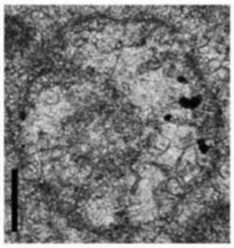
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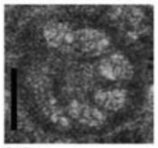
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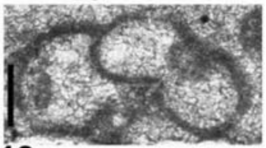
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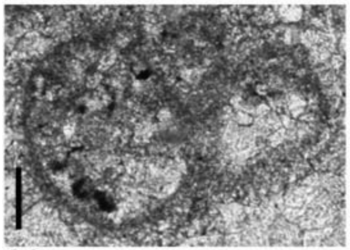
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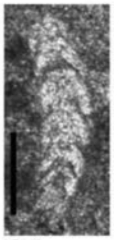
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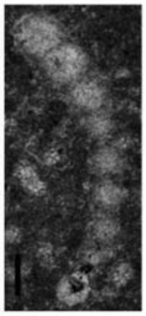
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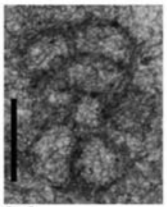
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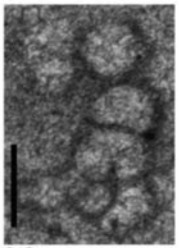
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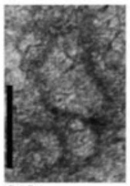
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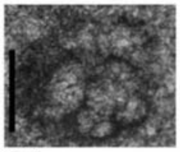
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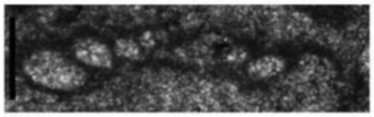
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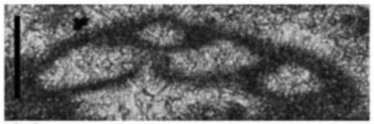
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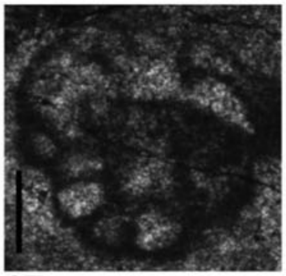
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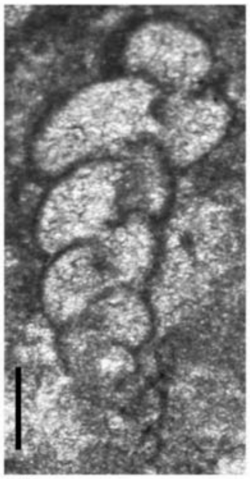
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Figure 20. All specimens are from Dawen (PDW), Dajiang (PDJ), Middle Triassic Dajiang (MDJ), Guandao (PGD), and Upper Guandao (PUG) sections. (**1–5**) Lamelliconinae?; (**6**) *Variostoma*? sp. 1; (**7**) *Variostoma*? sp. 2; (**8**) *Variostoma* sp. 1; (**9**) *Variostoma* sp. 2; (**10**) *Plagiostomella*? sp. (**11**) *Oberhauserella*? sp.; (**12, 13, 17, 18**) *Krikoumbilica pileiformis* He, 1984; (**14**) *Diplotremina* sp. 1; (**15, 16**) *Diplotremina* sp. 2; (**19**) *Abriolina*? sp.; (**20**) *Abriolina mediterranea* Luperto, 1963; (**21**) *Polarisella elabugae* (Cherdyntsev, 1914); (**22, 24**) *Polarisella hoae* (Trifonova, 1967); (**23**) *Protonodosaria exploita* (Trifonova, 1978c); (**25**) *Dentalina*? sp. 1; (**26**) *Dentalina*? sp. 2; (**27, 28**) *Geinitzinita* sp.; (**29**) *Nodosinelloides*? sp.; (**30**) *Austrocolomia* sp. (**31–34**) Unknown foraminifera 1; (**35–37**) Unknown foraminifera 2; (**38**) Unknown foraminifera 4; (**39**) Unknown foraminifera 3. (**1, 3–5**) PUG-029; (**2**) PUG-043; (**6**) PUG-137; (**7**) PUG-111; (**8**) PUG-063; (**9, 15**) PUG-081; (**10**) PUG-065; (**11**) PUG-037; (**12**) MDJ-39; (**13**) PUG-027; (**14**) PUG-031; (**16**) PGD-217; (**17**) PGD-185; (**18**) PUG-039; (**19, 24**) PUG-091; (**20**) PUG-093; (**21**) MDJ-07; (**22**) PUG-097; (**23**) PGD-225; (**25**) PUG-019; (**26**) PUG-041; (**27**) PUG-109; (**28**) PUG-017; (**29**) PUG-085; (**30**) PUG-145; (**31–34**) PDW-340; (**35, 37**) PGD-211; (**36**) PGD-212; (**38**) PDJ-058; (**39**) MDJ-47. Scale bars = 100 µm.

different morphogroups recognized in thin section to different variostomatid taxa with open nomenclature.

Genus *Krikoumbilica* He, 1984
Krikoumbilica pileiformis He, 1984
Figure 20.12, 20.13, 20.17, 20.18

Remarks.—*Krikoumbilica pileiformis* has been recognized in the Chinese material in the Spathian of the Guandao section (Fig. 11), the upper Bithynian to Longobardian of the Upper Guandao section (Figs. 8, 9), and the Illyrian of the Middle Triassic Dajiang section (Fig. 10). It is characterized by a large umbilicus and plano-convex test. Following the description of *K. pileiformis* from the Anisian–Ladinian of Guizhou, south China, by He (1984), this species has been partly or fully illustrated as *Diplotremina* or *D. astrofimbriata* Kristan-Tollmann, 1960 in some studies from Italy (Senowbari-Daryan et al., 1993), Japan (Kobayashi et al., 2005), Thailand (Kobayashi et al., 2006), and Laos (Miyahigashi et al., 2017). In Song et al. (2015), the axial sections of *K. pileiformis* have been reported as *Duotaxis* spp. from the Anisian of Qingyan section, south China.

Genus *Variostoma* Kristan-Tollmann, 1960

Remarks.—Four different trochospiral forms of varying degree have been assigned to *Variostoma*. Two of these populations (*Variostoma*? sp. 1 and *V.*? sp. 2), characterized by a rather wider umbilicus, have been doubtfully assigned to the genus.

Variostoma? sp. 1
Figure 20.6

Remarks.—*Variostoma*? sp. 1 has been found in the Cordevolian of the Upper Guandao section (Fig. 9).

Variostoma? sp. 2
Figure 20.7

Remarks.—*Variostoma*? sp. 2 has been found in the Fassanian–Longobardian of the Upper Guandao section (Fig. 9).

Variostoma sp. 1
Figure 20.8

Remarks.—*Variostoma* sp. 1 has been recognized in the Spathian of the Guandao section (Fig. 11) and the Longobardian of the Upper Guandao section (Fig. 9).

Variostoma sp. 2
Figure 20.9

Remarks.—*Variostoma* sp. 2 has been recorded in the Spathian to Aegean of the Guandao section (Fig. 11) and the Illyrian of the Upper Guandao section (Fig. 8).

Genus *Diplotremina* Kristan-Tollmann, 1960

Remarks.—Low trochospiral morphogroups have been assigned to the genus *Diplotremina.*

Diplotremina sp. 1
Figure 20.14

Remarks.—*Diplotremina* sp. 1 has been recorded from the Pelsonian of the Upper Guandao section (Fig. 8).

Diplotremina sp. 2
Figure 20.15, 20.16

Remarks.—*Diplotremina* sp. 2 is found in the Spathian to Bithynian of the Guandao section (Fig. 11), the Aegean to Pelsonian of the Upper Guandao section (Fig. 8), and the Longobardian of the Middle Triassic Dajiang section (Fig. 10).

Genus *Plagiostomella* Kristan-Tollmann, 1960
Plagiostomella? sp.
Figure 20.10

Remarks.—A very low trochospiral form with nearly pseudoplanispiral coiling assigned to *Plagiostomella*? sp. has been recognized from the uppermost Pelsonian in the Upper Guandao section (Fig. 9), earlier than the known stratigraphic range of the genus, which is Carnian (Zaninetti, 1976).

Family Oberhauserellidae? Fuchs, 1970
Genus *Oberhauserella* Fuchs, 1967
Oberhauserella? sp.
Figure 20.11

Remarks.—The family Oberhauserellidae, as an aragonitic taxon, has been classified in the Order Robertinida in recent literature (Rigaud et al., 2015). Very rare, small specimens, doubtfully assigned to *Oberhauserella*? sp., have been recorded in the Pelsonian of the Upper Guandao section (Fig. 8). These forms are characterized by very low trochospiral axial sections with a convex spiral side and a depressed umbilicus probably covered by an apertural flap.

Class Nodosariata Mikhalevich, 1993
Family Protonodosariidae Mamet and Pinard, 1992

Remarks.—This family, which originated in the latest Carboniferous and occurs frequently in the Permian, is a Permian-Triassic boundary survivor and its stratigraphic range extends up to the end of the Triassic (Vachard, 2016, 2018). Two well-known genera from the Paleozoic, *Protonodosaria* and *Polarisella*, are present in the Triassic of the GBG. The genus *Nodosinelloides* is questionably present. *Austrocolomia* has been included under the family Protonodosariidae in this study.

Genus *Polarisella* Mamet and Pinard, 1992
Polarisella elabugae (Cherdyntsev, 1914)
Figure 20.21

Remarks.—Characterized by thick-walled spherical chambers and a small, igloo-shaped, reduced lumen, the *elabugae* population is described as *Polarisella elabugae* (Cherdyntsev, 1914) in this study. This form was described for the first time by Cherdyntsev (1914) as *Nodosaria elabugae*. Two distinct forms, *N. abriolinae* described from the Abriola Limestone in Italy by Luperto (1963) and '*N*'. *armeniensis* described from the Caucasus by Efimova (1974), are synonyms of the *elabugae* population. It is common in the Changhsingian limestone of the Taurus Mountains (Lys and Marcoux, 1978; Altıner, 1981, 1984; Groves et al., 2005) and is thus a Permian-Triassic boundary survivor. In our material, this form has been recorded from the Pelsonian of the Upper Guandao and Middle Triassic Dajiang sections (Figs. 8, 10). Recently, it also has been reported from south China as '*N*.' *elabugae* from the *Hindeodus parvus* Zone of the Griesbachian Substage (Dai et al., 2018) and Permian-Triassic boundary beds of Slovenia (Kolar-Jurkovšek et al., 2018).

