The benthic foraminifer *Stomatorbina binkhorsti* (Reuss, 1862): Taxonomic review and ecological insights

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Abstract

The benthic foraminifer *Rosalina binkhorsti* Reuss, 1862, was cosmopolitan in Late Cretaceous to early Paleogene shallow-water seas. It possesses a distinctive composite wall made of a continuous, agglutinated layer discontinuously covered by secondary hyaline outer deposits. Its taxonomic position, phylogeny, morphology, wall structure, and composition have been debated for a long time. Based on abundant, well-preserved material from the Danian of the Kambühel Formation in the Northern Calcareous Alps, Austria, we identify elements in the here emended species *Stomatorbina binkhorsti* which support a strong affinity to the order Textulariida, within the genus *Stomatorbina* Dorreen, 1948. Usually regarded as free (non-fixing), *S. binkhorsti* is here illustrated attached to small bioclasts in high-energy carbonate settings. The attached specimens are juvenile forms with a wall covered by massive hyaline deposits. This observation suggests that secondary lamellar parts added to the wall may have served for stabilisation or fixation to the substrate.

Rosalina binkhorsti Reuss, 1862, war eine in den Flachwassermeeren der Oberkreide und des frühen Paläogens kosmopolitische benthonische Foraminifere. Sie besitzt eine zusammengesetzte Wand, bestehend aus einer kontinuierlichen agglutinierten Lage welche diskontinuierlich von äusseren sekundär-hyalinen Abschnitten bedeckt ist. Ihre taxonomische Position, Phylogenie, Morphologie, Wandstruktur und –zusammensetzung ist seit langem umstritten. Basierend auf gut erhaltenem und reichhaltigem Material aus dem Danium der Kambühel Formation in den Nördlichen Kalkalpen von Österreich, werden Charakteristika identifiziert, welche nachhaltig eine Affinität zur Gattung *Stomatorbina* Dorreen, 1948 innerhalb der Ordnung Textulariida belegen. Diese Foraminiferenart, gewöhnlich als frei lebend (nicht fixiert) angesehen, wird illustriert fixiert an kleine Bioklasten in einem hochenergetischen karbonatischen Ablagerungsmilieu. Die fixierten Formen sind gewöhnlich juvenile Exemplare deren Wand mehr oder weniger massiv von hyalinen Ablagerungen bedeckt ist. Dies lässt vermuten, dass sekundäre lamellare Ablagerung, die der Wand hinzugefügt werden, eine Rolle in der Stabilisierung oder der Fixierung auf dem Substrat spielten.

1. Introduction

The cosmopolitan species *Stomatorbina binkhorsti* (see synonymy) was first described from isolated specimens recovered from the Maastrichtian type area by Reuss (1862) as *Rosalina binkhorsti*. Since then, the higher-level taxonomic position of this species remained uncertain. Largely regarded as a calcitic rotaliid (e.g., Reuss, 1862; Hofker, 1927; Brown and Brönnimann, 1957; Reiss, 1958, 1963; McGowran, 1966), *S. binkhorsti* has also been assigned to the aragonitic order Robertinida (e.g., Loeblich and Tappan, 1964) or to the calcitic microgranular order Fusulinida (Hofker, 1963). Two major reasons explain this long-standing ordinal taxonomic uncertainty: (i) the species is discontinuously covered by calcitic hyaline lamellar ("rotaliid-like") deposits, and non-covered areas were, as remarked by Hofker (1976), erroneously interpreted as secondary apertures (e.g., in Uchio, 1952; Loeblich and Tappan, 1964) and (ii) the type species of *Stomatorbina* was reported to be aragonitic by X-ray determination (Loeblich and Tappan, 1964). But in their 1987 monography, Loeblich and Tappan placed *Stomatorbina* in the superfamily Discorbacea, family Mississippinidae, and subfamily Stomatorbininae. The lower, generic rank of *S. binkhorsti* is also controversial: the species has been assigned to a total of nine different genera since its first description. This taxonomic confusion has considerably limited phylogenetic approaches. As most scientists focussed on the above-mentioned wall and apertural issues, other important aspects of the species, such as its internal morphology and ecology, have been disregarded. This paper aims at clarifying the taxonomic position of *S. binkhorsti* and also at improving our understanding of the structure, morphology, and mode of life of this distinctive but divisive foraminiferal species.

2. Geological settings and studied material

The Kambühel Formation (Tragelehn, 1996) or Kambühel Limestone (sensu Tollmann, 1976), with its type locality Kambühel, near Ternitz, Lower Austria (Fig. 1), represents a Maastrichtian–upper Palaeocene carbonate platform that developed along the southern rim of the Northern Calcareous Alps. The Kambühel Formation

is well exposed in the easternmost part of the Northern Calcareous Alps and in the Mürzalpen Nappe (Plöchinger, 1967; Lein, 1982; Tragelehn 1996). Tragelehn (1996) provided a detailed microfacies and stratigraphic analysis of the Kambühel Limestone occurrences. Most discoveries are large olistoliths reworked in deeper water facies of the time-equivalent Upper Gosau Subgroup. Findings in the early Paleogene Zwieselalm Formation (Kollmann and Summesberger, 1982; Schlagintweit at al., 2003; Krische et al., 2012) are the westernmost known occurrences of such olistoliths.

The uppermost Maastrichtian part of the Kambühel Formation is rich in orbitoidal foraminifera (*Orbitoides*, *Lepidorbitoides*), *Siderolites calcitrapoides* Lamarck, meandropsinids [*Nummofallotia cretacea* (Schlumberger)] and rotaliids. The planktic foraminiferal index species *Pseudoguembelina hariaensis* Nederbragt allows to identify the upper Maastrichtian zone CF 3 (Keller, 2014, table 1). Here, *S. binkhorsti* is present but rare. This facies

is sharply overlain, above an iron-impregnated hard ground, by lower Danian limestones of similar facies, but displaying different foraminiferal fauna. The Danian limestones, dated by planktic foraminifera (det. Gerta Keller), comprise the major part of the Kambühel Formation. These are rich in bryozoans and benthic foraminifera, lacking larger taxa. A typical association includes *S. binkhorsti*, *Planorbulina uva* Scheibner, and *Cibicidoides* gr. *succedens* (Brotzen), and polymorphinids (Schlagintweit et al., 2018, fig. 3) (Fig. 2). *Solenomeris* sp. is also often observed, forming acervulinid macroids. Between the Danian limestones that comprise the lower part of the succession and the Selandian-Thanetian limestones above, neither a clear-cut boundary surface nor a sharp change of facies were identified. Up-section, large thick-walled *Gyroidinoides* Brotzen, *Cocoarota*? *orali* Inan and fragments of encrusting *Haddonia praeheissigi* Hagn are common. The latter two species become more significant in the following micritic, mostly bioclastic coral limestones (floatstones, boundstones) together with large-sized dasycladaleans [*Neomeris* (*Larvaria*) *deloffrei* Tragelehn, *Dactylopora bystricki* Dieni, Massari, and Radoičić]. The larger biocalcifyers (corals, *Parachaetetes*) are locally encrusted by sessile foraminifera (*Haddonia*, *Placopsilina*, *Miniacina*, *Planorbulina*) and crustose coralline algae. The thalli of the red algae are often affected by tiny bioeroding foraminifera. In the micritic matrix *Stomatorbina* sp., a rather small-sized form with rounded periphery occurs (Fig. 3, above). *S. binkhorsti* was not observed from these horizons. These limestones are exposed only near the southeastern edge of Kambühel. A schematic, composite (based on different outcrops) reconstruction of the
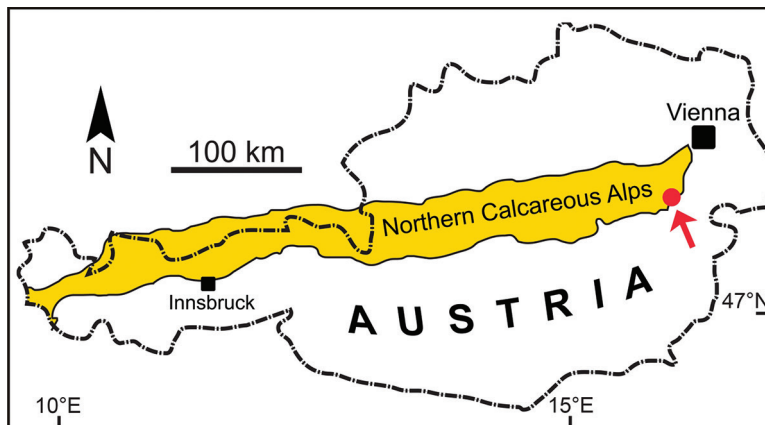

