



# Upper Triassic foraminifera from the Northern Calcareous Alps, Austria

## Zgornjetriasne foraminifere iz Severnih apneniških Alp, Avstrija

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**Ključne besede:** zgornji trias, zgodnja jura, Pötschenkalk, Zlambach formacija, Kössen formacija, Kendlbach formacija, morfoskupina

### Abstract

Foraminiferal assemblages and proportions of foraminiferal morphogroups were determined from Upper Triassic deposits of the Eiberg Basin and the Hallstatt Zone of the Northern Calcareous Alps in Austria (Eastern Alps). Foraminifera were hand-picked from the residue of marl samples taken from the upper Norian Pötschenkalk Formation, the middle–upper Rhaetian Zlambach Formation, and the uppermost Rhaetian Tiefengraben Member of the Kendlbach Formation. In total, 72 species from 31 genera were determined. Foraminiferal assemblages from the Pötschenkalk Formation at the Thälerergraben section are relatively diverse. *Dentalina*, *Ammodiscus*, *Nodosaria*, and *Glomospirella* dominate. Foraminiferal assemblages from the Zlambach Formation at the Rossmoos-/Stambachgraben section are also abundant and diverse. The most common foraminifera are *Reophax*, *Dentalina*, and *Annulina*. The uppermost Kössen Formation at the Schlossgraben section is dominated by hyaline taxa. The most common genera are *Ichthyolaria*, *Lenticulina*, and *Nodosaria*. At the Fonsjoch section, the uppermost Kössen Formation contains *Lenticulina*, *Astacolus*, and *Trochammina*. An increase in opportunists suggests variations in oxygen levels during the deposition of the uppermost Kössen Formation. The Kendlbach Formation at the Schlossgraben section is dominated by Lagenida over agglutinated taxa. *Astacolus*, *Lenticulina*, and *Trochammina* are the most common genera. At the Fonsjoch section, the Kendlbach Formation contains mostly *Astacolus*, followed by *Trochammina*, *Ammobaculites*, *Reophax*, and *Lenticulina*. Increases in opportunists point to increased stressful conditions. An increase in nodosariid foraminifera higher up the section indicates a return to better oxygenated conditions.

### Izvilleček

V okviru pričujoče raziskave smo določili foraminiferne združbe in foraminiferne morfoskupine iz zgornjetriasnih in spodnje spodnjajurskih plasti bazena Eiberg in območja Hallstatt današnjih Severnih Apneniških Alp v Avstriji (Vzhodne Alpe). Foraminifere so bile ročno pobrane iz netopnega ostanka vzorcev laporja iz zgornjenorijske Pötschenkalk formacije, srednje–zgornjeretijske Zlambach formacije in zgornjeretijskega dela Tiefengraben člena Kendlbach formacije. Skupno je bilo določenih 72 vrst, ki pripadajo 31 rodovom. Foraminiferne združbe Pötschenkalk formacije v profilu Thälerergraben so vrstno razmeroma bogate. Prevladujejo rodovi *Dentalina*, *Ammodiscus*, *Nodosaria* in *Glomospirella*. Foraminiferne združbe iz Zlambach formacije v Rossmoos-/Stambachgraben profilu so podobno raznolike in številčne. Najbolj pogosti rodovi so *Reophax*, *Dentalina* in *Annulina*. V najvišjih delih Kössen formacije profila Schlossgraben prevladujejo foraminifere s hialinsko steno. Najbolj pogosti rodovi so *Ichthyolaria*, *Lenticulina* in *Nodosaria*. Zgornja Kössen formacija pri Fonsjochu vsebuje foraminifere rodov *Lenticulina*, *Astacolus* in *Trochammina*. Porast deleža oportunistov v vrhnjem delu Kössen formacije kaže na spreminjajočo količino kisika. V Kendlbach formaciji profila Schlossgraben prevladuje skupina Lagenida. Preostanek pripada aglutiniranim primerkom. Najbolj pogosti rodovi so *Astacolus*, *Lenticulina* in *Trochammina*. V profilu Fonsjoch Kendlbach formacija od foraminifer vsebuje večinoma rod *Astacolus*. Sledijo *Trochammina*, *Ammobaculites*, *Reophax* in *Lenticulina*. Porast v deležu oportunistov kaže na stresne pogoje. Tem kmalu sledijo bolje prezračene razmere in večji delež nodosariid.

## Introduction

Foraminifera have been used as an instrument in palaeoecological studies for over 90 years (cf. Jorissen et al., 2007), with the practice progressing considerably with the growth of oil exploration (Van der Zwaan et al., 1999). The distribution of recent taxa and the composition of modern communities at the higher taxonomic levels is commonly translated to “young” fossil associations for interpretation regarding depositional environment and/or habitat. This uniformitarian approach, however, cannot be used for interpreting foraminiferal associations from “deep” geological time due to the increasing proportion of extinct taxa, the introduction of new habitats and/or the elimination of habitats, the changing environmental requirements of taxa, and changing environmental conditions (Murray, 1991, 2006). Kitazato (1984), Corliss (1985), and Jones and Charnock (1985), among others, showed that the general morphologies of the foraminiferal tests reflect their microhabitat, motility, and feeding strategies, and it was proposed that proportions among general shapes, as opposed to actual species and genera, could be used to interpret past environmental conditions, bridging the taxonomic differences between the past and the present (Kitazato, 1984; Bernhard, 1986; Kaiho, 1991; Kaiho & Hasegawa, 1994). Based on modern species of agglutinated foraminifera, Jones and Charnock (1985) established several morphogroups, and their concept was later followed by different authors working with fossil associations to interpret past changes in oxygen levels and/or food resources (e.g. Koutsoukos & Hart, 1990; Valchev, 2006; Mailliot et al., 2009; Nagy et al., 2009; Cetean et al., 2011; Reolid et al., 2012, 2013; Nikitenko et al., 2013; Rita et al., 2016; Setoyama et al., 2017; Reolid et al., 2019; Caratelli & Archuby, 2023). Despite attractions of the approach, actual observations of some modern species do not always confirm the expectations (e.g., Tremblin et al., 2021; McGann et al., 2025).

Even though the morphogroup analysis method was applied to assemblages as old as late Permian (Peng & Li, 2023), and even Devonian (Holcová & Slavík, 2013), it has not yet been employed in the interpretation of Triassic assemblages. One drawback is that Triassic foraminifera are usually determined from thin sections, for which proportions among the species cannot be determined accurately. Isolated, well preserved Triassic assemblages are less commonly dealt with. Examples include foraminiferal assemblages from friable marlstone of the Norian-Rhaetian Zlambach Formation, and the Rhaetian Kössen Formation

in the Northern Calcareous Alps (NCA), Austria (Kristan, 1957; Kristan-Tollmann, 1960, 1964a, b; Fuchs, 1967; Tollmann & Kristan-Tollmann, 1970; Hohenegger & Piller, 1975; Kristan-Tollmann et al., 1991; di Bari & Laghi, 1996; Hillebrandt & Urlichs, 2008; Clémence et al., 2010), assemblages from marlstone and claystone of the Ladinian–Carnian San Cassiano Formation, Italy (Vettorel, 1988; di Bari & Laghi, 1996; di Bari, 1997; di Bari et al., 1997; di Bari, 1998; di Bari & Baracca, 1998; di Bari & Laghi, 1998; di Bari, 1999), foraminifera from several Lower to Upper Triassic formations in the Balkan Mts. (Trifonova, 1965, 1967, 1992, 1993, 1994) and the Carpathians (Salaj et al., 1983, 1988), and assemblages from the Upper Triassic limestone from North Dobrogea, Romania (Mirăuța & Gheorghian, 1975; Grădinaru et al., 1989; Gale et al., 2021, 2022).

Assemblages from the Zlambach and Kössen Formations bear historical reputation due to dedicated, detailed work the resulting descriptions of many new taxa, especially by Kristan (1957), Kristan-Tollmann (1960, 1964a), and Fuchs (1967). Previous research of foraminifera from these formations also includes the work of Kristan (1959), Kristan-Tollmann and Tollmann (1964), Kristan-Tollmann (1970), Urlichs (1972), Kuss (1983), Matzner (1986), Hillebrandt et al. (2007), Clémence et al. (2010), and Mette et al. (2012, 2023). Earlier taxonomic work on Upper Triassic foraminifera from the NCA was done prior to the advent of electron microscopy in micropalaeontological studies, and the majority of the isolated type material from the NCA is thus shown in hand-drawn illustrations (e.g. Kristan, 1957; Kristan-Tollmann, 1964a, b; Fuchs, 1967; Tollmann & Kristan-Tollmann, 1970). Upper Triassic assemblages from the NCA were also studied for palaeoecological purposes. The spatial distribution of foraminifera along the platform-to-basin transect was studied by Hohenegger and Lobitzer (1971), Schäfer and Senowbari-Daryan (1978), Schäfer (1979), Schäfer and Senowbari-Daryan (1981), and Kuss (1983). Research by Kristan-Tollmann (1964a), and Tollmann and Kristan-Tollmann (1970) also showed large differences in foraminiferal assemblages among the different sections of the Zlambach Formation. Tollmann and Kristan-Tollmann (1970) distinguished between the Involutinida-rich “Plackles-” and the Lagenida-dominated “Fischerwiese-type” assemblages. Palaeoenvironmental interpretations of oxygen levels and organic input have been done by Weiland (1991) and Mette et al. (2019) for part of the Zlambach Formation, and by Mette et al.

(2012, 2023) for the upper Kössen and the Kendlbach Formations. Studies of foraminifera have also focused on the Triassic/Jurassic boundary interval and its impact on the evolution of benthic foraminifera. Hillebrandt (2008), Hillebrandt et al. (2007), Hillebrandt and Urlichs (2008), Clémence et al. (2010), Clémence and Hillebrandt (2013), and Hillebrandt et al. (2013) investigated foraminifera in detail from the uppermost Rhaetian and lowermost Hettangian parts of the Kendlbach Formation (Tiefengraben Member).

The scope of our research is to document foraminiferal assemblages from the NCA, Austria in the upper Norian Pötschenkalk (Thälerergraben section), the middle–upper Rhaetian Zlambach Formation (Rossmoos–Stambachgraben composite section), the upper Rhaetian Eiberg Member of the Kössen Formation (Schlossgraben section), and the Tiefengraben Member of the Kendlbach Formation (Schlossgraben and Fonsjoch sections). Foraminifera were obtained from marly intervals, with the majority of the specimens parautochthonous to autochthonous, and not redeposited. In total, 72 species from 31 genera were determined. Some are described briefly and an abridged synonymy is given. Despite the questionable use of the morphogroup approach, the determined

genera were nevertheless assigned into morphogroups. The diversity, generic composition, and composition of the assemblages according to morphogroups were subsequently compared between formations and localities. Finally, trophic levels (oxygen and food availability) were estimated based on morphogroup associations and compared with the previous interpretations.

### Geological framework

The NCA are a WSW–ENE-striking fold and thrust belt some 500 km long and 20–50 km wide of the Austroalpine domain comprising sedimentary successions of the former western margin of the Tethys Ocean (Tollmann, 1976; Mandl, 2000; Schmid et al., 2008). The studied sections belong to different tectonic units and different palaeogeographic and palaeoenvironmental settings of the NCA (Linzer et al., 1995; Kuerschner et al., 2007; Gawlick & Missoni, 2013). The Rossmoosgraben and Stambachgraben sections are located some 4 km east of Bad Goisern and belong to the Dachstein Nappe (Fig. 1). The Thälerergraben section is located near Unken as part of the Hallstätter Nappe. These sections belong to the Hallstatt Zone (sensu Lein 1985, 1987) and represent deposits of Tethyan deeper shelf to basinal palaeoenviron-

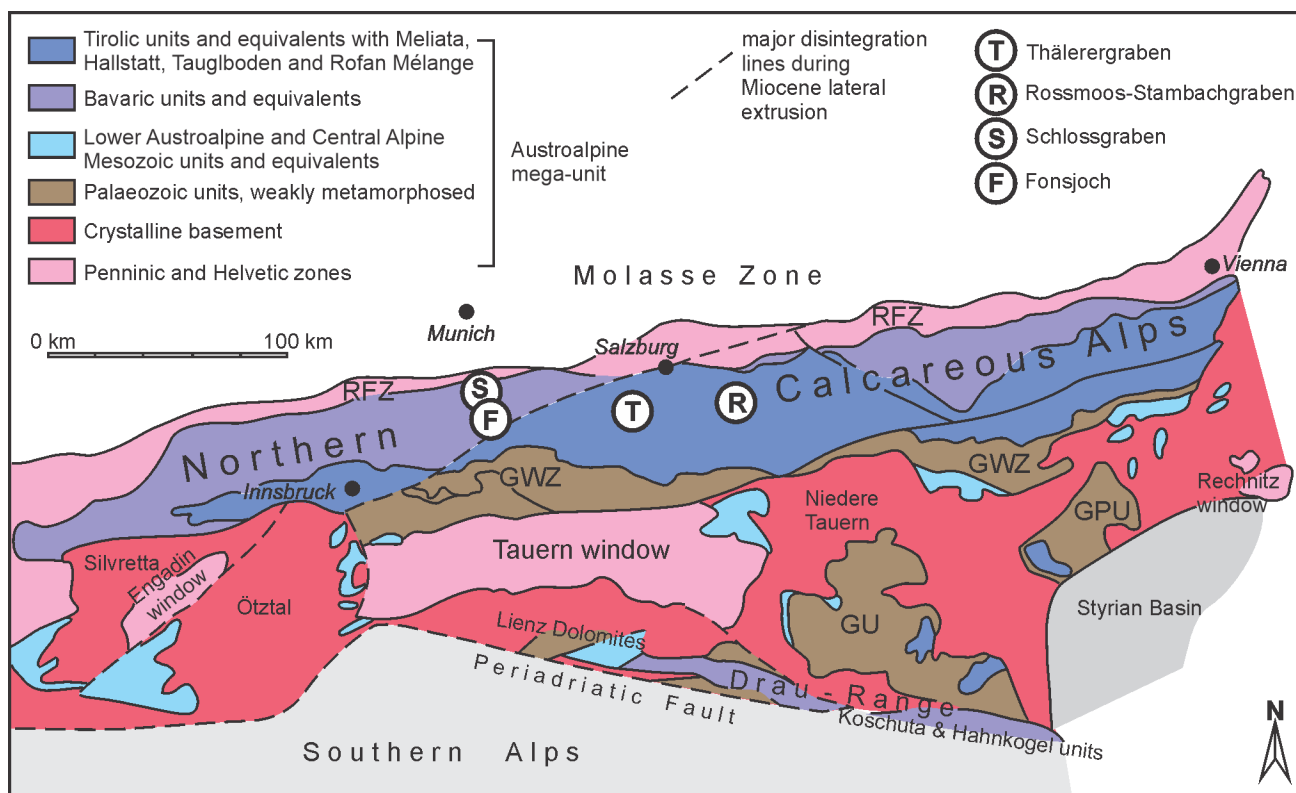


Fig. 1. Tectonic map of the Eastern Alps with locations of the studied sections. Modified after Tollmann (1977), Frisch & Gawlick (2003), Gawlick & Missoni (2013). GPU Graz Paleozoic unit, GU Gurktal unit, GWZ Greywacke Zone, RFZ Rhenodanubian Flysch Zone.

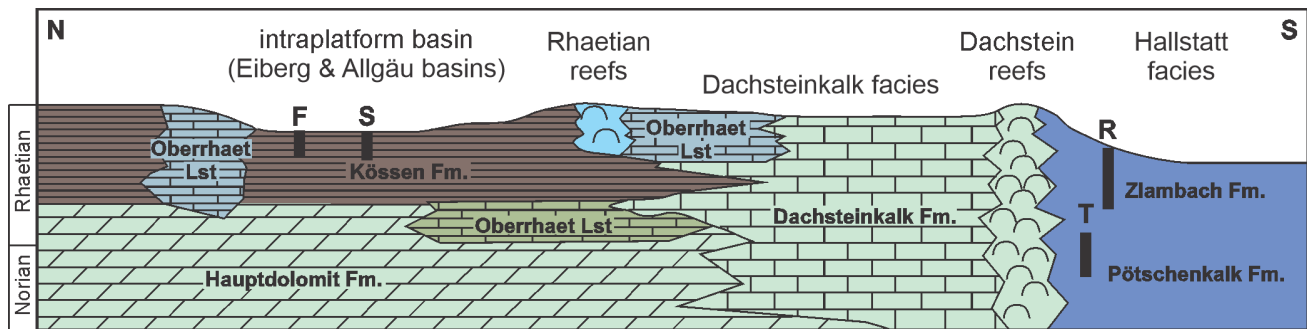


Fig. 2. Late Triassic facies of the Northern Calcareous Alps. Modified after Hüssner et al. (1996), Krystyn et al. (2005), Mette et al. (2012). An approximate stratigraphic range of the sections is indicated by black vertical bars: F- Fonsjoch, R- Rossmoos, S- Schlossgraben, T- Thälerergraben. The stratigraphic position of the Thälerergraben is somewhat uncertain (upper Norian or also lower Rhaetian – see text).

ments that were located near the Dachstein Carbonate Platform (Fig. 2). The Schlossgraben and Fonsjoch sections are located in the western NCA north and northwest of the Achensee as part of the Inntal Nappe. The uppermost Kössen Formation and the lower Kendlbach Formation exposed there were deposited in an intraplateform basinal setting (the ‘Eiberg Basin’, Krystyn et al., 2005; Mette et al., 2023) some tens of metres deep (Stanton & Flügel, 1997; Mette et al., 2023). The different palaeogeographic and palaeoenvironmental settings are expressed by the different taxonomic compositions of the microfossil assemblages, in particular with regard to the ostracod associations (e.g. Kristan-Tollmann, 1970, 1971, 1991; Mette et al., 2012, 2023).

The Thälerergraben section comprises a succession identified as the upper Pötschenkalk Formation (Kristan-Tollmann, 1969, Tollmann & Kristan-Tollmann, 1970). It consists of intercalated marly limestones and marls that do not include calciturbidites. The ostracod assemblages are different from the assemblages of the middle and upper Zlambach Formation. Although biostratigraphically indicative fossils have not yet been recorded, the Thälerergraben section was attributed to the upper Norian based on the ostracods (Kristan-Tollmann, 1969). The relatively extensive presence of marly beds suggests that this succession is stratigraphically transitional to the lowermost Zlambach Formation, which likely indicates latest Norian (?)– early Rhaetian age.

At the Rossmoosgraben and Stambachgraben sections the middle and upper Rhaetian part of the Zlambach Formation is exposed. Both sections have been combined into a composite section based on the correlation of lithostratigraphic and carbon isotope data (Mette et al., 2019). The intercalated marls and marly limestones yield ammonoids and bivalves and are very rich in ostracods, foraminifera,

and nannofossils. The lithostratigraphic pattern and trace element data indicate depositional cycles that are most distinctly developed in the lower and middle part of the Rossmoosgraben section (Mette et al., 2019). These cycles were probably affected by fluctuations in sea levels, which is also indicated by the presence of several calciturbiditic limestones beds (Mette et al., 2019). Analysis of the age, structure, and taxonomic composition of ostracod assemblages from the intercalated marls, however, has revealed that they were not strongly affected by redeposition and can thus be interpreted as parautochthonous to autochthonous (Mette et al., 2019).

The upper Rhaetian uppermost Kössen Formation exposed at the Schlossgraben and Fonsjoch sections is represented by medium- to thick-bedded limestones and intercalated marls with rich microfossil assemblages of ostracods and foraminifera, which suggest shallow subtidal carbonate platform (Fonsjoch section) and deep subtidal environments (Mette et al., 2023). The end-Triassic extinction event is characterized by a distinct fossiliferous marly bed (T-bed) with a bituminous shale at the top, indicating a short anoxic event (Hillebrandt & Kment 2009; Mette et al., 2023). The uppermost Rhaetian to lower Hettangian Kendlbach Formation is a succession of shales that are generally poor in macro- and microfossils, pointing to adverse environmental conditions except for the lowermost marly beds with abundant foraminifera (Hillebrandt & Kment 2009, Mette et al., 2023). It is currently considered that the Triassic/Jurassic boundary lies higher in the succession, and not in the sampled interval (Mette et al., 2023). Hillebrandt and Urlichs (2023) subdivided the Tiefengraben Member into the Schlossgraben Beds, an interval of reddish shales called the Schattwald Beds, and the Tiefengraben Member s. str.

## Materials and methods

### Sampled localities and data collection

Five stratigraphic sections were logged in the middle and western parts of the NCA: the upper Pötschenkalk Formation – Thälerergraben (47°36'40.73" N, 12°41'48.63" E), the Zlambach Formation – Rossmoosgraben (47°39'10.79" N, 13°38'48.59" E), Stambachgraben (47°39'01.01" N, 13°39'10.61" E), the Kössen Formation – Schlossgraben (47°28'31.70" N, 11°28'54.90" E), the Kössen Formation and the Kendlbach Formation – Fonsjoch (47°28'14.00" N, 11°39'20.50" E). Each section was sampled for microfossils at intervals of 10–40 cm, depending on the lithology. Thirty-six samples of marl were collected from the Rossmoosgraben and Stambachgraben sections. Eleven samples were taken from the Thälerergraben section, 19 samples from the Schlossgraben section, and 11 samples from the Fonsjoch section. Samples were processed and analysed for microfossils. Each sample was dried at 80 °C and treated with petroleum and 15 % hydrogen peroxide. The dissolved residue was washed using sieves of 1.0 mm, 0.3 mm, 0.1 mm, and 0.063 mm mesh-size. Foraminifera were handpicked from residues under a stereomicroscope using a fine brush and needle. Collecting was non-selective so that original proportions between taxa were maintained.