Polarisella hoae (Trifonova, 1967)
Figure 20.22, 20.24

Remarks.—*Polarisella hoae* was originally described as *Dentalina hoi* and is characterized by nearly conical, thick-walled chambers circumscribing small conical lumina. It is a Permian-Triassic boundary survivor because it is present in the Changhsingian and in Lower Triassic strata of southern Turkey (Groves et al., 2005). In China, it is present in the entire Triassic (Ho, 1959; Lin, 1987; He and Cai, 1991; He, 1993). In the GBG material, it has been recorded from the Pelsonian to Fassanian of the Upper Guandao section (Figs. 8, 9) and the Illyrian of the Middle Triassic Dajiang section (Fig. 10). In recent literature, it has been reported from the Lower Triassic Khuff Formation of Saudi Arabia (Vachard et al., 2005) and from the PTB transitional beds of western Slovenia (Kolar-Jurkovšek et al., 2018).

Genus *Protonodosaria* Gerke, 1959
Protonodosaria exploita (Trifonova, 1978c)
Figure 20.23

Remarks.—Characterized by spherical chambers, each perched high atop the previous one, and a rather large proloculus, *Protonodosaria exploita* has been found in the Aegean to Bithynian deposits of the Guandao section (Fig. 11) and the Bithynian to Pelsonian of the Upper Guandao section (Fig. 8). This species is known mostly from the Anisian of Bulgaria (Trifonova, 1978b), China (Kristan-Tollmann, 1983), Japan (Kobayashi, 1996), and Turkey (Groves et al., 2005). Recently, it has been reported from the Griesbachian of Italy (Groves et al., 2007), south China (Song et al., 2009), and western Slovenia (Nestell et al., 2011).

Genus *Nodosinelloides* Mamet and Pinard, 1992
Nodosinelloides? sp.
Figure 20.29

Remarks.—Sections of probable protonodosariid foraminifera reported as *Nodosinelloides*? sp. in this study are characterized by uniserial, hemispherical to subquadratic chambers. However, it is not certain whether the sections in the GBG material are characterized by a simple terminal opening, as is the case in *Nodosinelloides*, which is a late Carboniferous–Permian taxon. If the forms that we recognize are true *Nodosinelloides*, then this taxon should also be a Permian/Triassic boundary survivor. *Nodosinelloides*? sp. has been recorded from the Spathian to Bithynian in the Guandao section (Fig. 11) and the Bithynian to Cordevolian in the Upper Guandao section (Figs. 8, 9). According to Song et al. (2007, 2011b), *Nodosinelloides* (given as *N. aequiampla* [Zolotova and Baryshnikov, 1980]) is present in the Griesbachian of south China.

Genus *Austrocolomia* Oberhauser, 1960
Austrocolomia sp.
Figure 20.30

Remarks.—*Austrocolomia* sp. is possibly an intermediate form between *A. cordevolica* Oberhauser, 1967 and *A. marschalli* Oberhauser, 1967, and is characterized by the gradual increase in the width of uniserial hemispherical to subquadratic chambers with marked shoulders at chamber corners and a simple terminal aperture. This form has been found in the Cordevolian of the Upper Guandao section (Fig. 9).

Family Geinitzinidae Bozorgnia, 1973
Genus *Geinitzinita* Sellier de Civrieux and Dessauvagie, 1965
Geinitzinita sp.
Figure 20.27, 20.28

Remarks.—*Geinitzinita*, a member of the Family Geinitzinidae that appeared and flourished in the Permian (Vachard, 2016, 2018), occurs rarely in the Chinese material. Characterized by low and wide chambers in the longitudinal frontal sections, the diagnostic feature of the genus is visible in oblique longitudinal lateral sections with centrally arched chambers. *Geinitzinita* sp. has been recorded from the Bithynian to Longobardian of the Upper Guandao section (Figs. 8, 9).

Family Nodosariidae? Ehrenberg, 1838
Genus *Dentalina* Risso, 1826

Remarks.—Two arcuate nodosariid forms with an unknown type of terminal aperture have been questionably assigned to the genus *Dentalina*. These questionable forms are found in the Anisian of the Guandao and Upper Guandao sections (Fig. 8, 11).

Dentalina? sp. 1
Figure 20.25

Remarks.—See Remarks under Genus *Dentalina*.

Dentalina? sp. 2
Figure 20.26

Remarks.—See Remarks under Genus *Dentalina*. In the literature, specimens close to our *D.*? sp. 2 were illustrated as *Dentalina vadaszi* Oberhauser, 1960 by Song et al. (2011a, 2015) from the Olenekian to Anisian of south China.

Family Abriolinidae Zaninetti and Rettori in Zaninetti et al., 1992b
Genus *Abriolina* Luperto, 1963
Abriolina sp.
Figure 20.19

Remarks.—When initially created by Zaninetti and Rettori in Zaninetti et al. (1992), Abriolinidae was placed in the superfamily Geinitzinacea, which is considered one of the main taxonomic units of the Class Nodosariata (Vachard, 2016, 2018). Although it is reasonable on morphological grounds to place this double-wall-bearing group in the superfamily Geinitzinacea, which originated in the Paleozoic, our observations of the Chinese material suggest that the family Abriolinidae might be a morphologically convergent form that evolved during the Triassic. Trochospiral forms morphologically similar to trochamminid-like forms in the Illyrian of the Upper Guandao section (Fig. 8) could represent a population ancestral to Abriolinidae. We classify such forms as *Abriolina*? sp. (Fig. 20.19) due to the presence of a rudimentary and discontinuous outer hyaline layer covering the main microgranular to finely agglutinated inner layer.

Abriolina mediterranea Luperto, 1963
Figure 20.20

Remarks.—The true abriolinid taxon, *Abriolina mediterranea*, is found in the late Illyrian–Fassanian interval in the Upper Guandao section (Figs. 8, 9). This taxon was created based on specimens from the Abriola Limestone in southern Italy by Luperto (1963), who erroneously considered this form as a Late Permian foraminiferan. Emmerich et al. (2005) illustrated the typical specimens of this species from the Illyrian to Ladinian of the Latemar platform (Dolomites, Italy). These low trochospiral forms with a large proloculus and subglobular to subangular chambers are also characterized by a double wall, an inner microgranular to granular layer, and an outer with consistently occurring hyaline fibrous layer.

Unknown foraminifera

Remarks.—Four foraminiferal populations could not be named and are left with an open nomenclature in the Chinese material.

Unknown foraminifera 1
Figure 20.31–20.34

Remarks.—Unknown foraminifera 1 is probably a calcivertellid and characterized by tests with a coiled stage followed by an uncoiled stage with a folded tubular chamber making zigzag bends. This population has been recorded from the Smithian of the Dawen and the Spathian of the Guandao sections (Fig. 5, 11).

Unknown foraminifera 2
Figure 20.35–20.37

Remarks.—Unknown foraminifera 2 is a multilocular form, probably a trochamminid, with at least four whorls and a broad depression toward the umbilicus. It has been found in the Aegean of the Guandao section (Fig. 11).

Unknown foraminifera 3
Figure 20.39

Remarks.—Unknown foraminifera 3 is characterized by a reduced coiled stage and an uncoiled portion comprising biserial chambers with a hook-shaped valvular tooth extending from septal edges to protect the aperture. This interesting form is found in the Fassanian of the Middle Triassic Dajiang section (Fig. 10).

Unknown foraminifera 4
Figure 20.38

Remarks.—Unknown foraminifera 4 is possibly a porcelaneous tubular form coiled in various planes. It could be a Permian survivor and referred to one of the populations of *Hemigordiellina*, as emended by Vachard in Vachard and Beckary (1991). However, this form is rare in the Griesbachian of Dajiang section (Fig. 6) and not well enough preserved to decide on the correct taxonomic position.

Biostratigraphy

Several authors emphasized the biostratigraphic importance of Lower–Middle Triassic foraminifera (Zaninetti, 1976; Vachard and Fontaine, 1988; Altıner and Koçyiğit, 1993; Rettori et al., 1994; Rettori, 1995; Muttoni et al., 1996; Marquez, 2005; Kobayashi et al., 2006; Lehrmann et al., 2015). There have been numerous studies of the Lower–Middle Triassic foraminiferan biostratigraphy, but the resulting biostratigraphic zones have rarely been used in geological studies or for long-distance correlations.

The first attempts were focused on the European Triassic, particularly in the western Carpathians (Salaj, 1969, 1978; Salaj et al., 1983), Carpatho-Balkans (Salaj et al., 1988), Bulgaria (Trifonova, 1978a, b, 1992, 1993), southern Poland (Gazdzicki et al., 1975), the Transdanubian Range of Hungary

(Orovecz-Scheffer, 1987), and the Prealps in Switzerland (Zaninetti et al., 1972b). Further attempts addressed western Asia, including the Kocaeli Peninsula of Turkey (Zaninetti and Dağer, 1978) and the Caucasus of the Russian territory (Efimova, 1991). None of these studies developed a complete zonal scheme for the entire Lower Triassic–Anisian interval. Apart from taxonomic problems in some of these studies, poor calibration of the ranges of taxa used in the zonation schemes and the strong facies control on the stratigraphic distribution of foraminiferal taxa hindered the use of these zones as standard in the Geologic Time Scale.