Figure 1: Location of the Kambühel hill (red dot) in the southeastern part of the Northern Calcareous Alps, Austria.
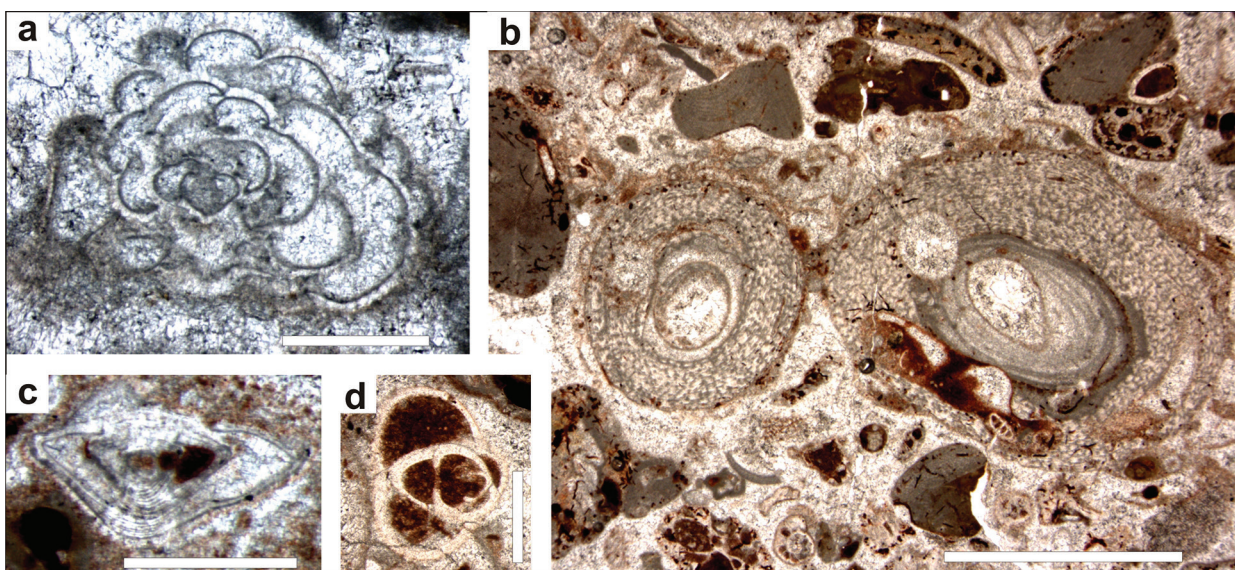

Figure 2: Typical foraminiferal assemblages associated with *S. binkhorsti* (Reuss) in the early Danian Kambühel Formation of the type locality. (a) *P. uva* Scheibner, thin section KB 23. (b) Microfacies with *Solenomeris* macroids, thin section KB 112/133-2. (c) *C.* gr. *succedens* (Brotzen), thin section KB 36. (d) Polymorphinid, thin section KB 121. Scale bars 0.2 mm (a, c–d), 1.0 mm (b).

Late Cretaceous–early Paleogene succession at Kambühel with the distribution of *S. binkhorsti* (Reuss), and *Stomatorbina* sp. is shown in Figure 3.

The Palaeocene part of the Kambühel Formation (Piller et al., 2004) is the type locality of diverse fossil taxa, for example, a foraminifer (Schlagintweit et al., 2016: *Clypeorbis*? *ultima*), dasycladalean algae (Tragelehn, 1996), a brachiopod (Dulai et al., 2008: *Basiliocostella kambuehelensis*), and a decapod crustacean (Verhoff et al., 2008: *Titanocarcinus kambuehelensis*). In the framework of his PhD Thesis, Tragelehn (1996) treated only the benthic foraminifera occurring in limestone of reefal affinity (mainly encrusting taxa). The species *S. binkhorsti* was not mentioned in his work and was recorded only recently, for the first time, from the Kambühel Formation (Schlagintweit et al., 2018). The numerous specimens, especially from the early Danian limestone, allow us to gain further insights into the taxonomic position, biometric variability, wall structure, and mode of life of this distinctive foraminiferal species, particularly during its juvenile stage (Figs. 4–7).

The thin sections from which the present study is based are deposited at the University of Innsbruck (collection Diethard Sanders). The carbonate rock outcrops, from which the herein studied thin sections were made, are from the following coordinates:

Sample KB 21, KB 23: 47°44'49,982"N, 16°01'51,570"E
Samples KB 34, KB 42, KB 121: 47°44'45,436"N, 16°01'46,5"E
Samples KB 100, KB 101, KB 104, KB 105, KB 107, KB 112, KB 121, KB 181: 47°44'42"N, 16°01'52"E
Samples KB 88, KB 92, KB 96, KB 98: 47°45'01"N, 16°02'02"E for *S. binkhorsti*
Samples KB 10a, KB 11, KB 157–158: 47°44'43"N, 16°02'03"E for *Stomatorbina* sp.

3. Higher-level classification

In the literature, the species *S. binkhorsti* has been alternately regarded as a rotaliid (e.g., Reuss, 1862; Hofker, 1927; Brown and Brönnimann, 1957; Reiss, 1958, 1963; McGowran, 1966), a robertinid (e.g., Loeblich and Tappan, 1964), a discorbid (Loeblich and Tappan, 1987), or as a fusulinid (e.g., Hofker, 1963), entailing doubts about its high-rank classification. Foraminifers with a composite agglutinated/microgranular and hyaline radial or fibrous calcitic wall were traditionally classified within Fusulinana or Nodosariata (Loeblich and Tappan, 1987; Vachard et al., 2010). However, following the Permo-Triassic mass extinction, foraminifers displaying such composite walls are extremely rare and systematic classifications are more ambiguous. As a result, post-Palaeozoic foraminifers possessing a composite wall have been
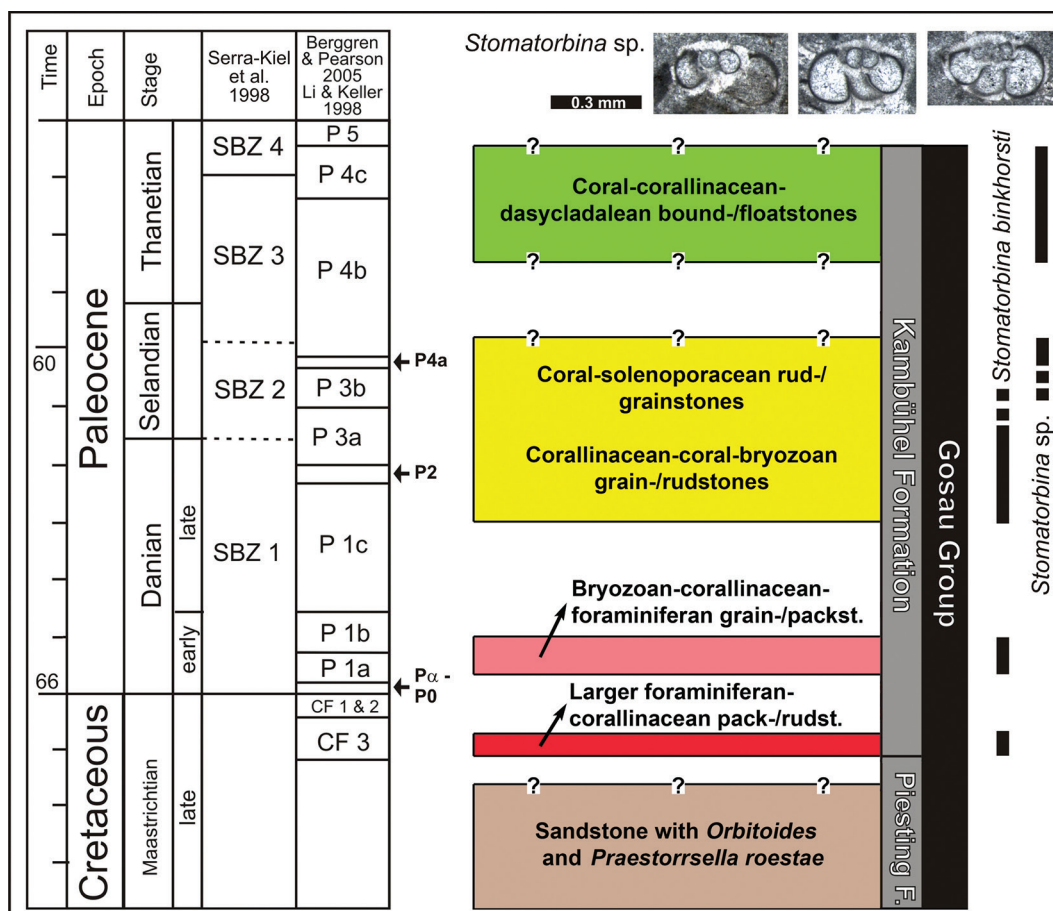

