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Taxonomic reassessment and palaeobiogeographical patterns of some Miogypsinidae species, larger benthic foraminifera

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Abstract. The Miogypsinidae comprise orbitoidal larger benthic foraminifera with generally eccentric position of the nepionic stage and a fan of equatorial chamberlets; the members of this family are widely used in biostratigraphy of upper Oligocene–middle Miocene deposits. Here, a taxonomic review of the genus *Miogypsinella* Hanzawa, 1940 (type species: *M. borodinensis* Hanzawa, 1940) and *Miogypsinoides lateralis* Hanzawa, 1940 is presented based on the reassessment of the type specimens. The palaeobiogeographical patterns of these taxa are discussed based on a compilation of the geographical and stratigraphical ranges of all their reported occurrences including illustrations. The computed tomography (CT)-scan analysis of the type material of *M. borodinensis*, from the Chattian of the central Indo-Pacific (Kitadaito Jima), indicates that it is a valid species different from *Miogypsinoides complanatus*. Two *Miogypsinella* species (*M. borodinensis*, *M. ubaghsi*) are widespread in the Chattian–Aquitanian of the Indo-Pacific region and one species (*M. bermudezi*) in the Aquitanian of the eastern Pacific (Mexico). *Miogypsinella* appeared in the Chattian in the central Indo-Pacific, reached Central America, and disappeared in the Aquitanian in both areas. The American Oligocene faunas of larger benthic foraminifera were, therefore, not distinctly isolated as previously proposed. *Miogypsinoides lateralis* is a clearly distinct species that is an exception to the presumed morphological trend within the *Miogypsinoides* species lineage. *Miogypsinoides lateralis* possesses morphometric values comparable to those of the Burdigalian–Langhian *M. indica* but occurring earlier, in the Aquitanian. The latest Aquitanian initiation of the Indonesian Seaway restriction and widespread drowning of former carbonate platforms likely brought about the extinction of *Miogypsinella borodinensis*, *M. bermudezi*, *M. ubaghsi*, and *Miogypsinoides lateralis*.

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1 Introduction

Miogypsinids (Miogypsinidae Vaughan, 1928 family) constitute a group of orbitoidal larger benthic foraminifera (LBF) with hyaline–lamellar perforated shell, spiral-arranged nepionic chambers with later equatorial chamberlets, and spiral and intraseptal canals (e.g. de Bock, 1976; Chaproniere, 1984; Loeblich and Tappan, 1987; Drooger, 1993). This group differs from other orbitoidal forms in having a generally eccentric position of the nepionic stage, located near the apex of the shell, and the development of equatorial chamberlets in one sector only (e.g. de Bock, 1976; Drooger, 1993). A total of 5 miogypsinid genera were accepted by Loeblich and Tappan (1987), 7 by BouDagher-Fadel and Price (2013), 8 by BouDagher-Fadel (2018), and 14 by Hayward et al. (2021). *Miogypsinoides* Yabe and Hanzawa, 1928 and *Miogypsina* Sacco, 1893 have so far been the most studied taxa, recorded from the western Tethys through Indo-Pacific areas and to Central America (Drooger, 1952, 1953, 1963; Drooger and Socin, 1959; Raju, 1974; BouDagher-Fadel and Price, 2013).

Miogypsinids have been used in biostratigraphy of Oligocene–middle Miocene deposits in both the western Tethys and in Indo-Pacific areas (e.g. Raju, 1974; Adams, 1984; Drooger and Laagland, 1986; Cahuzac and Poignant, 1997; Lunt and Allan, 2004; BouDagher-Fadel, 2018).

Based on Indonesian material, Tan (1936a, b, 1937a, b) found that the number of the nepionic chambers (hereafter, X value; i.e. nepionic stage) progressively decreased in the populations through time, with primitive forms (i.e. *Miogypsinoides*) having a longer nepionic stage, a trend named nepionic acceleration. This temporal morphological change was applied together with other shell characters in morphometric taxonomy with biostratigraphical aims, which has been historically prevailing in miogypsinid studies (e.g. Drooger, 1963, 1993; Raju, 1974; Schiavinotto, 1985; Özcan et al., 2009; Schiavinotto and Benedetti, 2021). In orbitoidal or radial foraminifera, the shell morphology may be very different at the beginning and end of the lineages. For these groups, including miogypsinids, Drooger (1993) proposed to split the individual lineages into segments based on morphometric data. These segments, which have been called species, are defined by a morphometric range (Pignatti, 1998). This species concept circumscribes artificial units with well-defined but arbitrarily chosen morphometric limits (e.g. Drooger, 1993; Özcan et al., 2007, 2009; Less, 1987).

The origin of the family is uncertain, and the geographical location of the ancestral forms is still debated. Mexico, south-western France, and Spain have been proposed as possible centres of origination of an Oligocene ancestor (Salmeron, 1972; Cahuzac and Poignant, 1987; Laagland, 1990). Two miogypsinid species, *Miogypsinella borodinensis* Hanzawa, 1940 (type species of the genus) and *Miogypsinella bermudezi* (Drooger, 1951), have alternatively been considered as possible ancestors of the family (Drooger, 1951, 1963; BouDagher-Fadel and Price, 2013). The hypotheses about the primitive forms were based on morphometric data (e.g. proloculus diameter, length of the nepionic stage), generally comparing them to those of *Miogypsinoides complanatus* (Schlumberger, 1900), considered by some authors to be the oldest species of the family (e.g. Drooger, 1993; BouDagher-Fadel, 2018). Both hypotheses, however, were deeply influenced by their unclear taxonomic position.

The shell architecture and systematic position of *Miogypsinella* have been repeatedly discussed in the literature, and it has been often placed in or considered a synonym of the genus *Miogypsinoides* (e.g. Drooger, 1952; Loeblich and Tappan, 1987; Sirel and Işık, 2011; Matsumaru et al., 2010; Gedik, 2018; Mitchell, 2026). According to Drooger (1993), the frequent changes in species names and concepts and the lack of morphometric details make it difficult to evaluate various reports of *Miogypsinella* from Pacific areas (e.g. Cole, 1954, 1969). Uncertainties stem from conflicting descriptions of *Miogypsinella borodinensis* and related species, in many cases incomplete or incorrect (e.g. Sirel and Işık, 2011; Matsumaru et al., 2010; Gedik, 2018), and from different interpretations of some shell structures (and the terminology applied to them). Rigorous descriptions of shell structures, besides their taxonomic value, are important to understand the functional morphology of the test and the relationships of shell architecture to cytoplasmic differentiation (Hottinger and Dreher, 1974; Hottinger, 1978; Hottinger and Leutenegger, 1980). A detailed morphological analysis and taxonomic assessment of the *Miogypsinella* species are, therefore, needed to circumscribe them, to narrow down their biostratigraphical range, and to discuss their possible phylogenetic relationships.

In the collection of Hanzawa (1940), in addition to *Miogypsinella borodinensis*, a second miogypsinid species is present: *Miogypsinoides lateralis* Hanzawa, 1940. Due to its peculiar nepionic stage characterized by a low number of chambers, it has been mixed up with *Miogypsinoides* species of Oligocene faunas from the western Tethys (Mediterranean) and the Indo-Pacific, and it has only been reported from the central Indo-Pacific (e.g. Hanzawa, 1957, 1962; Cole, 1957b, 1969). The species was later synonymized with *Miogypsinoides dehaartii*, hampering its use in biostratigraphical schemes (Lunt and Luan, 2022).

This study presents direct observations of shell structure and architecture of two miogypsinid species, *Miogypsinella borodinensis* and *Miogypsinoides lateralis*, as well as their systematic implications. The shell characters were observed by computed tomography (CT) scans. This advanced technology allowed us a detailed examination of shell characters, leading to a better understanding of species delimitation and evolutionary relationships. This morphological analysis permits (1) understanding the species taxonomy, (2) setting speciation and extinction events of *Miogypsinella* species, and (3) tracing the Oligocene–early Miocene biostratigraphical

and palaeobiogeographical scenarios for these miogypsinids in the western Tethyan and Indo-Pacific areas. Three species of *Miogypsinella* can be separated by the proloculus diameter, the number of nepionic chambers, the inclination of the planispiral whorl with respect to the equatorial plane, and the arc length of nepionic spiral from embryonic chambers to the apical point of test.

2 Materials and methods

This study was carried out on material preserved both as thin sections and isolated specimens in the collection of Hanzawa (1940) deposited in the Tohoku University Museum (Sendai, Japan). Oriented sections of LBF specimens in the collection of Hanzawa (1940) from Kitadaito Jima were housed at the Institute of Geology and Paleontology (IGPS), Faculty of Science (currently Department of Earth Science, Graduate School of Science).

The structural and morphological terms are those used by de Bock (1976), Drooger (1993), Hottinger et al. (1991), and Hottinger (2006). The suprageneric classification follows Loeblich and Tappan (1987). The descriptions of the analysed *Miogypsinella* species are ordered according to their stratigraphical appearance. References to published species records include only those in which structural diagnostic features were described and illustrated.