Toward the end of the 20th century, two important studies helped to clarify the overall biostratigraphic subdivision of the Lower–Middle Triassic. The first of these studies focused on northwest Sichuan and southern Shaanxi, China (He, 1993). Although incomplete, three main zones were used, namely *Arenovidalina chialingchiangensis* and *Meandrospira pusilla* zones for the Scythian and a *Glomospira densa-Meandrospira dinarica* Zone for the Anisian. These zones were further divided into subzones using critical species such as *Glomospirella vulgaris* and *Glomospira sinensis*. A second, more important study, illustrating the zones of foraminifera and biochronohorizons for the Triassic of the Tethyan Realm, has come out in the 'Mesozoic–Cenozoic of Western European Basins' volume of de Graciansky et al. (1998). In the Griesbachian (Induan)–Illyrian (Anisian) interval, Hardenbol et al. (1998; see also Kamoun et al., 1998) described the *Rectocornuspira kalhori* Zone from the Griesbachian, a non-characterized interval spanning from Dienerian to Smithian, the *Meandrospira pusilla* Zone from the Spathian, the *Meandrospira dinarica* Zone from the Aegean to Bithynian, the *Paulbronnimannia judicariensis* Zone from the Pelsonian, and the *Pilammina densa* Zone from the Illyrian.

There have been no meaningful improvements to the Lower Triassic–Anisian foraminiferal zonation since the study of Hardenbol et al. (1998). Among different versions of foraminiferal biostratigraphy proposed for limited intervals of Lower–Middle Triassic, the studies of Muttoni et al. (1998), Faletti and Ivanova (2003), Vachard et al. (2005), Korngreen and Benjamini (2006), Velić (2007), Vuks (2007), Korchagin (2008), and Maurer et al. (2008) can be given as examples.

Griesbachian (Induan)–Illyrian (Anisian) foraminiferal biostratigraphy in the Great Bank of Guizhou

In the Great Bank of Guizhou, 12 biozones and two unnamed intervals have been defined from the base of the Griesbachian (Induan) to the top of the Illyrian (Anisian).

Postcladella kalhori-Postcladella grandis *Zone*.—The type section of this biozone is in the Dawen section and defined as a 107.5 m thick limestone succession between 9.0–116.5 meters of the section. The zone is fixed by the successive first occurrences of *Postcladella kalhori* and *P. grandis* (Figs. 2, 21; samples 11–87 in Fig. 5). *Postcladella kalhori* makes its first appearance <2 m above the end-Permian extinction horizon, marked by an abrupt contact between fossiliferous pre-extinction limestone and post-extinction thrombolitic microbialite, thus the lower boundary of this zone approximates the Permian-Triassic boundary. The limestone lithology of the zone consists of thrombolites, micritic to high-energy limestones, oolitic dolomites, and thrombolite-bearing cyclic limestone deposits. *Postcladella kalhori* is usually associated with *Earlandia* sp. 1 and *E.* sp. 2 in the samples. The zone is also present in the Dajiang section, but absent in the Guandao section, probably due to unfavorable facies consisting of shales, allodapic breccias, and unfossiliferous carbonate mudstones.

The *Postcladella kalhori-Postcladella grandis* Zone is defined for the first time in the Triassic literature. It has the potential to be recognized also in the western Tethys because the first appearance of *P. grandis* always postdates the first appearance of *P. kalhori*, both in Turkey (Altıner and Zaninetti, 1981) and in the Transdanubian Range, Hungary (Orovecz-Scheffer, 1987).

The *Postcladella kalhori-Postcladella grandis* Zone corresponds to an important part of the Griesbachian Substage. In Song et al. (2009, 2016), *P. kalhori* was reported from the *H. parvus*, *I. staeschei*, and *I. isarsica* conodont zones (Griesbachian) of the Dajiang section. No conodonts have been recorded from the levels corresponding to the *P. kalhori-P. grandis* Zone in the Dawen section. However, Chen et al. (2009) reported some Griesbachian conodont zones from the Dawen section, which is at least partially equivalent to the lower part of our zone. Finally, *P. kalhori* has been reported from the uppermost Permian in some recent literature (Firi et al., 2016; Tian et al., 2018). However, mentioned or poorly illustrated specimens do not, in our view, belong to the *kalhori* population in these studies, and there is no need to extend this zone into the uppermost Permian.

Postcladella grandis *Zone*.—Between 116.5 and 160 meters of the Dawen section, a 43.5 m thick, thrombolite-bearing cyclic limestone interval is the type section of the *Postcladella grandis* Zone. It is a taxon-range zone defined by the first and last occurrences of *P. grandis* (Figs. 2, 21; samples 87–140 in Fig. 5). The zone also has been recognized in the Dajiang section. The last appearance of *P. grandis* is very close to the Griesbachian-Dienerian boundary, which is correlated with the Guandao section on the basis of carbon-isotope and conodont data (Payne et al., 2004; Lehrmann et al., 2015).

In the zone, *P. grandis* is associated with *P. kalhori*, *Earlandia* sp. 2, *Cornuspira mahajeri*?, and unknown foraminifera 4. Although not properly defined, this zone is surely present in the Taurides (Turkey) (Altıner and Zaninetti, 1981) and the Transdanubian Range in Hungary (Orovecz-Scheffer, 1987). The marker of the zone is also present in the Werfen Formation (Austria) (Krainer and Vachard, 2011, pl. 5, figs. 9, 10, 14). The upper part of the Griesbachian Substage could be characterized in the future after the definition of this zone in this part of Europe.

Postcladella grandis-Postcladella kalhori *Zone*.—The type section of this zone measures 24 m, between 160 and 184 meters of the Dawen section, and is fixed on the basis of successive last occurrences of *P. grandis* and *P. kalhori* (Figs. 2, 21; samples 143–167 in Fig. 5). The *Postcladella grandis-Postcladella kalhori* Zone, consisting of a thrombolite-bearing cyclic limestone succession, is assigned to the lower part of the Dienerian Substage. This interpretation is based on the carbon isotope correlation and conodonts obtained from the Guandao section, where the

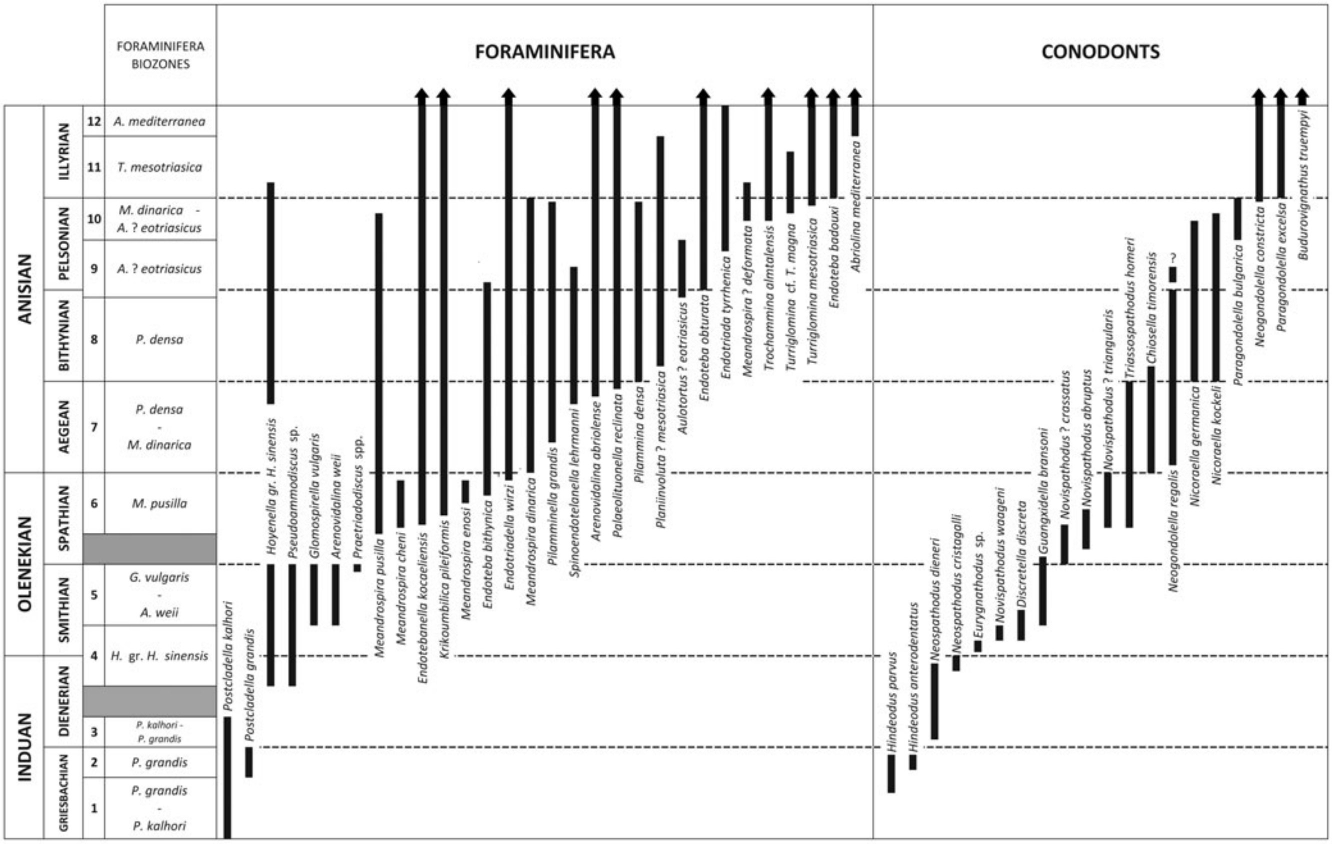

Figure 21. Biozones of foraminifera (1–12) and stratigraphic ranges of important foraminifera and conodont species. *P. kalhori*: *Postcladella kalhori*; *P. grandis*: *Postcladella grandis*; *H.* gr. *H. sinensis*: *Hoyenella* gr. *H. sinensis*; *A. weii*: *Arenovidalina weii*; *G. vulgaris*: *Glomospirella vulgaris*; *M. pusilla*: *Meandrospira pusilla*; *M. dinarica*: *Meandrospira dinarica*; *P. densa*: *Pilammina densa*; *A.*? *eotriasicus*: *Aulotortus*? *eotriasicus*; *T. mesotriasica*: *Turriglomina mesotriasica*; *A. mediterranea*: *Abriolina mediterranea*.