Figure 3: A schematic geological scheme of the Late Cretaceous–early Paleogene succession at Kambühel (based on different outcrops) with the distribution of *S. binkhorsti* (Reuss), and *Stomatorbina* sp. (modified from Schlagintweit et al., 2018, fig. 2).
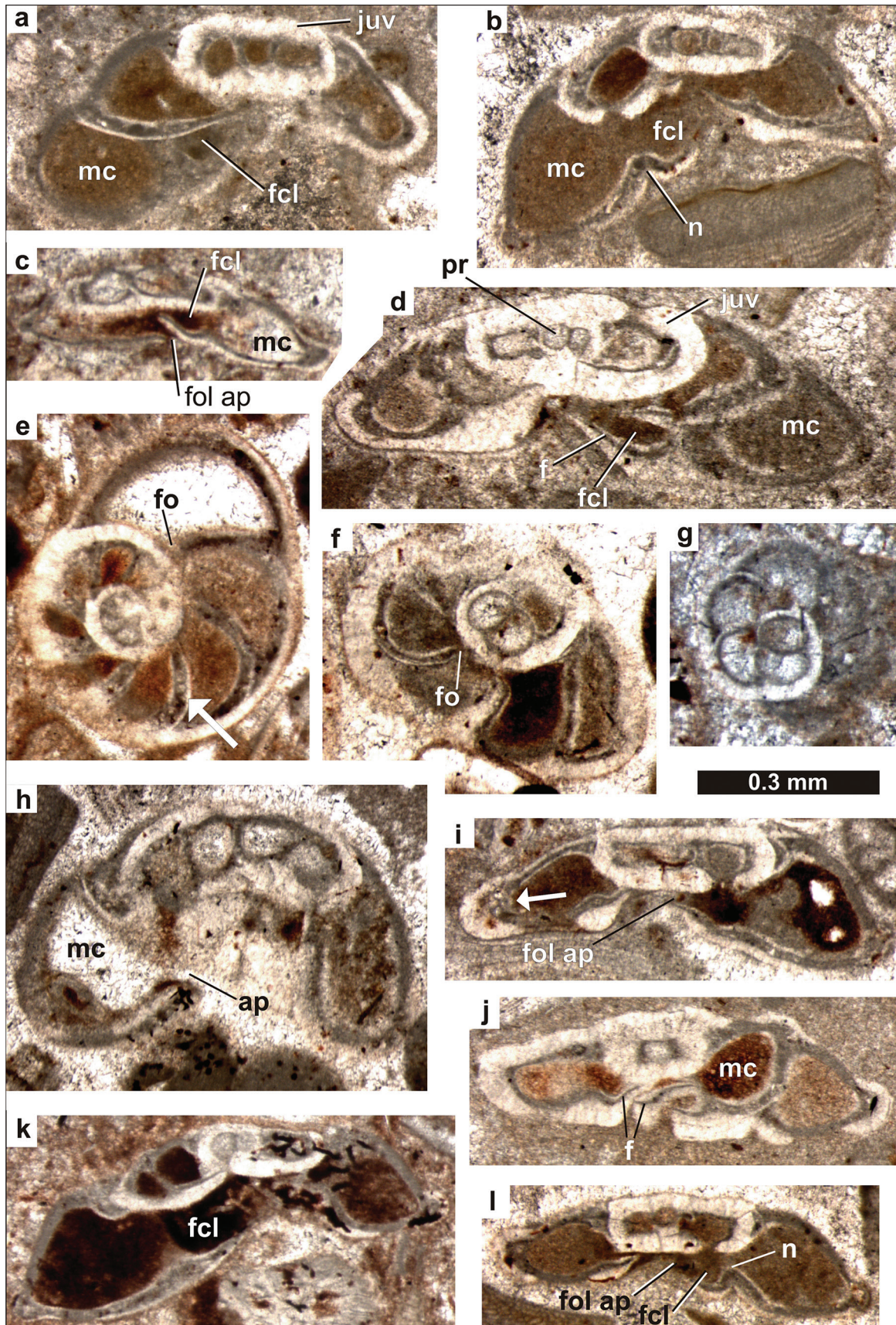
Figure 4: Thin-section photographs of *S. binkhorsti* (Reuss) from the early Paleogene (Danian–Selandian) of the Kambühel Formation. (a–b, d, i–l) Axial and sub-axial sections; thin sections KB 23, KB 105, KB 116, KB 107. (e, g, h) Equatorial and sub-equatorial sections; thin sections KB 88, KB 34, KB 84-4. (c, f) Oblique sections; KB 121, KB 92. Note the presence of large, originally aragonitic particles in specimen E, and I (arrows). Note the presence of three successive layers of lamellar deposits in the umbilical region in specimen J. Abbreviations: ap = aperture, f = folium, fcl = foliar chamberlet lumen, fo = foramen, fol ap = foliar aperture, juv = juvenarium, mc = main chamber, n = notch, pr = proloculus. Arrows in (e) and (i): agglutinated grains.

taxonomically assigned to either fusulinans (e.g., Septfontaine, 1978; Schlagintweit et al., 2015), nodosariats (e.g., Rigaud and Schlagintweit, 2016), rotaliids, textulariids, robertinids (Loeblich and Tappan, 1987), or spirillinids (Rigaud et al., 2018). Rigaud and Schlagintweit (2016) noticed that despite similarities in their wall appearance, post-Palaeozoic foraminifers with composite hyaline

calcitic/agglutinated microgranular walls can be separated into two distinct categories: those with continuously bilayered (or double-layered) walls (e.g., *Archaeosepta* or *Nodocantabricus*: see Wernli, 1970; Rigaud and Schlagintweit, 2016) and those with secondarily built hyaline calcitic layers, which may encompass several chambers or distinct parts of the test (e.g., *Altamirella*, *Murgeina* or
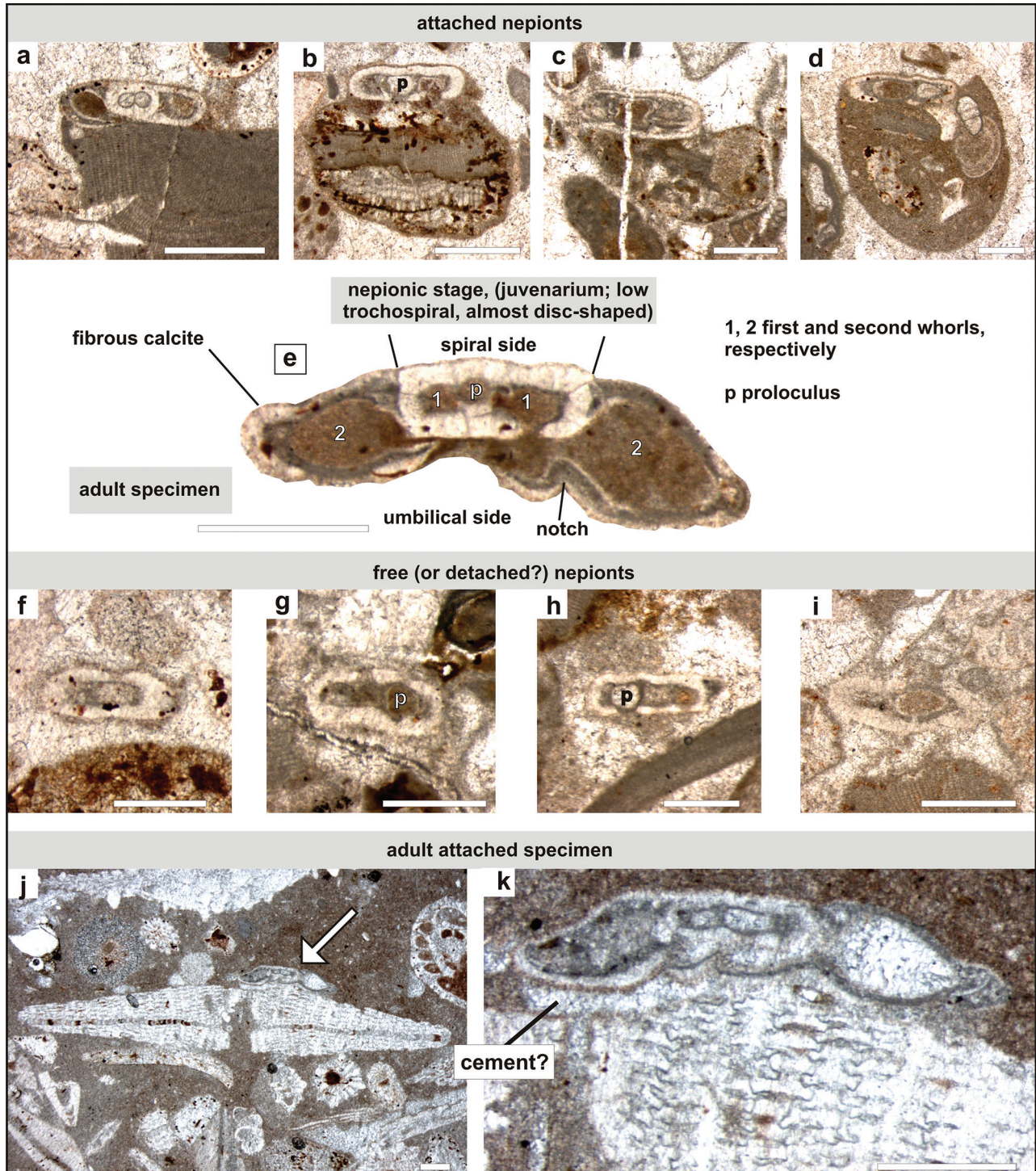