### Investigation of specimens

In order to make preliminary taxonomic determinations many specimens were first photographed in reflected light using a high-resolution digital optical microscope Keyence VHX-7000 available at the Geological Survey of Slovenia. For some of the better-preserved specimens of the order Lagenida investigation under reflected light also allowed for the observations of their internal structure. In some cases, immersing specimens in glycerine yielded better results. Back-scattered electron images of selected uncoated specimens were subsequently made using a JEOL JSM 6490LV SEM at 20 kV accelerating voltage, 10 mm working distance in a low vacuum. High magnifications allowed identification of coarsely agglutinated walls, whereas Energy-Dispersive X-ray Spectroscopy (EDS) with an Oxford INCA Penta FETx3 Si(Li) detector was used to distinguish between pure calcium carbonate walls and finely agglutinated walls made of quartz and/or silicates. Processing of mineral spectra was done using INCA Energy 350 software, with the acquisition times of 30–60 s.

## Biodiversity indices

The biodiversity of the foraminiferal assemblages was expressed as the number of genera and species in a sample (Taxa\_S) and with the Fisher alpha index (Fisher et al., 1943). The latter was computed with PAST software (ver. 4.03) (Hammer et al., 2001; Hammer & Harper, 2006). Undetermined species were also included in the calculation of diversity. The number of species in our samples is likely underestimated due to large similarities within the *Lenticulina*, *Astacolus*, '*Dentalina*' (*Prodentalina* and *Mesodentalina*), and *Nodosaria* genera (compare the number of species from these genera determined in this study and in the previous study by Kristan-Tollmann, 1964a, although some taxa might previously have been over-split – cf. Hillebrandt & Urlichs, 2008). Nevertheless the obtained values show true differences between the samples, as the same principles were applied to all samples.

### Foraminiferal morphogroup analysis

Agglutinated foraminifera were assigned to morphogroups according to Murray et al. (2011). Papers by Nagy et al. (1995), Reolid et al. (2008), Nagy et al. (2009), Nikitenko et al. (2013), and Setoyama et al. (2017) were also consulted. Morphogroups of calcareous taxa were determined according to Reolid et al. (2008, 2012), and Setoyama et al. (2017) (Fig. 3). We refrained from inferring life positions and feeding strategies from foraminiferal morphology due to the unreliability of the organizing principle and the many exceptions to the general rule (see Murray et al., 2011). Morphotypes that are present among calcareous as well as agglutinated foraminifera, are marked as distinct morphogroups, as is usual in such case studies (e.g. Tyska, 1994; Setoyama et al., 2017), even though the composition of the wall should not play a significant role in the morphogroup analysis.

## Results

In total, 72 foraminiferal species from 31 genera were determined within the scope of this study. Of these, 15 are left in open nomenclature due to the failure to find appropriate species in the literature. A condensed synonymy and abridged descriptions of determined species are given in Appendix 1. Selected specimens are illustrated in Figures 4–9. Note that specimens were photographed under reflected light (some also immersed in glycerin), as well as under a SEM, but that we chose to present only the most illustrative photos and specimens. Specimens that are not shown in reflected light

a)

| Mor. | Test form                                                                 | Genera                                                                              |                                                                                   |
|------|---------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|
| A    | Unilocular/multilocular tubular or branching                              | <i>Hyperammina</i> ,<br><i>Jaculella</i> ,<br><i>Bathysiphon</i>                    |  |
| B1   | Unilocular globular                                                       | <i>Annulina</i>                                                                     |  |
| B2   | Unilocular coiled, flattened                                              | <i>Ammodiscus</i><br><i>Glomospirella</i><br><i>Glomospira</i>                      |  |
| B3   | Multilocular, planispiral/ trochospiral globular or biconvex              | <i>Haplophragmoides</i> ,<br>„ <i>Endoteba</i> “                                    |  |
| B4   | Unilocular/multilocular irregular, conical, concavo-convex attached forms | <i>Tolypammina</i>                                                                  |  |
| C1   | Multilocular elongated, mixed growth                                      | <i>Reophax</i><br><i>Ammobaculites</i> ,<br><i>Gaudryina</i> ,<br><i>Textularia</i> |  |
| D    | Multilocular trochospiral                                                 | <i>Trochammina</i><br><i>Duotaxis</i><br>„ <i>Tetrataxis</i> “                      |  |

Fig. 3. Morphogroups of benthic foraminifera in Pötschen, Zlam-bach, Kössen and Kendlbach Formations from the Northern Cal-careous Alps. Different naming schemes are applied to agglutinated and calcareous taxa. Microhabitat and feeding strategies are not shown due to the substantial differences displayed among recent taxa belonging to the same morphogroup, and the lack of research in this area (see Murray et al., 2011).

b)

| Mor. | Test form                                                        | Genera                                                                                                                                                                                                                    |                                                                                     |
|------|------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| M1   | Plano-convex, meandering; initial phase coiled                   | <i>Planinivoluta</i>                                                                                                                                                                                                      |   |
| M2   | Discoidal flattened (planispiral), plano-convex trochospiral     | Duostominidae,<br>Oberhauserellidae,<br><i>Involutina</i>                                                                                                                                                                 |  |
| M3   | Discoidal flattened spiral, elongated                            | <i>Ophthalmidium</i> ,<br><i>Quinqueloculina</i>                                                                                                                                                                          |  |
| M4   | Multilocular elongated uniserial, some with initial coiled phase | <i>Nodosaria</i> ,<br><i>Prodentalina</i> ,<br><i>Mesodentalina</i> ,<br><i>Dentalinoides</i> ,<br><i>Paralingulina</i> ,<br><i>Pseudonodosaria</i> ,<br><i>Vaginulina</i> ,<br><i>Grillina</i> ,<br><i>Nodobacularia</i> |  |
| M5   | Elongated flattened                                              | <i>Astacolus</i> ,<br><i>Vaginulinopsis</i> ,<br><i>Ichthyolaria</i><br><i>Palmula</i> ,<br><i>Planularia</i>                                                                                                             |  |
| M6   | Elongated with straight periphery                                | <i>Eoguttulina</i>                                                                                                                                                                                                        |  |
| M7   | Biconvex (lenticular) planispiral                                | <i>Lenticulina</i>                                                                                                                                                                                                        |  |
| M8   | Conical, trochospiral, periphery broadly rounded                 | <i>Variostoma</i>                                                                                                                                                                                                         |  |

Fig. 4. Upper Triassic foraminifera from the Northern Calcareous Alps. **1:** *Jaculella* sp. A. Sample Th5, Thälerergraben. **2:** *Bathysiphon* cf. *salebrosus* (Kristan-Tollmann). Sample Th5, Thälerergraben. **3:** *Hyperammina* cf. *eulimbata* Kristan-Tollmann. Sample Th3, Thälerergraben. **4:** *Glomospira* *gordialis* (Jones & Parker). Sample RO75base2, Rossmoos. **5:** *Glomospira* sp. A. Sample RO75base2, Rossmoos. **6:** *Glomospira* *perplexa* Franke? Sample RO147, Rossmoos. **7:** *Ammodiscus* *incertus* (d'Orbigny). Sample Th4, Thälerergraben. **8:** *Ammodiscus* *infimus* (Strickland). Sample RO123base, Rossmoos. **9:** *Ammodiscus* *asper* (Terquem). Sample RO45, Rossmoos. **10:** *Glomospirella*? sp. A. Sample RO123base, Rossmoos. **11:** *Ammobaculites* *eumorphos* Kristan-Tollmann. Sample RO45, Rossmoos. **12:** *Ammobaculites* *zlambachensis* Kristan-Tollmann. Sample Fo15, Fonsjoch. **13:** *Reophax* cf. *rudis* Kristan-Tollmann. Sample Th14, Thälerergraben. **14:** *Ammobaculites* *rhaeticus* Kristan-Tollmann. Sample RO75base2, Rossmoos. **15:** *Ammobaculites* *rhaeticus* Kristan-Tollmann. Sample Th14, Thälerergraben. **16:** *Reophax* *densa* Tappan. Sample RO12.3, Rossmoos. **17:** *Ammobaculites* cf. *rhaeticus* Kristan-Tollmann. Sample RO75base2, Rossmoos.

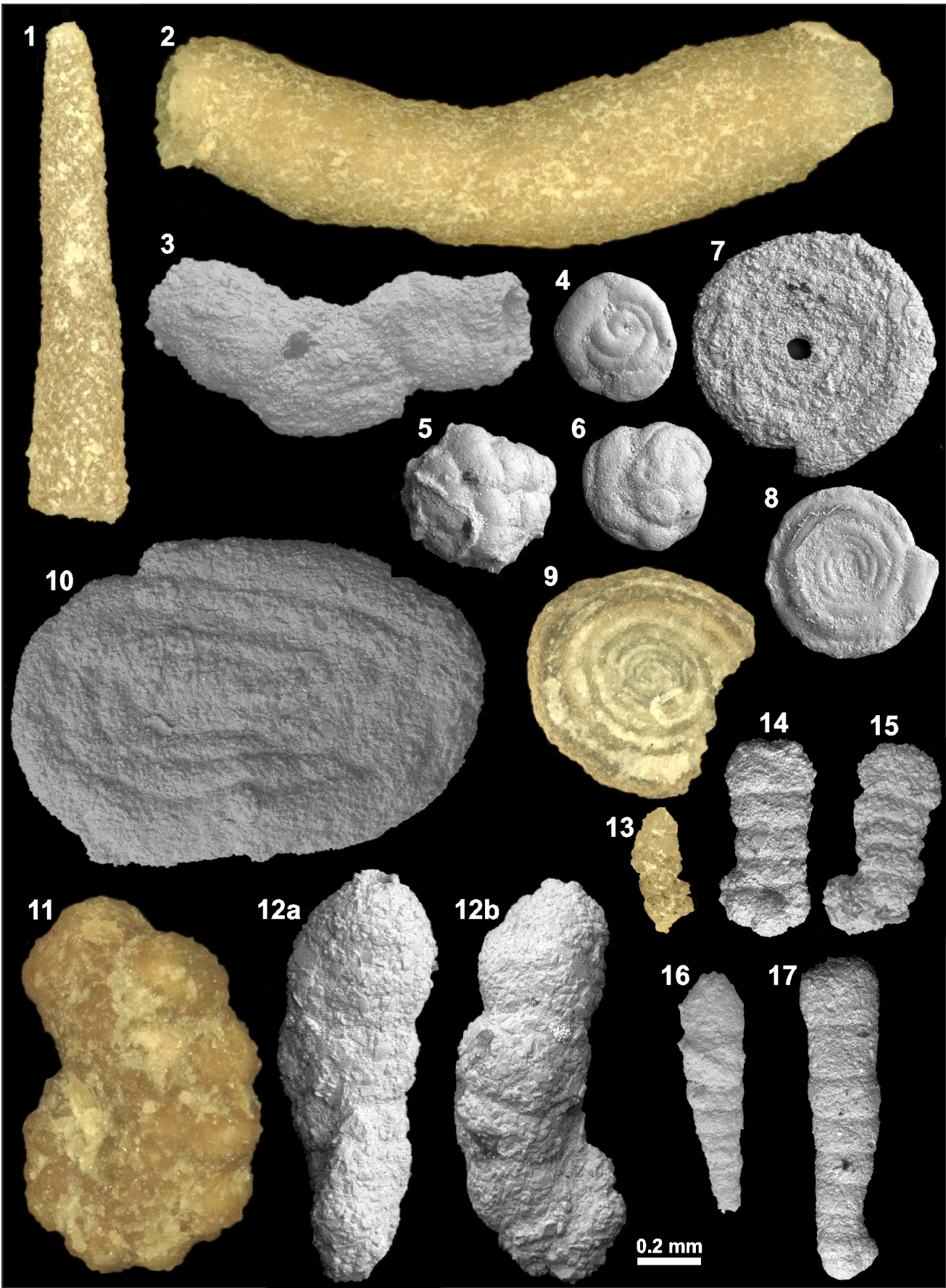


Fig. 4.

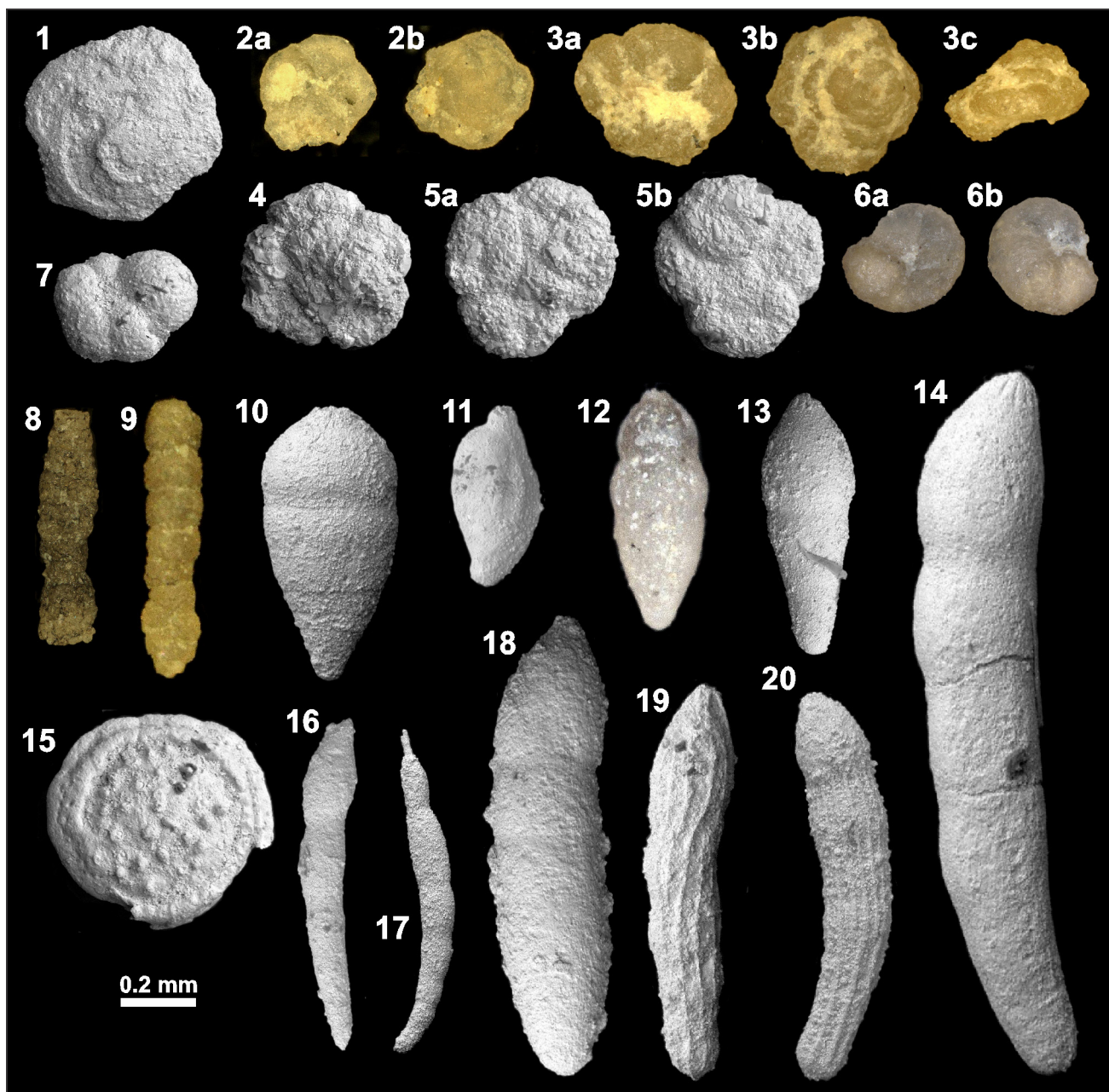


Fig. 5. Upper Triassic foraminifera from the Northern Calcareous Alps. **1:** *Tetrataxis humilis* Kristan. Sample RO69, Rossmoos. **2:** *Trochammina jaunensis* Brönnimann & Page. Sample RO12.3, Rossmoos. 2a- umbilical side. 2b- spiral side. **3:** *Trochammina alpina* Kristan-Tollmann complex. Slightly distorted specimen. Sample RO12.3, Rossmoos. 3a- umbilical side. 3b- spiral side. 3c- side view. **4:** *Trochammina alpina* Kristan-Tollmann complex. Compacted specimen. Sample RO12.3, Rossmoos. **5:** *Trochammina alpina* Kristan-Tollmann complex. Compacted specimen. Sample RW02, Rossmoos. 5a- spiral side. 5b- umbilical side. **6:** *Haplophragmoides?* sp. A. Sample RW01, Rossmoos. **7:** *Endothyra kuepperi* Oberhauser, umbilical side. Sample RO75base2, Rossmoos. **8:** Undetermined fragment of a textulariid with pyri-form/flask-like chambers. **9:** *Gaudryinella elegantissima* Kristan-Tollmann. Sample RO109, Rossmoos. **10:** *Pseudonodosaria obconica* (Reuss). Sample Th12, Thälerergraben. **11:** *Karaburunia atsabensis* Haig & McCartain. Sample RO262, Rossmoos. **12:** *Pseudonodosaria major pleiothalamia* (Kristan-Tollmann). Sample SC23, Schlossgraben. **13:** *Pseudonodosaria* sp. A. Sample Th2, Thälerergraben. **14:** *Prodentalina bicornis* (Terquem)? Sample RO45, Rossmoos. **15:** *Involutina liassica* (Jones in Brodie) complex. Sample RO45, Rossmoos. **16:** *Prodentalina paucicurvata* (Franke). Sample RO115, Rossmoos. **17:** *Prodentalina* sp. A. Sample Th4, Thälerergraben. **18:** *Prodentalina bicornis* (Terquem)? Sample RO08top, Rossmoos. **19:** *Mesodentalina tenuistriata* (Terquem). Sample RO115, Rossmoos. **20:** *Mesodentalina* sp. A. Sample Th4, Thälerergraben.

Fig. 6. Upper Triassic foraminifera from the Northern Calcareous Alps. **1:** *Nodosaria vermicularis* (Terquem). Sample TGL19r, Thälerergraben. **2:** *Nodosaria zlabachensis* Kristan-Tollmann. Sample RO177mid, Rossmoos. **3:** *Nodosaria liratella* Tappan. Sample RO2, Rossmoos. **4:** *Nodosaria zlabachensis* Kristan-Tollmann. Sample Fo15, Fonsjoch. **5:** *Nodosaria shublikensis* Tappan. Sample Sch2b, Schlossgraben. **6:** *Nodosaria levifracta* Kristan-Tollmann. Sample TGL19r, Thälerergraben. **7:** *Pseudonodosaria plurimicostata* (Kristan-Tollmann). Sample RO173, Rossmoos. **8:** *Nodosaria nitidana* Brand. Sample Th4, Thälerergraben. **9:** *Pseudonodosaria oveyi* (Barnard). Sample Th12-2, Thälerergraben. **10:** *Pseudonodosaria plurimicostata* (Kristan-Tollmann). Sample Th11, Thälerergraben. **11:** *Nodosaria cf. setulosa* Tappan. Sample Th12, Thälerergraben. **12:** *Paralingulina longiscata* (Terquem). Sample Fo7, Fonsjoch. **13:** *Pseudonodosaria simpsonensis* (Tappan)? Sample RO115, Rossmoos. **14:** *Nodosaria pupiformis* (Terquem). Sample Fo7, Fonsjoch. **15:** *Nodosaria* sp. A. Sample Sc5, Schlossgraben. **16:** *Pseudonodosaria ploechingeri* (Oberhauser). Sample TGL19r, Thälerergraben. **17:** *Ichthyolaria* sp. Sample RO12.3, Rossmoos. **18:** *Nodosaria* sp. B. Sample Ro45, Rossmoos. **19:** *Nodosaria* sp. C. Sample Th3, Thälerergraben. **20:** *Ichthyolaria terquemi squamosa* (Terquem & Berthelin). Sample SC2, Schlossgraben. **21:** *Ichthyolaria terquemi squamosa* (Terquem & Berthelin). Sample RO123base, Rossmoos. **22:** *Ichthyolaria terquemi squamosa* (Terquem & Berthelin). Sample Fo15, Fonsjoch. **23:** *Nodobacularia? vujisici* Urošević & Gaždžicki. Sample RO12.3, Rossmoos. **24:** *Ichthyolaria xiphoidea* (Kristan-Tollmann). Sample Th11, Thälerergraben. **25:** *Ichthyolaria xiphoidea* (Kristan-Tollmann). Sample Th1, Thälerergraben.