The isolated specimens were micro-CT-scanned at the Centro de Instrumentación Científica, Universidad de Granada, Spain. The micro-CT scanning system Zeiss Xradia 510 Versa with granite-based vibratory insulation was used. The source voltage used was 30–160 kV, with 2000×2000 pixel noise detector suppression at full charge. Non-destructive three-dimensional advanced image solutions were formed with high-contrast images and submicron resolution (700 nm). The true spatial resolution was 0.7 µm and 70 nm voxel size. The micro-computed tomographic scanning 3D models were rendered using Molcer Plus (Ver. 1.6) with the shell removed to highlight the volumes occupied by protoplasm within the shell and the arrangement and communications among chambers.

3 Systematic palaeontology

Superfamily Rotalioidea Ehrenberg, 1839

Family Miogypsinidae Vaughan, 1928

Genus ***Miogypsinella*** Hanzawa, 1940

Type species. *Miogypsinella borodinensis* Hanzawa, 1940, pp. 779–780, pl. 39, figs. 1–9.

Diagnosis. Test flat and concavo-convex, rarely conical; embryo near test apex consisting of a large sub-spheroidal protoconch and reniform deuteroconch separated by an imperforated wall and both surrounded by a perforated wall; protoconchal stolon lies in the opposite side of the deuteroconchal aperture; row of peri-embryonic chambers in a single spiral; equatorial chamberlets asymmetrical and ogival; apertural lip; septal flap; intraseptal interlocular space occurring around each embryonic, nepionic, and equatorial chamber and chamberlet; cover on intraseptal interlocular space; consecutive toothplates interconnected in adaxial position producing a primary spiral canal; intraseptal canal system shows vertical branches which issue from the spiral canal and extend to ventral side only; subsutural canals; very thin single-layered bilamellar outer shell wall in the equatorial chambers and chamberlets.

Remarks. *Miogypsinella* differs from *Miogypsinoides* in having a cover on intraseptal interlocular space, an apertural lip, and subsutural canals (Table 1). The higher number of planispiral nepionic chambers (Drooger and Raju, 1973; de Bock, 1976; Matsumaru, 2012), a broader flange becoming laterally heavily thickened, and a weakly trochospiral initial coil (Hanzawa, 1962, figs. 1–11; Loeblich and Tappan, 1987; BouDagher-Fadel et al., 2000; Matsumaru, 2012; BouDagher-Fadel and Price, 2013; BouDagher-Fadel and Wilson, 2000) have been used so far as distinctive shell characters to separate *Miogypsinoides* from *Miogypsinella*. These characters, however, are not supported by morphological evidence. The use of a "stronger predominance of pillars and pustules" to circumscribe *Miogypsinoides*, implying that *Miogypsinella* is its younger synonym (Cole in Cushman, 1948, p. 376; Drooger, 1953, p. 120; Drooger, 1993, p. 81), is not based on distinctive characters at the genus level and, therefore, cannot be accepted.

Drooger (1953) stated that *Miogypsinoides* differs from *Miogypsinella* in having side walls of distinctly lamellar structure, whereas the latter shows "dominating vertical structures" (Hanzawa, 1940; pillars and pustules in Drooger, 1993; BouDagher-Fadel and Price, 2013) in these lateral walls. After recognizing that these characters do not provide a sharp demarcation between the two taxa, he considered *Miogypsinella* to be a junior synonym of *Miogypsinoides*, including in this genus all species without lateral chamberlets (Drooger, 1953, p. 120, 122; Drooger, 1993, p. 81). According to this author, the occurrence of "some cavities of various kinds in the side walls" (i.e. intraseptal interlocular space) and nepionic characters (i.e. trochoid or planispiral whorl) may be regarded as diagnostic at species level (Drooger, 1953, p. 120).

Sirel and Işık (2011) and Gedik (2018) distinguished *Miogypsinella* from *Miogypsinoides* in having the "early rotaloid stage with pillars". Some *Miogypsinoides* species were transferred to *Miogypsinella* without any taxonomic comparisons and remarks (Sirel, 2010; Sirel and Işık, 2011; Sirel and Gedik, 2011; Gedik, 2018). Similar taxonomic misconceptions of *Miogypsinoides complanatus*/*Miogypsinella complanata* (Schlumberger) (e.g. Sirel and Işık, 2011; Matsumaru et al., 2010; Gedik, 2018) have caused confusion

Table 1. Comparison of diagnostic shell characteristics of *Miogypsinella* and *Miogypsinoides*. Based on data from [1] Hanzawa (1940), Drooger (1952, 1993), BouDagher-Fadel and Price (2013), and this study. [2] de Bock (1976), Loeblich and Tappan (1987), Drooger (1952, 1963, 1993), BouDagher-Fadel and Price (2013), and this study. Abbreviations: co, cover on intraseptal interlocular space; iis, intraseptal interlocular space; li, apertural lip; ssc, subsutural canals; sf, septal flap; spc, primary spiral canal; ssc, subsutural canals; tlw, thickness of the lateral walls; tp, toothplate; vcs, vertical canal system.

	co	iis	li	ssc	sf	spc	ssc	tlw	tp	vcs
Miogypsinella[1]	x	x	x	x	x	x	x	thin	x	ventral side only
Miogypsinoides[2]		x			x			thick	x	on both sides

in the stratigraphical range of this species as well as in its palaeobiogeographical distribution.

Hanzawa (1957, p. 86) considered *Miogypsinella* to be a junior synonym of *Miogypsinoides* because both genera show nepionic chambers trochospirally arranged ("asymmetrical between the ventral and dorsal sides"). As remarked above, neither this arrangement nor the mere number of nepionic chambers (de Bock, 1976, p. 59) can be used to separate the two genera.

Tan (1936a, p. 51) established *Conomiogypsinoides* providing two illustrations from thin-sectioned material: a paraxial section and an oblique equatorial section. These specimens show a heavily thickened wall with a vertical canal system on both sides of the shell, suggesting a possible ascription to *Miogypsinoides* (Hanzawa, 1940, p. 775; Hanzawa, 1962, p. 153).

The World Register of Marine Species (Hayward et al., 2021) reports *Miogypsinella* Hanzawa, 1940 as a subjective junior synonym of *Miogypsinoides* Yabe and Hanzawa, 1928 (opinion of Loeblich and Tappan, 1987), and lists seven *Miogypsinella* species (as *Miogypsinoides*): *M. borodinensis* Hanzawa, 1940; *M. boninensis* Matsumaru, 1996; *M. bornea* BouDagher-Fadel and Price, 2013; *M. cyprea* BouDagher-Fadel and Price, 2013, *M. elongata* BouDagher-Fadel and Price, 2010; *M. sanjosensis* Hanzawa, 1940; *M. ubaghsi* Tan, 1936a. *Miogypsinella akcadagensis* (Gedik and Sirel) and *Miogypsinella bermudezi* (Drooger) are not listed as such in Hayward et al. (2021).

Miogypsinella boninensis Matsumaru, 1996 (see also Sharaf et al., 2005, 2014), *Miogypsinella bornea* BouDagher-Fadel and Price, 2013, *Miogypsinella cyprea* BouDagher-Fadel and Price, 2013, *Miogypsinella elongata* BouDagher-Fadel and Price, 2010, and *Miogypsinella matsumaria* BouDagher-Fadel and Price, 2010 have not been sufficiently described and illustrated to assess their status as separate species. In particular, no key information about the apertural lip, spiral canal, subsutural canal, and vertical canal system is given in their descriptions. All these species are characterized by a thickened lateral shell wall, which reasonably allows their assignment to *Miogypsinoides* (de Bock, 1976; BouDagher-Fadel and Price, 2013; Table 1). Novandaru et al. (2025, fig. 5l–o) identified *Miogypsinella bornea* from the Chattian of West Java. The proposed shell structures do not clearly distinguish *Miogypsinella* and *Miogypsinoides* (Novandaru et al., 2025, table 1).

Miogypsinella akcadagensis (Gedik and Sirel) was first ascribed to *Miogypsinoides* by Gedik and Sirel (2009) and later placed in *Miogypsinella* by Gedik (2018). This species shows a thickened lateral wall, suggesting that it belongs to *Miogypsinoides* rather than to *Miogypsinella* (Table 1). This conclusion is supported by later records of this species and its illustrations (Gedik and Sirel, 2009; Sirel and Gedik, 2011; Gedik, 2014, 2015, 2018). *Miogypsinella bermudezi* (Drooger) is described and discussed in the following chapter.

Gedik (2018) proposed that *Miogypsinoides* (*Miogypsinoides*) *complanatus* (Schlumberger) forma *bantamensis* Tan, 1936a, *Miogypsinoides bantamensis*, and *Miogypsinoides bermudezi* Drooger, 1951 are younger synonyms of *Miogypsinella borodinensis* based on the number of nepionic (spiral) chambers. This synonymy cannot be accepted due to the different shell characteristics of *Miogypsinoides* and *Miogypsinella*.

The *Miogypsinella* species dealt with herein are exclusively fossil (*M. borodinensis*, *M. bermudezi*, and *M. ubaghsi*; Table 3). The proloculus diameter, the number of nepionic chambers, the inclination of the planispiral whorl in relation to the equatorial chamber plane, and the arc length of the nepionic spiral starting from embryonic chambers and ending at the apical point of test (i.e. clockwise spiral; hereinafter, angle γ; Amato and Drooger, 1969) are reliable characters to distinguish the species of this genus (Table 2).