Griesbachian-Dienerian boundary is placed on the basis of the first occurrence of *Neospathodus dieneri* following the last occurrence of *Hindeodus parvus* in the underlying Griesbachian (Payne et al., 2004; Lehrmann et al., 2015). Consistent with our study, Galfetti et al. (2008) properly identified the stratigraphic distribution of *P. kalhori* based on conodont data from the Nanpanjiang Basin. This study confirms the chronostratigraphic value of our zone, covering at least the lower part of the Dienerian Substage.

Unnamed interval in the Dienerian.—The interval consisting of thrombolite-bearing cyclic limestones, between 184 and 253 meters of the Dawen section and 250 and 326 meters of the Dajiang section, does not contain any foraminifera. Therefore, this interval could not be zoned within the biostratigraphic framework of this study. This interval in the platform interior sections probably corresponds in age to breccia deposits in the Guandao slope section in the GBG, an unfavorable setting for the occurrence of foraminifera.

Hoyenella *gr.* H. sinensis *Zone.*—The type section of this zone is defined in the Dawen section. It consists of a 68 m thick, thrombolite-bearing cyclic limestone between 253 and 321 meters of the section (Figs. 2, 21; samples 246–340 in Fig. 5). Successive first occurrences of *Hoyenella* gr. *H. sinensis* and *Glomospirella vulgaris* define the lower and upper boundaries. The zone is slightly thicker in the Dajiang section, and only the upper part is recognized in the Guandao section. The marker of the zone is associated with *H.* gr. *H. shengi*, transitional forms to *Meandrospira*, *Pseudoammodiscus* sp., *Glomospira* sp. (=*Pilammina praedensa*?), and unknown foraminifera 1 in the Dawen, Dajiang, and Guandao sections. The zone corresponds to the upper part of the Dienerian Substage and the lower part of the Smithian, thus encompassing the Induan-Olenekian boundary (Figs. 2, 21). This boundary is recognized in the Dawen section on the basis of carbon isotope chemostratigraphy and conodont biostratigraphy of the Guandao section, where it is delineated by the first occurrences of *Eurygnathodus*, *Novispathodus waageni*, and *Nv. posterolongatus* following the last occurrence of Dienerian marker *Neospathodus dieneri*. In recent literature, the first occurrence of *Hoyenella* gr. *H. sinensis* in south China (Galfetti et al., 2008), Israel (Korngreen et al., 2013), and India (Baud and Bhat, 2014) has been reported in the Dienerian, based on conodonts.

Glomospirella vulgaris-Arenovidalina weii *Zone.*—The zone is 34 m thick and corresponds to the interval between 160 and 194 meters of the Guandao section. It is made up of limestone intercalated with distinct allodapic breccia levels (Figs. 2, 21;

samples 96–132 in Fig. 11). The lower and upper boundaries are defined based on the first and last occurrences of *Glomospirella vulgaris* and *Arenovidalina weii* n. sp., respectively. In addition to these taxa, the zone contains *Hoyenella* gr. *H. sinensis*, *H.* gr. *H. shengi*, *Pseudoammodiscus* sp., and, in the upper part, the oldest involutinid taxa, *Praetriadodiscus zaninettiae* and *P. tappanae* (see Altıner and Payne, 2017). In China, as previously reported by He (1993), the *Glomospirella vulgaris* Subzone of the *Arenovidalina chialingchiangensis* Zone occurs below the Spathian *Meandrospira pusilla* Zone, and probably corresponds to our zone.

In our biostratigraphic framework, the *Glomospirella vulgaris-Arenovidalina weii* Zone, assigned a middle to upper Smithian age, corresponds to the upper part of the *Discretella discreta* and *Guangxidella bransoni* conodont zones, defined in the Guandao section by Lehrmann et al. (2015) (see also Fig. 21).

Unnamed interval in the Spathian.—In the Guandao section between 194 and 238 meters, an unfavorable lithology consisting of dolomite and allodapic breccia, did not yield any foraminifera (Fig. 2, 21). This interval, ∼44 m thick, does contain conodonts and, specifically, the first occurrence of *Novispathodus*? *crassatus* constrains the position of the Smithian-Spathian boundary in the Guandao section (Lehrmann et al., 2015). The unnamed interval is located below the first occurrence of conodonts *Novispathodus*? *triangularis* and *Triassospathodus homeri*, and corresponds to the lower Spathian.

Meandrospira pusilla *Zone.*—This zone, ∼39 m thick and entirely composed of limestone, measures between 238 and 277 meters of the Guandao section. It is defined on the basis of successive first occurrences of *Meandrospira pusilla* and *M. dinarica*, and corresponds to an important part of the Spathian Substage (Fig. 2, 21; samples 149–195 in Fig. 11). In the type section, the first occurrence of *M. pusilla* is above the unnamed interval in the Spathian and is nearly coeval with the first occurrence of *Novispathodus*? *triangularis* and *Triassospathodus homeri* (Lehrmann et al., 2015). At the upper boundary, the first occurrence of *M. dinarica* coincides with the turnover in conodont assemblages represented by *Chiosella timorensis*, *Neogondolella regalis*, and *Gladiogondolella tethydis*. As defined in this study, the zone is incomplete because the lower boundary, marked by the first occurrence of *M. pusilla*, is facies-controlled. If facies had been suitable, *M. pusilla* may well have appeared much lower in the succession.

In the zone, in addition to *Hoyenella* gr. *H. sinensis* and unnamed foraminifera 1, which range into the underlying zones, several important Triassic species make their first appearances, including *Meandrospira cheni*, *M.*? *enosi* n. sp., *M.*? sp., *Endoteba bithynica*, *Endotebanella kocaeliensis*, Endotebidae, *Endotriadella wirzi*, *Trochammina*? sp.1, *Verneuilinoides*? *azzouzi*, *Krikoumbilica pileiformis*, *Variostoma* sp. 1, *Variostoma* sp. 2, *Diplotremina* sp. 2, and *Nodosinelloides*? sp.

Although the marker of the zone has been used sometimes under different invalid species names, the *Meandrospira pusilla* Zone is one of the most frequently cited biostratigraphic units from the Lower Triassic. It has been reported from the western Carpathians or Carpatho-Balkan Range (Salaj, 1969, 1978; Trifanova, 1978a; Salaj et al., 1983, 1988), the Transdanubian Range of Hungary (Orovecz-Scheffer, 1987), the Kocaeli Peninsula from Turkey (Zaninetti and Dağer, 1978), southern China (He, 1993), Tunisia (Kamoun et al., 1998), and as a standard zone of Spathian age in the European basins volume (de Graciansky et al., 1998) by Hardenbol et al. (1998).

Meandrospira dinarica-Pilammina densa *Zone.*—This zone, corresponding to the Aegean Substage, is 14 m thick and measures from 18–32 meters in the Upper Guandao section. The lower and upper boundaries of the zone are defined on the basis of successive first occurrences of *Meandrospira dinarica* and *Pilammina densa* (Figs. 2, 21; samples 7–14 in Fig. 8). The first occurrence of *M. dinarica* is in the thin limestone layer overlying the first prominent ash layer of latest Spathian age (Fig. 2) and nearly coincides with the first occurrence of *Chiosella timorensis*, the index conodont used to draw the Olenekian-Anisian boundary (Lehrmann et al., 2015). At the upper boundary, the first occurrence of *P. densa* is nearly coeval with the first occurrence of the conodont *Nicoraella germanica* and approximates the Aegean-Bithynian boundary.

In addition to taxa with ranges from the Lower Triassic into the Aegean, such as *Hoyenella* gr. *H. sinensis*, *H.* gr. *H. shengi*, *Meandrospira pusilla*, *Endoteba bithynica*, *Endotebanella kocaeliensis*, *Endotriadella wirzi*, *Diplotremina* sp. 2, and *Variostoma* sp. 2, the zone contains several other taxa that first occur in the Aegean. These are *Arenovidalina abriolense*, *Meandrospiranella* cf. *M. samueli*, *Glomospirella* sp. 2, *Tolypammina gregaria*, *Pilamminella grandis, Reophax* sp. 2, *Reophax* sp. 5, *Palaeolituonella reclinata*, *Gaudryina* sp., *Placopsilina* sp., *Earlandia tintinniformis*, *Spinoendotebanella lehrmanni* n. gen., n. sp., Lamelliconinae?, and unknown foraminifera 2.

Although *M. dinarica* has been recognized as a very important marker for Anisian biostratigraphy by several authors (Salaj, 1969; Salaj et al., 1988; Zaninetti et al., 1972b; He, 1993), it was Rettori et al. (1994) who noticed the first occurrence of *M. dinarica* lower in the Anisian and close to the Olenekian-Anisian boundary, based on conodont data from the Eros Limestone in Greece. In the standard zonation of Hardenbol et al. (1998; see also Kamoun et al., 1998), the *M. dinarica-P. densa* Zone has been assigned to the Aegean–Bithynian based on the successive occurrences of *M. dinarica*, *Paulbronnimannia judicariensis* (Premoli Silva, 1971), and *Pilammina densa*. In this study, this interval has been shortened to the Aegean because the first occurrence of *P. densa* is very close to the Aegean-Bithynian boundary, based on reliable conodont data.

Pilammina densa *Zone.*—This zone is defined on the basis of the successive first appearances of *Pilammina densa* and *Aulotortus*? *eotriasicus*. It comprises 23 m of limestone between 32–55 meters in the Upper Guandao section (Figs. 2, 21; samples 15–23 in Fig. 8). The zone corresponds to the Bithynian Substage, except the topmost part where *A.*? *eotriasicus* makes its first appearance. The first occurrence of *P. densa* coincides nearly with the first occurrences of *Nicoraella germanica* and *Ni. kockeli*, index conodonts used to draw the Aegean-Bithynian boundary (Lehrmann et al., 2015). The upper boundary of the zone in the Upper Guandao section has been fixed slightly below the Bithynian-Pelsonian boundary. According to the conodont study, the

Bithynian-Pelsonian boundary is loosely constrained because of the late occurrence of the Pelsonian index *Paragondolella bulgarica* and some taxonomic problems regarding *Neogondolella* ex gr. *N. regalis*. We have decided on the lowest level as the Bithynian-Pelsonian boundary, among the possible positions of the boundary suggested by Lehrmann et al. (2015), considering also the stratigraphic position of characteristic Pelsonian foraminiferal associations.