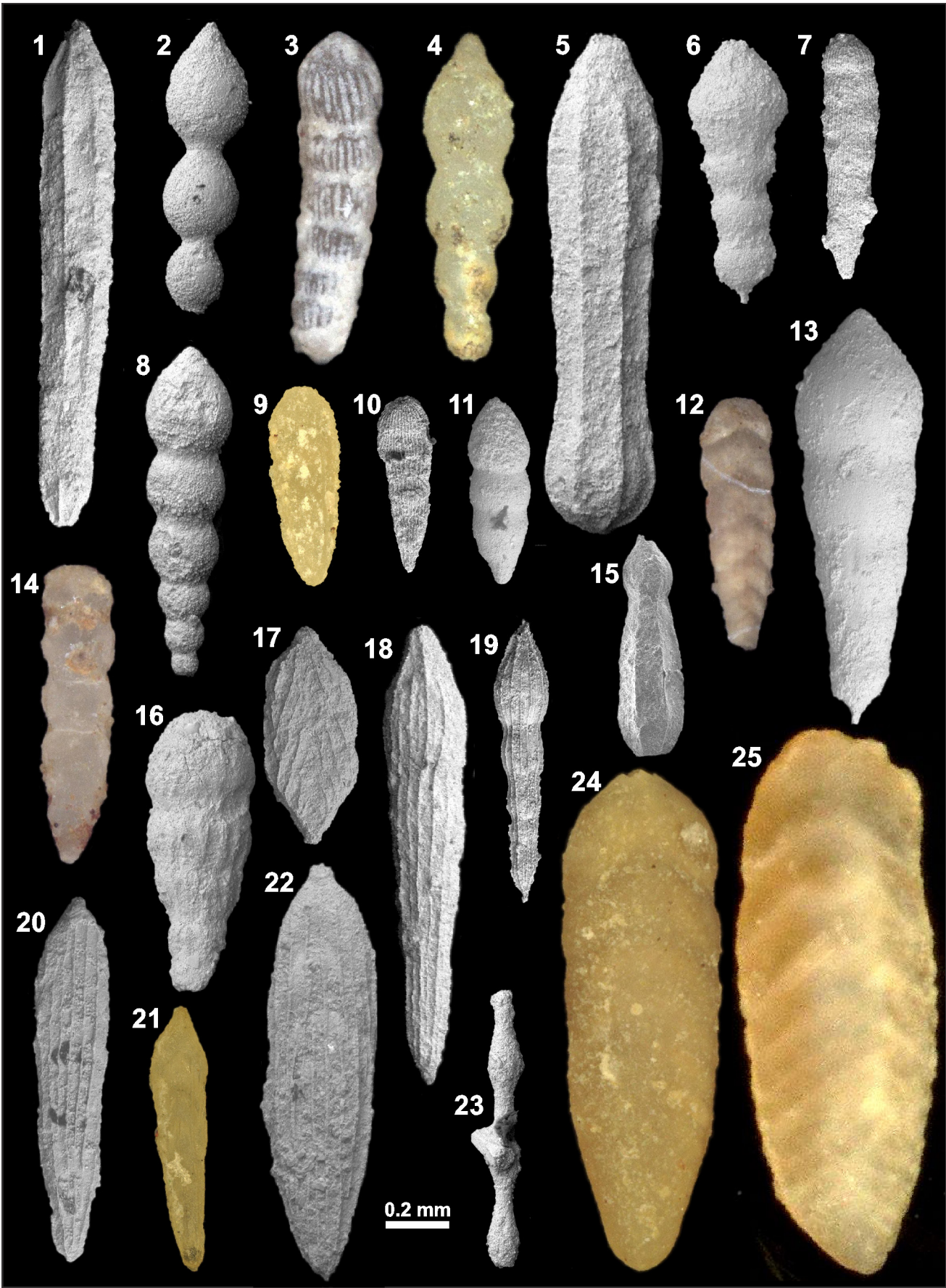


Fig. 6.

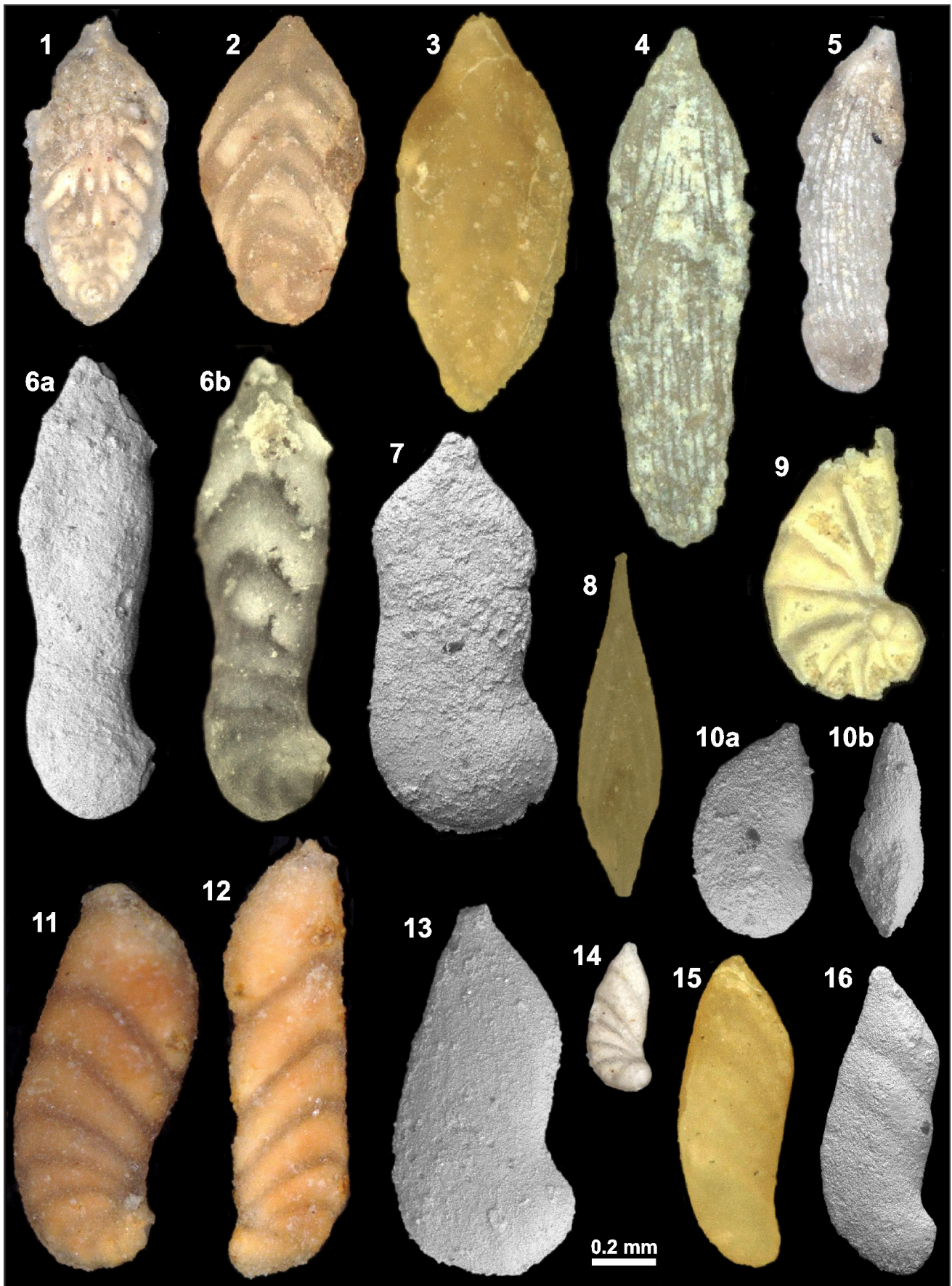


Fig. 7.

Fig. 7. Upper Triassic foraminifera from the Northern Calcareous Alps. **1:** *Ichthyolaria rhaetica* (Kristan-Tollmann). Sample SCH 1, Schlossgraben. **2:** *Palmula arignota* (Kristan-Tollmann). Sample Sc-2, Schlossgraben. **3:** *Ichthyolaria rhaetica* (Kristan-Tollmann). Sample Th11, Thälerergraben. **4:** *Palmula* sp. A. Sample Sc-2, Schlossgraben. **5:** *Palmula* sp. A. Sample Sc-2, Schlossgraben. **6:** *Palmula* sp. B. Sample RO 45, Rossmoos. 6a- SEM image. 6b- Image taken in reflected light. **7:** *Palmula* sp. C. Sample Th1, Thälerergraben. **8:** *Ichthyolaria phyllodea* (Kristan-Tollmann). Sample RO 109, Rossmoos. **9:** *Lenticulina nautiloides* (Bornemann). Sample F07, Fonsjoch. **10:** *Lenticulina nautiloides* (Bornemann). Sample TGL19r, Thälerergraben. 10a. Equatorial view. 10b. Axial view. **11:** *Vaginulinopsis acrolus* Tappan. Sample Sc-23.5, Schlossgraben. **12:** *Astacolus* sp. A. Sample Sc-23.5, Schlossgraben. **13:** *Astacolus arietis* (Terquem). Sample Th1, Thälerergraben. **14:** *Astacolus pediacus* Tappan?. Sample Sc-24, Schlossgraben. **15:** *Astacolus pediacus* Tappan?. Sample RO 45, Rossmoos. **16:** *Vaginulinopsis cryptospira* (Paalzow). Sample RO-2-12, Rossmoos.

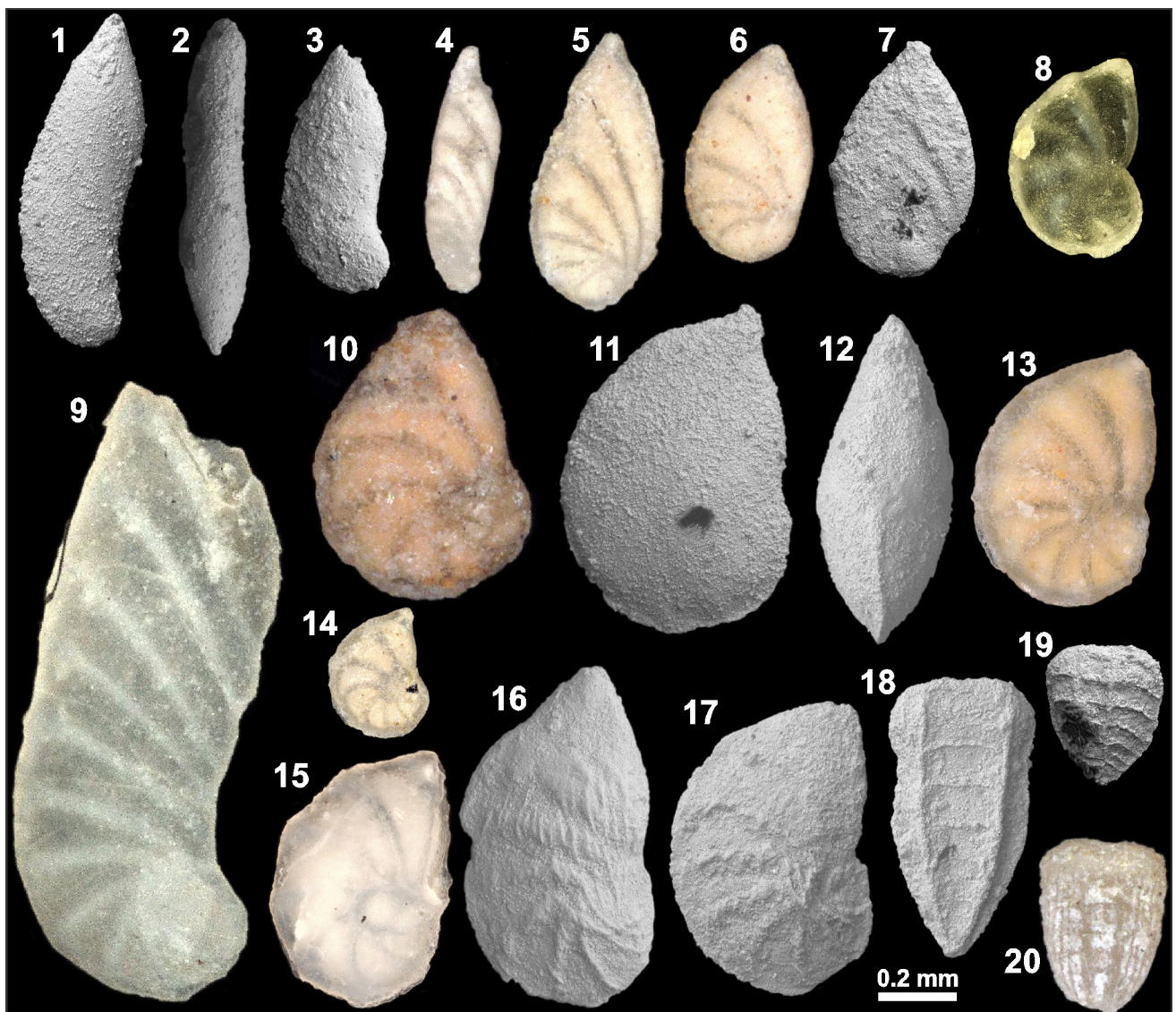


Fig. 8. Upper Triassic foraminifera from the Northern Calcareous Alps. **1–2:** *Astacolus pediacus* Tappan?. Sample Th4, Thälerergraben. 1- equatorial view; 2- axial view. **3:** *Astacolus pediacus* Tappan?. Sample Sc-24, Schlossgraben. **4:** *Astacolus cf. pediacus* Tappan. Sample Sch3b', Schlossgraben. **5:** *Astacolus cf. pediacus* Tappan. Sample Sc-24, Schlossgraben. **6:** *Lenticulina varians* (Bornemann) plexus. Sample Sc-24, Schlossgraben. **7:** *Lenticulina varians* (Bornemann) plexus. Sample Sc-24, Schlossgraben. **8:** *Lenticulina* sp. Sample RO 45, Rossmoos. **9:** *Planularia cf. protracta* (Bornemann). Sample Th1, Thälerergraben. **10:** *Lenticulina gottlingensis* (Bornemann). Sample Th1, Thälerergraben. **11:** *Lenticulina gottlingensis* (Bornemann). Sample F08, Fonsjoch. **12:** *Lenticulina gottlingensis* (Bornemann). Sample F08, Fonsjoch. **13:** *Lenticulina gottlingensis* (Bornemann). Sample Sc-24y, Schlossgraben. **14:** *Lenticulina cf. gottlingensis* (Bornemann). Sample Sc-24, Schlossgraben. **15:** *Lenticulina gottlingensis* (Bornemann). Slightly damaged specimen. Sample Th15, Thälerergraben. **16:** *Lenticulina stenocostata* Kristan-Tollmann?. Sample Sc-5, Schlossgraben. **17:** *Lenticulina stenocostata* Kristan-Tollmann?. Sample Sc-5, Schlossgraben. **18:** *Paralingulina grilli* (Kristan-Tollmann). Sample RO2-7, Rossmoos. **19:** *Lingulina lingua* Kristan-Tollmann. Sample RO115, Rossmoos. **20:** *Lingulina lingua* Kristan-Tollmann. Sample Sc-24, Schlossgraben.

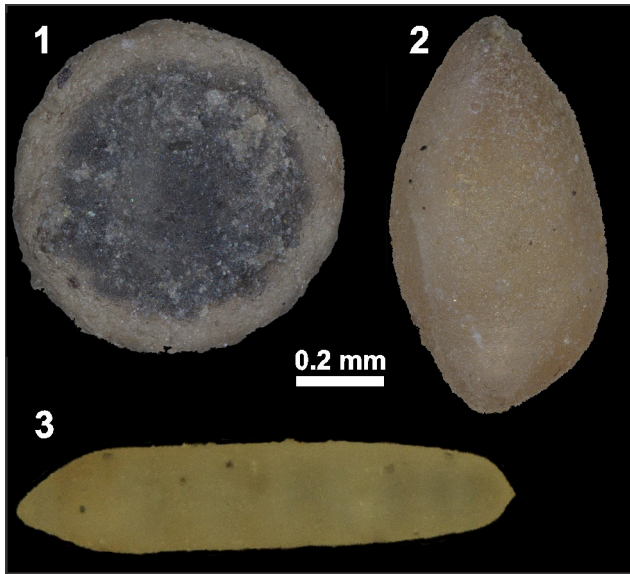


Fig. 9. Upper Triassic foraminifera from the Northern Calcareous Alps. **1:** *Annulina metensis* Terquem. Sample RO2-12, Rossmoos. **2:** *Eoguttulina kuhni* (Franke). Sample RO2-12, Rossmoos. **3:** *Dentalinoides?* sp. A. Sample RO 45, Rossmoos.

are additionally illustrated in Appendix 2 in the online version of the paper. The occurrence of species within formations and localities are given in Table 1. Some specimens were determined only to the genus level, mostly due to a lack of preserved species-diagnostic features. The EDS investigation of the walls of the specimens shows that, apart from possible recrystallization and/or neomorphic changes of aragonite, the chemistry of the wall was not changed during diagenesis. Calcareous, as well as agglutinated tests are preserved, so no bias was likely introduced. The assemblages were collected from marl layers and represent parautochthonous or autochthonous fauna (Mette et al., 2019). Some of the specimens (e.g. *Reophax*, *Trochammina*) show deformation as the result of the compaction of the sediment. Table 2 summarizes important information concerning the composition of the assemblages from each section and formation. Some intervals are inadequately covered, and samples

Table 1. List of taxa from the investigated Upper Triassic formations from the Northern Calcareous Alps.

| Formation (Section)                      | List of foraminiferal taxa                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Zlambach Formation<br>(Rossmoos section) | <i>Annulina metensis</i><br><i>Hyperammina cf. eulimbata</i><br><i>Ammodiscus incertus</i><br><i>Ammodiscus infimus</i><br><i>Ammodiscus asper</i><br><i>Glomospira gordialis</i><br><i>Glomospira</i> sp. A<br><i>Glomospira perplexa?</i><br><i>Glomospirella?</i> sp. A<br><i>Reophax densa</i><br><i>Ammobaculites eumorphos</i><br><i>Ammobaculites rhaeticus</i><br><i>Ammobaculites cf. rhaeticus</i><br><i>Haplophragmoides?</i> sp. A<br><i>Trochammina jaunensis</i><br><i>Trochammina alpina</i> complex<br><i>'Tetrataxis' humilis</i><br><i>Endothyra kuepperi</i><br><i>Karaburunia atsabensis</i><br><i>Nodobacularia?</i> <i>vujisici</i><br><i>Involutina liassica</i> complex<br><i>Pseudonodosaria plurimicostata</i><br><i>Pseudonodosaria obconica</i><br><i>Pseudonodosaria major pleiothalama</i><br><i>Pseudonodosaria simpsonensis</i><br><i>Pseudonodosaria</i> sp. A<br><i>Nodosaria vermicularis</i> | <i>Nodosaria liratella</i><br><i>Nodosaria zlambachensis</i><br><i>Nodosaria levifracta</i><br><i>Nodosaria shublikensis</i><br><i>Nodosaria nitidana</i><br><i>Nodosaria</i> sp. B<br><i>Nodosaria?</i> sp. C<br><i>Dentalinoides?</i> sp.<br><i>Ichthyolaria xiphoidea</i><br><i>Ichthyolaria phyllodea</i><br><i>Ichthyolaria rhaetica</i><br><i>Ichthyolaria terquemi squamosa</i><br><i>Paralingulina grilli</i><br><i>Mesodentalina tenuistriata</i><br><i>Prodentalina paucicurvata</i><br><i>Prodentalina bicornis?</i><br><i>Prodentalina</i> sp. A<br><i>Eoguttulina kuhni</i><br><i>Palmula</i> sp. B<br><i>Astacolus pediacus</i><br><i>Astacolus</i> sp. A<br><i>Vaginulinopsis cryptospira</i><br><i>Lenticulina nautiloides</i><br><i>Lenticulina gottingensis</i><br><i>Lenticulina stet.</i><br><i>Lingulina lingua</i> |

|                                                |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
|------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Zlambach Formation<br>(Thälerergraben section) | <i>Annulina metensis</i><br><i>Bathysiphon</i> cf. <i>salebrosus</i><br><i>Hyperammina</i> cf. <i>eulimbata</i><br><i>Jaculella</i> sp. A<br><i>Ammodiscus incertus</i><br><i>Ammodiscus infimus</i><br><i>Ammodiscus asper</i><br><i>Glomospira perplexa</i> ?<br><i>Glomospirella</i> ? sp. A<br><i>Reophax</i> cf. <i>rudis</i><br><i>Ammobaculites rhaeticus</i><br><i>Ammobaculites</i> cf. <i>rhaeticus</i><br><i>Haplophragmoides</i> ? sp. A<br><i>Trochammina</i> sp.<br><i>'Tetrataxis' humilis</i><br><i>Gaudryinella elegantissima</i><br><i>Karaburunia atsabensis</i><br>Duostominidae<br><i>Pseudonodosaria oveyi</i><br><i>Pseudonodosaria plurimicostata</i><br><i>Pseudonodosaria obconica</i><br><i>Pseudonodosaria major pleiothalama</i> | <i>Pseudonodosaria ploechingeri</i><br><i>Pseudonodosaria</i> sp. A<br><i>Nodosaria vermicularis</i><br><i>Nodosaria zlambachensis</i><br><i>Nodosaria levifracta</i><br><i>Nodosaria nitidana</i><br><i>Nodosaria</i> sp. B<br><i>Nodosaria</i> sp. C<br><i>Nodosaria</i> cf. <i>setulosa</i><br><i>Ichthyolaria xiphoidea</i><br><i>Ichthyolaria rhaetica</i><br><i>Mesodentalina</i> sp. A<br><i>Prodentalina paucicurvata</i><br>? <i>Prodentalina bicornis</i><br><i>Prodentalina</i> sp. A<br><i>Palmula</i> sp. C<br><i>Astaculus pediacus</i><br><i>Astaculus</i> sp. A<br><i>Astaculus arietis</i><br><i>Lenticulina nautiloides</i><br><i>Lenticulina gottingensis</i><br><i>Planularia</i> cf. <i>protracta</i> |
| Kössen Formation<br>(Schlossgraben section)    | <i>Jaculella</i> sp. A<br><i>Reophax densa</i><br><i>Variostoma coniforme</i><br><i>Pseudonodosaria plurimicostata</i><br><i>Pseudonodosaria</i> sp.<br><i>Pseudonodosaria major pleiothalama</i><br><i>Pseudonodosaria</i> sp. A<br><i>Nodosaria vermicularis</i><br><i>Nodosaria levifracta</i><br><i>Nodosaria shublikensis</i><br><i>Nodosaria</i> sp. A<br><i>Nodosaria</i> sp. B<br><i>Ichthyolaria xiphoidea</i><br><i>Ichthyolaria phylloidea</i><br><i>Ichthyolaria rhaetica</i><br><i>Ichthyolaria terquemi squamosa</i>                                                                                                                                                                                                                            | <i>Prodentalina paucicurvata</i><br>? <i>Prodentalina bicornis</i><br><i>Eoguttulina kuhni</i><br><i>Palmula arignota</i><br><i>Palmula</i> sp. A<br><i>Astaculus pediacus</i><br><i>Astaculus</i> cf. <i>pediacus</i><br><i>Astaculus</i> sp. A<br><i>Vaginulinopsis acrolus</i><br><i>Lenticulina nautiloides</i><br><i>Lenticulina varians plexus</i><br><i>Lenticulina gottingensis</i><br><i>Lenticulina</i> cf. <i>gottingensis</i><br><i>Lenticulina stenocostata</i><br><i>Lingulina lingua</i>                                                                                                                                                                                                                    |
| Kössen Formation<br>(Fonsjoch section)         | <i>Trochammina alpina complex</i><br>? <i>Trochammina jaunensis</i><br><i>Endoteba</i> sp.<br><i>Paralingulina longiscata</i><br><i>Nodosaria pupiformis</i><br><i>Nodosaria</i> sp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          | <i>Pseudonodosaria</i> sp.<br><i>Ichthyolaria terquemi squamosa</i><br><i>Astaculus arietis</i><br><i>Lenticulina gottingensis</i><br><i>Lenticulina nautiloides</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Kendlbach Formation<br>(Schlossgraben section) | <i>Trochammina</i> sp.<br><i>Pseudonodosaria</i> sp.<br><i>Astaculus</i> cf. <i>pediacus</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  | <i>Lenticulina varians plexus</i><br><i>Lenticulina nautiloides</i><br>Nodosariidae                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Kendlbach Formation<br>(Fonsjoch section)      | <i>Glomospira</i> sp.<br>? <i>Reophax</i> sp.<br><i>Trochammina alpina complex</i><br>? <i>Trochammina</i> sp.<br><i>Ammobaculites zlambachensis</i><br><i>Endothyroidea</i><br><i>Pseudonodosaria plurimicostata</i><br><i>Pseudonodosaria</i> sp.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           | <i>Nodosaria levifracta</i><br><i>Ichthyolaria terquemi squamosa</i><br><i>Prodentalina paucicurvata</i><br><i>Astaculus pediacus</i><br><i>Astaculus</i> sp. A<br><i>Lenticulina nautiloides</i><br><i>Lenticulina gottingensis</i><br><i>Lenticulina</i> sp.                                                                                                                                                                                                                                                                                                                                                                                                                                                             |