Miogypsinella borodinensis Hanzawa, 1940
Figures 1–5.

non 1924 *Miogypsina complanata* Schlumberger; Silvestri, pl. 1, fig. 19.

? 1937 *Miogypsinoides complanata*; Barker and Grimsdale, pl. 5, fig. 6.

1937 *Miogypsinoides complanata*; Barker and Grimsdale, pl. 6, figs. 1–6, pl. 7, fig. 1; pl. 8, fig. 6.

1938 *Miogypsinella* Hanzawa, pp. 387–389.

1938 *Miogypsina* (*Miogypsinoides*) *complanata* Schlumberger; Cole, pl. 8, fig. 10.

Table 2. Comparison of diagnostic shell characteristics of *Miogypsinella* species and their stratigraphical distribution. Species are listed according to their first appearance reported in the literature. Based on data from [1] Barker and Grimsdale (1937), Hanzawa (1940, 1957, 1965), and this study. [2] Drooger (1951, 1963, 1993), Akers and Drooger (1957), and Hanzawa (1957). [3] Tan (1936a), Cole (1954, 1957b), Hanzawa (1957, 1965), and Mohiuddin et al. (2000). Abbreviations: angle γ, arc length of nepionic spirals starting from embryonic chambers and ending at the apical point of test; L, length (max); prol, proloculus diameter; pwd, planispiral whorl direction degree; nc, number of nepionic chambers.

	Age	L (mm)	prol (µm)	nc	pwd	nepionic whorl	angle γ
M. borodinensis[1]	Chattian–Aquitanian	1–1.2	80–110	7–12	ca. 30°	trochospiral	140–165°
M. bermudezi[2]	Aquitanian	1	50–70	13–19	0°	trochospiral	ca. 50–70°
M. ubaghsi[3]	Chattian–Aquitanian	1.5	80–130	13–16 (24)	0°	trochospiral	330° (400°)

v. 1940 *Miogypsinella borodinensis* n. sp., Hanzawa, pp. 779–780, pl. 39, figs. 1–9, text-fig. 2.

1940 *Miogypsinella sanjosensis* n. sp., Hanzawa, text-fig. 3.

1941 *Miogypsinoides complanata* (Schlumberger); Galloway and Heminway, pl. 36, figs. 6–9.

1951 *Miogypsina* (*Miogypsinella*) Drooger, p. 364 (*nom. transl.*).

? 1954 *Miogypsinoides borodinensis* (Hanzawa); Cole, pp. 600–601, pl. 221, figs. 6–8.

? 1957a *Miogypsinoides complanatus* (Schlumberger); Cole, pl. 25, figs. 1–2

1957 *Miogypsinoides borodinensis* (Hanzawa); Hanzawa, pp. 91–92, pl. 15, fig. 11; pl. 21, figs. 2–3.

1962 *Miogypsinoides complanatus* (Schlumberger); Hanzawa, pl. 7, fig. 11.

1962 *Miogypsinoides borodinensis* (Hanzawa); Hanzawa, pl. 7, fig. 15.

1965 *Miogypsinoides* [*borodinensis* (Hanzawa)]; Hanzawa, pl. 38, fig. 2a–b.

1967 *Miogypsinoides complanata* (Schlumberger); Cole, pl. 9, figs. 1, 3, 5, 8.

1974 *Miogypsina* (*Miogypsinoides*) cf. *bermudezi* Drooger; Raju, p. 77, pl. 1, figs. –5 (drawings); ? pl. 3, figs. 1–2 (outer views); pl. 5, figs. 1-3.

? 1984 *Miogypsinoides borodinensis* Hanzawa; Cahuzac, pl. 1, fig. 5.

1988 *Miogypsinella* Hanzawa; Loeblich and Tappan, p. 680.

1989 *Miogypsinoides* cf. *M. bermudezi* Drooger; Robinson and Persad, pl. 1, figs. 1–4.

? 2000b *Miogypsinella* cf. *borodinensis* Hanzawa; BouDagher-Fadel et al., p. 14, pl. 2, fig. 3.

2004 *Miogypsinella* sp. cf. *M. bermudezi*; Robinson, fig. 10a.

? 2010 *Miogypsinoides formosensis*; Matsumaru et al., pl. 1, figs. 8–10.

non 2010 *Miogypsinella complanata* (Schlumberger); Matsumaru et al., pl. 1, figs. 5–7.

2013 *Miogypsinella ubaghsi* Tan; BouDagher-Fadel and Price, p. 198, fig. A1f–g.

? 2013 *Miogypsinella borodinensis* Hanzawa; BouDagher-Fadel and Price, p. 197, fig. A1h.

non 2015 *Miogypsinella borodinensis* Hanzawa; Sirel, pl. 42, fig. 1; pl. 52, figs. 1–26; pl. 53, fig. 1.

2017 *Miogypsinella bermudezi* Akers and Drooger; Robinson et al., fig. 6a–b.

? 2018 *Miogypsinella borodinensis* Hanzawa; BouDagher-Fadel, pl. 6.30, fig. 3.

? 2023 *Miogypsinella*; Alvarado Sierra et al., fig. 9X.

2024 *Miogypsinoides bermudezi* Drooger; Mitchell et al., fig. 3.4–5.

Type reference and figures. *Miogypsinella borodinensis* Hanzawa, 1940, pp. 779–780, pl. 39, figs. 1–9 (figs. 1–4, isolated specimens), text-fig. 2 (hand drawing illustrating the specimen of pl. 39, figs. 8–9).

Repository data. Thin sections labelled "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, a", "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, b", and "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, c" (Fig. 1a) and isolated specimens in cell slide labelled "*Miogypsinella borodinensis* n. sp. Hanzawa, IGPS Coll. Cat. No. 21456" (Fig. 1b); housed at the IGPS, Tohoku University, Sendai, Japan.

Table 3. Stratigraphical and geographical distribution of *Miogypsinella borodinensis* Hanzawa, *Miogypsinella bermudezi* (Drooger), and *Miogypsinella ubaghsi* (Tan).

References	Referred to as	Age	Locality	Illustrations
Cole (1938)	*Miogypsina* (*Miogypsinoides*) *complanata*	?Oligocene	E Mexico	pl. 8, fig. 10
Hanzawa (1940)	*M. borodinensis*	Chattian	Kitadaito Jima	figs. 1–9, text-fig. 2
Hanzawa (1940)	*M. sanjosensis* n. sp.	Oligocene	E Mexico	text-fig. 3 (drawing)
Barker and Grimsdale (1937)	*Miogypsinoides complanata*	Chattian	E Mexico	pl. 6, figs. 1–6, pl. 7, fig. 1; pl. 8, fig. 6
Galloway and Heminway (1941)	*Miogypsinoides complanata*	Oligocene	Porto Rico	pl. 36, figs. 6–9
Cole (1957a)	*Miogypsinoides complanatus*	?Oligocene	Panama	pl. 25, figs. 1–2
Hanzawa (1957)	*Miogypsinoides borodinensis*	Oligocene	Saipan, Tinian, Rota	pl. 15, fig. 11, pl. 21, figs. 2–3
Cole (1967)	*Miogypsinoides complanata* (Schlumberger);	Chattian	E Mexico	pl. 9, figs. 1, 3, 5, 8
Raju (1974)	*Miogypsina* (*Miogypsinoides*) cf. *bermudezi* Drooger	Chattian	Kutch (India)	pl. 5, figs. 1–3
Robinson and Persad (1989)	*Moigypsinoides* cf. *M. bermudezi*	Chattian	Antigua	pl. 1, figs. 1–4
Drooger (1993)	*Miogypsina bermudezi*	Oligocene	Cuba	fig. 43 (left), fig. 44 (left)
BouDagher-Fadel et al. (2000a)	*M.* cf. *borodinensis*	Chattian, lower Te	NE Borneo	pl. 2, fig. 3
BouDagher-Fadel et al. (2000b)	*M. borodinensis*	Chattian, lower Te	NE Borneo	no illustration
Robinson (2004)	*Miogypsinella* sp. cf. *M. bermudezi*	Chattian	Jamaica	fig. 10a
BouDagher-Fadel and Price (2013)	*M. borodinensis*	Late Oligocene (Te 2, 3, 4)	Borneo	fig. A1h
Robinson et al. (2017)	*Miogypsinella bermudezi*	Chattian	Antigua	fig. 6a–b
BouDagher-Fadel (2018)	*M. borodinensis*	Chattian	NE Borneo	pl. 7.14, fig. 3
Matsumaru et al. (2010)	*?Miogypsinoides formosensis*	Chattian	Menderes-Taurus Platform, Turkey	pl. 1, figs. 8–10
Mitchell et al. (2024)	*Miogypsinoides bermudezi* Drooger	Chattian	Americas	fig. 3.4–5
Mohler (1949)	*Miogypsina* (*M'oides*) *ubaghsi*	Chattian	Borneo	no illustration
Cole (1957b)	*Miogypsinoides ubaghsi* Tan	Chattian (Te 2–3)	Eniwetok	pl. 243, figs. 15–16

Table 3. Continued.