Figure 5: Attached specimens of *S. binkhorsti* (Reuss) from the late Maastrichtian (j, k) and Danian (a–i) of the Kambühel Formation, Austria. (a–d) Juvenile specimens attached to coralline algae and other bioclasts; thin sections KB 96-1, KB 98-1, KB 104-11, KB 101-7. (e) Adult specimens, axial sections, with some descriptive terms used herein; thin section KB 107-1. (f–i) Free (or detached) nepionts; thin sections KB 34-B-11, KB 21-1, KB 112-1, KB 100-2. (j, k) Adult specimens attached to an orbitoidid foraminifer; thin section KB 181-1-10. Scale bars 0.2 mm.

Mohlerina: see Schlagintweit, 2012; Schlagintweit et al., 2015).

The wall structure is therefore the key to a taxonomic approach. In *S. binkhorsti*, the finely agglutinated layer is continuous and forms the framework of the test (= primary wall sensu Hofker, 1963, 1978; e.g., Fig. 4e, j). Conversely, hyaline outer deposits are discontinuous in all observed specimens (e.g., Fig. 4a). Moreover, they do not (or rarely or partially) cover the septa (Fig. 4e). Hence, the composite wall of *S. binkhorsti* cannot be regarded as bilayered *sensu stricto*. It is primarily finely agglutinated and should be assigned to the Textulariida. Like in *Altamirella*, hyaline outer deposits are secondary, as first explained by Hofker (1963), and a single hyaline deposit may encompass several chambers (Fig. 4a, b, d–l). These calcitic deposits may be observed along the outer surface and more scarcely along the inner surface of the finely agglutinated primary wall. Interestingly, *S. binkhorsti* may preferentially select aragonitic particles (e.g., see recrystallised or reprecipitated, originally recrystallised particles in Figs. 4g; 5j) to form its finely agglutinated test, as noticed first by Hofker (1963, 1978).

The presence of large, originally aragonitic particles can be traced in our specimens (Fig. 5j). Due to their unstable nature, aragonitic particles are extremely rarely preserved in the fossil record. In our material, gastropods and dasycladalean green algae, which are known to originally possess an aragonitic skeleton, are always fully reprecipitated or recrystallised into mosaic sparite, in the same way as the here illustrated originally aragonitic particles. Other portions of the test of *S. binkhorsti* (i.e., calcitic cement and secondary deposits) are comparatively remarkably well preserved. Such aragonitic particles were most likely inadvertently analysed by Loeblich and Tappan (1964) in the type species of *Stomatorbina*, misleading them into classifying this form in Robertinida. Recent specimens of *Stomatorbina* have been analysed (? the cement) by Blackmon and Todd (1959) and McGowran (1966) as being made of high magnesian calcite. The origination and diversification of a new aragonitic group of foraminifers in Late Cretaceous–Paleogene strata are unlikely since, during that time period, aragonitic forms, including representatives of the order Robertinida, were rare and poorly diversified (see Rigaud et al., 2013, 2015, 2016; Rigaud and Blau, 2016).

A debate regarding the wall structure of *S. binkhorsti* is particularly recurrent in the literature. Some authors regarded the species as bilamellar (e.g., Reiss, 1958, 1963; Hansen, 1979), whereas others regarded it as monolamellar (McGowran, 1966). As previously stated by Hofker (1963), the hyaline outer deposits are secondary and *S. binkhorsti* is an agglutinated, non-lamellar species. Whether the secondary deposits are monolamellar or bilamellar is therefore of minimal taxonomic importance and depends on the part of the test under investigation, as lamellar deposits may be multiple (e.g., note the three layers of lamellar deposits in the umbilical region of the specimen illustrated in Fig. 4j).

4. Generic affinity

As previously mentioned, the taxonomy of this Late Cretaceous–early Paleogene (Maastrichtian to Palaeocene, e.g., Di Carlo et al., 2010) species is highly controversial. *S. binkhorsti* has been assigned to almost 10 different genera (see synonymy list later). In the literature of the last decades, however, two main generic attributions usually remain: *Mississippina binkhorsti* (Reuss) or *S. binkhorsti* (Reuss). Both genera were first regarded as synonyms by Hofker (1956). Notwithstanding, in Loeblich and Tappan (1987), the stratigraphic ranges of *Mississippina* Howe and that of *Stomatorbina* Dorreen are distinct: lower Oligocene to Holocene, and Eocene to Holocene, respectively. The two genera are traditionally positioned within the family Mississippinidae Saidova (e.g., Loeblich and Tappan, 1987, 1992; Sirel, 1998; Di Carlo et al., 2010).

As vividly debated in the literature (e.g., Dorreen, 1948; Uchio, 1952; Hofker, 1956, 1969; Todd, 1965), the genera *Mississippina* and *Stomatorbina* show strong structural and morphological affinities. According to Hofker (1969: p. 73), "*Stomatorbina* differs … from *Mississippina*, only in minor, specific characteristics". Yet, Loeblich and Tappan (1987), based on differences in test shape (*Stomatorbina* is distinctly trochoid whereas *Mississippina* is flattened trochospiral with nearly planispiral coils), regarded the two genera as being part of two distinct subfamilies. As Dorreen (1948: p. 296) observed, "in *Mississippina* the whorls embrace both dorsally and ventrally and the aperture extends from the ventral side, across the periphery, to the dorsal side. Dorsal sutures are not limbate, as in *Stomatorbina*, but are depressed". The latter observation was also made by Todd (1965: p. 24). An additional difference may exist between the two genera: while all illustrations of the type species of *Stomatorbina* (*Lamarckina torrei* Cushman and Bermúdez, e.g., Dorreen, 1948: pl. 39, fig. 4; Loeblich and Tappan, 1987: pl. 600, figs. 13–15) display a clear notch, which is an outer expression of the presence of an internal chamber wall infold, available illustrations of the type species of *Mississippina* (*M. monsouri* Howe; Howe, 1930: pl. 27, fig. 4; Loeblich and Tappan, 1987: pl. 600, figs. 7–9) suggest that such infold is far less pronounced in the latter genus.

In view of (1) the trochoid test (Fig. 3a, b, d), (2) the ventral position of the chambers (Fig. 4a–d, i–l), (3) the common presence of secondary hyaline deposits above the sutures (Fig. 4d–h), and (4) the presence of a well-pronounced notch in our specimens (Fig. 4a–d, l), we strongly recommend to name the species described by Reuss (1862, *R. binkhorsti*) as *S. binkhorsti* (Reuss, 1862).

