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

Felix SCHLAGINTWEIT<sup>1,\*</sup> & Sylvain RIGAUD<sup>2</sup>

<sup>1)</sup> Lerchenauerstr. 167, 80935 München, Germany

<sup>2)</sup> Asian School of the Environment, 62 Nanyang Drive, 637459 Singapore

\*) Corresponding author: felix.schlagintweit@gmx.de



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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 higherlevel 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



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

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 thickwalled 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 cor-

al 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 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-Palaeo-zoic 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).

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



**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 applutinated 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, I; 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. bink*horsti 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 21/2 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.





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;



**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.

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 highenergy depositional environments. Such structures are common in homeomorphic proved epibenthic forms such as Tetrataxis or Mohlerina and may represent convergent evolution strategies.

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Felix SCHLAGINTWEIT<sup>1),\*</sup> & Sylvain RIGAUD<sup>2)</sup>

<sup>1)</sup>Lerchenauerstr. 167, 80935 München, Germany

<sup>2)</sup> Asian School of the Environment, 62 Nanyang Drive, 637459 Singapore

\*) Corresponding author: felix.schlagintweit@gmx.de

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