References	Referred to as	Age	Locality	Illustrations
Mohiuddin et al. (2000)	*Miogypsinella ubaghsi* (Tan, 1936a)	Chattian	Komahashi-daini Seamount	figs. 7.2, 8.2, 8.3
Cole (1954)	*Miogypsinoides borodinensis*	Aquitanian	Bikini	pl. 221, figs. 6–8
Hanzawa (1965)	*Miogypsinoides* [*borodinensis* (Hanzawa)]	Aquitanian	Kitadaito Jima	pl. 38, figs. 2a–b
BouDagher-Fadel and Price (2013)	*M. ubaghsi* (Tan Sin Hok)	Aquitanian (Te 2–Te 5)	Papua New Guinea	fig. A1f–g
Tan (1936a)	*Miogypsinoides ubaghsi*	Aquitanian	East Borneo	pl. 1, figs. 1–3, 7
Hanzawa (1940)	*Miogypsinella ubaghsi* (Tan)			text-fig. 4 (drawing)
Cole (1954)	*Miogypsinoides ubaghsi* Tan	Aquitanian	Bikini	pl. 221, figs. 9–17, no 18, pl. 222, figs. 13, 15
Cole (1954)	*Miogypsinoides borodinensis* (Hanzawa)	Aquitanian	Bikini	pl. 221, figs. 6–8
BouDagher-Fadel and Price (2013)	*Miogypsinella ubaghsi* Tan	early Aquitanian (Te 5)	Borneo, Papua New Guinea	fig. A1f–g
BouDagher-Fadel (2018)	*Miogypsinella ubaghsi* (Tan Sin hok	early Aquitanian, early Te 5	Papua New Guinea	pl. 7.14, figs. 4, 8
BouDagher-Fadel et al. (2000a)	*Miogypsinella ubaghsi* (Tan, 1936a) *Miogypsinella boninensis* Matsumaru	Burdigalian (lowermost upper Te) Chattian (lower Te)	Papua New Guinea NE Borneo	pl. 3, figs. 1–2 pl. 2, figs. 1–2, 4
Sharaf et al. (2005)	*Miogypsinella boninensis*	Upper Oligocene (lower Te)	East Java, Kujung	p. 1, fig. 1
Drooger (1951)	*Miogypsinoides (M.) bermudezi*	Aquitanian	Pinar del Rio, Cuba	figs. 1a–6
Akers and Drooger (1957)	*Miogypsina (Miogypsinoides) bermudezi*	Early Miocene	Gulf Coast	no illustrations

Diagnosis. Nepionic stage with 7–12 chambers in trochospiral whorl near the shell apex. Proloculus ranges from 80 to 110 µm in diameter (Table 2). Angle γ ca. 140–165°. The nepionic planispiral whorl is inclined about ca. 30° with respect to the subsequent equatorial chambers.

Lectotype. Hanzawa (1940) did not designate a type. The illustrated syntypes of Hanzawa (1940) occur in three thin sections (Fig. 1a). Three isolated specimens are also present (Hanzawa, 1940; pl. 39, figs. 1–4). In accordance with Art. 74 of ICZN (1999), we hereby designate as lectotype the specimen in thin section "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, a" (Fig. 1a), originally illustrated by Hanzawa (1940, pl. 39, figs. 5–6), with the purpose of clarifying the application of this name. The specimens of the other two thin sections illustrated in Fig. 1a thus become paralectotypes, as well as those in cell slide IGPS Coll. No. 21456.

Remarks. Hanzawa (1940) studied upper Oligocene material (see Iryu et al., 2010, for dated core data) collected from cores in the Kitadaito Jima borehole. The specimens illustrated in pl. 39, figs. 5–7, by Hanzawa (1940) show an apertural lip and subsutural canals, which are characters diag-

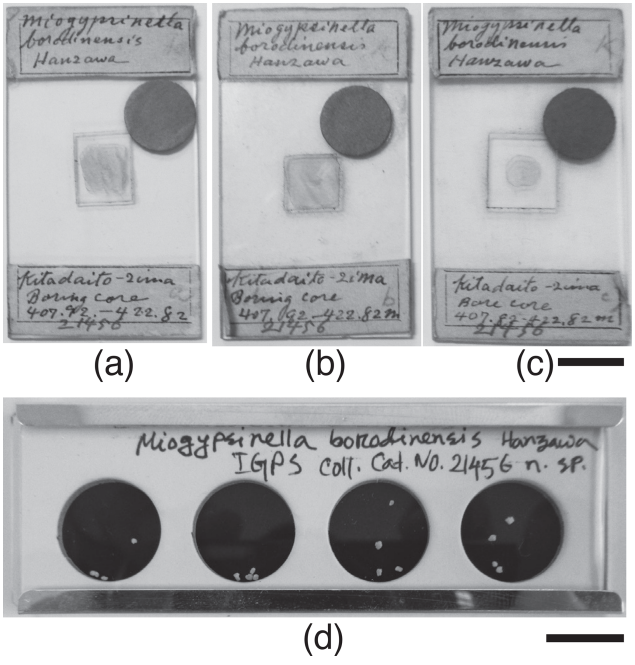

Figure 1. *Miogypsinella borodinensis* Hanzawa, 1940, thin sections of types and isolated specimens; Hanzawa's collection, IGPS, Tohoku University, Sendai, Japan. **(a)** "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, a"; lectotype, designated herein. **(b)** "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, b"; paralectotype, designated herein. **(c)** "*Miogypsinella borodinensis* Hanzawa, Kutadaito Jima Boring core 407.92–422.82 m, c"; paralectotypes, designated herein. **(d)** "*Miogypsinella borodinensis* n. sp. Hanzawa, IGPS Coll. Cat. No. 21456"; paralectotype, designated herein. Scale bar represents 1 cm.

nostic for *Miogypsinella*. The micro-CT-scanned specimens show the occurrence of the cover on intraseptal interlocular space, intraseptal interlocular space, apertural lip, subsutural canals, septal flap, primary spiral–umbilical canal, thickness of the lateral walls, toothplate, and vertical canal system. In the analysed Hanzawa specimens, the proloculus diameter, angle γ, and inclination of the nepionic planispiral whorl confirm its status as a distinct species (Figs. 1–5, Table 2).

Hanzawa (1940, pp. 766–767, fig. 1) considered "*Miogypsina complanata* Schlumberger, 1900" described by Nuttall (1933) and by Barker and Grimsdale (1937) to be *Miogypsinella* based on the occurrence of sub-quadrate chambers in the spiral whorl covered by a compact layer of laminated structure on both sides of the shell (pp. 771–772). However, these characters cannot be considered valid for including *M. complanata* in *Miogypsinella* (e.g. Loeblich and Tappan, 1987; BouDagher-Fadel, 2018; Table 1).

Hanzawa (1940, p. 775) referred to "*Miogypsina complanata* Schlumberger" of Nuttall (1933, pl. 24, figs. 9, 11, 13–14) and to *Miogypsinoides complanata* of Barker and Grimsdale (1937; pl. 8, fig. 6), both from the upper Oligocene of eastern Mexico (Méson Formation; Vaughan and Cole, 1936; Wilson, 1987), to establish the new species *Miogypsinella sanjosensis* Hanzawa (p. 766). Hanzawa (1940) did not designate a holotype.

Later, Hanzawa (1957, p. 92) corrected the status of his species *Miogypsinella sanjosensis*, considering it to be a synonym of *Miogypsinoides complanatus* based on its "rotaloid stage", which is not a distinctive character at the genus level (Table 1). The specimens of Nuttall (1933) show a biconvex test, 14 nepionic chambers ($X = 14$), angle γ ca. 180°, and lateral chamberlets (pl. 24, fig. 11). The occurrence of lateral chamberlets rules out the ascription of these specimens to *Miogypsinella*.

In contrast, the specimens of Barker and Grimsdale (1937, pl. 8, fig. 6) show a spiral canal "… from which spring offshoots passing into, and along, the radial septa" (p. 163; i.e. the intraseptal interlocular space and subsutural canals). According to these shell characters, along with the septal flap, toothplate, and vertical canal system on ventral side only, those specimens can be ascribed to *Miogypsinella* rather than to *Miogypsinoides* (Table 1). No information about the collection storage was provided by Barker and Grimsdale (1937), and the original material described and illustrated could not be located. The studied isolated specimens were illustrated as equatorial (pl. 6, figs. 1–6; pl. 7, fig. 1) and axial sections (pl. 8, fig. 6). The nepionic stage shows 8–12 chambers in trochospiral whorl with an angle γ of ca. 130°. The proloculus ranges from 80 to 110 µm in diameter. The nepionic planispiral whorl direction angle is nearly 30° with respect to the later equatorial chambers. These characters correspond to *Miogypsinella borodinensis* (Table 2). The specimens illustrated by Barker and Grimsdale (1937) and the single drawing reported by Hanzawa (1940, fig. 3) cannot be morphologically separated from the types of *Miogypsinella borodinensis*, and, therefore, *M. sanjosensis* cannot be considered a distinct species.