Several major foraminiferal taxa with first occurrences in older zones occur also in the Bithynian: *Hoyenella* gr. *H. sinensis*, *H.* gr. *H. shengi*, *Meandrospira pusilla*, *M. dinarica*, *Arenovidalina abriolense*, *Pilamminella grandis*, *Palaeolituonella reclinata*, *Earlandia tintinniformis*, *Endoteba bithynica*, *Spinoendotebanella lehrmanni* n. gen., n. sp., *Endotebanella kocaeliensis*, *Endotriadella wirzi*, *E. wirzi*?, and Lamelliconinae?. The following taxa occur for the first time in the *P. densa* zone: *Planiinvoluta*? *mesotriasica*, *Hoyenella*? sp. 2, *Ophthalmidium*? Sp. 5, *Reophax* sp. 3, *Endoteba controversa*, *Endotebanella* sp. 2, *Endotriada* sp. 1, *Protonodosaria exploita*, *Geinitzinita* sp., *Dentalina*? sp. 1, and *Dentalina*? sp. 3.

The *P. densa* Zone has been used in previous studies to distinguish chronostratigraphic intervals within the Anisian Stage (Salaj, 1969, 1976; Zaninetti et al., 1972b; Gazdzicki et al., 1975; Zaninetti and Dağer, 1978; Salaj et al., 1983, 1988; Orovecz-Scheffer, 1987; Budurov et al., 1993; He, 1993; Hardenbol et al., 1998; Kamoun et al., 1998; Faletti and Ivanova, 2003). In this study, the lowest occurrence of *P. densa* coincides with the Aegean-Bithynian boundary, which is consistent with the interpretation of Muttoni et al. (1996) based on conodont data. Therefore, this zone is a reliable index for the Bithynian substage, if its upper boundary is fixed with a reliable taxon such as *A.*? *eotriasicus*.

Aulotortus? eotriasicus *Zone.*—Corresponding to the interval between the lowest and highest occurrences of *Aulotortus*? *eotriasicus*, the zone is ~51 m thick and measures from 55–106 meters in the Upper Guandao section (Figs. 2, 21; samples 23–45 in Fig. 8). Chronostratigraphically, it corresponds to the uppermost Bithynian and lower Pelsonian, and is composed primarily of limestone interrupted by one prominent allodapic breccia level. In the Pelsonian, *A.*? *eotriasicus* occurs above the last true *Neogondolella regalis* and is associated with the conodonts *Nicoraella germanica* and *Ni. kockeli*, extending from the Bithynian into the Pelsonian (Lehrmann et al., 2015). The last individuals of *A.*? *eotriasicus* occur below the first occurrence of the Pelsonian index conodont *Paragondolella bulgarica*, which is partially present in the Pelsonian of the Upper Guandao section (Lehrmann et al., 2015).

Major foraminiferal taxa that occur in lower zones of the Anisian and range into the *A.*? *eotriasicus* Zone include *Planiinvoluta*? *mesotriasica*, *Meandrospira dinarica*, *Pilammina densa*, *Pilamminella grandis*, *Palaeolituonella reclinata*, *Spinoendotebanella lehrmanni* n. gen., n. sp., and *Endotriadella wirzi*. In addition, the following foraminiferal taxa appear for the first time within the *A.*? *eotriasicus* zone: *Hoyenella*? sp. 1, *Glomospirella* sp. 1, *Reophax* sp. 4, *Reophax* sp. 7, *Endoteba obturata*, *Endotebanella* sp. 1, *Endotriada tyrrhenica*, *Endotriadella lombardi*, *Triadodiscus* sp., *Oberhauserella*? sp.1, and *Polarisella elabugae*.

This zone, largely corresponding to the Pelsonian Substage, is surely present in the Dinarids (Bosnia-Herzegovina) and Greece (Brönnimann et al., 1973a; Rettori et al., 1994; Zaninetti et al., 1994); however, no biozonation has been suggested in these studies. Muttoni et al. (1998) reported *A.*? *eotriasicus* from the base of the Illyrian of Albania, higher than its previously known range within the Anisian, and assigned this interval to the '*pragsoides*' Zone, adopted from the *A. pragsoides* Zone of Salaj et al. (1988). However, the conodonts reported in their study are highly fragmentary and true Illyrian markers seem to be absent to calibrate this zone.

Aulotortus? eotriasicus-Meandrospira dinarica *Zone.*—The zone is defined on the basis of successive last occurrences of *Aulotortus*? *eotriasicus* and *Meandrospira dinarica*. It is composed of a 95 m thick limestone interval interrupted by some important carbonate breccia levels between 106 and 201 meters of the Upper Guandao section (Figs. 2, 21; samples 47–65 in Fig. 8). The zone corresponds to the middle and upper part of the Pelsonian Substage, and the upper boundary nearly coincides with the last occurrence of the index conodont *Paragondolella bulgarica*, approximating the Pelsonian-Illyrian boundary.

Several major taxa, including *M. dinarica*, *Pilammina densa*, and *Pilamminella grandis*, range into this zone from underlying zones of the Anisian Stage. Among these taxa, only *Spinoendotebanella lehrmanni* n. gen., n. sp. makes its last appearance close to the lower boundary of the zone. In addition, the following foraminiferan species occur for the first time within the zone: *Meandrospira*? *deformata*, *Meandrospiranella irregularis*?, *Turriglomina* cf. *T. magna*, *T. mesotriasica*, *Ophthalmidium* sp. 3, *Gsollbergella*? sp. 2, *Reophax* sp. 1, *Reophax* sp. 6, *Trochammina almtalensis*, *Malayspirina* sp., *Endoteba* sp., *Endotriada* sp. 2, *Plagiostomella* sp., *Diplotremina* sp. 1, and *Polarisella hoae*.

Across the Tethys, the last occurrence of *M. dinarica* has been reported at or very close to the Pelsonian-Illyrian boundary (Zaninetti, 1976; Salaj et al., 1988; Rettori, 1995; Hardenbol et al., 1998; Kamoun et al., 1998; Muttoni et al., 1998). Therefore, using this last appearance as a boundary in the definition of the upper *M. dinarica* zone is very useful for the characterization of the Pelsonian substage in the Middle Triassic biostratigraphy.

Turriglomina mesotriasica *Zone.*—Corresponding to an important part of the Illyrian Substage and composed of limestone intercalated with carbonate breccia levels, this zone measures 75 m between 201–276 meters of the Upper Guandao section. The zone is defined based on the last occurrence of *Meandrospira dinarica* and the first occurrence of *Abriolina mediterranea*. A third taxon, *Turriglomina mesotriasica*, has been used to name this zone. Its first occurrence is in the uppermost part of the underlying upper *M. dinarica* Zone, very close to the Pelsonian-Illyrian boundary (Figs. 2, 21; samples 67–89 in Fig. 8). The lower boundary of this zone coincides with the last occurrence of Pelsonian index conodont *Paragondolella bulgarica* and the first occurrence of *P. excelsa*, index conodont of the Illyrian (Lehrmann et al., 2015). The upper boundary lies at a datum lower than the Anisian-Ladinian boundary, which is delineated by the first occurrence of *Budurovignathus truempyi*, the index conodont for the base of Fassanian.

Some biostratigraphically important taxa, including *Meandrospira pusilla*, *M. dinarica*, *Pilammina densa*, and *Pilamminella grandis*, which first appear in the Olenekian and older Anisian zones, make their last appearances close to the Pelsonian-Illyrian boundary and do not extend into this zone. However, several taxonomically well-established taxa, including *Planiinvoluta*? *mesotriasica*, *Arenovidalina abriolense*, *M.*? *deformata*, *Turriglomina* cf. *T. magna*, *Malayspirina* sp., *Verneuilinoides*? *azzouzi*, *Endoteba controversa*, *E. obturata*, *Endotebanella kocaeliensis*, *Endotriada tyrrhenica*, *Endotriadella wirzi*, *E. lombardi*, and *Krikoumbilica pileiformis*, extend into this zone. The following species occur for the first time within the zone: *Turriglomina* sp., *Endoteba badouxi*, *Endotriada* sp. 3, and *Piallina*? sp.

Although *Pilammina densa* is the preferred foraminiferal marker of the upper Anisian in the European basins (Zaninetti et al., 1972b, Salaj et al., 1988; Rettori, 1995; Hardenbol et al., 1998), its stratigraphic range does not extend higher than Pelsonian in the Great Bank of Guizhou. Here we use the *Turriglomina mesotriasica* Zone to recognize the Illyrian Substage because it is well calibrated with conodont data.

Abriolina mediterranea *Zone.*—In the upper Illyrian, this zone is defined on the basis of the successive first occurrences of *Abriolina mediterranea* and *Agathammina*-like forms (*Agathammina*? sp.) displaying coiling in five planes, as in *Quinqueloculina*, but without septation. The zone is represented by 18 m of limestone with the intercalation of one prominent breccia and measures between 276–294 meters of the Upper Guandao section (Figs. 2, 21; samples 91–95 in Fig. 8). The appearance of coiling in five planes in *Agathammina*? sp., never observed in the Anisian stratigraphy, is coeval with the first occurrence of the index conodont of the Fassanian, *Budurovignathus truempyi*.

Nearly all foraminiferal assemblages recognized in the underlying *Turriglomina mesotriasica* Zone are recorded in this zone. *Abriolina*? sp. and *Palaeolituonella* sp. occur for the first time.

Abriolina mediterranea is used for the first time as a zonal marker in this study. Although not formally defined, the zone is probably present in the Latemar platform (Dolomites, Italy), where *A. mediterranea* has been reported from Illyrian to Ladinian strata by Emmerich et al. (2005).