5. Mode of life: insights from the test structure and appearance

The thin sections of Danian grainstones of the Kambühel Formation yielded several specimens of *S. binkhorsti*, predominantly juvenile forms that are demonstrably fixed to other bioclasts (Fig. 5). Specimens of *S. binkhorsti* attached to hard substrates had, according to our knowledge, never been illustrated before. Morphologically

and structurally comparable foraminifers (e.g., *Tetrataxis*, *Mohlerina*, *Altamirella*) are also commonly found in attached position (Cossey and Mundy, 1990; Vachard et al., 2010; Schlagintweit, 2012; Schlagintweit et al., 2015). Observed attached specimens of *S. binkhorsti* are mostly juveniles (nepionts). The nepiont, ranging in diameter from 0.22 to 0.45 mm (Table 1), usually consists of a spherical proloculus and the first whorl that almost planispirally surrounds the proloculus. Note that due to the rapid widening of the chambers, the proloculus does not appear centred in axial sections (Figs. 4d, l; 5b). Nepionts lack the angular margin of adult forms as they are thickly covered by distinctive secondary hyaline deposits. They are sometimes observed free (? detached) between other skeletal grains (Fig. 5f–i). In rare cases, we observed fully grown attached specimens (e.g., Fig. 5i, j). Note that in the illustrated adult attached specimen from the late Maastrichtian, the pore space (now filled with sparitic, diagenetic cement) is observed between the specimen and the substrate (a larger benthic foraminifera) on which it attached. The presence of this empty space suggests that a non-calcified, probably organic anchorage structure existed between the foraminifer and the substrate on which it attached, hampering sediment infiltration (see also specimens in Fig. 5c). Such structure is also observed in several morphologically and structurally similar foraminifers (e.g., see Schlagintweit, 2012: fig. 7 for micro-aquarium in *Tetrataxis* and *Mohlerina*). The observation of numerous attached specimens points to an epibenthic, at least intermittently attached mode of life for *S. binkhorsti*. For small species like *S. binkhorsti*, which can be easily eroded and transported by currents, attachment is certainly an advantage. Transport and associated attrition could represent an important limitation for the development of foraminifers in high-energy settings. In view of its wall structure, *S. binkhorsti* seems very well adapted to limit transport and its undesirable effects: (1) in juvenile specimens, hyaline secondary deposits thicken the test (by a factor of 2–4), and specimens adopt attachment strategies so that higher flow velocities are needed for transport and erosion and (2) in adult forms, the most fragile and/or vital parts of the test (i.e., test margin and apertural system) are more heavily covered by hyaline lamellar deposits, increasing the resistance of *S. binkhorsti* to erosional processes and fragmentation.

The mode of life and wall structure of *S. binkhorsti* may therefore result from adaptation to shallow, high-energy environments. Secondary hyaline deposits may have played an important role to stabilise and protect both attached and free specimens of *S. binkhorsti*. Interestingly, the initial embryonic part of *Altamirella*, *Stomatorbina*, and *Sabaudia* (juvenarium sensu Charollais and Brönnimann, 1965) is almost structurally identical: the whole juvenarium is commonly surrounded by hyaline deposits, which form a protective envelope. Note that laminar deposits around the juvenarium are mostly formed following the formation of the first whorl, not affecting early dispersal. Schlagintweit et al. (2015) proposed that

not only this hyaline cover may have limited transport and test damage but also it serves as a protection from predators and unfavourable environmental conditions. This might be true for juvenile specimens that are almost fully enveloped but the strategic position of laminar deposits in adult specimens of *S. binkhorsti* rather points to a search for more robustness, and resistance to attrition.

6. Systematic Palaeontology

For glossary of terms used for shell description, reference is made to Hottinger (2006). Terms like notch, folia, foliar aperture, and foliar chamberlet are typical structures described in lamellar rotaliids (e.g., Hottinger, 2014). This, however, does not exclude their usage in other groups and these structures or equivalents are not restricted to Rotaliida. Several Robertinids display an umbilical notch (= diaphragm in Höglund, 1947, see, e.g., modern *Ceratocancris* or *Robertina*) that is related to an internal wall infolding that fully or partially subdivides chambers. Folia-like structures, usually named umbilical flaps, lobes, or tips (see diagnoses in Loeblich and Tappan, 1987), are well known in agglutinated forms such as *Discorinopsis*, *Asteroparatrochammina*, *Lepidodeuterammina*, *Rotaliammina*, or *Tiphotrocha*.

Phylum Foraminifera d'Orbigny, 1826

Class Globothalamea Pawlowski et al., 2013
Order "Textulariida" Delage and Hérouard, 1896; sensu Pawlowski et al., 2013
Family Mississippinidae Saidova, 1981
Genus *Stomatorbina* Dorreen, 1948
Type species: *Lamarckina torrei* Cushman and Bermúdez, 1937
Stomatorbina binkhorsti (Reuss, 1862), emend.
Figs. 4–5

1862 *Rosalina binkhorsti* Reuss, p. 317, pl. 2, fig. 3a–c.
1899 *Discorbina binkhorsti* (Reuss); Egger, p. 164, pl. 18, figs. 28–30.
1927 *Pulvinulina binkhorsti* (Reuss); Hofker, p. 126, text-figs. 4–11.
1936 *Conorbina binkhorsti* (Reuss); Brotzen, p. 145.
1946 *Discorbis binkhorsti* (Reuss); Schijfsma, p. 82, text-fig. 4a–c.
1950 *Gavelinella binkhorsti* (Reuss); Visser, p. 265, pl. 5, fig. 6a–c, pl. 10, fig. 12.
1951 *Discopulvinulina binkhorsti* (Reuss); Hofker, p. 20, text-figs. 22a–e, 23a–c.
1952 *Stomatorbina binkhorsti* (Reuss); Bermudez, p. 33.
1957 *Stomatorbina binkhorsti* (Reuss); Brown and Brönnimann, p. 36, text-figs. 26–38.
1958 *Mississippina binkhorsti* (Reuss); Hofker, figs. 1–6.
1963 *Mississippina binkhorsti* (Reuss); Hofker, p. 157–160, figs. 1–5.
1972 *Mississippina binkhorsti* (Reuss); Samuel et al., pl. 36, figs. 1, ?2–4.
non 1991 *Mississippina binkhorsti* (Reuss); Radoičić, pl. 6, figs. 4–6, non 7 (= *Sistanites iranica* Rahaghi).

1998   *Mississippina binkhorsti* (Reuss); Sirel, p.103, pl. 1, figs. 2–5, 8–9.

2008   *Mississippina binkhorsti* (Reuss); Özgen Erdem, pl. 1, fig. 3.

?2008   *Stomatorbina binkhorsti* (Reuss); Pignatti et al., pl. 6, figs. 1–2.

2010   *Stomatorbina binkhorsti* (Reuss); Di Carlo et al., p. 66, pl. 1, fig. 11.

2012   *Mississippina binkhorsti* (Reuss); Leszczyński et al., fig. 9c.

??2014   *Stomatorbina binkhorsti* (Reuss); Hosseinzadeh et al., p. 479, fig. 3a-b.

2015   *Stomatorbina binkhorsti* (Reuss); Sirel, pl. 28, figs. 6–15.

2016   *Mississippina binkhorsti* (Reuss); Matsumaru, pl. 8, fig. 8.

2017   *Stomatorbina* (*Mississippina*) *binkhorsti* (Reuss); Buček and Köhler, p. 75, pl. 29, figs. 2, 5.

2019   *Stomatorbina binkhorsti* (Reuss); Schlagintweit and Rashidi, pl. 6, fig. 18.

2019   *Stomatorbina binkhorsti* (Reuss); Consorti and Köruğlu, fig. 10i.

Emended description: Test small, hemispherical to rounded sub-trapezoid (see characteristic trapezoid sections in Fig. 4i, l), with a flat, slightly irregular to depressed umbilical side and a keeled margin, more pronounced in adult forms. The juvenarium (Fig. 5b–d, f–i), almost completely covered by hyaline laminar deposits, is formed by a globular proloculus and 1–1.5 whorl(s) of extremely low trochospirally coiled first hemispherical then sub-trapezoid, sometimes double-keeled chambers (about 5–6 chambers per whorl), increasing fairly rapidly in size. Subsequent chambers, the shape of rounded trapezoid prisms, are coiled in a more pronounced trochospiral arrangement, forming one to two additional whorl(s), with 6–7 chambers per whorl. Slightly inflated, these chambers are only partly covered by hyaline laminar deposits, typically near the apertural system, along the sutures (spiral suture included), and at the test margin. Sutures, largely covered by hyaline laminar deposits, appear broad and distinct, raising above the (comparatively sunken) chamber surface. An internal infold of the chamber wall partially separates the main chamber from a foliar chamberlet, forming a distinct umbilical notch. Wall composite, made of a primary, continuous agglutinated layer (thickness up to 0.03 mm) discontinuously covered by secondary hyaline, prismatic calcitic outer deposits (thickness up to 0.08 mm). Foramen, single, a narrow slit in interio-marginal, sub-peripheral position, as the aperture. Supplementary (foliar) aperture, a long slit at the base of the folium.

Dimensions: The observed test diameters range from 0.51 to 1.2 mm; the height ranges from 0.12 to 0.55 mm (see Fig. 6). For the nepiont data, see Table 1. The plot of test diameter against height (or thickness) shows that the two parameters are directly correlated. It also gives evidence that the larger the tests, the greater the variability (ratio D/H).