By studying material from the Aquitanian of Bikini, Cole (1954) considered *Miogypsinella borodinensis* to be *Miogypsinoides* (p. 600) with no detailed systematic remarks (see also Cole, 1969, table 2). The illustrated specimens show more than 12 chambers in the nepionic stage and a proloculus diameter of ca. 80 µm. These characters are comparable to those of *Miogypsinella ubaghsi* rather than to those of *M. borodinensis* (Table 2).

Cole (1967, pl. 9, figs. 1, 3, 5, 8) reported as *Miogypsinoides complanatus* four specimens from the Chattian Méson Formation of eastern Mexico, from where the specimens of Barker and Grimsdale (1937) originated (see remarks above). In the equatorial sections of the illustrated specimens, the occurrence of ca. 10 nepionic chambers close to the shell apex, the intraseptal interlocular space, and subsutural canals suggests their ascription to *Miogypsinella*. This confirms that the specimens of Barker and Grimsdale (1937) and Cole (1967) from eastern Mexico represent the same species (i.e. *Miogypsinella borodinensis*).

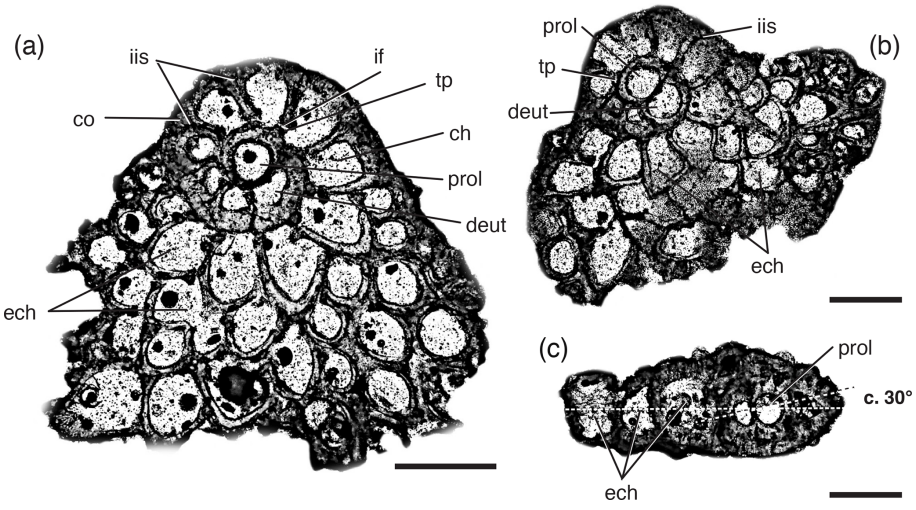

Figure 2. *Miogypsinella borodinensis* Hanzawa, 1940; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. **(a)** Equatorial section of an isolated specimen (Hanzawa, 1940, pl. 39, fig. 6). **(b)** Sub-equatorial section of an isolated specimen (Hanzawa, 1940, pl. 39, fig. 7). **(c)** Axial section of an isolated specimen (Hanzawa, 1940, pl. 39, fig. 8). Scale bar represents 0.250 mm. Abbreviations: ch, chamber; co, cover on intraseptal interlocular space; deut, deuteroconch; ech, equatorial chamberlet; if, intercameral foramen; iis, intraseptal interlocular space; prol, proloculus; tp, toothplate.

Matsumaru et al. (2010) and Matsumaru (2017, p. 165) regarded *Miogypsinella sanjosensis* Hanzawa (1940) as a junior synonym of *Miogypsinoides complanatus* based on upper Oligocene materials from Turkey and the Philippine archipelago. The illustrated specimens clearly show heavily thickened lateral walls and vertical canal systems to both sides of the test confirming the ascription of these specimens to *Miogypsinoides* and ruling out a possible affinity to *Miogypsinella*.

Cole (1957c) described *Miogypsinoides bantamensis* from the Aquitanian of Saipan and considered *Miogypsinella borodinensis* to be its synonym (p. 328). The illustrated specimens (pl. 110, figs. 8–18; pl. 111, figs. 1–4) show heavily thickened lateral walls and vertical canal systems on both sides of the test, suggesting that this synonymy cannot be accepted.

Miogypsina (*Miogypsinoides*) cf. *bermudezi* recorded from the Chattian of Kutch (India; Raju, 1974) was illustrated by drawings (pl. 1, figs. 1–5); by their outer surfaces (pl. 3, figs. 1–2); and by three equatorial sections, which show nepionic chambers comparable in number ($X = 11$–12; Raju, 1974; pl. 5, figs. 1–3) and in angle γ (130–150°) to those of *M. borodinesis*. This record of *bermudezi* likely corresponds to *borodinensis* (Tables 2 and 3). However, these Chattian records need further confirmation since no axial sections were illustrated (Raju, 1974). Random sub-axial sections of these Indian specimens show a thick lateral wall, suggesting possible affinities with *Miogypsinoides*.

Gedik (2018) reported *Miogypsinella borodinensis* from the Chattian of Malatya (Turkey). Gedik (2018) concluded that *Miogypsinoides bantamensis, Miogypsinella borodinensis*, and *Miogypsinella bermudezi* are synonyms of *Miogypsinella borodinensis* because of their number of nepionic chambers. This synonymy cannot be accepted due to the different shell characteristics of these species (Table 2). The thickness of the outer shell walls of the illustrated Malatya specimens suggests they are *Miogypsinoides*.

The Chattian records of *Miogypsinella borodinensis* from the western Tethys (Turkey; Sirel, 2003, 2015; Sirel and Gedik, 2011; Sirel and Işık, 2011; Hakyemez et al., 2016; Gedik, 2018) and the central Indo-Pacific (Borneo; BouDagher-Fadel, 2018) show planispiral nepionic chambers, heavily thickened lateral walls, and a vertical canal system to both sides of the test (Table 1). Therefore, these records belong to *Miogypsinoides*. The comparison between the proloculus diameter and the number of nepionic chambers of the recorded *Miogypsinoides* species in the Mediterranean areas (Schiavinotto and Benedetti, 2021, fig. 6) and *M. borodinensis* confirm this conclusion.

The single record of *Miogypsinella borodinensis* from the Chattian of Aquitaine (France; Cahuzac, 1984, pl. 1, fig. 5) does not clearly show its shell characters. Similarly, the single record of *Miogypsinella* from the Chattian of Brazil needs further confirmation since a thickened outer shell wall is likely present in the illustrated specimen (Alvarado Sierra et al., 2023).

Two drawings of axial sections of *Miogypsinoides complanatus* from the Oligocene of north-western Italy (as *Miogypsina* (*Miogypsinoides*) *complanata* in Ferrero Mortara (1987, fig. 4a–b) are similar to *Miogypsinella borodinensis*. However, due to the lack of information about the cover on intraseptal interlocular space, apertural lip, subsutural canals,