Table 2. Main characteristics of foraminiferal assemblages from the Rossmoos/Stambachgraben (Zlambach Formation), Thälerergraben (Pötschenkalk Formation – lowermost Zlambach Formation), Schlossgraben (Kössen Formation, Kendlbach Formation), and Fonsjoch (Kendlbach Formation) sections.

|                                                       | <b>Rossmoos/<br/>Stambachgraben:<br/>Zlambach Fm.</b>      | <b>Thälerergraben:<br/>Pötschenkalk Fm.</b>                                          | <b>Schlossgraben:<br/>Kössen Fm.</b>                           | <b>Fonsjoch: Kössen Fm.</b>                                   | <b>Schlossgraben:<br/>Kendlbach Fm.</b>                                             | <b>Fonsjoch: Kendlbach<br/>Fm.</b>                                                                  |
|-------------------------------------------------------|------------------------------------------------------------|--------------------------------------------------------------------------------------|----------------------------------------------------------------|---------------------------------------------------------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------|
| No. of samples                                        | 36                                                         | 11                                                                                   | 15                                                             | 2                                                             | 4                                                                                   | 9                                                                                                   |
| Main genera                                           | <i>Reophax</i> , ' <i>Dentalina</i> ',<br><i>Annullina</i> | ' <i>Dentalina</i> ', <i>Ammodiscus</i> ,<br><i>Nodosaria</i> , <i>Glomospirella</i> | <i>Ichthyolaria</i> , <i>Lenticulina</i> ,<br><i>Nodosaria</i> | <i>Lenticulina</i> , <i>Astacolus</i> ,<br><i>Trochammina</i> | <i>Astacolus</i> , <i>Lenticulina</i> ,<br><i>Trochammina</i> ,<br><i>Nodosaria</i> | <i>Astacolus</i> , <i>Trochammina</i> ,<br><i>Ammodiscus</i> , <i>Reophax</i><br><i>Lenticulina</i> |
| Dominant morphogroups                                 | M4 (32%), C1 (26%), B2<br>(13%), B1 (10%)                  | M4 (41%), B2 (33%), M5<br>(9.6%)                                                     | M5 (39.7%), M4 (29.2%),<br>M7 (28.9%)                          | M5 (37.1%), M7 (34.7%), D<br>(23.9%)                          | M5 (43.5%), D (25%), M7<br>(14.1%), M4 (6.5%)                                       | M5 (31.5%), C1 (25.8%), D<br>(10.3%)                                                                |
| Other morphogroups<br>present (≤5%)                   | M5 (5%), M2 (5%), M7<br>(4.6%), M6, D, B4, B3, A           | M7 (4.4%), B1, B4, C1, M1,<br>A, D, B3, M2, M3                                       | M8, M6, D, C1, A                                               | M4, B3                                                        |                                                                                     | M4, B2, B3                                                                                          |
| Average % of epifauna                                 | 18.7                                                       | 40.2                                                                                 | 0.6                                                            | 24.6                                                          | 25                                                                                  | 16.3                                                                                                |
| Average % of infauna                                  | 79.9                                                       | 59.6                                                                                 | 97.9                                                           | 75.4                                                          | 75                                                                                  | 71.4                                                                                                |
| No. specimens per<br>sample                           |                                                            |                                                                                      |                                                                |                                                               |                                                                                     |                                                                                                     |
| Min.                                                  | 2                                                          | 9                                                                                    | 1                                                              | 3                                                             | 1                                                                                   | 1                                                                                                   |
| Max.                                                  | 295                                                        | 120                                                                                  | 219                                                            | 164                                                           | 115                                                                                 | 122                                                                                                 |
| Average                                               | 73.2                                                       | 54.7                                                                                 | 43.7                                                           | (83.5)                                                        | 37.5                                                                                | 32.2                                                                                                |
| No. species<br>per sample                             |                                                            |                                                                                      |                                                                |                                                               |                                                                                     |                                                                                                     |
| Min.                                                  | 2                                                          | 4                                                                                    | 1                                                              | 3                                                             | 1                                                                                   | 1                                                                                                   |
| Max.                                                  | 39                                                         | 25                                                                                   | 19                                                             | 14                                                            | 3                                                                                   | 8                                                                                                   |
| Average                                               | 12.14                                                      | 14                                                                                   | 8.2                                                            | 8.5                                                           | 1.5                                                                                 | 3.44                                                                                                |
| No. genera<br>per sample                              |                                                            |                                                                                      |                                                                |                                                               |                                                                                     |                                                                                                     |
| Min.                                                  | 2                                                          | 4                                                                                    | 1                                                              | 3                                                             | 1                                                                                   | 1                                                                                                   |
| Max.                                                  | 18                                                         | 14                                                                                   | 9                                                              | 7                                                             | 2                                                                                   | 6                                                                                                   |
| Average                                               | 8.64                                                       | 9.45                                                                                 | 4.8                                                            | 5                                                             | 1.25                                                                                | 2.89                                                                                                |
| Fisher<br>alpha per<br>sample                         |                                                            |                                                                                      |                                                                |                                                               |                                                                                     |                                                                                                     |
| Min.                                                  | 0                                                          | 2.7                                                                                  | 0                                                              | 0                                                             | 0                                                                                   | 0                                                                                                   |
| Max.                                                  | 15.54                                                      | 9.89                                                                                 | 6.59                                                           | 3.65                                                          | 0.56                                                                                | 4.32                                                                                                |
| Average                                               | 5.67                                                       | 6.6                                                                                  | 3.78                                                           | 1.83                                                          | 0.29                                                                                | 1.32                                                                                                |
| Average % of agglutinates                             | 50.7                                                       | 42.3                                                                                 | 0.3                                                            | 24.6                                                          | 25                                                                                  | 42.1                                                                                                |
| Average % of porcelaneous                             | 0.1                                                        | 2.1                                                                                  | 0                                                              | 0                                                             | 0                                                                                   | 0                                                                                                   |
| Average % of hyaline                                  | 49.2                                                       | 51.3                                                                                 | 99.7                                                           | 75.4                                                          | 75                                                                                  | 57.9                                                                                                |
| Average % of uniserial<br>lagenids                    | 26.1                                                       | 36.8                                                                                 | 26.1                                                           | 3.1                                                           | 6.5                                                                                 | 3.5                                                                                                 |
| Average % of <i>Lenticulina</i><br>+ <i>Astacolus</i> | 8.8                                                        | 11                                                                                   | 34.8                                                           | 68.7                                                          | 68.5                                                                                | 40.8                                                                                                |

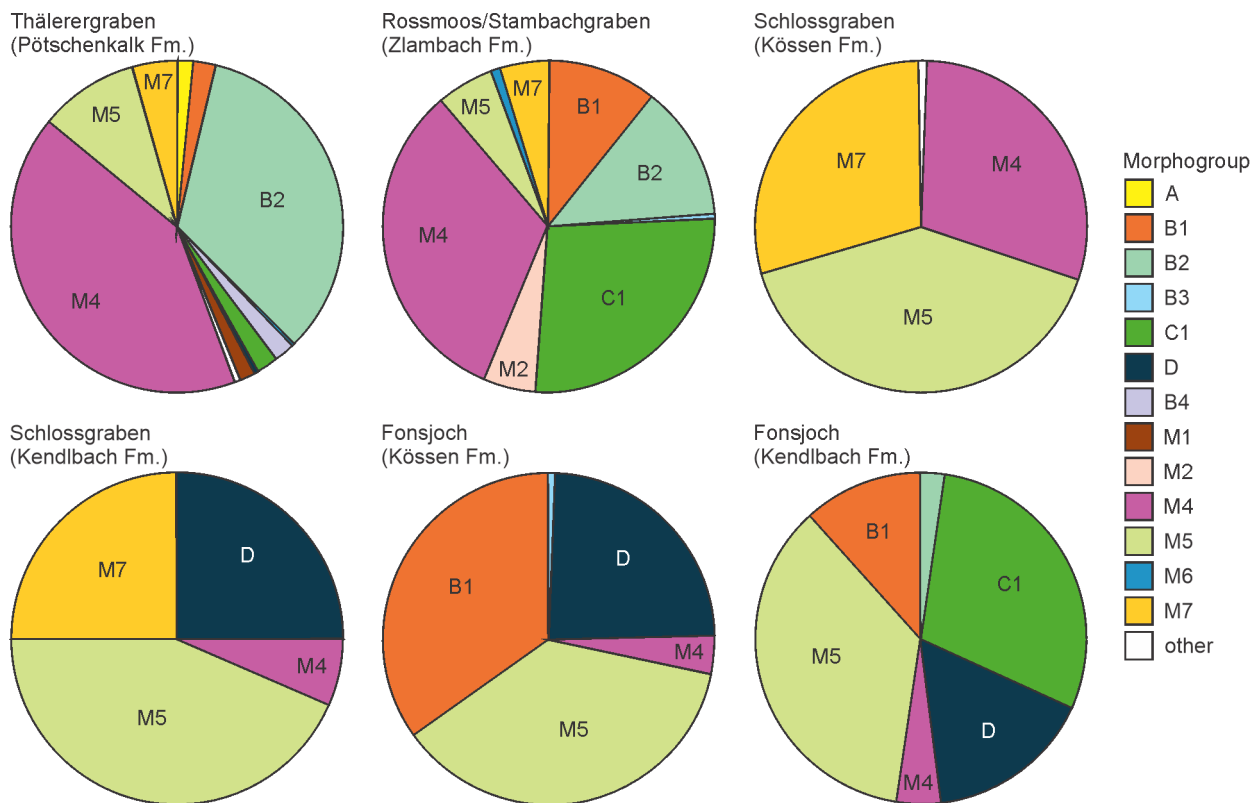


Fig. 10. Foraminiferal morphogroups in the studied sections of the Pötschenkalk, Zlambach, Kössen and Kendlbach Formations.

were not of the same weight. The average number of specimens and species must thus be treated with considerable caution. Figure 10 shows morphogroup composition per formation and section.

Foraminiferal assemblages from the Pötschenkalk Formation at the Thälerergraben section (Fig. 11) are relatively rich in species (14 on average) and genera (9.45 on average). The ratio between agglutinated specimens and specimens belonging to Lagenida is 42.3 % against 51.3 %. The most common genera are *Dentalina* (27 % of the specimens) and *Ammodiscus* (23 % of the specimens), followed by *Nodosaria* (9.9 % of the specimens) and *Glomospirella* (8.2 % of the specimens). Subordinate are *Astacolus* (6.6 % of the specimens), *Lenticulina* (4.4 % of the specimens), *Pseudonodosaria* (4.4 % of the specimens), *Ichthyolaria* (3 % of the specimens), *Glomospira* (2.6 % of the specimens), *Annulina* (2.1 % of the specimens), and *Tolypammina* (2 % of the specimens). Other genera represent less than 2 % of all specimens. Elongated uniserial forms dominate (M4, 41 % of the specimens), followed by flattened unilocular coiled forms (B2, 33 % of the specimens), and elongated flattened tests (M5, 9.6 % of the specimens).

Foraminiferal assemblages from the Zlambach Formation at the Rossmoos section (middle to upper Rhaetian; Fig. 12) are similarly abundant and diverse (on average 12.14 species per sample, and 8.64 genera per sample). Agglutinated taxa on average represent 50.7 % of the specimens, and Lagenida 49.2 %. The most common foraminifera are *Reophax* (on average 21 % of the specimens), *Dentalina* (on average 22 % of the specimens), and *Annulina* (10 % of the specimens). Subordinate are *Glomospira* (6.7 % of the specimens), *Ammobaculites* (5.1 % of the specimens), *Involutina* (4.9 % of the specimens), *Lenticulina* and *Ammodiscus* (4.6 % of the specimens each), *Astacolus* (4.2 % of the specimens), *Nodosaria* (3.9 % of the specimens), and *Pseudonodosaria* (3.4 % of the specimens). Less than 2 % of the specimens belong to other genera. Proportions between species vary, but no clear trend was observed along the section. The most common morphogroups are elongated uniserial forms with or without early coiled phase (M4 and C1, together 58 % of the specimens), followed by flattened unilocular coiled tests (B2; 13 % of the specimens), and uniserial globular tests (B1; 10 % of the specimens).

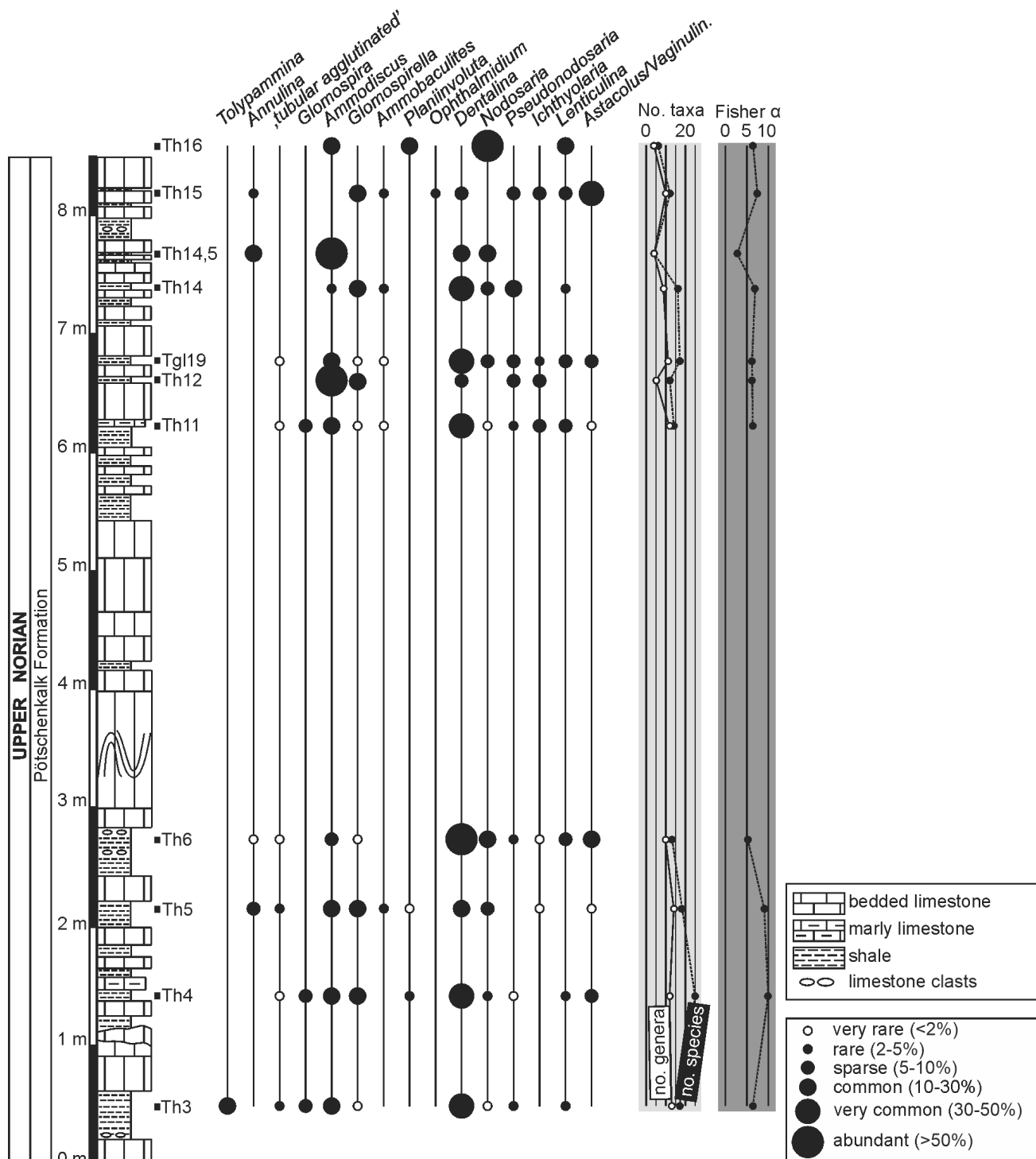


Fig. 11. Distribution of foraminiferal genera within the uppermost Pötschenkalk at the Thälerergraben section. Note that taxa that represent less than 2 % in all samples are not included. Only samples that contained foraminifera are shown. The diversity index was calculated from the number of species (some also left undetermined), whereas only determined genera are shown in the figure.

From the Kössen Formation at the Schlossgraben section (Fig. 13) a total of 32 taxa were determined. The average number of species per sample is 8.2, and the average number of genera per sample is 4.8. The assemblage is dominated by hyaline taxa (99.7 % of the specimens). The most common genera are *Ichthyolaria* (32.1 % of the speci-

mens), *Lenticulina* (28.9 % of the specimens), and *Nodosaria* (19.5 % of the specimens). Elongated flattened tests dominate (M5, 39.7 % of the specimens), followed by multilocular elongate uniserial tests (M4, 29.2 % of the specimens), and lenticular planispiral forms (M7, 28.9 % of the specimens).

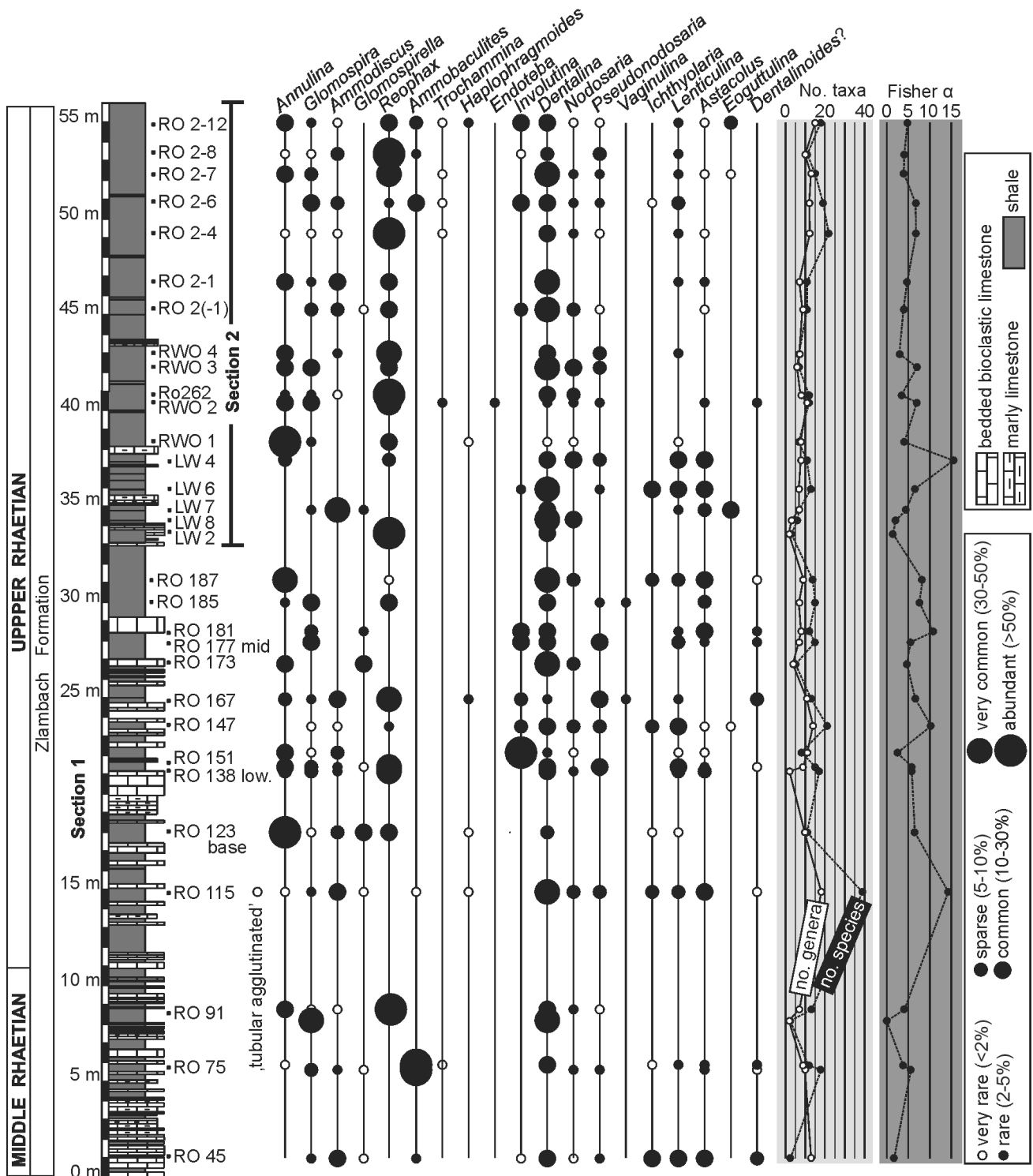


Fig. 12. Distribution of foraminiferal genera within the Zlambach Formation at the combined Rossmoos/Stambachgraben section. Note that taxa that represent less than 2 % of all samples are not included. Only samples that contained foraminifera are shown. The diversity index was calculated from the number of species (some also left undetermined), whereas only determined genera are shown in the figure.