Remarks: The original description of the species *R. binkhorsti* by Reuss (1862, p. 317, translated) from calcareous marls of the Maastrichtian type area (the Netherlands) was based on isolated specimens (not thin sections): "Rather rare. Size 0.88 mm. Almost circular or broad oval, very strongly depressed, flake-like, with acute margin. Spiral side slightly curved, with 2½ to 3 whorls, the internal ones not clearly discernible; the last (Remark: whorl) with 4 to 5 broad arched chambers, all surrounded by a rounded strip-like fringe. The umbilical side is depressed towards its centre; the last chamber is very large. All (Remark: chambers) terminating towards the umbilicus by means of a tongue-like appendage being the largest in the latest chambers. The test surface is finely perforate". Important information such as the wall type and structure, the aperture type and position, the chamber partition, and the presence of a juvenarium were not stated, leading to several taxonomic controversies. The here emended description includes this information.
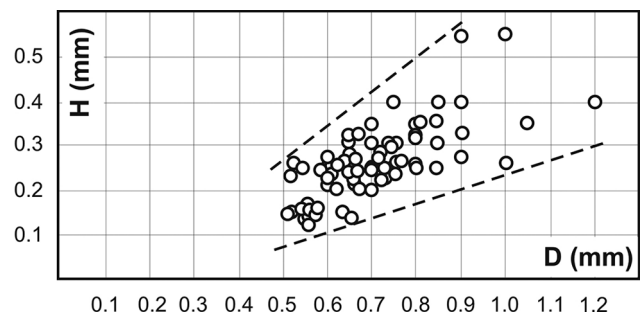

Figure 6: Bivariate scatterplot of test diameter (*D*) against height (*H*) of *S. binkhorsti* (Reuss) from the Danian Kambühel Formation. Nepionic stages are excluded (see Table 1).

	attached and free nepionts										mean
diameter nepiont (D)	0.27	0.27	0.27	0.3	0.25	0.31	0.28	0.29	0.45	0.22	0.29
thickness nepiont (H)	0.11	0.14	0.10	0.14	0.09	0.14	0.08	0.08	0.17	0.10	0.12
ratio D/H	2.45	1.90	2.70	2.10	2.80	2.20	3.50	3.60	2.64	2.20	2.61
diameter proloculus	0.050	0.050	-	0.060	0.060	-	0.065	-	-	0.050	0.056
	free adult specimens										
diameter nepiont (D)	0.29	0.32	0.26	0.28	0.32	0.26	0.21	0.23	0.21	0.23	0.26
thickness nepiont (H)	0.09	0.12	0.10	0.12	0.15	0.13	0.09	0.07	0.08	0.07	0.10
ratio D/H	3.20	2.67	2.60	2.30	2.10	2.00	2.30	3.30	2.60	3.30	2.64
diameter proloculus	-	0.06	0.05	0.05	0.05	0.05	0.06	-	0.05	0.06	0.054

Table 1: Dimension measurements of investigated *Stomatorbina* specimens, both attached and free, during nepionic stage (in mm, except ratio *D/H*).

The notch or chamber wall infold or indentation (Hofker, 1978) (Fig. 7) is well identifiable in both isolated and sectioned specimens (see Figs. 4a–d, l; 5e). It partially separates the main chamber from the foliar chamberlet but does not form a true plate. Such internal partition produced by an infolding of the wall is sporadically found in all known major groups of Globothalamea (e.g., in Rotaliida with *Rosalina*, in ?Robertinida with *Ceratobuliminoides*, and in "Textulariida" with *Valvulammina*). Sections of *S. binkhorsti* and relative species strongly resemble sections of the coeval rotaliid genus *Rotalispirella*. However, as noticed by Consorti et al. (2017), the latter genus displays possibly fused foliar piles and possesses large pores, a canal system, and true umbilical plates (*S. binkhorsti* only shows a wall infolding).

The family Mississippinidae Saidova, 1981 includes the genera *Mississippina*, *Schlosserina* and *Stomatorbina*. As noted by previous authors (e.g., Uchio, 1952; Hofker, 1978), these three genera are extremely similar and only differ in their apertural characteristics and chamber arrangement (Loeblich and Tappan, 1987). A taxonomic revision of the family is beyond the scope of the present manuscript, but here we confirm that the wall of the oldest representative of this homogeneous group is finely agglutinated.

7. Phylogenetic relationships

In 1966, McGowran studied Oligocene and recent specimens of *S. concentrica* (Parker and Jones) in oriented thin sections and stated that the "agglutinating" layer sensu Hofker (1963) represents an opaque, granular, monolamellar primary wall. McGowran (1966), therefore, proposed that *S. binkhorsti* could have originated from the optically granular genus *Valvalabamina*. The presence of coccoliths, small foraminifers, and other calcareous agglutinated grains (Hofker, 1963) within this "granular" layer, however, refutes McGowran's statement. In view of its finely agglutinated wall and low trochospiral coiling, *S. binkhorsti* more likely originated from a trochamminoid ancestor, a group particularly well diversified during the Upper Cretaceous. As the earliest known representative of the family Mississippinidae Saidova, 1981, *S. binkhorsti* possibly flourished and gave rise to several taxa that are yet to be described (Fig. 2).

Despite their atypical structural similarities (juvenarium, secondary hyaline deposits, probable micro-aquarium;

see Vachard and Krainer, 2001 for details), *Altamirella biscayana* (Schlagintweit et al., 2015) and *S. binkhorsti* are not phylogenetically related. More than 20 million years separate the two species. *A. biscayana* and *S. binkhorsti* display very distinct test and chamber shapes and apertural systems. However, the two species share the same epibenthic mode of life. In the Phanerozoic, several epibenthic foraminifers developed a juvenarium (*Altamirella*, *Sabaudia*, and *Stomatorbina*) and built secondary laminar hyaline deposits (*Altamirella*, *Mohlerina, Stomatorbina, Tetrataxis*), and/or a micro-aquarium (in ?*Altamirella*, *Mohlerina,* ?*Stomatorbina*, *Tetrataxis*). These forms are all dark microgranular to agglutinated (sensu Rigaud et al., 2015) but share very few other morphological or structural characteristics (*Sabaudia*, e.g., is biserial and displays a sub-epidermal network), and they do not appear phyletically correlated. We propose that these traits were acquired independently as a result of a convergent (?or parallel) evolution. The presence of a juvenarium, of secondary laminar hyaline deposits, or of a micro-aquarium, has therefore no taxonomic value but should serve as valuable information to reconstruct the mode of life of a fossil form.

8. Conclusions

The cosmopolitan benthic foraminifer *S. binkhorsti* (Reuss) is one of the most frequent taxa in moderate to high-energy nearshore carbonates of the Kambühel Formation at its type locality. Due to its primary finely agglutinated wall structure, it should not be included in the Rotaliidae but, instead, be positioned within "Textulariida" (sensu Pawlowski et al., 2013). Usually regarded as free, specimens of *S. binkhorsti* were found attached to hard substrates, especially juvenile forms. A non-calcified, probably organic anchorage structure existed between the foraminifer and its substrate, limiting detachment. Secondary hyaline deposits are mainly observed over the most fragile or vital parts of the test, and likely served as a protective envelope that added weight and robustness to the test to limit transport and erosion, and cope with the downside of an epibenthic mode of life in high-energy depositional environments. Such structures are common in homeomorphic proved epibenthic forms such as *Tetrataxis* or *Mohlerina* and may represent convergent evolution strategies.
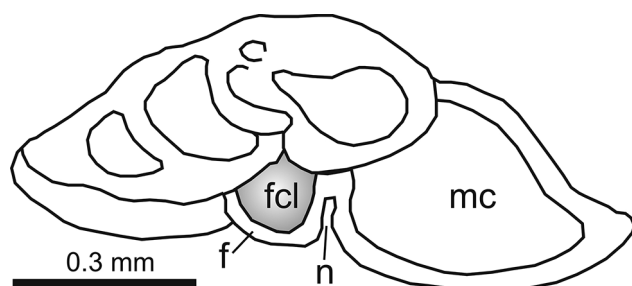
Figure 7: Schematic drawing of *S. binkhorsti* (Reuss), modified after Hofker (1978, pl. 9, fig. 2, *M. binkhorsti*). Abbreviations: f = folium, fcl = foliar chamberlet lumen, mc = main chamber, n = notch.

References

Berggren, W.A., Pearson, P.N., 2005. Revised tropical to subtropical Paleogene planktonic foraminiferal zonation. Journal of Foraminiferal Research, 35, 279–298.

Bermúdez, P.J., 1952. Estudio sistematico de los foraminíferos rotaliformes. Boletín de Geologia, Venezuela, 2/4, 1–230.

Blackmon, P.D., Todd, R., 1959. Mineralogy of some foraminifera as related to their classification and ecology. Journal of Paleontology, 1–15.