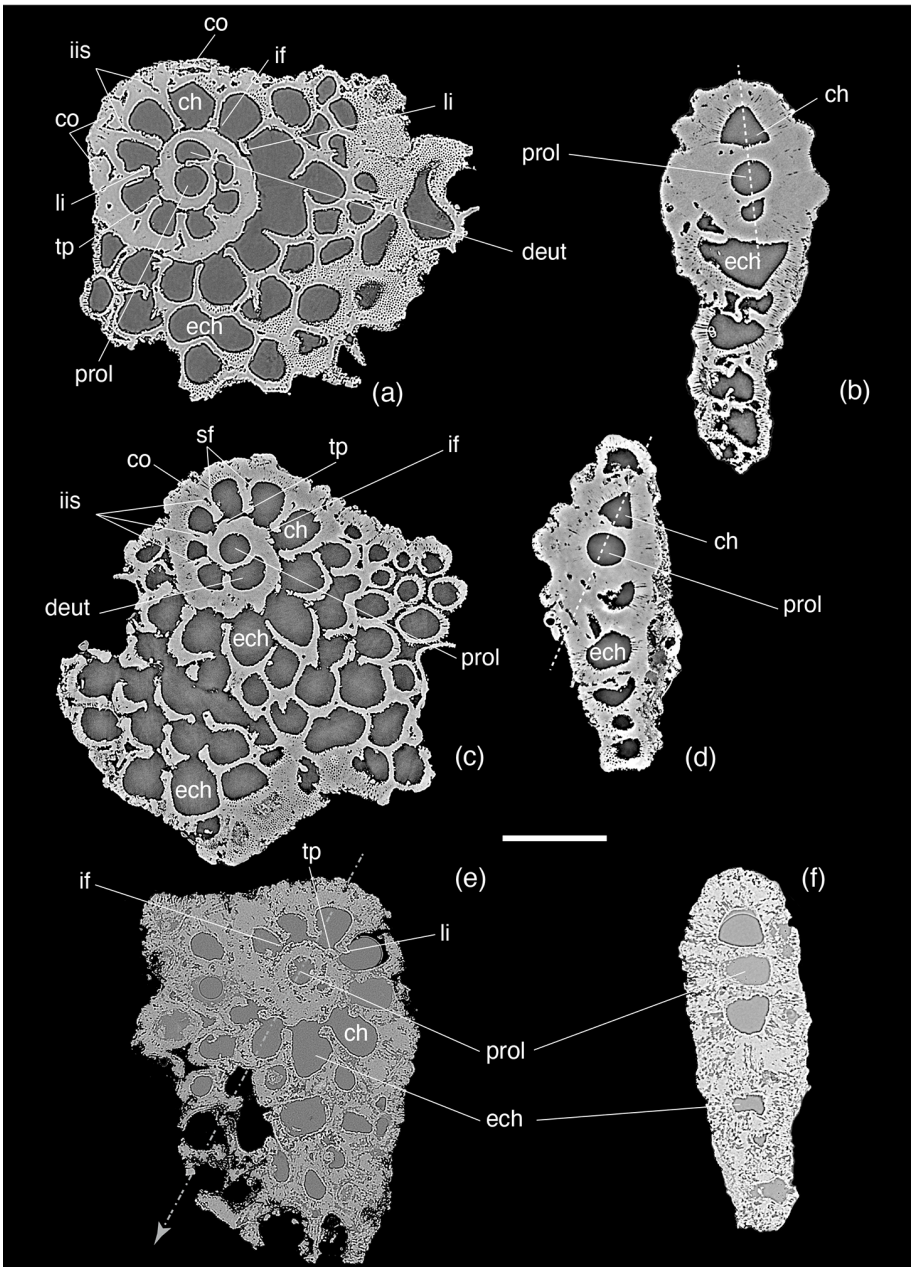

Figure 3. *Miogypsinella borodinensis* Hanzawa, 1940; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. Micro-computed tomographic analysis of megalospheric specimens. Scale bar represents 0.250 mm. For abbreviations see Fig. 2; li, apertural lip; sf, septal flap; tp, toothplate.

and spiral canal, these specimens cannot be ascribed with certainty to *Miogypsinella*.

Geographical and stratigraphical distribution. *Miogypsinella borodinensis* appears in the Chattian in the central Indo-Pacific area (Figs. 6 and 7, Table 3). Central Indo-Pacific records of this species are from NE Borneo (BouDagher-Fadel et al., 2000a, b; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018) and Kitadaito Jima (Hanzawa, 1940, 1965), Saipan (Hanzawa, 1957), and the Bikini Atoll (Cole, 1954). The Central American records are from the Chattian of eastern Mexico (Barker and Grimsdale, 1937; Cole, 1967), Antigua, and Jamaica (Robinson and Persad, 1989; Robinson, 2004; Robinson et al., 2017; Mitchell et al., 2024). The last occurrences are from the Aquitanian of Kitadaito Jima (Hanzawa, 1965) and Bikini (Cole, 1954) (Fig. 6).

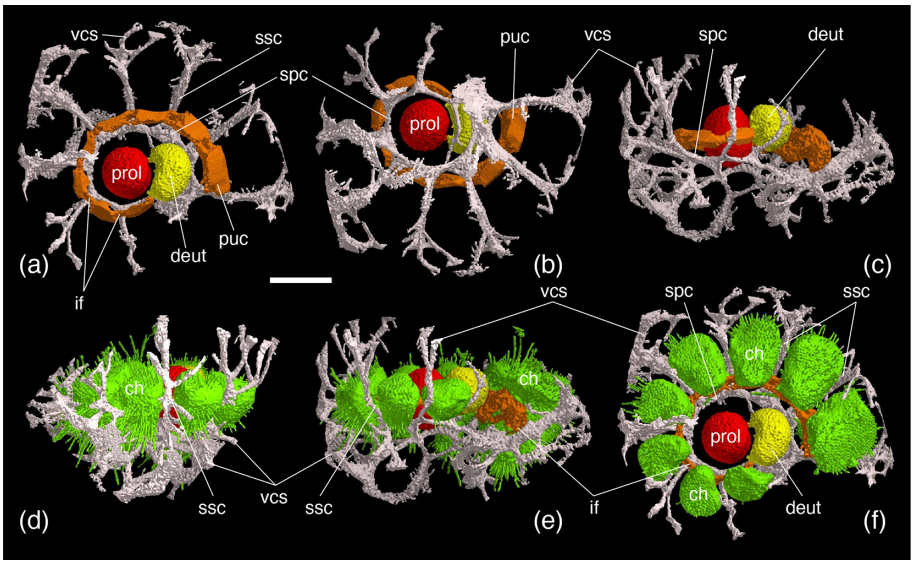

Figure 4. *Miogypsinella borodinensis* Hanzawa, 1940; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. Micro-computed tomographic scanning 3D-rendered models with shell removed (rendering by Shunichi Kinoshita). Primary spiral–umbilical canal is tubular (puc). The vertical canal system (vcs), issuing from the spiral canal (spc), connects successive volutions of the spiral canal. Subsutural canals (ssc; i.e. sutural fissures in de Bock, 1976) issue from deep interseptal spaces in the ultimate intercameral suture. For abbreviations see Fig. 2; sf, septal flap. Scale bar represents 0.100 mm.

Miogypsinella bermudezi (Drooger, 1951)

1951 *Miogypsina* (*Miogypsinella*) *bermudezi* n. sp., Drooger, pp. 357–359, figs. 1a–6.

1952 *Miogypsina bermudezi* Drooger; Drooger, p. 47.

? 1957 *Miogypsina* (*Miogypsinoides*) *bermudezi* Drooger; Akers and Drooger, pp. 670, 674.

1957 *M. bermudezi* (Drooger) (1951) (= *M. ubaghsi* Tan); Hanzawa, p. 86.

1993 *Miogypsina bermudezi*; Drooger, fig. 43 (left), fig. 44 (left).

non 2003 *Miogypsinella bermudezi* Drooger; Sirel, pl. 14, figs. 1–27.

Type reference and figures. *Miogypsina* (*Miogypsinella*) *bermudezi* Drooger, 1951, pp. 357–359, figs. 1a–6; figs. 1a–c, 2a–c, 3a–b (holotype).

Repository data. Unfortunately, the original material described by Drooger (1951) could not be located at the Department of Earth Sciences, Faculty of Geosciences, Utrecht University.

Diagnosis. Nepionic stage with 13–19 chambers in trochospiral whorl near the shell apex. Proloculus ranges from 50 to 70 µm in diameter (Table 2). Angle γ ca. 300°. The nepionic planispiral whorl is nearly horizontal with respect to the subsequent equatorial chambers.

Remarks. Drooger (1951) introduced this *Miogypsinella* species from the Miocene of Cuba. The holotype is an isolated specimen illustrated by drawings (figs. 1a–c, 2a–c, 3a–b), whereas three specimens (paratypes) are represented by equatorial (fig. 4) and axial sections (figs. 5–6). The paratypes show intraseptal interlocular space, subsutural canals, septal flap, primary spiral canal, subsutural canals, thickness of the lateral walls, toothplate, and a vertical canal system, indicating that they belong to *Miogypsinella*. They show 12 nepionic chambers, arranged in a planispiral whorl nearly horizontal (i.e. planispiral whorl direction degree 0°; figs. 5–6), with a proloculus 50–70 µm in diameter (Drooger, 1951, p. 359). The angle γ is ca. 300° (Drooger, 1951, fig. 4).

This species suffered the taxonomic uncertainties regarding the distinction between *Miogypsinoides* and *Miogypsina*. Drooger (1952, 1993) ascribed *M. bermudezi* to *Miogypsina* but afterwards regarded the species as *Miogypsinoides bermudezi* (1963, fig. 4; Drooger and Raju, 1973). The distinctive short nepionic stage and the "difference in thickness of the solid side wall" with respect to *Miogypsinoides* (Drooger, 1993, p. 76, 89, fig. 43) suggest a separate status of this species as *Miogypsinella bermudezi*. This status is further confirmed by the occasional occurrence of intraseptal interlocular space and subsutural canals, referred to by Drooger (1993, p. 83) as "lateral chambers".