Early Triassic–early Middle Triassic diversity and recovery

Following one of the most severe mass extinctions in Earth's history, at the Permian-Triassic boundary of ∼252 my ago, the recovery of marine ecosystems was both protracted and non-monotonic, with variation in recovery dynamics among higher taxa as well as interruptions of recovery due to later environmental disturbances (Hallam, 1991; Kidder and Worsley, 2004; Payne et al., 2004, 2006; Lehrmann et al., 2006; Payne and Kump, 2007; Fraiser and Bottjer, 2007a; Galfetti et al., 2007, 2008; Knoll et al., 2007; Algeo et al., 2011; Chen and Benton, 2012; Sun et al., 2012, 2015; Song et al., 2014; Tian et al., 2014; Wei et al., 2015; Lau et al., 2016; Penn et al., 2018; Zhang et al., 2018; Goudemand et al., 2019). The combined effects of extinction and recovery led to replacement of the Paleozoic Fauna by the Modern Fauna (Sepkoski, 1984; Fraiser and Bottjer, 2007b). In addition to foraminifera, recovery dynamics have been studied in microfossil groups such as radiolarians (Feng et al., 2007; Feng and Algeo, 2014) and conodonts (Orchard, 2007; Stanley, 2009), as well as invertebrate clades such as corals (Senowbari-Daryan et al., 1993; Flügel, 2002), brachiopods (Rodland and Bottjer, 2001; Z.Q. Chen et al., 2005; J. Chen et al., 2015), bryozoans (Powers and Pachut, 2008), gastropods (Erwin and Pan, 1996; Fraiser and Bottjer, 2004; Nützel, 2005; Payne, 2005; Brayard et al., 2010), ammonoids (McGowan, 2004; Brayard et al., 2006, 2009; Stanley, 2009), and echinoderms and vertebrates (Twitchett and Oji, 2005; Chen and McNamara, 2006), yielding valuable information on recovery patterns during the Early Triassic and their correlation with ongoing environmental disturbances.

The foraminiferal fauna of the Great Bank of Guizhou was studied recently by Payne et al. (2011) to investigate the tempo and mode of biotic recovery from the end-Permian mass extinction. They reported gradual increases in the diversity, evenness, and sizes of foraminifera through the Early Triassic and earliest Middle Triassic, with stable values reached early in the Anisian. Payne et al. (2011) stated that the recovery patterns on the GBG correspond well with available global data and appear to parallel those of many benthic invertebrate clades. Based on the metrics of standing diversity, evenness, and size, the recovery trajectory in foraminifera appears to have been more gradual than those of pelagic taxa, such as ammonoids and conodonts (Brayard et al., 2009; Stanley 2009), suggesting a decoupling of recovery processes between benthic and pelagic environments. However, these metrics do not capture species-level changes in the composition of the foraminiferal biota and their implications for recovery dynamics. Consequently, some similarities between the foraminiferan and pelagic recovery dynamics may have been overlooked.

In this study, a more detailed, species-level taxonomy has been carried out on the material of the GBG used by Payne et al. (2011), which has revealed further details on the recovery pattern and diversity in the Early Triassic. The species-level data shed new light on recovery dynamics and, furthermore, highlight the ways in which analyses at higher taxonomic levels may capture some aspects of recovery dynamics, but also obscure or distort other aspects.

Ninety-seven foraminifera populations recognized at species rank have been plotted in a range chart from the base of Griesbachian (Permian-Triassic boundary) to the upper limit of the Illyrian (Anisian-Ladinian boundary) (Fig. 22). In actuality, the number of distinct, species-level taxa is probably >100 because four of these taxa given in the list of Figure 22 (Variostomatidae, Endotebidae, unknown Nodosariata, and Lamelliconinae?) probably contain more than one taxon. Within the foraminiferal biostratigraphic framework, calibrated by conodont biostratigraphy, we recognize three groups of taxa whose stratigraphic ranges and phyletic relationships to one another demarcate three major phases in the Early–Middle Triassic recovery of foraminiferan communities.

Step1: Griesbachian–early Dienerian: disaster taxa and their evolutionary derivatives.—The foraminiferan community that characterizes the interval from the end-Permian extinction

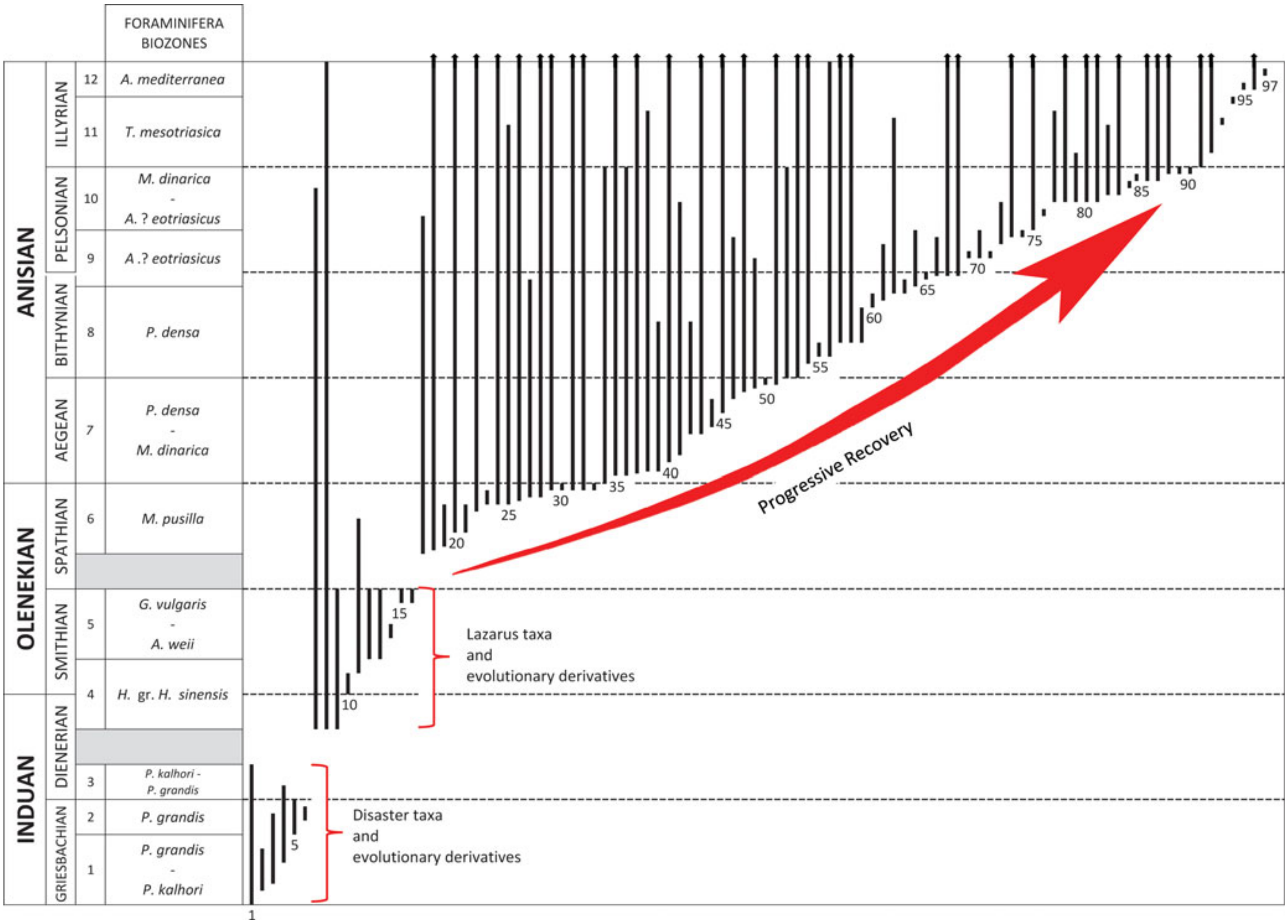

Figure 22. Range chart showing the delayed and progressive recovery phases of foraminifera. For the abbreviations of biozone markers of foraminifera, see Figure 21. 1 = *Postcladella kalhori*; 2 = *Earlandia* sp. 1; 3 = Unknown foraminifera 4; 4 = *Earlandia* sp. 2; 5 = *Postcladella grandis*; 6 = *Cornuspira mahajeri*?; 7 = *Hoyenella* gr. *H. sinensis*; 8 = *Hoyenella* gr. *H. shengi*; 9 = *Pseudoammodiscus* sp.; 10 = *Glomospira* sp.; 11 = Unknown foraminifera 1; 12 = *Glomospirella vulgaris*; 13 = *Arenovidalina weii*; 14 = Transitional forms to *Meandrospira*; 15 = *Praetriadodiscus zaninettiae*; 16 = *Praetriadodiscus tappanae*; 17 = *Meandrospira pusilla*; 18 = *Endotebanella kocaeliensis*; 19 = *Meandrospira cheni*; 20 = *Krikoumbilica pileiformis*; 21 = *Trochammina*? sp. 1; 22 = *Nodosinelloides*? sp.; 23 = *Meandrospira? enosi* n. sp.; 24 = *Variostoma* sp. 1; 25 = *Variostoma* sp. 2; 26 = *Verneuilinoides*? *azzouzi*; 27 = *Endoteba bithynica*; 28 = *Diplotremina* sp. 2; 29 = *Endotriadella wirzi*; 30 = *Hoyenella* ? sp.; 31 = Variostomatidae; 32 = Endotebidae; 33 = *Meandrospira*? sp.; 34 = *Meandrospira dinarica*; 35 = *Endotriadella wirzi*?; 36 = *Pilamminella grandis*; 37 = Unknown Nodosariata; 38 = *Reophax* sp. 2; 39 = *Glomospirella* sp. 2; 40 = *Earlandia tintinniformis*; 41 = *Gaudryina* sp.; 42 = *Placopsilina* sp.; 43 = *Tolypammina gregaria*; 44 = Unknown foraminifera 2; 45 = *Reophax* sp. 5; 46 = *Spinoendotebanella lehrmanni* n. gen., n. sp.; 47 = *Arenovidalina abriolense*; 48 = Lamelliconinae ?; 49 = *Protonodosaria exploita*; 50 = *Meandrospiranella samueli*; 51 = *Palaeolituonella reclinata*; 52 = *Pilammina densa*; 53 = *Triadodiscus* sp.; 54 = *Endoteba controversa*; 55 = *Ophthalmidium*? sp. 5; 56 = *Planiinvoluta? mesotriasica;* 57 = *Geinitzinita* sp.; 58 = *Reophax* sp. 3; 59 = *Dentalina*? sp. 1; 60 = *Hoyenella*? sp. 2; 61 = *Dentalina*? sp. 2; 62 = *Endotebanella* sp. 2; 63 = *Endotriada* sp. 1; 64 = *Aulotortus*? *eotriasicus*; 65 = *Hoyenella* ? sp. 1; 66 = *Glomospirella* sp. 1; 67 = *Endotriadella lombardi*; 68 = *Endoteba obturata*; 69 = *Endotebanella* sp. 1; 70 = *Reophax* sp. 4; 71 = *Oberhauserella*? sp.; 72 = *Polarisella elabugae*; 73 = *Endotriada tyrrhenica*; 74 = *Reophax* sp. 7; 75 = *Ophthalmidium* sp. 3; 76 = *Gsollbergella*? sp. 2; 77 = *Endoteba* sp.; 78 = *Endotriada* sp. 2; 79 = *Meandrospira*? *deformata*; 80 = *Reophax* sp. 6; 81 = *Trochammina almtalensis*; 82 = *Turriglomina* cf. *T. magna*; 83 = *Polarisella hoae*; 84 = *Gandinella* sp. 1; 85 = *Meandrospiranella irregularis*?; 86 = *Reophax* sp. 1; 87 = *Turriglomina mesotriasica;* 88 = *Malayspirina* sp.; 89 = *Plagiostomella*? sp.; 90 = *Diplotremina* sp. 1; 91 = *Endoteba badouxi*; 92 = *Turriglomina* sp.; 93 = *Endotriada* sp. 3; 94 = *Piallina*? sp.; 95 = *Abriolina*? sp.; 96 = *Abriolina mediterranea*; 97 = *Palaeolituonella* sp.