Only two samples of the uppermost Kössen Formation were taken at the Fonsjoch section (Fig. 14). Their generic composition is almost the same. However, it is clear from these two samples that the number of species in the assemblage (on average 8.5) correlates with the number of collected specimens. *Lenticulina* (34.7 % of the speci-

mens), *Astaculus* (34.0 % of the specimens), and *Trochammina* (23.9 % of the specimens) dominate. The main morphogroups are calcareous elongated flattened (M5), planispiral lenticular (M7), and agglutinated trochospiral (D).

Following the uppermost Triassic extinction event, which was marked by the deposition of bi-



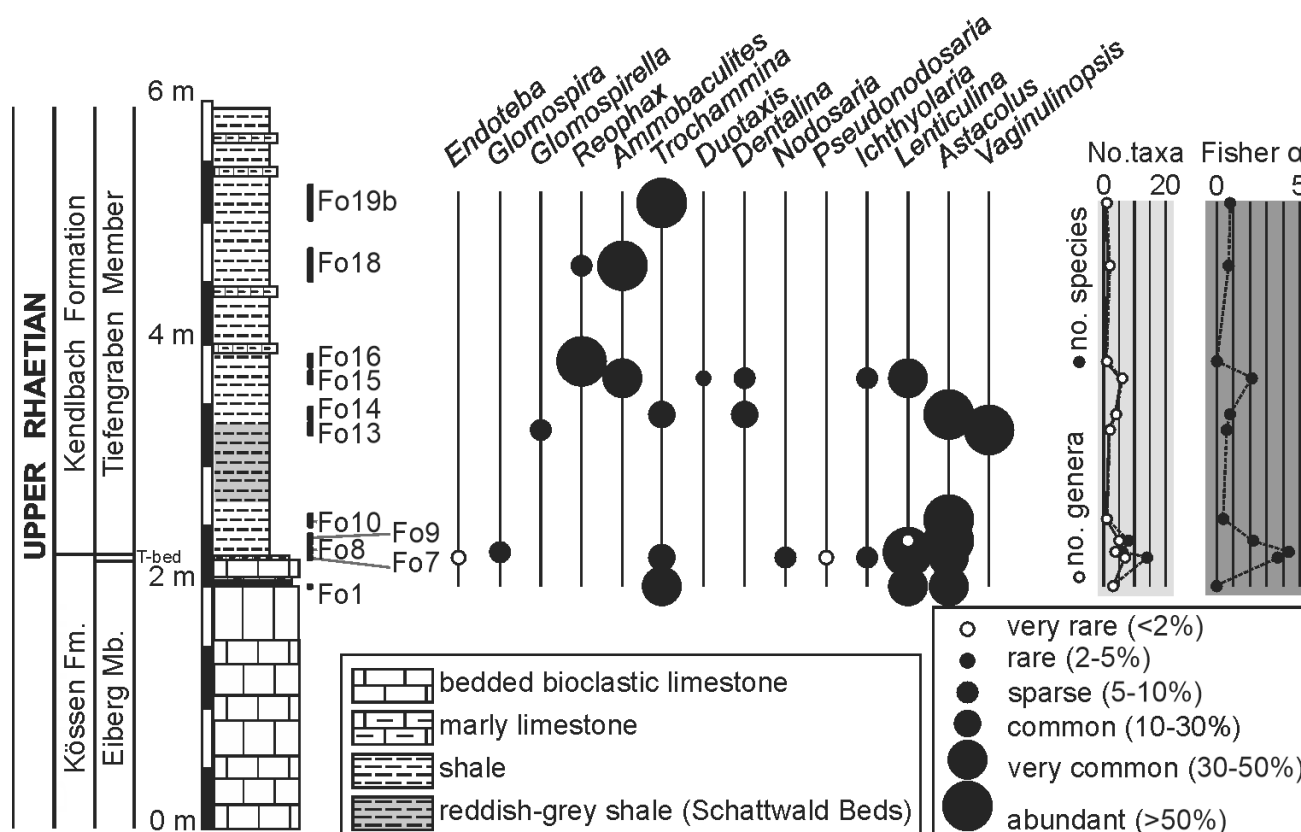


Fig. 14. Distribution of foraminiferal genera within the uppermost Kössen Formation and Kendlbach Formation at the Fonsjoch section. Note that taxa that represent less than 2 % of all samples are not included. Only samples that contained foraminifera are shown. The diversity index was calculated from the number of species (some also left undetermined), whereas only determined genera are shown in the figure.

In samples from the Kendlbach Formation at the Fonsjoch section (Fig. 14), the number of species in a single assemblage varies between 1 and 8 (average 3.44), and the number of genera between 1 and 6 (on average 2.89). *Astacolus* (30.5 % of the specimens) is the dominant genus, followed by *Trochammina* (13.8 % of the specimens), *Ammobaculites* (13.7 % of the specimens), *Reophax* (12.1 % of the specimens), and *Lenticulina* (10.3 % of the specimens). Agglutinated taxa represent 42.1 % of the specimens, and hyaline taxa 57.9 % of the specimens. The proportion of uniserial lagenids, however, is low (3.5 % of the specimens). Notable is the larger proportion of morphogroup C1 in higher samples. In other samples, the same morphogroups dominate as in the Schlossgraben section (except for morphogroup M4, which plays a minor role in these samples).

## Discussion

### Foraminifera from the Pötschenkalk and Zlambach Formation

Although Kristan-Tollmann (1969) and Tollmann and Kristan-Tollmann (1970) described ostracods from the upper Norian Pötschenkalk

at the Thälerergraben section, foraminifera from this locality were not yet mentioned. On the other hand, foraminifera of the Rossmoos-/Stambachgraben section were previously described by Weiland (1991) and Mette et al. (2019). Due to the dominance of lagenids and agglutinated taxa, the foraminiferal fauna of both localities (Figs. 10–12) corresponds to the 'Fischerwiese-type' fauna (also Kristan-Tollmann, 1964a). The taxonomic composition of the assemblages is very similar. The most notable difference between them is the presence of *Involutina* (first occurrence at ~18 m), the presence of *Eoguttulina*, and an abundance of *Reophax* (incl. *Scherochorella* sensu Haig & McCartain, 2010) in the Rossmoosgraben/Stambachgraben section (Fig. 12). Rare tubular agglutinated foraminifera (*Hyperammina*, *Bathysiphon*, *Jaculella*) are present in both sections. In the modern assemblages, such forms are more typical of continental slopes and basin plains (Murray et al., 2011), and are only rarely reported from shallower settings (Tyszka, 1994). Their presence correlates with the basin-ward position of the Hallstat zone (Mandl, 2000). The relatively high diversity of foraminiferal fauna suggests oxygenated conditions (Murray, 2006; Setoyama et al., 2017). Most of the speci-

mens are probably autochthonous in position, as suggested by the absence of taxa characteristic of the platform-top, such as aulotortids and milioliporids (Hohenegger & Lobitzer, 1971; Schäfer & Senowbari-Daryan, 1978; Wurm, 1982; Chablais et al., 2011; Gale, 2012).

The main morphogroups in the two sections are multilocular elongated uniserial calcareous and agglutinated tests (M4, C1), unilocular coiled flattened tests (B2), elongated and flattened (M5), and unilocular globular tests (B1) (Fig. 10). Morphogroup B comprises proven or interpreted surface-dwelling (shallow epifaunal to epifaunal) species (Jones & Charnock, 1985; Murray et al., 2011). *Ammodiscus* and *Glomospira* are today most commonly present in deeper marine environments (Jones & Charnock, 1985). In the modern seas of NW Europe, groups B1 and B2 are present from the upper bathyal to the abyssal zone (Murray et al., 2011). Morphogroup C largely consists of sediment-dwelling species, yet also includes some epifaunal species. Morphogroup C1 is distributed from the inner shelf to the abyssal but is dominant in the NE European margin from the inner shelf to the upper bathyal (Murray et al., 2011).

Literature data on the distribution of calcareous taxa is lacking. However, morphogroup M4 can be considered the equivalent of morphogroup C1. Morphogroup M5 does not have a true equivalent among morphogroups of agglutinated taxa. These foraminifera are interpreted as epifauna or shallow infauna (Fig. 3).

Despite the nearly identical association of morphogroups, the two sections differ in their proportions of presumed epifauna and infauna. According to the TROX model (Jorissen et al., 1995; Van der Zwaan et al., 1999), similar proportions of both epifauna and infauna at the Thälerergraben section suggests meso- to oligotrophic conditions. In contrast, the predominance of infaunal forms at the Rossmoos-/Stambachgraben section and the high proportion of *Reophax*, which is considered deep infauna (Setoyama et al., 2017), suggest more meso- to eutrophic conditions. *Eoguttulina*, which is only occasionally present in samples at the Rossmoos-/Stambachgraben section, is an opportunist and may proliferate under oxygen-restricted conditions (Rita et al., 2016). The high number of deposit-feeding Bairdioidea in ostracod assemblages at the Rossmoos-/Stambachgraben section, however, indicates that oxygen deficiency occurred only occasionally (Mette et al., 2019, 2023).

In contrast to the 'Fischerwiese-type' fauna, the 'Plackles-type' assemblages commonly con-

tain trochospiral and planispiral involutinids, and less numerous Lagenida (Tollmann & Kristan-Tollmann, 1970). Within the typical 'Plackles-type' assemblages from the Zlambach marls at Krautgartenalm, Tollmann and Kristan-Tollmann (1970) also recorded *Galeanella*, *Cornuspira*, Dufrenoyiidae and a larger variety of Ophthalmitidae, which indicates proximity to the platform. These taxa are either missing or very rare at the Thälerergraben and Rossmoos-/Stambachgraben sections. Besides these differences, however, the 'Plackles-type' fauna at Krautgartenalm contains many of the same species as the 'Fischerwiese-type' fauna at Thälerergraben and Rossmoos-/Stambachgraben.

### Foraminifera from the Kössen Formation

The Kössen Formation was relatively well sampled at the Schlossgraben section (Fig. 13), while only two samples were taken from its uppermost part at the Fonsjoch section (Fig. 14). Foraminifera from the Schlossgraben section were previously investigated by Clémence et al. (2010), and Mette et al. (2023). The studied interval already falls into the interval of end-Triassic changes in global conditions and regional changes in the depositional environment. From the T-Bed, *Lenticulina* and *Astacolus* were identified as the most abundant, followed by *Nodosaria*, *Ichtyolaria*, *Paralingulina*, and *Trochammina* (Clémence et al., 2010). Based on diverse and common Nodosariidae, well-oxygenated normal marine mesotrophic conditions of outer shelf to open-sea environments were suggested (Clémence et al., 2010). Even though no significant influence of the end-Triassic sea-level drop was evident, Mette et al. (2023) observed successive decreases in diversity, followed by the disappearance of ostracod taxa within the T-Bed, which was likely the result of a drop in O<sub>2</sub> levels.

The Fonsjoch section (Fig. 14) was previously researched by Mette et al. (2023). According to the latter authors, deposition took place in a somewhat shallower setting between the storm wave base and the fair-weather wave base. Similar to the Schlossgraben section, diverse and abundant assemblages of *Astacolus*, *Lenticulina*, *Marginulinopsis*, *Trochammina*, *Ichtyolaria*, and *Dentalina* were noted from the T-Bed (Mette et al., 2023).

Our results confirm a high number of *Lenticulina* specimens in the Schlossgraben section (Fig. 13). However, compared to the results of Clémence et al. (2010), a somewhat lower share of *Astacolus* was determined; and no *Paralingulina* were identified. We need to point out that our study differs

from previous research in terms of the scale of the study; that is, Clémence et al. (2010) sampled only two beds of the uppermost T-Bed, but at a much finer scale. In our study, similar assemblages to that from the T-Bed were also recovered from samples lying approximately 1 m and 3 m lower in the Eiberg Member, which suggests that the depositional environment and conditions did not drastically change towards the top of the Kössen Formation (that is, at the level of this study). The exception might be the somewhat higher proportion of *Lenticulina* in the T-Bed (abundant, as opposed to being very common below the T-Bed). Previous studies of the Fonsjoch section can also be confirmed. Here, the proportions of Nodosariidae are lower than at Schlossgraben, but are nonetheless present. *Astacolus* and *Trochammina* are more common than they are at Schlossgraben (Fig. 14).

An increase of highly mobile opportunist *Lenticulina* within the infaunal microhabitat could suggest variations in oxygen levels during the deposition of the T-Bed (Tyszka, 1994; Reolid et al., 2008, 2012, 2013, 2014; Rita et al., 2016; Giraldo-Gómez et al., 2022) and thus confirms the previous interpretation by Mette et al. (2023). According to Reolid et al. (2013), flat compressed tests, such as those of *Ichthyolaria* or *Astacolus*, are also suitable for oxygen-poor conditions, as the high surface-to-volume ratio allows for easier exchange of gases. *Trochammina* is also considered an opportunist that tolerates fluctuations in salinity (not expected in the sampled sections due to their deposition at few tens of metres depth) and hypoxic conditions (Nagy et al., 2010; Nikitenko et al., 2013). Trochamminids are epiphytal, but also infaunal down to 60 cm in the sediment (Murray et al., 2011). The dominant morphogroups in both sections (Fig. 10) are interpreted as epifauna (D), shallow infauna (M4, M5), and epifauna to deep infauna (M7, *Lenticulina*) (Tyszka, 1994; Reolid et al., 2008; Nikitenko et al., 2013), confirming previous interpretations of mesotrophic conditions.

Stratigraphic distribution of foraminifera within the upper Kössen Formation was also studied at the Kuhjoch (Hillebrandt et al., 2007; Hillebrandt & Urlichs, 2008), Eiberg, and Tiefengraben sections (Clémence et al., 2010) representing other parts of the Eiberg Basin, as well as at the Wolfsschlucht section which belongs to the separate intraplatform Allgäu Basin (Hillebrandt & Urlichs, 2023). The Tiefengraben sections represent a succession deposited closer to the platform margin, so the Eiberg Member is more limestone-dominant at the top. *Pseudonodosaria*, *Dentalina* (*Prodentalina*), and *Eoguttulina* were determined from the

marl interval approximately 11–12 m below the contact with the Kendelbach Formation (Clémence et al., 2010). Due to the presence of diverse and abundant Nodosariidae, Clémence et al. (2010) interpreted mesotrophic conditions and high levels of dissolved oxygen; it should be pointed out, however, that *Eoguttulina* proliferated under low-oxygen conditions (Rita et al., 2016). The Eiberg Member at the Eiberg section also deposited in a more distal setting. From this section, Clémence et al. (2010) observed a shift from assemblages dominated either by *Lenticulina*, Nodosariidae, and *Ichthyolaria*, or by *Eoguttulina*, to assemblages dominated by agglutinated *Ammobaculites* and *Ammomarginulina*. This change from calcareous to agglutinates-dominated assemblages coincides with high  $\delta^{18}\text{O}$  values and was interpreted as the consequence of a short-term cooling event and/or change in seawater chemistry. The Eiberg section ends with a new shift to *Trocholina*-dominated assemblages, which probably reflects a relative drop in sea level (Clémence et al., 2010). In the Kuhjoch section, marls 2.5 and 1 m below the Kendelbach Formation contain *Trochammina*, *Ammodiscus*, and polymorphinids, whereas the T-Bed contains Nodosariidae and a few Textulariina (Hillebrandt et al., 2007; Hillebrandt & Urlichs, 2008).

The Kössen Formation in the Allgäu Basin deposited in an occasionally restricted marine, shallow neritic environment. Hiatuses are more frequent, especially at the top of the formation. From the Wolfsschlucht section of the Allgäu Basin, only moulds of a planispiral foraminifera (*Cornuspira*, *Ammodiscus* or *Glomospirella*?; see fig. 9 in Hillebrandt & Urlichs, 2023), small nodosariids, and *Eoguttulina* were found in the uppermost Kössen Formation (Hillebrandt & Urlichs, 2023).

### Foraminifera from the Kendlbach Formation

According to Clémence et al. (2010), the deposition of the lowermost Kendelbach Formation coincides with the maximal environmental perturbations. Foraminifera from the Kendlbach Formation within the Eiberg Basin were previously investigated by Hillebrandt (2008), Hillebrandt et al. (2007), Hillebrandt and Urlichs (2008), Hillebrandt and Kment (2009), Clémence et al. (2010), Clémence and Hillebrandt (2013), Hillebrandt et al. (2013), and Mette et al. (2023). The Kendlbach Formation in the Allgäu Basin was researched for foraminifera by Hillebrandt and Urlichs (2023).

Marls underlying the Schattwald Beds were named the Schlossgraben Beds by Hillebrandt and Urlichs (2023). From the Eiberg Basin, the greatest abundance of *Trochammina* was recorded at

Schlossgraben, Tiefengraben, and Kendelbachgraben (Hillebrandt & Kment, 2009; Clémence et al., 2010) and interpreted as a consequence of stressful conditions, temporarily lower pH, and in proximal settings also brackish conditions. Hillebrandt and Kment (2009), and Mette et al. (2023) determined abundant lagenid foraminifera from the Schlossgraben section, dominated by *Astacolus*, *Dentalina*, *Nodosaria*, and *Pseudonodosaria*. From the Fonsjoch section, Mette et al. (2023) recorded low diversity assemblages of *Marginulinopsis*, *Lenticulina*, *Astacolus*, and *Ichthyolaria*. *Trochammina*, *Nodosariidae* and/or *Marginulinopsis* are present below the Schattwald Beds in the Kuhjoch section (Hillebrandt & Urlichs, 2008). In the Allgäu Basin, the Schlossgraben Beds contain *Trochammina* (in Hillebrandt & Urlichs, 2008 misidentified as *Oberhauserellidae* – see Hillebrandt & Urlichs, 2023, p. 100), *Eoguttulina*, some *Nodosariidae*, and rare *Ammodiscus* (Hillebrandt & Urlichs, 2023). Our study confirms the seemingly contrasting results of previous investigations for the Schlossgraben section (Fig. 13). The lowermost part of the Schlossgraben Beds contain a relatively more diverse assemblage of *Nodosariidae*, *Ichthyolariidae*, *Astacolus* and *Lenticulina*, but a little higher up assemblages are completely dominated by *Trochammina*, *Lenticulina*, or *Astacolus* (Fig. 13). This indicates that high oxygen levels characterised the deposition of the lowermost Schlossgraben Beds; later, however, conditions became more stressful. The same can be said of the Fonsjoch section (Fig. 14), even though the greatest abundance of *Trochammina* was not recorded there.

The following Schattwald Beds in the Eiberg Basin are dominated by *Hippocrepina*, accompanied by *Trochammina* and *Marginulinopsis* (Hillebrandt et al., 2007; Hillebrandt & Urlichs, 2008), while in the Allgäu Basin, the Schattwald Beds are barren of foraminifera (Hillebrandt & Urlichs, 2023). The dominance of *Hippocrepina* was interpreted as a sign of unfavourable environmental conditions (Hillebrandt & Urlichs, 2008). In our study, only one sample was taken from the top of the Schattwald Beds (sample Fo13 in Fig. 14), which was dominated by *Vaginulinopsis*, with a minor presence of *Glomospirella*. The latter is assigned to morphogroup B2 and represents epifauna (Nikitenko et al., 2013), while *Vaginulinopsis* represents shallow infaunal morphogroup M5 (Ansari et al., 2021). This indicates availability of oxygen also within the upper part of the sea floor, and mesotrophic to oligotrophic conditions (Jorissen et al., 1995; Van der Zwaan et al., 1999).

A foraminiferal assemblage consisting of rare agglutinated *Ammobaculites* and *Ammomarginulina*, as well as *Pseudonodosaria* was determined from marls overlying the Schattwald Beds (the Tiefengraben Member s.str.) at the Tiefengraben section in the Eiberg Basin, followed upwards by more diverse *Nodosariidae* (Hillebrandt & Urlichs, 2008; Clémence et al., 2010). This was interpreted as a gradual re-establishment of more open marine conditions in the lowermost Hettangian (Clémence et al., 2010). At the Fonsjoch, assemblages above the Schattwald Beds comprise relatively diverse *Nodosarioidea*, associated with *Ammobaculites* and *Trochammina*, which is also suggestive of a return to more oxygenated conditions (Mette et al., 2023). *Oberhauserellidae* first occur in this interval (Hillebrandt et al., 2007; Hillebrandt & Urlichs, 2008). According to Hart et al. (2003) and Clémence and Hillebrandt (2013), however, oberhauserellids tolerated low-oxygen conditions, which suggests fluctuating rather than stable oxygen levels.