Brotzen, F., 1936. Foraminiferen aus dem schwedischen untersten Senon von Eriksdal in Schonen. Sveriges geologiska undersökning (ser. C, no. 396), 30 (1936), 3, 1–206.

Brown, N.K., Brönnimann, P., 1957. Some Upper Cretaceous rotaliids from the Caribbean region. Micropaleontolgy, 3/1, 29–38.

Buček, S., Köhler, E., 2017. Palaeocene reef complex of the Western Carpathians. Slovak. Geological Magazine, 17/1, 3–163.

Charollais, J., Brönnimann, P., 1965. Première note sur les foraminifères du Crétacé inférieur de la région genevoise: *Sabaudia* Charollais et Brönnimann, n. gen. Archives des Sciences, 18, 615–624.

Consorti, L., Köruğlu,F., 2019. Maastrichtian-Paleocene larger Foraminifera biostratigraphy and facies of the Şahinkaya Member (NE Sakarya Zone, Turkey): Insights into the Eastern Pontides arc sedimentary cover. Journal of Asian Earth Sciences, 183, 103965. https://doi.org/10.1016/j.jseaes.2019.103965

Consorti, L., Villalonga, R., Caus, E., 2017. New Rotaliids (benthic foraminifera) from the Late Cretaceous of the Pyrenees in northeastern Spain. Journal of Foraminiferal Research, 47/3, 284–293. https://doi.org/10.2113/gsjfr.47.3.284

Cossey, P.J. and Mundy, D.J.C., 1990. *Tetrataxis*: a loosely attached limpet-like foraminifer from the Upper Palaeozoic. Lethaia, 23, 311–322.

Cushman, J.A., Bermúdez, P.J., 1937. Further new species of foraminifera from the Eocene of Cuba. Contributions from the Cushman Laboratory for Foraminiferal Research, 13, 1–29.

Delage, Y., Hérouard, E., 1896. Traité de Zoologie Conrète. Vol. 1, La Cellule et les Protozoaires. Paris, Schleicher Frères.

Di Carlo, M., Accordi, G., Carbone, F., Pignatti, J., 2010. Biostratigraphic analysis of Paleogene lowstand wedge conglomerates of a tectonically active platform margin (Zakynthos Island, Greece). Journal of Mediterranean Earth Sciences, 2, 31–92.

Dorreen, J.M., 1948. A foraminiferal fauna from the Kaiatan stage (upper Eocene) of New Zealand. Journal of Paleontology, 281–300.

Dulai, A., Bittner, M.A., Müller, P., 2008. A monospecific assemblage of a new rhynchionellid brachiopod from the Paleocene of Austria. Fossils & Strata, 54, 193–201.

Egger, J.G., 1899. Foraminiferen und Ostrakoden aus den Kreidemergeln der Oberbayerischen Alpen. Abhandlungen der Mathematisch-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften, 21, 1–230.

Hansen, H.J., 1979. Test structure and evolution in the Foraminifera. Lethaia, 12, 173–182.

Höglund, H., 1947. Foraminifera in the Gullmar Fjord and the Skagerak. Zoologiska Bidrag Fran Uppsala, 26, 1–328.

Hofker, J. 1927. Die Foraminiferen aus dem Senon Limburgens. Natuurhistorisch Maandblad, 16/9, 125–128.

Hofker, J., 1951. The toothplate Foraminifera. Archives Néerlandaises de Zoologie, 8/4, 353–372.

Hofker, 1956. Foraminifera dentata. Foraminifera of Santa Cruz and Thatch-Island Virginia archipelago West-Indies. Spolia Zoologica Musei Hauniensis, 15, 1–237.

Hofker, J., 1958. Foraminifera from the Cretaceous of South Limburg, XXXVI. The evolution of Mississippina binkhorsti Reuss. Natuurhistorisch Maandblad, 47/1-2, 101–103.

Hofker, J., 1963. Foraminifera from the Cretaceous of South Limburg, LXX. The finer structure of the test of *Mississippina binkhorsti* (Reuss, 1862) and its bearing on the taxonomic position of *Mississippina*. Natuurhistorisch Maandblad, 52/11, 157–160.

Hofker, J., 1969. Recent foraminifera from Barbados. Studies fauna Curaçao and other Caribbean Islands, 115, 1–158.

Hofker, J., 1978. Biological results of the Snellius expedition XXX. The foraminifera collected in 1929 and 1930 in the eastern part of the Indonesian archipelago. Zoologische Verhandelingen, 164, 1–69.

Hosseinzadeh, M., Daneshian, J., Moallemi, S.A. and Solgi, A., 2014. First report of *Stomatorbina binkhorsti* in Upper Paleocene-Lower Eocene deposits in Jahrum Formation, eastern part of the coastal Fars (Southern Iran). Advances in Environmental Biology, 8/24, 477–480.

Hottinger, L., 2006. Illustrated glossary of terms used in foraminiferal research. Carnets de Géologie/Notebooks on Geology, Memoir 2006/02 (CG2006_M02).

Hottinger, L., 2014. Paleogene larger rotaliid foraminifera from the Western and Central Neotethys. Springer, Heidelberg, 196 pp.

Howe, H.V., 1930. Distinctive new species of foraminifera from the Oligocene of Mississippi. Journal of Paleontology, 4, 327–331.

Keller, G. 2014. Deccan volcanism, the Chicxulub impact, and the end-Cretaceous mass extinction: coincidence? Cause and effect? Geological Society of America Special Papers, 205, 29–55. https://doi.org/10.1130/2014.2505(03)

Kollmann, H.A., Summesberger, H., 1982. Excursions to Coniacian-Maastrichtian in the Austrian Alps. Exkursionsführer 4th Meeting Working Group Coniacian-Maastrichtian Stages,Vienna, 105 pp.

Krische, O., Gawlick, H.-J., Schlagintweit F., 2012. Resedimented Late Palaeocene shallow-water clasts of the Kambühel Formation of the Weitenau area and

their tectonic implications (Salzburg Calcareous Alps, Austria). Austrian Journal of Earth Sciences, 105/3, 38–47.

Lein R., 1982, Vorläufige Mitteilungen über ein Vorkommen von flyschoider Gosau mit Komponenten paleozäner Riffkalke in den Mürztaler Alpen. Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten in Österreich, 28, 121–132.

Li, L., Keller, G., 1998. Maastrichtian climate, productivity and faunal turnovers in planktic foraminifera in South Atlantic DSDP Sites 525A and 21. Marine Micropaleontology, 33, 55–86.

Loeblich, A.R., Tappan, H., 1964. Sarcodina chiefly "Thecamoebians" and Foraminiferida. In Moore, R., Ed., Treatise on Invertebrate Paleontology. Geological Society of America. Part C. Protista, 2, 1–653.

Loeblich, A.R., Tappan, H., 1987. imprinted 1988. Foraminiferal genera and their classification. Van Nostrand Reinhold, New York, 2, 1182.

Matsumaru, K., 2016, Larger foraminiferal biostratigraphy of the upper Cretaceous (Campanian) to Paleogene (Lutetian) sedimentary rocks in the Haymana and Black Sea regions, Turkey. Micropaleontology, 62/1, 1–68.

McGowran, B., 1966. Bilamellar walls and septal flaps in the Robertinacea. Micropaleontology, 12/4, 477–488.

Orbigny, A., d', 1826. Tableau méthodique de la classe des Céphalopodes. Annales des Sciences Naturelles, 7, 245–314.

Özgen Erdem, N., 2008. Biostratigraphy of Thanetian-Illerdian benthic foraminifera in the Akçataş – Cebeci (NW Tosya – SE Kastamanonu) Region. Bulletin of the Mineral Research and Exploration, 137, 49–59.

Pawlowski, J., Holzmann, M., Tyszka, J., 2013. New supraordinal classification of Foraminifera: Molecules meet morphology. Marine Micropaleontology, 100, 1–10. https://doi.org/10.1016/j.marmicro.2013.04.002

Pignatti, J., Di Carlo, M., Benedetti, A., Bottino, C., Briguglio, A., Falconi, M., Mateuucci, R., Perugini, G., Ragusa, M., 2008. SBZ 2-6 Larger foraminiferal assemblages from the Apulian and Pre-Apulian domains. Atti del Museo civico di storia naturale di Trieste, suppl. 53, 131–146.

Piller,W.E., Egger, H., Erhart, C.W., Gross, M., Harzhauser, M., Hubmann, B., Van Husen, D., Krenmayr, H., Krystin, L. and Lein,R., 2004. Stratigraphische Tabelle von Österreich 2004 (sedimentäre Schichtfolgen). Kommission für die paläontologische und stratigraphische Erforschung Österreichs, Österreichische Akademie der Wissenschaften und Österreichische Stratigraphische Kommission, Wien.