horizon through the Griesbachian and into the mid-Dienerian has low diversity and a distinctive taxonomic composition (Fig. 22). The community largely belongs to three genera: *Postcladella* (previously known as *Rectocornuspira*), *Cornuspira*, and *Earlandia*. The later appearance of *P. grandis*, which most likely evolved from *P. kalhori*, illustrates that the community was not entirely static; rather, it contains evidence of evolutionary trends that may reflect recovery from the mass extinction event or some amelioration of environmental constraints on recovery.

Defined by Fischer and Arthur (1977) as opportunistic species that proliferated at times of biotic crises, 'disaster taxa' have been further described by Kauffman and Harries (1996) as species that undergo very short-term, large-scale population blooms immediately following biotic crises, early in the survival phase. The studied samples of the Great Bank of Guizhou reveal a distinct pattern of low-diversity, high-dominance foraminiferal assemblages that persist through the Griesbachian before disappearing by the end of the early Dienerian (Fig. 23). This long interval of dominance by a few species may explain why it is also associated with internal evolutionary trends, such as the increase in size from *P. kalhori* to *P. grandis*. However, the lineages that dominated this early post-extinction interval do not appear to have played a role in the later Early Triassic recovery of foraminifera.

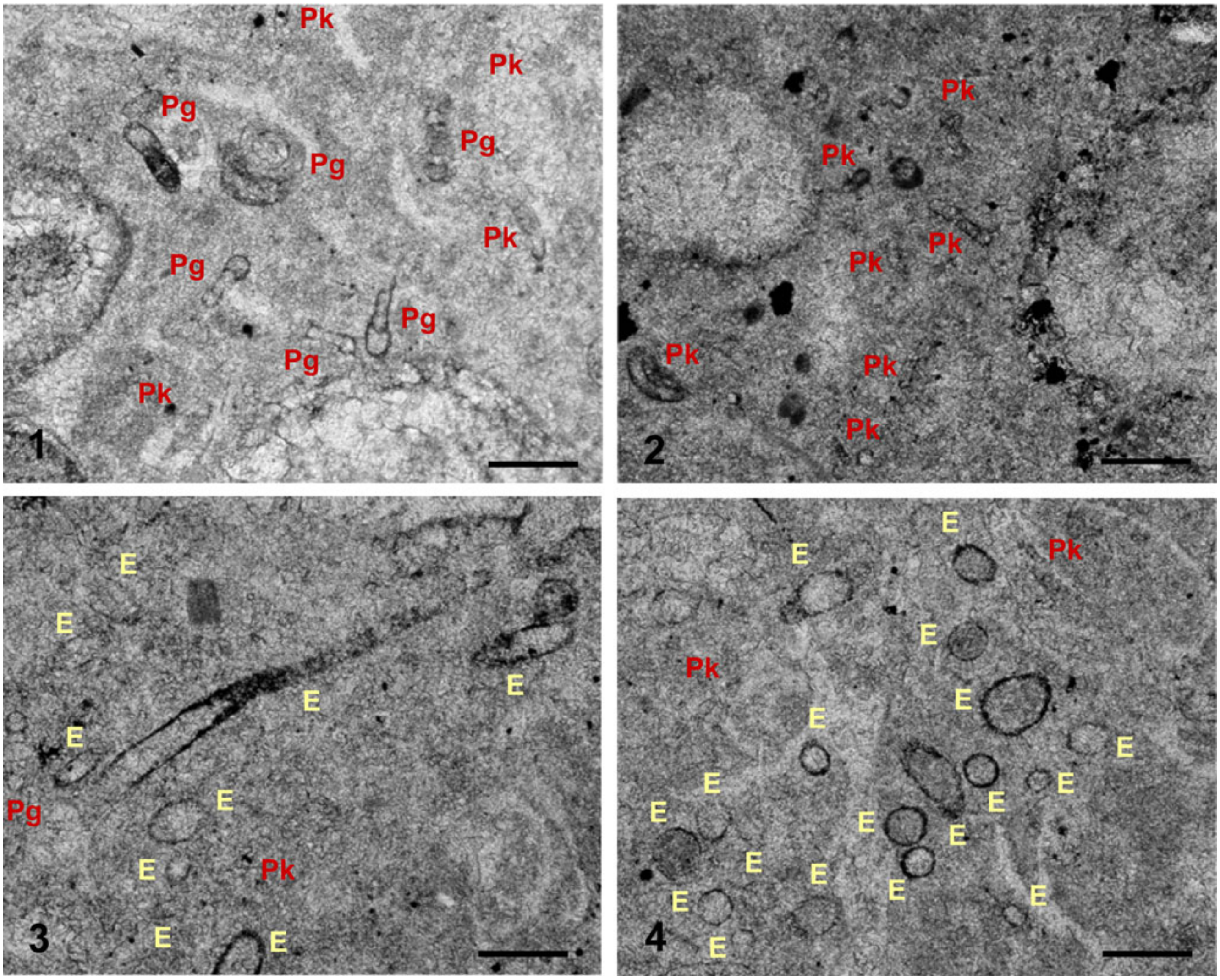

Figure 23. Disaster taxa from Dawen (PDW) and Dajiang (PDJ) sections. (**1**) *Postcladella* (Pk: *P. kalhori*; Pg: *P. grandis*) from the *Postcladella grandis* Zone (Griesbachian) (PDJ-174); (**2**) *Postcladella* (Pk: *P. kalhori*) from the *Postcladella kalhori-Postcladella grandis* Zone (Griesbachian) (PDW-011); (**3**) *Earlandia* (E: *E.* sp. 2) associated with *Postcladella* (Pk: *P. kalhori*; Pg: *P. grandis*) from the *Postcladella grandis* Zone (Griesbachian) (PDW-120); (**4**) *Earlandia* (E: *E.* sp. 2) associated with *Postcladella* (Pk: *P. kalhori*) from the *Postcladella grandis* Zone (Griesbachian) (PDW-120). Horizontal bars = 200 μm.

Similar Griesbachian to lowermost Dienerian foraminiferan assemblages have been reported across the Tethyan belt. Hallam and Wignall (1997), based mainly on data from south China, were the first to characterize an Early Triassic foraminiferan genus, *Earlandia* spp., explicitly as a disaster taxon. Later, Altıner et al. (2005), Groves and Altıner (2005), and Groves et al. (2005, 2007) characterized a group of species, consisting of *P. kalhori*, *C. mahajeri,* and *Earlandia* spp., as disaster taxa that make their first appearances in the thrombolitic facies directly overlying the Changhsingian carbonates, both in Turkey and Italy. Later, Song et al. (2009, 2016), from south China, and Krainer and Vachard (2011), from southern Austria, described similar taxa from similar facies in lowermost Triassic strata. According to Altıner et al. (2005), this assemblage of disaster taxa is usually associated in the early Griesbachian with several well-known Permian forms that survived the end-Permian mass extinction. These surviving taxa, including *Globivalvulina*, *Kamurana*, *Geinitzina*, *Syzrania*, and maybe several others, survived the immediate extinction interval, but did not leave any further descendants in the Triassic as part of the long-term recovery process (‘failed crisis progenitors’ of Kauffman and Harries, 1996). In a more recent paper by Song et al. (2016), a distinct population of *Globivalvulina* (*G. lukachiensis* Nestell et al., 2011), known from the Capitanian–Changhsingian stages of the Permian, has been erroneously classified as a disaster taxon from the lower Griesbachian of south China. This taxon is more likely a failed survivor (Altıner et al., 2005).