Miogypsinella bermudezi differs from *M. borodinensis* in having a smaller proloculus (50–70 µm versus 90 µm), a higher number of nepionic chambers (X = 13–19 versus X = 7–12), a higher angle γ (ca. 300° *versus* 140–165°), and a horizontal early trochospiral whorl (Table 2). *Miogypsinella bermudezi* is similar to *M. ubaghsi* (Table 2)

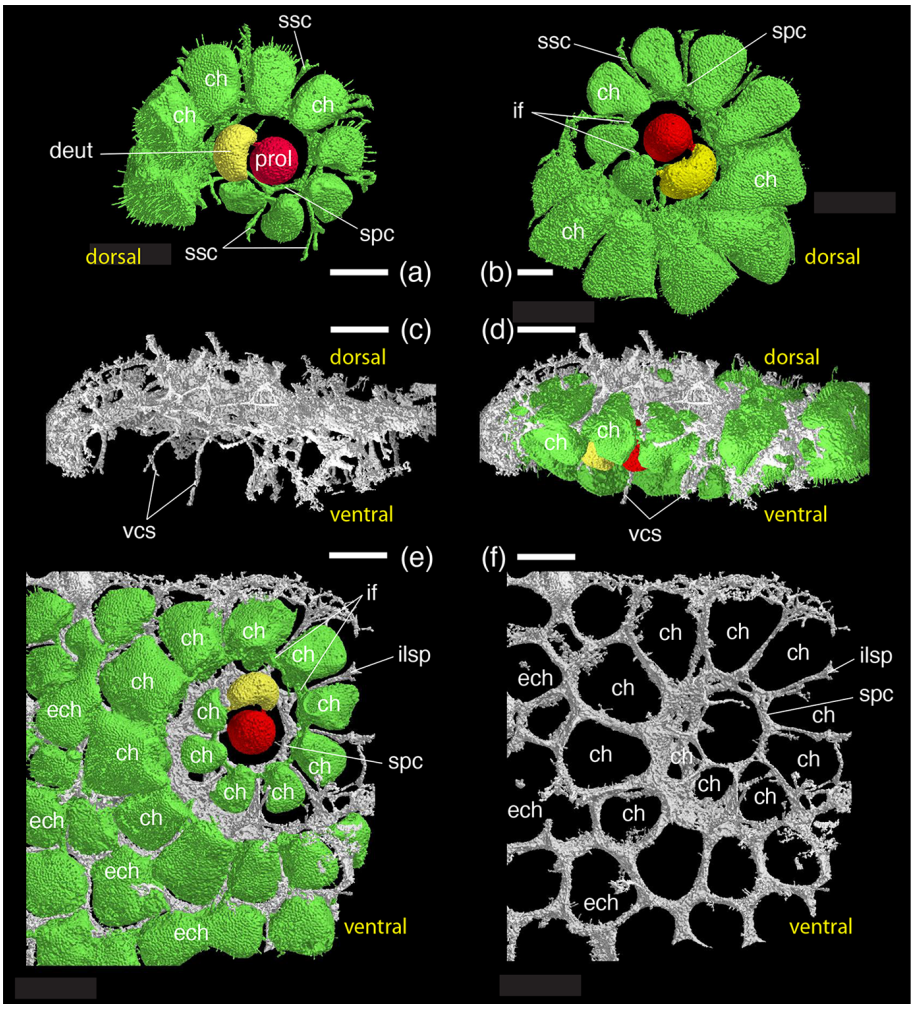

Figure 5. *Miogypsinella borodinensis* Hanzawa, 1940; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. Micro-computed tomographic scanning 3D-rendered models with shell removed (rendering by Shunichi Kinoshita). The ventral side of the shell is characterized by the vertical branches of the intraseptal canal system. Scale bars represent 0.100 mm. For abbreviations see Figs. 2–4.

except for the proloculus diameter (50–70 µm versus 80–130 µm).

Since no illustrations were published, Early Miocene records from the Louisiana Gulf Coast (Akers and Drooger, 1957; see Poag, 1975, for stratigraphy) and Puerto Rico (Gordon, 1961) need further study. Nonetheless, Akers and Drooger (1957) described "thicker side walls and pustules" which do not support the ascription to the thinner-walled *Miogypsinella*.

Chattian specimens from Antigua and Jamaica (Robinson, 2004) are characterized by thinner lateral side walls, proloculus size, and number of nepionic chambers comparable to those of *Miogypsinella borodinensis* rather than to *M. bermudezi* (Table 2).

Miogypsinoides nigeriana (Küpper, 1960), from the Burdigalian of Cameroon, is characterized by very thin lateral walls and a sub-horizontal planispiral nepionic whorl resembling those of *Miogypsinella bermudezi*. However, because in *Miogypsinoides nigeriana* the canal system occurs at both sides of the test, this species was correctly ascribed to *Miogypsinoides* (Drooger, 1966). The Chattian record of *Miogypsinella bermudezi* from the western Tethys (Turkey; Sirel, 2003, pl. 14, figs. 1–27) shows shell characters distinctive of *Miogypsinoides* (Table 1).

Stratigraphical distribution. Drooger (1951) attributed his material from Baños in Pinar del Rio Province, western Cuba, to the "Early Middle Oligocene" (p. 359). According to the stratigraphical reassessment of the Oligocene–Miocene stratigraphy of Cuba, the Baños succession was formalized as the Baños Formation (Iturralde-Vinent, 1972). This formation consists of two members: the lower member (Oligocene–lowermost Miocene) with deep-water benthic foraminifera and lepidocyclinids and the upper member (Miocene) consisting of sandy limestone with lepidocyclinids, nummulitids, and miogypsinids. The material of

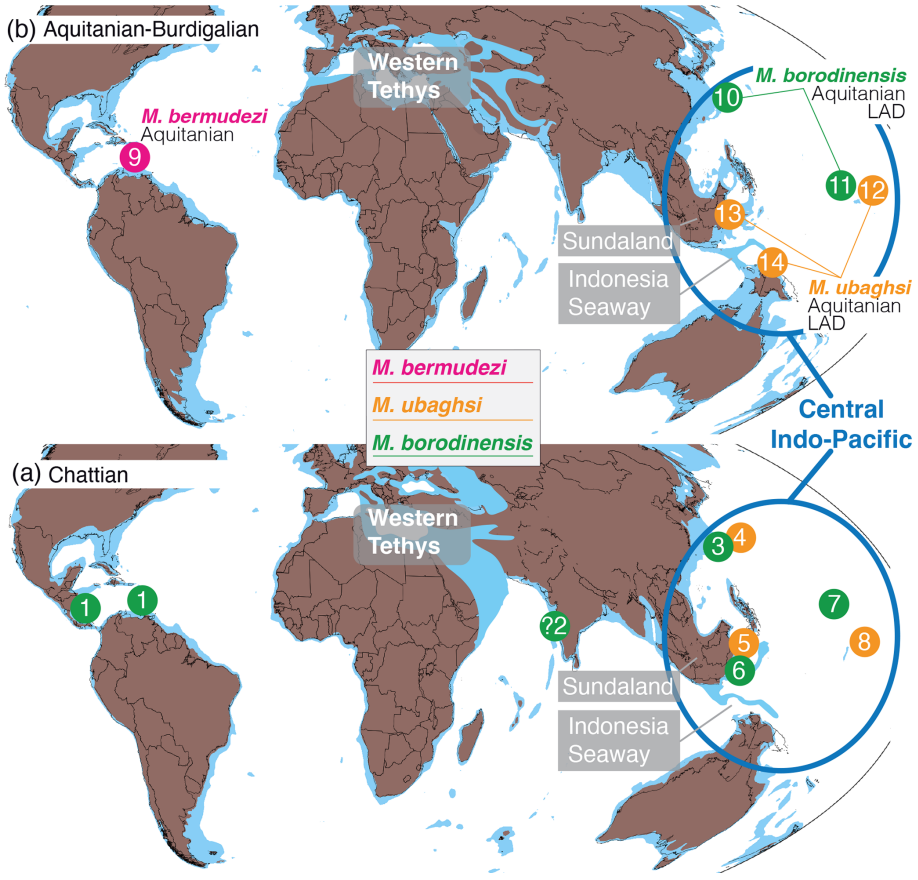

Figure 6. Palaeogeographical locations of the early Oligocene **(a)**–early Miocene **(b)** *Miogypsinella* species. Abbreviations: Mbe, *Miogypsinella bermudezi*; Mbo, *Miogypsinella borodinensis*; Mu, *Miogypsinella ubagshi*; LAD, last appearance datum. In America, *Miogypsinella borodinensis* has so far been identified in the Chattian of eastern Mexico, Jamaica, and Antigua only (1, Barker and Grimsdale, 1937; Cole, 1967; Robinson, 2004; Robinson et al., 2017). *Miogypsinella borodinensis* appeared in the Chattian of Kitadaito Jima (3, Hanzawa, 1940), Saipan (7, Hanzawa, 1957), and north-eastern Borneo (6, BouDagher-Fadel et al., 2000a; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018). Its last occurrences are from the Aquitanian of Kitadaito Jima (10, Hanzawa, 1965) and Bikini (11, Cole, 1954). *Miogypsinella ubaghsi* ranges from the Chattian to the Aquitanian. This species occurs in the Chattian of Chichi Jima (4), north-eastern Borneo (5), and Eniwetok (8) (Tan, 1936a, b; Mohler, 1949; Cole, 1954, 1957b; Matsumaru, 2012; BouDagher-Fadel and Price, 2013; Mohiuddin et al., 2000; BouDagher-Fadel, 2018) as well as the Aquitanian of Bikini (12), north-eastern Borneo (13), and Papua New Guinea (14) (Tan, 1936a; Cole, 1954; Hanzawa, 1940; BouDagher-Fadel et al., 2000a; BouDagher-Fadel and Price, 2013). The single record of *Miogypsinella bermudezi* is from the early Miocene of Cuba (9, Drooger, 1951). Numbers refer to localities. 1: Barker and Grimsdale (1937; Mbo, eastern Mexico), Cole (1938, 1957a, 1967; Mbo, eastern Mexico, Panama). 2: Raju (1974; Mbo, Kutch). 3: Hanzawa (1940; Mbo, Kitadaito Jima), Matsumaru (2012; Mbo, Kitadaito Jima), this study. 4: Matsumaru (2012; Mbo, Mu, Chichi Jima). 5: BouDagher-Fadel et al. (2000a, b; Mbo, Mu, NE Borneo), BouDagher-Fadel and Price (2013; Mbo, Borneo), BouDagher-Fadel (2018; Mbo, NE Borneo). 7: Hanzawa (1957; Mbo, Saipan). 8: Hanzawa (1962; Mu, Eniwetok). 9: Drooger (1951; Mbe, Pinar del Rio, Cuba). 10: Hanzawa (1965; Mbo, Kitadaito Jima). 11: Cole (1954; Mbo, Bikini). 12: Cole (1954; Mu, Bikini). 14: BouDagher-Fadel et al. (2000a; Mu, NE Borneo, Papua New Guinea), BouDagher-Fadel and Price (2013; Mu, NE Borneo, Papua New Guinea), BouDagher-Fadel (2018; Mu, Papua New Guinea). Palaeogeographical maps modified from Hall (2013) and Kocsis and Scotese (2021). Flooded continental areas are indicated with light blue; terrestrial areas are coloured brown.