According to our study, the marls immediately overlying the Schattwald Beds at Fonsjoch contain *Trochammina*, *Dentalina*, and *Astacolus*, and then *Ammobaculites*, some *Duotaxis*, *Dentalina*, *Ichthyolaria*, and *Lenticulina* (Fig. 14). Epifaunal, shallow infaunal, and deep infaunal morphogroups are represented, which is evidence of mesotrophic conditions on the sea floor (Jorissen et al., 1995; Van der Zwaan et al., 1999). Approximately 1 m above the Schattwald Beds, a peak in *Reophax* was recorded. *Reophax*, like *Lenticulina*, could shift its position within the sediment according to oxygen levels. Thus, its dominance could indicate fluctuations in redox boundary (Reolid et al., 2012). In and above this sample, the diversity and the abundance of foraminifera are again very low, with one sample containing *Ammobaculites*, and one *Trochammina* and *Eoguttulina*. We cannot exclude the diagenetic removal of calcareous tests from the assemblages, or the fact that the diversity is biased due to the low number of specimens recovered; however, both *Trochammina* and *Eoguttulina* are stress-tolerant species (Clémence et al., 2010; Reolid et al., 2012), and while the first is agglutinated, the latter has calcareous test, so it would seem that the composition of the assemblage is determined by stressful conditions rather than diagenesis. At the Adratsbach section from the Allgäu Basin, Hillebrandt, and Urlichs (2023) recorded assemblages with *Trochammina* and *Eoguttulina*, followed by *Ammobaculites* and *Trochammina*. At the Wolfsschlucht the Tiefengraben Beds first contain small *Nodosarioidea*, *Eoguttulina*, and *Oberhaus-*

erellidae, joined later by *Trochammina*, *Ammobaculites*, *Reophax*, and *Lagenammina* (Hillebrandt & Urlichs, 2023).

### Conclusions

Foraminifera belonging to 72 species from 31 genera were determined from the Upper Triassic Pötschenkalk, Zlambach, Kössen and Kendlbach Formations. The research presented clearly shows different proportions among morphological groups of foraminifera in the sampled formations. Further use of this data in interpretations of paleoecological conditions, however, requires some caution.

Relatively numerous and diverse assemblages were determined from the Pötschenkalk and Zlambach Formations. Agglutinated taxa predominate slightly over lagenids. The presence of astrorhizids confirms deposition in a more distal setting under oxygenated conditions. Similar numbers of presumed epi-, and infauna at the Thälerergraben section suggest meso- to oligotrophic conditions for the Pötschenkalk, and the predominance of presumed infauna in the Zlambach Formation at the Rossmoos-/Stambachgraben section points to meso- to eutrophic conditions.

Our findings for the Kössen Formation at the Schlossgraben and Fonsjoch sections appear largely in accordance with previous investigations. Compared to the Rossmoos and Thälerergraben faunas, the number of species and diversity in the uppermost Kössen Formation are much lower. However, the studied interval was already marked by regional changes in the environment, as well as global environmental perturbations of the latest Triassic. The T-Bed at Schlossgraben shows some increase in the proportion of *Lenticulina*. Mesotrophic conditions for both sections are determined based on the morphogroup composition.

Diverse assemblages with nodosariids indicate high oxygen levels for the lowermost part of the Kendlbach Formation (lower Schlossgraben Beds). However, peaks in *Trochammina*, *Astacolus*, and *Lenticulina* in low-diversity assemblages follow, which is interpreted as a general drop in oxygen levels in the Eiberg Basin. The uppermost Schattwald Beds and the Tiefengraben Member s.str. at Fonsjoch are already evidence of a return from stressful conditions and the establishment of meso- to oligotrophic conditions. However, the occasional dominance of *Trochammina* and *Eoguttulina* indicates that conditions varied.

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### Data availability

The dataset used in this study is published online as Appendix 2 and 3.

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## Appendix 1: Systematic palaeontology

**Remark:** Foraminiferal classification is currently in the state of rebuilding, as the most often used classifications based on wall composition and/or general test structure (e.g. Loeblich & Tappan, 1964, 1988, 1992; Mikhalevich, 2014; Mikhalevich & Kaminski, 2024) disagree with genetics of the living foraminifera (e.g. Pawlowski et al., 2013; Holzmann et al., 2022; Sierra et al., 2022). In addition to relatively low numbers of genetically analysed recent genera, genetic information cannot be obtained from extinct foraminiferal groups. For the classification below the family or subfamily level, we herein follow classification by Loeblich and Tappan (1988, 1992), Kaminski (2004), and Gaillot and Vachard (2007). For classification above the family level, we mostly follow Mikhalevich (2014) due to the completeness of the work, supplemented with opinions of Rigaud et al. (2015, 2016). Instead of the formal Monothalamaea we use the informal name “Monothalamids”, as suggested by Pawlowski et al. (2013), and followed by Pavel et al. (2023). It should be noted, however, that the choosing of classification does not affect the results of this research, as it is only a manner of sorting the specimens. The synonymy list primarily consists of specimens from the residue. These can be compared to the investigated material more reliably than the specimens illustrated from thin sections. Some species, however, were established based on specimens observed from thin sections. For those, the determination is less certain. The open nomenclature follows Copestake and Johnson (2014), and Sigovini et al. (2016). We give here only very condensed descriptions of the specimens.

Infrakingdom Rhizaria Cavalier-Smith, 2002

Phylum Retaria Cavalier-Smith, 1999

Subphylum Foraminifera d’Orbigny, 1826

“Monothalamids” Pawlowski et al., 2013 (paraphyletic)

Order Astrorhizida Lankester, 1885

Suborder Astrorhizina Lankester, 1885

Superfamily Astrorhizoidea Brady, 1881

Family Rhabdamminidae Brady, 1884

Subfamily Bathysiphoninae Avnimelech, 1952

Genus *Bathysiphon* M. Sars in G. O. Sars, 1872

(type species *Bathysiphon filiformis* Sars, 1872; Norway; Recent)

### *Bathysiphon* cf. *salebrosus* (Kristan-Tollmann, 1964)

Fig. 4.2

*Hyperammina salebrosa* Kristan-Tollmann, 1964, p. 25, pl. 1, fig. 8.

*Bathysiphon salebrosa* (Kristan-Tollmann, 1964). – Haig & McCartain, 2010, p. 371, figs. 3.8–3.9.

**Remarks:** The type material shows internally wrinkled wall. We observed only the exterior of the test.

Suborder Hippocrepinina Saidova, 1981

Superfamily Hippocrepinoidea Rhumbler, 1895

Family Hippocrepinidae Rhumbler, 1895

Subfamily Hyperammininae Eimer & Fickert, 1899

Genus *Hyperammina* Brady, 1878

(type species *Hyperammina elongata* Brady, 1878; Adriatic Sea; Recent)

### *Hyperammina* cf. *eulimbata* Kristan-Tollmann, 1964

Fig. 4.3

*Hyperammina eulimbata* Kristan-Tollmann, 1964, p. 26, pl. 1, figs. 3–5, 10–11.

**Remarks:** Characterised by restrictions on the outer surface. The inner wall of *Hyperammina eulimbata* varies in thickness, restricting the interior into funnel-like proto-chambers (Kristan-Tollmann, 1964). We did not observe the interior of the specimens. The wall is coarsely agglutinated, whereas Kristan-Tollmann (1964) writes that *H. eulimbata* has finely agglutinated wall.

Subfamily Jaculellinae Mikhalevich, 1995

Genus *Jaculella* Brady, 1879

(type species *Jaculella acuta* Brady, 1879; Brazil; Recent)

### *Jaculella* sp. A

Fig. 4.1

**Description:** The test is probably bilocular, high conical, rectilinear, slowly, but constantly enlarging in width. The wall is agglutinated, and virtually identical with the wall of *Hyperammina* cf. *salebrosa* (see above). The final test width is 0.32 mm, reached at the length of 1.56 mm. For the determination of species, the final lumen size should be measured as well. Hohenegger and Lein (1977) were of the opinion that specimens described from Triassic as “*Aeolisaccus*” or “*Earlandia*” in truth belong to genera *Jaculella* or *Hyperammina* based on having agglutinated and not “microgranular” wall.

**Remarks:** Differs from *Arenosiphon* Grubbs, 1939 in having constantly tapering test.

Class Spirillinata Mikhalevich, 1992 (=Tubothalamea Pawlowski et al., 2013)

Subclass Ammodiscana Mikhalevich, 1980

Order Ammodiscida Mikhalevich, 1980

Family Ammodiscidae Reuss, 1862

Subfamily Ammodiscinae Reuss, 1862

**Remarks:** Loeblich and Tappan (1992) put Ammodiscidae into the order Lituolida Lankester, 1885. Pawlowski et al. (2013) later incorporated most of the Lituolida into the paraphyletic order "Textulariida", placed under the class Globothalamea. Mikhalevich (2014) placed Ammodiscidae into the class Spirillinata Mikhalevich, 1992, which corresponds to Tubothalamea by Pawlowski et al. (2013).

Genus *Ammodiscus* Reuss, 1852

(type species *Orbis infimus* Strickland, 1846; England; Lower Jurassic)

***Ammodiscus incertus* (d'Orbigny, 1839a)**

Fig. 4.7

*Operculina incerta* d'Orbigny, 1839a, p. 49, pl. 6, figs. 16–17.

*Ammodiscus incertus* (d'Orbigny, 1839). – Kristan-Tollmann, 1964, p. 32, pl. 3, figs. 1–2.

*Ammodiscus* sp. – Resch, 1972, pl. 3, fig. 1.

**Description:** Bilocular. Second chamber planispirally enrolled in 5–6 coils, convolute to evolute. Test axially flattened, slightly biconcave. Outline circular. Aperture a simple opening at the end of the tube. Wall coarsely agglutinated. Test diameter 0.76–1 mm. Test thickness 0.09 mm. Height of the last coil 0.16 mm.

***Ammodiscus infimus* (Strickland, 1846)**

Fig. 4.8

*Orbis infimus* Strickland, 1846, p. 31, fig. a.

*Ammodiscus infimus* (Strickland, 1846). – Kristan-Tollmann, 1964, p. 32, pl. 8, figs. 6–7.

*Ammodiscus infimus* (Strickland, 1846). – Fuchs, 1970, p. 71, pl. 1, figs. 5–6.

*Ammodiscus infimus* (Strickland). – Tollmann & Kristan-Tollmann, 1970, pl. 3, fig. 8.

**Description:** The second chamber is coiled in 6–7 coils. The wall is finely agglutinated, thin,

translucent wall. Largest diameter 0.77 mm. Height of the last coil 0.15 mm.

**Remarks:** Differs from *A. incertus* in having more coils and in its wall.

***Ammodiscus asper* (Terquem, 1864)**

Fig. 4.9

*Involutina asper* Terquem. – Tappan, 1955, p. 38, pl. 8, figs. 10–13.

**Description:** The test diameter is 0.69–0.84 mm. The height of the last coil is 0.13 mm.

Subfamily Usbekistaniinae Vyalov, 1968

Genus *Glomospira* Rzehak, 1885

(type species *Trochammina squamata gordialis* Jones & Parker, 1860; Indian Ocean and Arctic Seas; Recent)

***Glomospira gordialis* (Jones & Parker, 1860)**

Fig. 4.4

*Glomospira gordialis* (Jones & Parker, 1860). – Kristan-Tollmann, 1964, p. 33, pl. 3, figs. 12–15.

*Glomospira gordialis* (Jones & Parker). – Tollmann & Kristan-Tollmann, 1970, pl. 3, fig. 11.

Cf. *Glomospira* cf. *gordialis* (Jones & Parker). – Resch, 1972, pl. 3, fig. 3.

*Gordiospira* sp. – Hohenegger & Piller, 1975, pl. 11, figs. 1–4.

**Description:** Only the undivided second chamber (deuterolocus) is visible, coiled in a globular shape. The deuterolocus makes approximately 4–5 coils; the second and the later coils are nearly perpendicular from the first coil and more-or-less strongly deviate from each other, thus in some specimens nearly approaching planispiral coil in the latter part of the test. The wall is thin, translucent, but built of well-sorted quartz grains, with some minor addition of accessory minerals (rutile). The test measures 0.28–0.46 mm in diameter. The final breadth of the deuterolocus is 0.06–0.1 mm.

***Glomospira* sp. A**

Fig. 4.5

**Remarks:** Although the specimen on Figure 4.5 looks similar to ?*Glomospira perplexa* Franke in Figure 4.6, the test of the former lacks translucency. It also has a larger number of coils.

***Glomospira perplexa* Franke, 1936?**

Fig. 4.6

? *Glomospira perplexa* Franke, 1936, p. 18, pl. 1, fig. 12.

*Glomospira perplexa* Franke, 1936. – Kristan-Tollmann, 1964, p. 33, pl. 3, figs. 3–11.

*Glomospira perplexa* Franke. – Tollmann & Kristan-Tollmann, 1970, pl. 3, fig. 14.

**Description:** Globular test; only undivided tubular deuterolocus is visible. It coils in approximately 4–7 (?) coils. The length of the coils varies, and the tube often makes meandering loops. The wall is finely agglutinated (quartz grains, some aluminosilicates or lithic grains). The width of the tube seems to vary along its length, but this could also be due to changing depth of the coil. The diameter of the test is 0.43–0.64 mm. The final width of the deuterolocus is 0.14 mm.

Order Ammovertellinida Mikhalevich, 1999

Family Ammovertellinidae Saidova, 1981

Subfamily Ammovertellininae Saidova, 1981

? Genus *Glomospirella* Plummer, 1945

(type species *Glomospira umbilicata* Cushman & Waters, 1927; Texas; Carboniferous)

***Glomospirella?* sp. A**

Fig. 4.10

**Description:** The test is bilocular, with a long tubular deuterolocus, elliptically (?) enrolled. Alternatively, the test could be circular and laterally compressed. The initial way of coiling is not visible; the outer part is formed of 3–4 planispiral coils. The aperture is a simple circular opening at the end of the tube. The wall is coarsely agglutinated. The larger axis measures 0.96–1.52 mm; the shorter diameter is 0.48–1.03 mm. The final diameter of the deuterolocus is 0.15–0.20 mm.

**Remarks:** The specimens are identified as a *Glomospirella* or as *Ammodiscus*, depending on whether the initial coiling is not or is planispiral. Lateral compression was not observed in other species of *Ammodiscus*.

Subclass Spirillinana Mikhalevich, 1992

Superorder Involutinoida Hohenegger & Piller, 1977

Order Involutinida Hohenegger & Piller, 1977

Superfamily Involutinoidea Bütschli, 1880

Family Involutinidae Bütschli, 1880

Subfamily Involutininae Bütschli, 1880

Genus *Involutina* Terquem, 1862, emend. Rigaud et al. (2015)

(type species *Involutina silicea* Terquem, 1862; France; Lower Jurassic)

***Involutina liassica* (Jones in Brodie, 1853) complex**

Fig. 5.15

*Nummulites liassicus* Jones in Brodie, 1853, p. 275.

*Involutina turgida* Kristan, 1957, p. 275, pl. 22, figs. 5–10.

*Involutina liassica* (Jones, 1853). – Kristan-Tollmann, 1964, p. 59, pl. 8, fig. 9.

*Involutina turgida* Kristan, 1957. – Kristan-Tollmann, 1964, p. 60, pl. 8, figs. 10–12.

*Involutinaliassica* (Jones). – Tollmann & Kristan-Tollmann, 1970, pl. 5, fig. 13.

*Involutina liassica* (Jones). – Hohenegger & Piller, 1975, pl. 9, figs. 1–4.

**Remarks:** Classification to the suborder level follows Rigaud et al. (2015). According to Koehn-Zaninetti (1969), Gušić (1975), Blau (1987), and Rigaud et al. (2015), *I. turgida* is a junior synonym of *I. liassica*. Based on our experience, *Involutina farinacciae* Brönnimann and Koehn-Zaninetti, 1969 differs from the *I. liassica*/*I. turgida* complex in smaller test size and occurs only in Lower Jurassic.

Class Nodosariata Mikhalevich, 1992

Subclass Hormosinana Mikhalevich, 1992

Order Hormosinida Mikhalevich, 1980

Superfamily Hormosinoidea Haeckel, 1894

Family Reophacidae Cushman, 1927

Genus *Reophax* de Montfort, 1808

(type species *Reophax scorpiurus* Montfort, 1808; Adriatic Sea; Recent)

***Reophax cf. rudis* Kristan-Tollmann, 1964**

Fig. 4.13

*Reophax rudis* Kristan-Tollmann, 1964, p. 29, pl. 2, fig. 1.

**Description:** Only one specimen, with the last four chambers preserved. The last chamber is characteristically larger from the preceding ones, tapering towards the aperture. The aperture is central, simple circular. The other chambers are on the outside wider than high, with distinct sutures. The wall is coarsely agglutinated. The specimen is

0.36 mm long; the length of the last chamber is 0.19 mm, its width is 0.16 mm.

**Remarks:** The type specimen measures 1.46 mm in length and 0.79 mm in width. The illustrated specimen is interpreted as *R. cf. rudis* based on the shape of the last chamber.

***Reophax densa* Tappan, 1955**

Fig. 4.16

*Reophax densa* Tappan, 1955, p. 35, pl. 8, figs. 1–6.

*Reophax eominutus* Kristan-Tollmann, 1964, p. 28, pl. 1, figs. 15–19.

*Reophax eominutus* Kristan-Tollmann. – Tollmann & Kristan-Tollmann, 1970, pl. 3, fig. 5.

*Scherochorella eominutus* (Kristan-Tollmann, 1964). – Haig & McCartain, 2010, p. 375, figs. 4.15–4.17.

**Description:** Specimens are laterally compressed. Multilocular test with uniserially arranged chambers. The initial part, often broken off, seems to consist of a circular proloculus, slightly larger from the following second chamber, although we cannot completely exclude that the initial part consists of a short planispiral part, as in *Ammobaculites*. The proloculus is followed by approximately 11 chambers. Sutures are slightly depressed, visible on the surface. The width of the test slowly increases and attains the largest width with the last chamber, which appears somewhat longer than the preceding chambers. The apertural face is rounded. The simple circular aperture is situated on the top. The wall is coarsely agglutinated. The complete specimens are up to 1.26 mm long, and 0.25 mm wide. The proloculus measures 0.08 mm in diameter.

**Remarks:** The type specimen is 0.63 mm long and 0.19 wide.

Class Miliolata Saidova, 1981

Subclass Miliammina Mikhalevich, 1980

Order Lituolida Lankester, 1885

Superfamily Lituoloidea de Blainville, 1827

Family Lituolidae de Blainville, 1827

Subfamily Ammomarginulinae Podobina, 1978

Genus *Ammobaculites* Cushman, 1910

(type species *Spirolina agglutinans* d'Orbigny, 1846; Austria; middle Miocene)

***Ammobaculites eumorphos* Kristan-Tollmann, 1964 [B-form]**

Fig. 4.11

*Ammobaculites eumorphos* Kristan-Tollmann, 1964, p. 38, pl. 5, figs. 3–4 [fig. 3 marked as 10 in pl. 5], pl. 6, figs. 1–5.

**Description:** Multichambered test consists of a large planispiral part and a shorter uniserial part. The planispiral part consists of 7–8 chambers, while the planispiral part comprises 2–3 chambers. Chamber width is larger than their height. The test outline is undulated, with depressed chamber sutures. The apertural face is rounded, low to high domical. The aperture is circular, in chambers of the uniserial part positioned centrally. The wall is coarsely agglutinated. The entire test is 1.35 mm long. The planispiral part is 0.38–0.61 mm in diameter. Chambers in the uniserial part are 0.69 mm wide.

***Ammobaculites zlabachensis* Kristan-Tollmann, 1964**

Fig. 4.12

*Ammobaculites zlabachensis* Kristan-Tollmann, 1964, p. 36, pl. 4, figs. 5–7.

***Ammobaculites rhaeticus* Kristan-Tollmann, 1964**

Fig. 4.14–4.15

*Ammobaculites rhaeticus* Kristan-Tollmann, 1964, p. 36, pl. 4, figs. 8–13.

***Ammobaculites cf. rhaeticus* Kristan-Tollmann, 1964**

Fig. 4.17

Cf. *Ammobaculites rhaeticus* Kristan-Tollmann, 1964, p. 36, pl. 4, figs. 8–13.

**Remarks:** Differs from *A. rhaeticus* in having smaller planispiral part. The test is uncompacted, circular in cross-section.

Subclass Miliolana Saidova, 1981

? Suborder Endothyroidea Fursenko, 1958

? Order Endothyroidea Fursenko, 1958

? Superfamily Endothyroidea Brady, 1884

? Family Endotebidae Vachard, Martini, Rettori & Zaninetti, 1994

Genus *Endothyra* Phillips, 1846

(type species *Endothyra bowmani*; England; Carboniferous)

***Endothyra kuepperi* Oberhauser, 1960**

Fig. 5.7

*Endothyra ? kuepperi* Oberhauser. – Tollmann & Kristan-Tollmann, 1970, pl. 4, figs. 16–17.

*Endothyra kuepperi* Oberhauser. – Kristan-Tollmann, 1983, p. 296, Fig. 1.1.

cf. *Endothyra* sp. – He Yan, 1999, pl. 1, fig. 8.

**Description:** The test is multilocular. Chambers are all or in majority arranged in a very low trochospire, so that the test almost appears planispiral. The initial part of the test is covered by the outer (last) coil. Five chambers are visible on the umbilical side of the test. They show gradual increase in size. Sutures are well visible, deepened. The last chamber is the largest,  $\frac{3}{4}$  of the test wide and broadly rounded. The umbilicus is shallow and broad. The aperture is not visible. The test wall is simple, agglutinated (quartz, aluminosilicates and/or lithic grains), and relatively smoothly finished. The test diameter is 0.4 mm.

**Remarks:** Specimens are very rare, so not enough material is available for sectioning of the specimens. The genus *Endoteba* was described as having secreted calcareous wall with agglutinated calcareous grains (Vachard et al., 1994; fig. 2b in Rigaud et al., 2014). The relationship between former *Fusulinana* and *Textulariana* is explained in Rigaud et al. (2014), and Mikhalevich (2014), among others. In contrast to endothyroids, *Trochammina* has a very clearly visible trochospiral coiling, even in very low specimens of the species *Trochammina jaunensis* Brönnimann and Page. Triassic *Trochammina* also presumably has a lower number of chambers (four) in the last coil. Oberhauserellids are similar in shape and size, but have aragonitic hyaline wall (Fuchs, 1969, 1975; Hillebrandt, 2012).