Assessing the evolutionary paleoecological dynamics of foraminifera during the immediate survival interval of the Griesbachian is further complicated by highly unusual foraminiferal taxa reported without any illustration in the study of Sun et al. (2015) from the Smithian–Spathian sections of south China. These authors reported the typical Griesbachian–early Dienerian disaster taxa *Postcladella* (given as *Rectocornuspira*) and *Earlandia*, as well as some Permian forms (*Paleotextularia*, *Cribrogenerina*, *Globivalvulina*, *Nodosinella*), from Smithian–Spathian strata in association with *Meandrospira pusilla* and *Hoyenella*. If this report does not reflect mistakes in taxonomic identifications, the mixed fauna most probably could be explained by reworking of Permian and Griesbachian–Dienerian specimens into Smithian–Spathian strata of the Jiarong and Mingtang sections of the Nanpanjiang Basin. These sections contain platform material that was transported and redeposited in slope sections, providing a potential mechanism for this scenario. The co-occurrences of taxa in these sections that have not been reported to co-occur elsewhere argue against an interpretation of the local survival of the Permian and Griesbachian forms into the Smithian and Spathian.

The stratigraphic range of the high-dominance, low-diversity foraminiferan assemblage extending from the base of Griesbachian to mid-Dienerian coincides in time with the strongest geochemical proxy evidence for persistent and expanded ocean anoxia (cf., Lau et al., 2016). According to Zhang et al. (2018), two successive expansions of anoxia occurred on the continental shelves within this time interval—the earlier event lasted from latest Changhsingian to earliest Griesbachian (C1), and the later event lasted from latest Griesbachian to earliest Dienerian (C2). The earlier event coincides with the range and extinction of failed survivors and with the first appearances of disaster taxa immediately following the end-Permian extinction. The second pulse corresponds to the continuation of the survival of disaster taxa from latest Griesbachian to earliest Dienerian, and finally to their extinction.

Step 2: Late Dienerian–Smithian: Lazarus taxa and their evolutionary derivatives.—Following a mid-Dienerian gap in the occurrence of foraminifera on the GBG in the studied sections, there is a substantial shift in the composition of foraminiferan communities and recovery dynamics during the late Dienerian to Smithian (Fig. 22). Most of the taxa that occur in this step are Lazarus taxa with Permian ancestors, but no obvious representatives in Griesbachian to lower Dienerian strata (e.g., *Hoyenella* spp., *Pseudoammodiscus* sp., *Glomospira* sp. [=*Pilammina praedensa*?], *Glomospirella vulgaris*, *Arenovidalina weii* n. sp., transitional forms to *Meandrospira*). *Hoyenella* and *Arenovidalina* originated in the late Paleozoic (Vachard, 2018), but they reappeared in the late Dienerian and in the Smithian, respectively. *Glomospira* and *Glomospirella* also originated in the late Paleozoic (Permian) (Vachard, 2018), and then reappeared in the late Dienerian–Smithian interval. The forms illustrated as *Glomospirella*? from the uppermost Changhsingian of southwestern Guangxi, south China by Gu et al. (2007) are certainly related to Early Triassic *Glomospirella* faunas. *Glomospirella*? *mamilla* Gu et al., 2007, which is similar or identical to *Glomospirella vulgaris*, is recognized as a Lazarus taxon in this study in the Smithian of the GBG. Apparently, such *Glomospirella* species of Guangxi adapted themselves to deeper-water environments (as a refugium?) close to the Permian-Triassic boundary and later, in the aftermath of the crisis, spread over the carbonate platform.

The pseudoammodiscid clade, which appeared in the Devonian and survived through the Permian, reappeared in the Early Triassic (Altıner and Payne, 2017). *Pseudoammodiscus* sp. first occurs in the upper Dienerian in China, as well as in Turkey (Altıner and Zaninetti, 1981). This form apparently survived into the Smithian and finally gave rise to *Praetriadodiscus* close to the Smithian-Spathian boundary. *Praetriadodiscus* is an ancestor or close relative of the last common ancestor of all involutinid taxa (Altıner and Payne, 2017). The genus *Meandrospira*, which occurs in the Spathian, has been interpreted as a Lazarus taxon representing the phyletic continuation of the Permian form assigned to *Streblospira* (Altıner et al., 2005). The specimens that we found in the Smithian of the Dajiang section probably belong to this Lazarus lineage.

Within the detailed biostratigraphic framework based on both conodonts and foraminifera, it appears that the recovery of Lazarus taxa in the late Dienerian–Smithian interval was interrupted by an extinction event. Several foraminiferal Lazarus taxa (*Pseudoammodiscus* sp., *Arenovidalina weii* n. sp., *Glomospirella vulgaris*, *Praetriadodiscus zaninettiae*, and *P. tappanae*) disappeared close to the Smithian-Spathian boundary (Figs. 21, 22). However, from these Lazarus taxa, the main species of the genus *Hoyenella* (*H.* gr. *H. sinensis* and *H.* gr. *H. shengi*) and the unknown foraminifera 1 survived and occur in the Spathian and Middle Triassic Series of the Great Bank of Guizhou.

The data from this study are not consistent with the data and interpretations given in Song et al. (2011a), in which it was suggested that benthic marine diversity began to recover in the early Smithian, little more than 1 Myr after the mass extinction. We interpret the coincidence of the first occurrences of several foraminiferal taxa in the Smithian in the dataset of Song et al. (2011a) to result either from taxonomic misassignments, which are impossible to assess due to the lack of illustrated material, or due to miscorrelation of studied sections. In Song et al. (2011a), several taxa that are well known from younger levels of the Lower Triassic, Anisian, or even from the Late Triassic (e.g., *Meandrospira dinarica*, *Pilammina densa*, *Trochammina almtalensis*, *Endotriadella wirzi*, and *Gsollbergella spiroloculiformis* [Oravecz-Scheffer, 1971]) are reported in the early Smithian. Because we did not observe these forms in our material, and they have not been reported from correlative stratigraphic horizons elsewhere, we cannot place strong weight on these reports.

An episode of expanded oceanic anoxia during the mid-late Smithian (the C3 event of Zhang et al., 2018) is correlated broadly with the extinction of several important Lazarus taxa. However, further assessment is required to determine how closely spaced in time these extinctions were and how closely they coincide to intervals of rapid environmental change, such as the Smithian-Spathian boundary crisis (Galfetti et al., 2007).

Step 3: Spathian–Anisian: progressive recovery.—The interval spanning from the base of the Spathian to the top of the Illyrian is characterized by the marked diversification of foraminifera (Fig. 22). Among the 80 taxa identified within this interval in this study, short-ranging taxa are generally populations defined with open nomenclature (*Reophax* spp. 1–7; *Ophthalmidium* spp. 1–5; etc.), based on our latest taxonomic interpretations (see taxonomy section). In the Spathian–Anisian interval, these taxa appeared in association with several well-established and wider ranging forms, such as *Meandrospira pusilla*, *M. dinarica*, *Pilammina densa*, and *Turriglomina mesotriasica*.

Several clear trends have been noted in the evolution of foraminifera during the Spathian. Three distinct populations, *M. pusilla*, *M. cheni*, and *M.*? *enosi* n. sp., were successively derived from the Lazarus taxon *Meandrospira* (Altıner et al., 2005). The Permian genus *Endoteba* reappeared in the Spathian and gave way to the first occurrences of *E. bithynica*, *Endotebanella kocaeliensis*, and *Endotriadella wirzi* in this interval. Species belonging to the well-known Triassic families Variostomatidae and Trochamminidae also made their first appearances in the Spathian.

The rest of the Anisian diversity increase continued at a fairly constant rate, within the constraints of available data, although there may have been an acceleration close to the Spathian-Aegean boundary (Fig. 22). Within this context of progressive recovery, the C4 event of Zhang et al. (2018), which corresponds to expansion of sea-floor anoxia at the Early-Middle Triassic transition, does not seem to have been associated with any obviously biological response in foraminiferan communities on the GBG. Although Zhang et al. (2018) recognized this end-Spathian event as a crisis of global extent, there is relatively little evidence at present for a large biological response in benthic marine communities.

Many of the foraminiferal populations recognized in the Anisian derived from ancestors that originated in the Olenekian (*Meandrospira dinarica* from *M. cheni*, species of *Turriglomina* and other meandrospirid forms from *M. pusilla*, derivation of *Ophthalmidium* spp. from *Arenovidalina* originated in the Smithian, *Spinoendotebanella lehrmanni* n. gen., n. sp. from *E. kocaeliensis*, *Endotriadella wirzi*? [large form] from *E. wirzi*, *Trochammina almtalensis* from the lineage originated from *Trochammina* sp. 1). Other species have obvious evolutionary precursors in the Anisian (progressively derived *Endoteba*, *Endotebanella*, *Endotriada*, and *Endotriadella* species). However, some other taxa also occur during this phase of recovery whose phylogenetic origins cannot be demonstrated with the available material from China. For example, *Pilammina praedensa*, a possible ancestor of *P. densa* and *Pilamminella grandis*, has been recorded only questionably in the Smithian (as *Glomospira* sp.). For the origin of *Reophax*, which first appears at the base of Anisian, no specimens have been recovered in the Lower Triassic. In addition to these taxa, the origins of some taxa first occurring in the Anisian (*Palaeolituonella reclinata*, *Aulotortus*? *eotriasicus*, *Glomospirella* sp. 1, *G.* sp. 2 [*Glomospirella lampangensis*?], *Gaudryina* sp. [*Gaudryina triadica*?]) remain unclear and are not well constrained by the studied material from the GBG.

In summary, foraminiferal standing diversity increased progressively through the late Early Triassic (Spathian) and into the Middle Triassic (Anisian). The maximum number of species encountered is nearly 20 in the Spathian, ∼40 in the Aegean/Bithynian, and 60 in the Pelsonian, whereas in the Griesbachian–Smithian, the diversity remained always <10. Following the extinction of far more than 100 calcareous foraminiferan species in the Changhsingian (Groves and Altıner, 2005), the Griesbachian to Smithian interval is characterized by two successive stages of recovery. The first is characterized by the high abundance of a few disaster taxa, with many failed survivors (Altıner et al., 2005; Groves et al., 2005; Song et al., 2009) during the Griesbachian to early Dienerian. The second consists of a fauna dominated by Lazarus taxa in the late Dienerian–Smithian. The taxa that dominated these two intervals produced few lineages that participated in the long-term recovery process. The diversification of taxa that contributed to the Middle Triassic diversification of foraminifera started in the Spathian with several new originations, and continued with these taxa becoming ancestors of many species that made their first appearances in the Anisian.

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