Radoičić, R., 1991. *Acicularia tavnae* sp. nov. and other Acetabulariaceae from the Paleocene of eastern Majevica (NE Bosnia, Dinarides). Geologija, Razprave in Porocila, 34, 57–75.

Reiss, Z., 1958. Classification of lamellar foraminifera. Micropaleontology, 4, 51–70.

Reiss, Z., 1963. Reclassification of perforate foraminifera. Bulletin of the Geological Survey of Israel, 35, 1–111.

Reuss, A.E., 1862. Paläontologische Beiträge II. Die Foraminiferen des Kreidetuffs von Maastricht. Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Classe, 44/1, 304–324.

Rigaud, S., Blau, J., 2016. New robertinid foraminifers from the Early Jurassic of Adnet, Austria and their evolutionary importance. Acta Palaeontologica Polonica, 61/4, 721–734. https://doi.org/10.4202/app.00250.2016

Rigaud, S., Schlagintweit, F., 2016. Initiation of a reversal to uniseriality in the polymorphinid *Nodocantabricus duplexmurus* n. gen., n. sp.: A double-layered Foraminifera from the lower-middle Cenomanian of Cantabria, N-Spain. Cretaceous Research, 63, 14–22. https://doi.org/10.1016/j.cretres.2016.02.008

Rigaud, S., Blau, J., Martini, R., Rettori, R., 2013. Taxonomy and phylogeny of the Trocholinidae (Involutinina). The Journal of Foraminiferal Research, 43/4, 317–339. https://doi.org/10.2113/gsjfr.43.4.317

Rigaud, S., Vachard, D. and Martini, R., 2015. Agglutinated versus microgranular foraminifers: end of a paradigm? Journal of Systematic Palaeontology, 13/2, 75–95. https://doi.org/10.1080/14772019.2013.863232

Rigaud, S., Vachard, D., Schlagintweit, F., Martini, R., 2016. New lineage of Triassic aragonitic Foraminifera and reassessment of the class Nodosariata. Journal of Systematic Palaeontology, 14, 919–938. https://doi.org/10.1080/14772019.2015.1112846

Rigaud, S., Schlagintweit, F., Bucur, I.I., 2018. The foraminiferal genus Neotrocholina Reichel, 1955 and its less known relatives: A reappraisal. Cretaceous Research, 91, 41–65. https://doi.org/10.1016/j.cretres.2018.04.014

Saidova, K., 1981. O sovremennom sostoyanii sistemy nadvidovykh taksonov Kaynozoyskikh bentosnykh foraminifer [On an up-to-date system of supraspecific taxonomy of Cenozoic benthonic foraminifera]. Institut Okeanologii P. Shirshova, Akademiya Nauk SSSR, 73 pp. (in Russian.)

Samuel, O., Borza, K., Köhler, E., 1972, Microfauna and lithostratigraphy of the Paleogene and adjacent Cretaceous of the Middle Váh Valley (Western Carpathians). Geol. Ust. Dionyza Stura, Bratislava, 246 pp.

Schijfsma, E., 1946. The foraminifera from the Hervian (Campanian) of southern Limburg. Mededelingen van de Geologische Stichting, ser. C, 5/7, 1–174.

Schlagintweit, F., 2012. *Mohlerina basiliensis* (Mohler, 1938): a Middle Jurassic-Early Cretaceous facultative (?) epilithic benthic foraminifer. Facies, 58/4, 637–647.

Schlagintweit, F., Rashidi, K., 2019. *Serrakielina chatorshiana* gen. et sp. nov., and other (larger) benthic Foraminifera from Danian-Selandian carbonates of Mount Chah Torsh (Yazd Block, Central Iran). Micropaleontology, 65/4, 305–338.

Schlagintweit, F., Rigaud, S., Wilmsen, M., 2015. The new benthic foraminifer *Altamirella biscayana* n. gen., n. sp. from the Early Cenomanian of Cantabria, N-Spain: a post-Palaeozoic fusulina? Cretaceous Research, 52, 1–8. https://doi.org/10.1016/j.cretres.2014.08.001

Schlagintweit, F., Švábenická, L. and Lobitzer, H., 2003. An occurrence of Paleocene Reefal Limestone in the Zwieselalm Formation of Gosau (Upper Austria). In: J.T. Weidinger, H. Lobitzer, I. Spitzbart (Eds): Beiträge zur Geologie des Salzkammergutes. Gmundner Geo-Studien, 2, 173–180.

Schlagintweit, F., Studeny, M., Sanders, D., 2016. *Clypeorbis*? *ultima* n. sp. from the uppermost Maastrichtian of Austria: the youngest representative of the Clypeorbinae Sigal, 1952 (calcareous benthic foraminifera)? Cretaceous Research, 66, 163–170. https://doi.org/10.1016/j.cretres.2016.06.006

Schlagintweit, F., Sanders, D., Studeny, M., 2018. The nepionic stage of *Solenomeris* Douvillé, 1924 (Acervulinidae, Foraminiferida): new observations from the uppermost Maastrichtian-early Danian of Austria (Kambühel Formation, Northern Calcareous Alps). Facies, 64, 27. https://doi-org/10.1007/s10347-018-0540-5

Septfontaine, M., 1978. Présence d'*Archaeosepta platierensis* Wernli 1970 dans le Jurassique briançonnais des Préalpes. Importance stratigraphique, relations avec le microfaciès et la paléogéographie. Notes du Laboratoire de Paléontologie de Genève, 2/1, 1–6.

Serra-Kiel J., Hottinger, L., Caus, E., Drobne, K., Ferràndez, C., Jauhri, A.K., Less, G., Pavlovec, R., Pignatti, J., Samsó, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. Bulletin de la Société Geologique de France, 169, 281–299.

Sirel, E., 1998. Foraminiferal description and biostratigraphy of the Paleocene-lower Eocene shallow-water limestones and discussion on the Cretaceous-Tertiary boundary in Turkey. General Directorate of the mineral research and exploration, Ankara, Monograph series, 2, 117 pp.

Sirel, E., 2015. Reference sections and key localities of the Paleogene stage and discussion C-T, P-E and E-O boundaries by the very shallow-shallow water foraminifera in Turkey. Ankara University Yayinlari 461, 171 p.

Todd, R., 1965. The Foraminifera of the Tropical Pacific Collections of the "Albatross", 1899-1900. Part 4. Rotaliform families and planktonic families [End of Volume]. Bulletin U.S. National Museum, 161, 139 pp.

Tollmann A., 1976. Monographie der Nördlichen Kalkalpen. Teil II. Analyse des klassischen nordalpinen Mesozoikums. Stratigraphie, Fauna und Fazies der Nördlichen Kalkalpen. Franz Deuticke, Wien, 540 pp.

Tragelehn, H., 1996. Maastricht und Paläozän am Südrand der Nördlichen Kalkalpen (Niederösterreich, Steiermark) – Fazies, Stratigraphie Paläogeographie und Fossilführung des "Kambühelkalkes" und assoziierter Sedimente. Diss. Naturwiss. Fak. University Erlangen, 216 pp.

Uchio, T., 1952. An interesting relation between *Stomatorbina* Dorreen, 1948, and *Mississippina* Howe, 1930, of Foraminifera. Transactions and proceedings of the Paleontological Society of Japan, New series, 1952/7, 195–200.

Vachard, D., Krainer, K., 2001. Smaller foraminifers of the Upper Carboniferous from the Auernig Group, Carnic Alps (Austria/Italy). Rivista Italiana di Paleontologia e Stratigrafia, 107, 147–168

Vachard, D., Pille, L. and Gaillot, J., 2010. Palaeozoic Foraminifera: Systematics, palaeoecology and responses to global changes. Revue de Micropaléontologie, 53, 209–254.

Verhoff, J.R., Müller, P.M., Feldmann, P.R., Schweitzer, C.E., 2008. A new species of Tumidocarcinidae (Decapoda, Carpilioidea) from the Kambühel Formation (Paleocene) of Austria. Annalen Naturhistorisches Museum Wien, 111A, 225–232.

Visser, A.M., 1950. Monograph of the foraminifera of the type-locality of the Maestrichtian (South-Limburg, the Netherlands). Leidse Geologische Mededelingen, 16, 197–359.

Wernli, R. 1970. *Archaeosepta platierensis* Wernli, n. gen., n. sp., un nouveau Foraminifère du Jurassique moyen du Jura méridional. Compte Rendu des Séances de la Société de Physique et d'Histoire Naturelle de Genève, 5, 87–93.

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