Superorder Milioloida Delage & Herouard, 1896

Order Nubeculariida Jones in Griffith & Henfrey, 1875

Superfamily Nubecularioidea Jones in Griffith & Henfrey, 1875

Family Nubeculariidae Jones in Griffith & Henfrey, 1875

Subfamily Nodobaculariinae Cushman, 1927

? Genus *Nodobacularia* Rhumbler, 1895

(type species *Nodobacularia tibia* Rhumbler, 1895; Atlantic Ocean; Recent)

***Nodobacularia? vujisici* Urošević & Gaździcki, 1977**

Fig. 6.23

*Nodobacularia vujisici* Urošević & Gaździcki, 1977, p. 97, pl. 1, figs. 1–6.

*Nodobacularia? vujisici* Urošević & Gaździcki, 1977. – Oselj et al., 2023, p. 116, Fig. 6a–g. [cum syn.]

Family Ophthalmitidae Wiesner, 1920

Genus *Karaburunia* Langer, 1968

(type species *Karaburunia rendeli* Langer, 1968; Turkey; Anisian)

***Karaburunia atsabensis* Haig & McCartain, 2012**

Fig. 5.11

Cf. *Quinqueloculina nucleiformis* Kristan-Tollmann, 1964, p. 61, pl. 9, figs. 9–11.

Cf. *Quinqueloculina nucleiformis* Kristan-Tollmann, 1964. – Fuchs, 1970, p. 75, pl. 2, fig. 2.

*Karaburunia atsabensis* Haig & McCartain, 2012, p. 43, pl. 1, figs. 14–18; pl. 2, figs. 1–32.

**Remarks:** The aperture of the specimen is partly obscured, but most likely simple, rounded, slightly raised.

Class Rotaliata Mikhalevich, 1980 (=Globothalamea Pawłowski et al., 2013)

Subclass Textulariana Mikhalevich, 1980

Order Nautiloculinida Mikhalevich, 2003

Superfamily Nautiloculinoidea Loeblich & Tappan, 1985

? Family Haplophragmoididae Maync, 1952

? Genus *Haplophragmoides* Cushman, 1910

(type species *Nonionina canariensis* d'Orbigny, 1839a; Canary Islands; Recent)

***Haplophragmoides? sp. A***

Fig. 5.6

*Haplophragmoides subglobosus* (G. O. Sars, 1872). – Kristan-Tollmann, 1964, p. 35, pl. 4, figs. 1–4.

**Description:** The test is flattened, lenticular, multilocular, with an involute coiling. The sides of the test are not completely symmetrical, but we nevertheless interpret the test as planispiral,

and somewhat deformed due to compaction (as are some of the specimens illustrated by Kristan-Tollmann, 1964). Only the last coil with approximately six chambers is visible. The height of the chambers seems to vary. Shallow depression is visible on both sides of the test. It is filled with calcite. Aperture is not visible. The test wall is simple, agglutinated (mostly from grains of quartz, rare albite), relatively smoothly finished, and nearly translucent. The test diameter is 0.33 mm.

**Remarks:** The species is distinguished from Endothyroidea by presumably planispiral coil, and from Oberhauserellidae in having non-calcareous, agglutinated wall. We dismiss the possibility of mineral replacement due to the fact that calcareous tests of other species in our material are well preserved. Specimens closely resemble the material published by Kristan-Tollmann (1964) as *Haplophragmoides subglobosus*, although Kristan-Tollmann's specimens are a little larger (0.47 mm in diameter). Kristan-Tollmann compared her specimens with Cushman (1910), but recent specimens in Cushman (1910) are notably larger (1–2.5 mm in diameter), and separated from Kristan-Tollmann's specimens by a large stratigraphic gap.

Order Trochamminida Saidova, 1981

Superfamily Trochamminoidea Schwager, 1877

Family Trochamminidae Schwager, 1877

Subfamily Trochammininae Schwager, 1877

Genus *Trochammina* Parker & Jones, 1859

(type species *Nautilus inflatus* Montagu, 1808; England; Recent)

***Trochammina jaunensis*  
Brönnimann & Page, 1966**

Fig. 5.2

*Trochammina jaunensis* Brönnimann & Page, 1966, p. 88, pl. 1, figs. 6–8.

**Remarks:** The type material is from thin sections. The herein illustrated specimen has been identified as *T. jaunensis* based on the low spire and somewhat smaller size (diameter 0.31 mm) compared to *T. alpina*? (diameter 0.43–0.50 mm). The type specimen of *T. jaunensis* is 0.29 mm in diameter (cf. Brönnimann & Page, 1966).

***Trochammina alpina* Kristan-Tollmann,  
1964 complex?**

Figs. 5.3–5.5

*Trochammina alpina* Kristan-Tollmann, 1964, p. 43, pl. 7, figs. 2–3.

*Trochammina almtalensis* Koehn-Zaninetti, 1969, p. 38, pl. 5, figs. E–F; fig. 6A–P.

? *Trochammina alpina* Kristan-Tollmann. – Tollmann & Kristan-Tollmann, 1970, pl. 4, figs. 4–5.

**Description:** Specimens are deformed (vertically flattened and distorted) due to compaction. Four chambers are visible on the umbilical side. The wall is agglutinated, although in some species it seems more fine-grained (Fig. P2.3) and in the others the wall is coarsely agglutinated (Figs. 5.4–5.5). The final diameter of the test of the fine-grained specimens is 0.43 mm; while the coarse-grained specimens measure 0.50–0.62 mm in diameter. Approximately four coils are visible, each with four chambers.

**Remarks:** The type material of *T. almtalensis* is from thin sections. The largest diameter of the type specimens is 0.3 mm. The type material of *T. alpina* are isolated specimens, measuring 0.53–0.54 mm in diameter. The herein observed specimens are of the intermediate size, and it is thus difficult to place them to either of the two species. Note that Koehn-Zaninetti (1969) described the wall of *T. almtalensis* as “microgranular or finely agglutinated”, while Kristan-Tollmann (1964) wrote that *T. alpina* has coarsely agglutinated wall. If *T. alpina* and *T. almtalensis* will be proved synonyms, then *T. almtalensis* holds priority.

Order Verneulinida Mikhalevich & Kaminski in Mikhalevich, 2003

Superfamily Verneulinoida Cushman, 1911

Family Verneulinidae Cushman, 1911

Subfamily Verneulinoidinae Suleymanov, 1973

Genus *Tetrataxis* Ehrenberg, 1854

(type species *Tetrataxis conica* Ehrenberg, 1854; Russia; Carboniferous)

***“Tetrataxis” humilis* Kristan, 1957**

Fig. 5.1

*Tetrataxis humilis* Kristan, 1957, p. 292, pl. 17, figs. 1–3.

*Tetrataxis humilis* Kristan. – Tollmann & Kristan-Tollmann, 1970, pl. 4, fig. 6.

**Remarks:** The presence of the genus *Tetrataxis* within the Triassic has been considered doubtful, as the Triassic specimens do not show the

double-layered wall of the true *Tetrataxis*, which belongs in the order Fusulinida (Loeblich & Tappan, 1988). A new genus needs to be established, probably phyletically close to the genus *Duotaxis* Kristan, 1957 (Falzoni et al., 2023). The illustrated specimen is somewhat smaller than the type material (diameter 0.56 mm compared to 0.79 mm and 0.93 mm for the paratype and the holotype, respectively).

Subfamily Verneulininae Cushman, 1927

Genus *Gaudryinella* Plummer, 1931

(type species *Gaudryinella delrioensis* Plummer, 1931; Texas; Lower Cretaceous)

***Gaudryinella elegantissima***

**Kristan-Tollmann, 1964**

Fig. 5.9

*Gaudryinella elegantissima* Kristan-Tollmann, 1964, p. 48, pl. 8, figs. 1–5.

**Description:** Matches description of the type material. The length of the specimen is 0.76 mm, which is slightly longer than that of the type material.

Foraminifera incertae sedis

Genus *Annulina* Terquem, 1862

(type species *Annulina metensis* Terquem, 1862; France; Lower Jurassic)

***Annulina metensis* Terquem, 1862**

Fig. 9.1

*Annulina metensis* Terquem, 1862, p. 433, pl. 5, figs. 6a, b.

*Thuraminoides metensis* (Terquem, 1862). – Haig & McCartain, 2010, p. 371, figs. 3.10–3.11.

Class Nodosariata Mikhalevich, 1992, emend. Rigaud et al., 2016

Subclass Nodosariana Mikhalevich, 1992

Order Nodosariida Calkins, 1926, emend. Rigaud et al., 2016

Suborder Nodosariina Calkins, 1926

Superfamily Nodosarioidea Ehrenberg, 1838

Family Nodosariidae Ehrenberg, 1838

Subfamily Nodosariinae Ehrenberg, 1838

Genus *Pseudonodosaria* Boomgaart, 1949 (= *Rectoglandulina* Loeblich & Tappan, 1955)

(type species *Glandulina discreta* Reuss, 1850; Austria; middle Miocene)

***Pseudonodosaria oveyi* (Barnard, 1953)**

Fig. 6.9

*Rectoglandulina oveyi* (Barnard, 1953). – Kristan-Tollmann, 1964, p. 90, pl. 14, figs. 10–12.

***Pseudonodosaria plurimicostata***

**(Kristan-Tollmann, 1964)**

Figs. 6.7, 6.10

*Rectoglandulina plurimicostata* Kristan-Tollmann, 1964, p. 89, pl. 13, figs. 23–27.

**Description:** Test is multilocular, elongated with circular cross-section, rectilinear or nearly rectilinear with uniserially arranged chambers. Approximately 7–9 chambers are visible, but the number of chambers in the initial part of the test is not clear. The proximal end of the test is narrow. The chambers are nearly globular, but the specimens are compressed. Outer sutures are poorly visible. The surface of the test is covered by thin parallel ribs; between 10 and 12 ribs are visible on one side of the test, running along the entire length of the test, but it appears that shorter and perhaps less pronounced ribs may be added in the last part of the test. The aperture is central, probably simple circular. The test length is 0.55–0.76 mm, the test width is 0.14–0.16 mm. The wall is made of calcium carbonate and transparent (hyaline).

**Remarks:** The test is smaller than in *Nodosaria lirata* and the initial part of the test is narrower (Fig. 6.3).

***Pseudonodosaria* sp. A**

Fig. 5.13

*Dentalina difformis* Terquem, 1864. – Kristan-Tollmann, 1964, p. 103, pl. 17, figs. 16–17.

**Description:** Test is multilocular, uniserial, curvilinear. Rounded proloculus is followed by 5–6 larger cylindrical chambers, approximately of the same dimensions. Sutures are poorly visible; they are slightly more obvious towards the end of the test. Test sides are parallel in the larger part of the test. The aperture is terminal radiate, positioned centrally and slightly pulled-out (raised) from the apertural face. The test is 1.35–1.45 mm long, 0.31–0.35 mm wide. The ratio between length and width of the test is 4.2.

**Remarks:** The specimen is considered nearly identical to the specimens depicted in Kristan-Tollmann

(1964) as *Dentalina difformis* (= *Pseudonodosaria difformis*, Hayward et al., 2024). However, we do not agree that Kristan-Tollmann's specimens belong to *Dentalina difformis* in Terquem (1864).

***Pseudonodosaria ploechingeri*  
(Oberhauser, 1960)**

Fig. 6.16

*Pseudoglandulina ploechingeri* Oberhauser, 1960, p. 27, pl. 1, figs. 1–41.

*Pseudonodosaria ploechingeri* (Oberhauser). – Kristan-Tollmann, 1983, pl. 1, figs. 1–6.

*Pseudonodosaria ploechingeri* (Oberhauser), 1960. – He Yan, 1999, pl. 4, fig. 11.

***Pseudonodosaria simpsonensis*  
(Tappan, 1951)?**

Fig. 6.13

? *Pseudoglandulina simpsonensis* Tappan, 1951, p. 12, pl. 3, figs. 9–14.

? *Rectoglandulina simpsonensis* (Tappan). – Tollmann & Kristan-Tollmann, 1970, pl. 7, fig. 20.

? *Pseudonodosaria simpsonensis* (Tappan), 1951. – He Yan, 1999, pl. 3, fig. 2.

**Description:** The test is fairly large, elongated, with gradually enlarging chambers (5 or 6 in total). These are wider than high, except for the last chamber, which is pyriform. Sutures are slightly deepened. The test surface is smooth. The apical end has a short spine. The aperture is central, radiate.

Genus *Nodosaria* Lamarck, 1812

(type species *Nautilus radicola* Linnaeus, 1758; Adriatic Sea; Recent)

**Remarks:** See discussion in Copestake and Johnson (2014, p. 160) about the morphology of this genus.

***Nodosaria vermicularis* (Terquem, 1866)**

Fig. 6.1

*Dentalina vermicularis* Terquem, 1866, p. 483, pl. 19, fig. 21.

*Nodosaria oculina vermicularis* (Terquem, 1866). – Kristan-Tollmann, 1964, p. 75, pl. 11, figs. 6–8.

**Description:** Test is very elongated rectilinear, multilocular, with chambers in uniserial arrangement. The initial part of the test is pointed, but in

most specimens abraded so that it appears rounded. The width of the test at first increases, but the sides of the test soon become semi-parallel. The exact number of chambers could not be determined – at least five can be counted in some specimens, which, however, lack the initial part of the test. Chambers have oval to pyriform shape. External sutures between the chambers are not visible, and the test's outline runs unbroken, except for the last chamber, where a slight indentation is hinted. Six strong ribs run along the length of the test. The aperture is at the end of the last chamber, centrally situated, raised upon a short neck. Wall is translucent and made of calcium carbonate (hyaline). The length of the illustrated specimen is 1.58 mm. The longest specimen measures 2.19 mm, with the final width of 0.24 mm.

**Remarks:** Loeblich and Tappan (1988) removed costate species from *Nodosaria* and placed them in the distinct genus *Pyramidulina*. Copestake and Johnson (2014), however, disagree with this decision, and consider the presence of ribs a species-specific feature.

***Nodosaria liratella* Tappan, 1951**

Fig. 6.3

*Nodosaria liratella* Tappan, 1951, p. 11, pl. 3, figs. 17–20.

? *Nodosaria raphanistriformis* (Gümbel, 1862), emend. E. & I. Seibold, 1955. – Kristan-Tollmann, 1964, p. 72, pl. 11, figs. 1–3.

***Nodosaria zlabachensis*  
Kristan-Tollman, 1964**

Figs. 6.2, 6.4

*Nodosaria zlabachensis* Kristan-Tollmann, 1964, p. 68, pl. 10, figs. 8–9.

**Description:** Test is multilocular, elongated. Four chambers are uniserially arranged. They gradually increase in size and are oval to pyriform in shape. Sutures are clearly visible. The test surface is smooth. The aperture is situated centrally on top of the last chamber, raised above the apertural face, probably radiate. The test is 1.04 mm long.

***Nodosaria levifracta* Kristan-Tollmann, 1964**

Fig. 6.6

*Nodosaria levifracta* Kristan-Tollmann, 1964, p. 69, pl. 10, figs. 10–11.

*Nodosaria levifracta* Kristan-Tollmann, 1964.  
– He Yan, 1999, pl. 3, fig. 9.

***Nodosaria shublikensis* Tappan, 1951**

Fig. 6.5

*Nodosaria shublikensis* Tappan, 1951, p. 11, pl. 3, figs. 1–4.

*Nodosaria anarthra* Kristan-Tollmann, 1964, p. 71, pl. 10, fig. 22.

**Description:** The test is large, linear, with no visible sutures. The initial part is wide and well-rounded, followed by somewhat narrower part of the test, which then gradually becomes wider. The last chamber is piriform, with centrally raised simple round aperture. The surface of the test is covered with six strong longitudinal ribs, which fade near the aperture. The length of the test is 1.58 mm.

***Nodosaria nitidana* Brand, 1937**

Fig. 6.8

*Nodosaria nitidana* Brand, 1937. – Kristan-Tollmann, 1964, p. 67, pl. 10, figs. 1–4.

***Nodosaria* cf. *setulosa* Tappan, 1955**

Fig. 6.11

cf. *Nodosaria setulosa* Tappan, 1955, p. 73, pl. 24, figs. 1–5.

**Description:** The test is small, elongated. Chambers (5 or 6?) at first increase rapidly, then more slowly, so that the later part of the test has nearly parallel sides. The apical end is rounded. Sutures are well visible, especially between the last and the penultimate chamber. The chambers are wider than high, except for the last chamber, which is higher and pyriform. The aperture is central, details are not visible. The test surface is smooth.

***Nodosaria pupiformis* (Terquem, 1864)**

Fig. 6.14

*Dentalina pupiformis* Terquem, 1864, p. 385, pl. 7, fig. 13.

cf. *Nodosaria pupiformis* Terquem, 1864. – Kristan-Tollmann, 1964, p. 82, pl. 14, fig. 15.

**Description:** A singular specimen. The test is elongated, uniserial, linear. The initial part of the test is narrow but rounded. Approximately eight chambers follow. Sutures are poorly visible in the

early part of the test, but distinct in the last stages of growth. The aperture is not visible, and the last chamber is perhaps not present. The test surface is smooth. The test wall is made of calcium carbonate, partly translucent (hyaline). The length of the specimen is 0.93 mm, the width is 0.23 mm.

***Nodosaria* sp. A**

Fig. 6.15

**Description:** The test is elongated, shaped like a sceptre, with broad, rounded initial part of the test, gradually becoming narrower, and ending with distinct large final chamber, onion-like or pyriform in shape. Except for the last chamber, the sutures are not visible. The number of chambers is not visible. Six strong ribs run longitudinal along the test's length from the juvenile part to the middle of the last chamber, probably not reaching the aperture. The aperture is raised on a short neck and radiate. The wall is made of calcium carbonate, hyaline.

**Remarks:** The specimen is similar to *Nodosaria archoidea* Kristan-Tollmann, 1964 in the number of ribs, if not in the general shape, but only one specimen of *N. archoidea* was illustrated. However, in *N. archoidea* the ribs are not present from the base of the test. Specimens determined in Kristan-Tollmann (1964) as *Nodosaria metensis robusta* Barnard, 1950 have more ribs. *Nodosaria cupaeformis* Kristan-Tollmann, 1964 has nine ribs. *Nodosaria fungiformis* Kristan-Tollmann is identical in shape but has a smooth surface. The specimen is in part also similar to *Nodosaria metensis* Terquem on plate 7, figures 6–7 in Copestake and Johnson (2014), but the latter have more ribs, better visible chamber sutures and less pronounced last chamber.

***Nodosaria* sp. B**

Fig. 6.18

*Dentalina* cf. *gracilistriata* Loeblich & Tappan, 1950. – Kristan-Tollmann, 1964, p. 91, pl. 11, figs. 16–17.

**Remarks:** Description is identical with the description given by Kristan-Tollmann (1964). The size of the specimen is 1.42 mm. The holotype of *Dentalina gracilistriata* Loeblich and Tappan (1950), however, is smaller (length 0.81 mm), has less numerous chambers, globular proloculus, rounded base, more pronounced sutures, and fainter ribs.

***Nodosaria* sp. C**

Fig. 6.19

*Nodosaria* cf. *minuta* Cordey, 1962. – Kristan-Tollmann, 1964, p. 79, pl. 12, fig. 3.

**Description:** Identical with the description given by Kristan-Tollmann (1964). The size of the specimen is 0.88 mm.

? Genus *Dentalinoides* Marie, 1941

(type species *Dentalinoides canulina* Marie, 1941; France; Upper Cretaceous)

***Dentalinoides?* sp. A**

Fig. 9.3

**Description:** Smooth, elongated test with chambers in uniserial arrangement. The proloculus bears a short spine. Chambers are chevron in shape. The length of the test is 1.1 mm.

Family Ichthyolariidae Loeblich & Tappan, 1986

Genus *Ichthyolaria* Wedekind, 1937

(type species *Fronidularia bicostata* d'Orbigny, 1850; Germany; Lower Jurassic)

***Ichthyolaria xiphoidea*  
(Kristan-Tollmann, 1964)**

Figs. 6.24–6.25

*Fronidularia xiphoidea* Kristan-Tollmann, 1964, p. 145, pl. 31, figs. 1–6.

*Fronidularia nitida* Terquem, 1858. – Fuchs, 1970, p. 89, pl. 5, fig. 10.

*Pachyphloides xiphoidea* (Kristan-Tollmann), 1964. – He Yan, 1999, pl. 3, fig. 17.

**Remarks:** According to Copestake and Johnson (2014), *Ichthyolaria* differs from *Fronidularia* in lacking secondary lamination. According to them, only some of the Middle Jurassic and younger species belong to *Fronidularia*. They dubiously considered *I. xiphoidea* to be a junior synonym of *Ichthyolaria brizaeformis* (Bornemann, 1854), but their specimens have higher ultimate chamber (pl. 11, fig. 30 in Copestake & Johnson, 2014).

***Ichthyolaria phyllodea*  
(Kristan-Tollmann, 1964)**

Fig. 7.8

*Fronidularia phyllodea* Kristan-Tollmann, 1964, p. 150, pl. 33, figs. 1–8.

***Ichthyolaria rhaetica*  
(Kristan-Tollmann, 1964)**

Figs. 7.1, 7.3

*Fronidularia rhaetica* Kristan-Tollmann, 1964, p. 146, pl. 32, figs. 1–8.

*Fronidularia rhaetica* Kristan-Tollmann, 1964. – Salaj & Jendrejáková, 1967, pl. 20, fig. 10.

*Fronidularia rhaetica* Kristan-Tollmann. – Tollmann & Kristan-Tollmann, 1970, pl. 8, fig. 15.

*Fronidularia rhaetica* (Kristan-Tollmann, 1964). – Kristan-Tollmann & Gramann, 1992, pl. 2, fig. 1.

***Ichthyolaria terquemi squamosa*  
(Terquem & Berthelin, 1875)**

Figs. 6.20–6.22

*Fronidularia bicostata* d'Orbigny, 1850 subsp. *intercosta* Kristan-Tollmann, 1964, p. 151, pl. 33, figs. 12–13.

? *Fronidularia pulchra* Terquem, 1858. – Fuchs, 1970, p. 90, pl. 5, fig. 6.

? *Fronidularia sulcata* Bornemann, 1854. – Fuchs, 1970, p. 90, pl. 5, fig. 3.

*Ichthyolaria terquemi squamosa* (Terquem & Berthelin, 1875). – Copestake & Johnson, 2014, p. 155, pl. 11, figs. 1, 7–9.

**Description:** The test is elongated, lanceolate, laterally compressed, probably uniserial throughout. Sides of the test are slightly flaring, in specimen on Figure 6.22 subparallel. Proloculus is followed by 9–10 chevron-like chambers, gradually increasing in size. Sutures are flush with the surface, poorly or not visible. The test surface is covered by longitudinal ribs; these are added along the test length, so that between 7 and 10 are visible on one side in the last part of the test. The radiate aperture is central, slightly raised on a short neck. A short spine is perhaps present on the apex of the test. The initial, more widely flaring part of the test is 0.04–0.08 mm long. The final length of the test is 0.84–1.38 mm. The final width of the test is 0.19–0.36 mm. The height of the last chamber is 0.11–0.16 mm. The distance between the ribs is 0.04–0.05 mm. The height of the apertural neck is 0.03–0.05 mm; its width is 0.05–0.07 mm.

Genus *Paralingulina* Gerke, 1969

(type species *Lingulina tenera* Bornemann, 1854; Germany; Lower Jurassic)

***Paralingulina grilli* (Kristan-Tollmann, 1964), comb. nov.**  
Fig. 8.18

*Grillina grilli* Kristan-Tollmann, 1964, p. 66, pl. 34, figs. 3–9.

*Grillina grilli* Kristan-Tollmann. – Tollmann & Kristan-Tollmann, 1970, pl. 7, fig. 13.

***Paralingulina longiscata* (Terquem, 1870)**  
Fig. 6.12

*Paralingulina longiscata longiscata* (Terquem, 1870). – Copestake & Johnson, 2014, p. 185, pl. 8, figs. 24, 29, 35.

**Description:** A single specimen. The test is uniserial, elongated, laterally compressed, with nearly parallel sides. Proloculus is not preserved. Most of the test consists of eight chevron-like chambers. Chambers are relatively higher than in other species recorded in this study. The sutures are also more pronounced. Numerous fine parallel ribs run longitudinally along the test. The specimen is 0.81 mm long and 0.22 mm wide. The last chamber is 0.12 mm long.

Genus *Mesodentalina* Norling, 1968  
(type species *Dentalina matutina* d'Orbigny, 1850; France; Lower Jurassic)

***Mesodentalina tenuistriata* (Terquem, 1866)**  
Fig. 5.19

*Dentalina tenuistriata* Terquem, 1866. – Kristan-Tollmann, 1964, p. 91, pl. 14, figs. 8–9.

Cf. *Mesodentalina tenuistriata* (Terquem, 1866). – Copestake & Johnson, 2014, p. 252, pl. 14, figs. 1, 2, 7, 8.

***Mesodentalina* sp. A**  
Fig. 5.20

**Description:** The test is curvilinear, uniserial throughout. Globular proloculus is rounded, followed by six or seven (?) chambers. The initial part of the test is unbroken, without sutures, thus obscuring the total number of chambers; sutures are somewhat more pronounced in the last part of the test. The last chamber is shaped like a high dome, with centrally positioned aperture. The type of the aperture is not determined. The test surface is covered by longitudinal ribs, not visible on the surface of the last chamber and in the first part of the proloculus. Additional ribs are inserted

as the test grows: approximately 6 or 7 ribs are thus visible on the initial part of the test, and approximately 14 on the penultimate chamber. The wall is calcareous, transparent (hyaline). The test is 1.0 mm long and 0.2 mm in width.

**Remarks:** The specimen differs from *Mesodentalina tenuistriata* Terquem in having more numerous ribs, which curve along the same line as the test, and in having shorter final chamber.

Genus *Prodentalina* Norling, 1968  
(type species *Dentalina terquemi* d'Orbigny, 1850; France; Lower Jurassic)

***Prodentalina paucicurvata* (Franke, 1936)**  
Fig. 5.16

*Dentalina paucicurvata* Franke, 1936. – Kristan-Tollmann, 1964, p. 101, pl. 17, figs. 5–6.

**Remarks:** Numerous specimens identical or similar to the illustrated were observed. Due to the small differences between the species of “*Dentalina*” (*Prodentalina* sensu Copestake & Johnson, 2014), not all of them belong to *P. paucicurvata* (see Kristan-Tollmann, 1964 for the diversity of “*Dentalina*”). The illustrated specimen was determined as *P. paucicurvata* based on flush sutures, large and elongated last chamber, and its size (length 0.85 mm).

***Prodentalina bicornis* (Terquem, 1870)?**  
Fig. 5.18

*Dentalina bicornis* Terquem, 1870, p. 370, pl. 29, figs. 13–17.

*Dentalina* ex gr. *subsiliqua* Franke. – Oberhauser, 1960, p. 24, pl. 6, figs. 1–3.

*Dentalina bicornis* Terquem, 1870. – Kristan-Tollmann, 1964, p. 95, pl. 15, figs. 3–9.

**Description:** Specimen identical to the one illustrated in Kristan-Tollmann (1964) on plate 15, figure 7. Size of the illustrated specimen is 2.04 mm.

***Prodentalina* sp. A**  
Fig. 5.17

**Description:** A single specimen with delicate, elongated, curved test. Initial part is angular. Eight or nine elongated chambers are uniserially arranged. The length of the chambers increases more strongly than their width. The last cham-

ber is distinctly smaller than the one before, and bears aperture on a long neck. Sutures are visible. The length of the specimen is 0.86 mm. The greatest width of the test is 0.09 mm. The length of the penultimate chamber is 0.20 mm. The length of the last chamber is 0.14 mm (without apertural neck), its width is 0.07 mm. The length of the apertural neck is 0.07 mm.

Order Polymorphinida Mikhalevich, 1980

Suborder Polymorphinina Mikhalevich, 1980

Family Polymorphinidae d'Orbigny, 1839b

Subfamily Polymorphininae d'Orbigny, 1839b

Genus *Eoguttulina* Cushman & Ozawa, 1930

(type species *Eoguttulina anglica* Cushman & Ozawa, 1930; England; Lower Cretaceous)

***Eoguttulina kuhni* (Franke, 1936)**

Fig. 9.2

*Eoguttulina kuhni* (Franke, 1936) subsp. *kuhni* (Franke). – Kristan-Tollmann, 1964, p. 160, pl. 37, figs. 1–4.

Order Vaginulinida Mikhalevich, 1993

Family Vaginulinidae Reuss, 1860

Subfamily Palmulinae Saidova, 1981

Genus *Palmula* Lea, 1833

(type species *Palmula sagittaria* Lea, 1833; New Jersey, USA; Upper Cretaceous)

**Remarks:** See discussion in Copestake and Johnson (2014) regarding synonymy of *Palmula* and *Falsopalmula*.

***Palmula arignota* (Kristan-Tollmann, 1964)**

Fig. 7.2

*Falsopalmula arignota* Kristan-Tollmann, 1964, p. 154, pl. 34, fig. 2.

*Falsopalmula arignota* Kristan-Tollmann, 1964. – Salaj & Jendrejáková, 1967, pl. 20, fig. 8.

*Falsopalmula arignota* Kristan-Tollmann. – He Yan & YueZhi-lan, 1987, pl. 6, figs. 9–10.

*Falsopalmula* sp. – He Yan & Norling, 1991, pl. 4, fig. 14.

p.p. *Pachyphloides oberhauseri* (Sellierde Givrieux & Dessauvagie, 1965). – Trifonova, 1994, p. 31, pl. 11, fig. 7.

***Palmula* sp. A**

Figs. 7.4–7.5

**Description:** The test is lanceolate, slightly flaring, laterally compressed. Proloculus is poorly

visible, followed by seven chambers in planispiral arrangement. Chambers increase their width faster than their height, so that the planispire is asymmetric, with proloculus positioned to the side. Before the completion of the spiral, the uniserial part follows, comprising up to seven chevron-like chambers. Sutures are generally poorly visible. The aperture is radiate, positioned centrally on top of a short neck. The surface of the test is covered by longitudinal to slightly oblique ribs. Approximately 13–19 ribs can be counted on each side of the test. The ribs may terminate or are added along the test's length. The total test height is 0.93–1.39 mm. The width of the test is 0.36–0.57 mm. The planispiral part is 0.13–0.15 mm in diameter. The height of the last chamber is 0.22 mm. The height of the apertural neck is 0.07–0.09 mm. The aperture is 0.10–0.13 mm wide. The distance between the ribs is 0.02–0.03 mm.

***Palmula* sp. B**

Figs. 7.6a–7.6b

**Description:** The test is leaf-like, laterally compressed. The initial part is a planispiral coil, in some specimens positioned next to the longest test axis, in others positioned more to the side and slightly sticking out. The globular proloculus is followed by 7–9 chambers that gradually increase in width, more slowly in height. The planispiral part is followed by a longer uniserial part, at first consisting of two cylindrical chambers that are identical in width and height, and then three or four chambers that become increasingly more chevron-shaped and are higher than previous chambers. The first two of the chevron-shaped chambers increase in width, then again decrease, so that the widest part of the test is approximately mid-way along the uniserial part. The position of the aperture probably shifts from the outside margin to the central position, probably raised on a short neck. The surface of the test is smooth. The wall is made of calcium carbonate, translucent (hyaline). The test is 1.46 mm long. The coiled part is 0.36 mm wide. The uniserial part is 0.41 mm wide. The diameter of the proloculus is 0.04 mm.

***Palmula* sp. C**

Fig. 7.7

**Description:** Like in *Palmula* sp. B, the specimen consists of initial planispiral part, which is larger than in the former species. The planispiral part is followed by uniserially arranged chevron-like chambers. The last one bears centrally

positioned aperture, sitting on top of a short neck. The width of the uniserial part is approximately constant. The interior of the test could not be observed. The wall is made of calcium carbonate (hyaline). The diameter of the planispiral part and the width of the chambers in the uniserial part of the test are the same: 0.52 mm.

Subfamily Marginulininae Wedekind, 1937

Genus *Astacolus* Montfort, 1808

(type species *Nautilus crepidula* Fichtel & Moll, 1798; Mediterranean Sea; Recent)

***Astacolus pediacus* Tappan, 1955?**

Figs. 7.14, 7.15, 8.1–8.3

? pars *Astacolus pediacus* Tappan, 1955, p. 56, pl. 17, fig. 5. [non figs. 1, 12–18]

? *Marginulina karnica* Oberhauser, 1960, p. 22, pl. 2, figs. 9–16, 21–24.

? *Lenticulina* (*Planularia*) *crepidula* (Fichtel & Moll, 1803). – Kristan-Tollmann, 1964, p. 130, pl. 26, fig. 8.

*Lenticulina* (*Astacolus*) *karnica* (Oberhauser, 1960). – Oraveczné-Scheffer, 1965, p. 194, pl. 4, figs. 1–4.

*Lenticulina* (*Astacolus*) *inquisita* (Terquem, 1870). – Salaj & Jendrejáková, 1967, pl. 20, fig. 7.

*L.* (*Vaginulinopsis*) *protracta* (Bornemann). – Tollmann & Kristan-Tollmann, 1970, pl. 8, fig. 10. cf. *Vaginulina* sp. – Resch, 1972, pl. 5, fig. 26.

***Astacolus* cf. *pediacus* Tappan, 1955**

Fig. 8.4

cf. pars *Astacolus pediacus* Tappan, 1955, p. 56, pl. 17, fig. 5. [non figs. 1, 12–18]

cf. *Lenticulina* (*Vaginulinopsis*) *protracta* (Bornemann, 1854). – Kristan-Tollmann, 1964, p. 124, pl. 24, figs. 1–2.

*Astacolus* sp. – Resch, 1972, pl. 5, fig. 20.

***Astacolus* sp. A**

Fig. 7.12

**Description:** The test is elongated, with an equally short or shorter initial planispiral part, followed by four or five chambers in uniserial arrangement. The growth turns early from planispiral to linear, approximately 15% up the test's length. Septa are dorsally curved backwards. Sutures are visible only on the ventral side. The aperture is positioned at the dorsal side of the apertural face, pointing slightly dorsally, surrounded by a short neck. The test surface is smooth. The

entire test is 1.39 mm long, and up to 0.37 mm wide. The planispiral part is 0.29 mm wide.

**Remarks:** The specimens differs from “*Lenticulina* (*Vaginulinopsis*) *cryptospira* Paalzow” (= *Vaginulinopsis cryptospira*) in Kristan-Tollmann (1964) in larger size and in than all of the sutures are visible on the ventral side. It differs from *Lenticulina* (*Vaginulinopsis*) *protracta* (Bornemann) (= *Planularia protracta*) in Kristan-Tollmann (1964) in visible sutures.

***Astacolus arietis* (Terquem, 1866)**

Fig. 7.13

*Astacolus arietis* (Terquem). – Tappan, 1955, p. 55, pl. 19, figs. 1–5.

**Remarks:** The specimen resembles *Palmula* sp. C (Fig. 7.7) but does not evolve chevron-like last chambers. Transition between the two species is possible (see Copestake & Johnson, 2014).

Genus *Vaginulinopsis* Silvestri, 1904

(type species *Vaginulina soluta* var. *carinata* Silvestri, 1898; Italy; Pliocene)

***Vaginulinopsis acrus* Tappan, 1951**

Fig. 7.11

*Vaginulinopsis acrus* Tappan, 1951, p. 10, pl. 3, figs. 21–23.

**Description:** The test is elongated, though relatively wide, and laterally compressed. It consists of a short initial planispiral part, which comprises approximately six chambers in a loose spire. The planispiral part is followed by five uniserially arranged chambers, first in curvilinear, then linear arrangement. The point of break is a little below one half of the total length of the test. The aperture is situated in the corner of the chambers, at the dorsal margin, pointing away from the direction in which the test is growing. It is positioned on a short neck, circular. The septa curve backwards near the dorsal margin of the test. Sutures are not visible on the outline of the test. The surface of the test is smooth. The test is 1.23 mm long. The planispiral part is 0.37 mm wide, and the uniserial part is 0.49 mm wide. The aperture is 0.12 mm in diameter.

**Remarks:** The specimen has smaller planispiral part than “*Lenticulina* (*Vaginulinopsis*) *deformis* (Bornemann, 1854)” (= *Astacolus deformis*)

in Kristan-Tollmann (1964) and *Lenticulina varians varians* in Copestake and Johnson (2014). In opinion of Copestake and Johnson (2014), the former is a junior synonym of the latter.

***Vaginulinopsis cryptospira* (Paalzow, 1917)**

Fig. 7.16

*Lenticulina* (*Vaginulinopsis*) *cryptospira* (Paalzow, 1917). – Kristan-Tollmann, 1964, p. 126, pl. 26, figs. 4–6.

non *Vaginulinopsis cryptospira* (Paalzow). – He Yan & Yue Zhi-lan, 1987, pl. 6, fig. 12.

*Astacolus vetusta* (d'Orbigny). – He Yan & Yue Zhi-lan, 1987, pl. 6, fig. 20.

non *Vaginulinopsis cryptospira* (Paalzow), 1917. – He Yan, 1999, pl. 5, fig. 11.

Subfamily Lenticulininae Chapman, Parr & Collins, 1934

Genus *Lenticulina* Lamarck, 1804

(type species *Lenticulites rotula* Lamarck, 1804; France; Eocene)

***Lenticulina nautiloides* (Bornemann, 1854)**

Figs. 7.9, 7.10

pars *Astacolus connudatus* Tappan, 1951, p. 10, pl. 2, fig. 9.

cf. *Lenticulina* (*Lenticulina*) *excavata* (Terquem, 1864). – Kristan-Tollmann, 1964, p. 110, pl. 20, fig. 6; pl. 21, figs. 6–7.

*Lenticulina* (*Lenticulina*) *nautiloides* (Bornemann, 1854). – Kristan-Tollmann, 1964, p. 111, pl. 21, fig. 1.

*Lenticulina* (*Astacolus*) *nautiloides* (Bornemann, 1854). – Fuchs, 1970, p. 93, pl. 5, figs. 7, 11.

"*Astacolus*" *variens* (Bornemann). – Hohenegger & Piller, 1975, pl. 7, figs. 1–4.

**Remarks:** The figured specimen is smooth, with no sutures visible on the outside.

***Lenticulina varians* (Bornemann, 1854)**

**plexus**

Figs. 8.6–8.7

pars *Astacolus pediacus* Tappan, 1955, p. 56, pl. 17, fig. 1.

*Lenticulina* (*Lenticulina*) *variens convoluta* (Bornemann, 1854). – Kristan-Tollmann, 1964, p. 112, pl. 26, figs. 12–13.

cf. pars *Lenticulina* aff. *variens* (Bornemann). – Apthorpe, 2003, p. 22, pl. 4, fig. 24.

*Lenticulina varians* (Bornemann, 1854) plexus. – Copestake & Johnson, 2014, p. 220, pl. 16, fig. 18; pl. 16, figs. 17, 19–21, 25.

**Remarks:** Identical specimen was illustrated by Tappan (1955) among the type material of *Astacolus pediacus* Tappan, 1955. However, the type material of the said species probably contains more than one species.

***Lenticulina gottingensis* (Bornemann, 1854)**

Figs. 8.10–8.13, 8.15

*Lenticulina* (*Lenticulina*) *gottingensis gottingensis* (Bornemann, 1854). – Kristan-Tollmann, 1964, p. 107, pl. 19, figs. 3–7.

*Lenticulina* (*Lenticulina*) *gottingensis gottingensis* (Bornemann). – Tollmann & Kristan-Tollmann, 1970, pl. 8, fig. 6.

*Lenticulina* (*Lenticulina*) *gottingensis polygonata* (Franke). – Tollmann & Kristan-Tollmann, 1970, pl. 8, fig. 7.

? *Lenticulina* sp. – Resch, 1972, pl. 5, fig. 25.

*Lenticulina gottingensis* Bornemann. – He Yan & Hu Lan-ying, 1978, pl. 3, fig. 4.

*Lenticulina nautiloides* (Bornemann). – He Yan & Hu Lan-ying, 1978, pl. 3, fig. 11.

? *Lenticulina gottingensis* (Bornemann). – He Yan & Yue Zhi-lan, 1987, pl. 7, fig. 3.

*Lenticulina gottingensis* (Bornemann), 1854. – He Yan, 1999, pl. 3, fig. 13; pl. 5, fig. 2.

**Description:** The test is multichambered, planispiral, oval in equatorial view, rhomboid in axial view. The surface is smooth; no sutures are visible. The proloculus is followed by 9–10 chambers, wider than high, and increasing in width faster than in height. Septa are convex, equally thick as the outer wall. The apertural face is also convex. The aperture is positioned dorsally, raised on a short neck, simple rounded. A small indentation is visible at the base of the apertural face, i.e. between the apertural face and the older part of the spire. The lower half of the test has a distinct keel. The wall is made of calcium carbonate, translucent (hyaline). The height of the specimens is 0.68–0.87 mm.

***Lenticulina* cf. *gottingensis* (Bornemann, 1854)**

Fig. 8.14

**Remarks:** The specimen is smaller (height 0.33 mm) than *L. gottingensis* on Figures 8.10–8.13, 8.15.

***Lenticulina stenocostata*****Kristan-Tollmann, 1964?**

Figs. 8.16–8.17

*Lenticulina* (*Lenticulina*) *stenocostata* Kristan-Tollmann, 1964, p. 114, pl. 29, fig. 14.

***Lenticulina* stet.**

Fig. 8.8

**Remarks:** The test has a more elongated oval shape in equatorial view, and the indentation at the base of the apertural face is more pronounced than in *L. gottingensis*. The height of the specimen is 0.50 mm.

Subfamily Vaginulininae Reuss, 1860

Genus *Planularia* DeFrance in Blainville, 1826

(type species *Planularia auris* DeFrance in Blainville, 1826; Mediterranean Sea; Recent)

***Planularia* cf. *protracta*****(Bornemann, 1854)**

Fig. 8.9

cf. *Lenticulina* (*Vaginulinopsis*) *protracta* (Bornemann, 1854). – Kristan-Tollmann, 1964, p. 124, pl. 24, figs. 1–2.

Family Lingulinidae Loeblich & Tappan, 1961, stat. elevated Mikhalevich, 2014

Subfamily Lingulininae Loeblich & Tappan, 1961

Genus *Lingulina* d'Orbigny, 1826

(type species *Lingulina carinata* d'Orbigny, 1826; Italy; Tertiary)

***Lingulina lingua* Kristan-Tollmann, 1964**

Figs. 8.19–8.20

*Lingulina lingua* Kristan-Tollmann, 1964, p. 139, pl. 30, figs. 1–3.

*Septalingulina tetrasetpta* He Yan & Norling, 1991, p. 26, pl. 4, figs. 5, 6, 8–10, 12, 13.

*Grillina grilli* Kristan-Tollmann, 1964. – Trifonova, 1994, p. 32, pl. 11, fig. 2.

**Description:** As for the type material. The test length is 0.37–0.60 mm, the test width is 0.29–0.44 mm. The ratio between length and width of the test is 1.19–1.36.

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