Drooger (1951) probably came from the upper member, early Miocene in age (Figs. 6–7, Table 3).

Miogypsinella ubaghsi (Tan, 1936)

1936a *Miogypsinoides ubaghsi* n. sp. Tan, pp. 47–48, pl. 1, figs. 1, 7.

non 1936a *Miogypsinoides ubaghsi* n. sp. Tan, pl. 1, figs. 3–6.

1940 *Miogypsinella ubaghsi* (Tan); Hanzawa, pp. 767–768, 775, text-fig. 4.

1949 *Miogypsina* (*Moides*) *ubaghsi*; Mohler, p. 526.

1954 *Miogypsinoides ubaghsi* Tan; Cole, pp. 603–604, pl. 221, ? fig. 5, figs. 9–17, no fig. 18, pl. 222, figs. 13, 15, no fig. 14.

1954 *Miogypsinoides borodinensis* (Hanzawa); Cole, p. 600, pl. 221, figs. 6–8.

1957b *Miogypsinoides ubaghsi* Tan; Cole, pp. 770–771, pl. 243, figs. 5–16.

non 1957b *Miogypsinoides ubaghsi* Tan; Cole, pl. 243, figs. 10–11, 13–14, 17–19.

1957 *Miogypsinella bermudezi* (Drooger); Hanzawa, p. 86.

? 1962 *Miogypsinoides ubaghsi* Tan; Hanzawa, pl. 7, figs. 16–17, 19 (drawings).

? 1984 *Miogypsinoides ubaghsi* Tan Sin Hok; Cahuzac, pl. 1, fig. 2.

? 1986 *Miogypsinoides ubaghsi*; Premoli Silva, pl. 1, figs. 1–3, 9.

? 1981 *Miogypsinoides ubaghsi*; Premoli Silva and Brusa, pl. 12, figs. 12–13, pl. 13, fig. 5.

? 1991 *Miogypsinoides ubaghsi*; Gibson and Margerum, fig. 8.

1996 *Miogypsinella boninensis* n. sp.; Matsumaru, pp. 50, 52, 54, pl. 7, figs. 12–13; figs. 23–24.

non 1996 *Miogypsinella boninensis* n. sp.; Matsumaru, pl. 5, figs. 1–7; pl. 6, figs. 1–12; pl. 7, figs. 1–11, 14–16.

2000a *Miogypsinella ubaghsi* (Tan Sin Hok); BouDagher-Fadel et al., pl. 3, figs. 1–2.

2000a *Miogypsinella boninensis* Matsumaru; BouDagher-Fadel et al., pl. 2, figs. 1–2, 4.

2000 *Miogypsinella ubaghsi* (Tan, 1936; Mohiuddin et al., p. 199, figs. 7.2, 8.2, 8.3.

2005 *Miogypsinella boninensis* Matsumaru, 1996; Sharaf et al., p. 10, pl. 1, fig. 1.

2018 *Miogypsinella ubaghsi* (Tan Sin Hok); BouDagher-Fadel, pl. 7.14, figs. 4, 8.

non 2020 *Miogypsinella ubaghsi*; Teillet et al., fig. 5A.

Type reference and figures. Tan (1936a), pp. 47–48, pl. 1, figs. 1–3, 7.

Repository data. The original material described and illustrated by Tan (1936a) could not be located.

Diagnosis. Nepionic stage with 13–16 (maximum 24) chambers in a trochospiral whorl near the shell apex. Proloculus ranges from 80 to 130 µm in diameter (Table 2). Angle γ ca. 330° (maximum 400°). The nepionic planispiral whorl is nearly horizontal with respect to the equatorial chambers.

Remarks. Tan (1936a) established the new species *Miogypsinoides ubaghsi* from the Aquitanian of Indonesia. Hanzawa (1940) considered *M. ubaghsi* to be congeneric with *Miogypsinella borodinensis*, both taxa having "a juvenarium of rotaloid spire and umbilical plugs" (p. 767). The occurrence of subsutural canals and a vertical canal system only in the ventral shell side in the types of *ubaghsi* (Tan, 1936a, pl. 1, figs. 1–3, 7) indicates that it belongs to *Miogypsinella*. *Miogypsinella ubaghsi* differs from the other species in having a larger proloculus, the highest number of nepionic chambers, and the lowest angle γ (Table 2).

In the Aquitanian of Eniwetok, Cole (1957b) identified *Miogypsinoides ubaghsi* with no detailed systematic remarks (see also Cole, 1969, table 2). The illustrated specimens show a thickened lateral shell wall, indicating their ascription to *Miogypsinoides*.

Miogypsinella boninensis Matsumaru, 1996, described from the Chattian of Minami-jima (Japan), was considered a species separated from *M. ubaghsi* essentially by having a proloculus ca. 90–140 µm in diameter and 23–28 nepionic chambers (Matsumaru, 1996, p. 52). However, the proloculus diameter and the number of the nepionic chambers, along with an unclear angle γ (Matsumaru, 1996, pl. 5, figs. 1–7; pl. 6 fig. 6, holotype; fig. 23/4), question the separation of the two species (see also Matsumaru, 1996, p. 54, no illustrated axial sections) and suggest that *M. boninensis* likely belongs to *Miogypsinoides*.

Cahuzac (1984) illustrated a single specimen from the Chattian of Aquitaine (France) but did not provide any information about the shell characters.

Most of the *Miogypsinella ubaghsi* (as *Miogypsinoides*) records are inadequately illustrated, and some shell characters do not fit with the species circumscription, as they show heavily thickened lateral walls and vertical canal systems to both sides of the test (Table 1; Cole, 1954, 1957b; Premoli Silva, 1986; Premoli Silva and Brusa, 1981; Gibson and Margerum, 1991; Teillet et al., 2020).

Stratigraphical distribution. The material of Tan (1936a) was collected from the Aquitanian of Indonesia. This species has been recorded from the Chattian in Borneo, Eniwetok, Chichi Jima, Komahashi-daini Seamount, Kitadaito Jima, and Kyushu-Palau ridge (Mohler, 1949; Hanzawa, 1962; Matsumaru, 1996, 2012; Mohiuddin et al., 2000) as well as the Aquitanian in Papua New Guinea (Cole, 1954, 1957b; BouDagher-Fadel et al., 2000a; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018) (Figs. 6 and 7, Table 3).

Genus ***Miogypsinoides*** Yabe and Hanzawa, 1928

Type species. *Miogypsina dehaartii* van der Vlerk, 1924, pp. 429–432, figs. 1a–c, figs. 2–3.

Diagnosis. Embryo near test apex; nepionic chambers in a single planispiral whorl with spherical proloculus and reni-

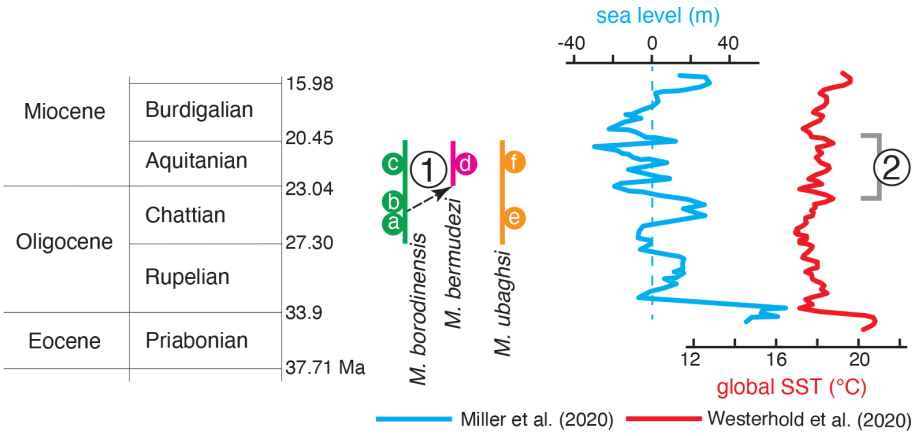

Figure 7. Biostratigraphical patterns of the lower Oligocene–lower Miocene *Miogypsinella* species compared with the global eustatic curves and global sea surface temperature (SST) estimates. *Miogypsinella borodinensis* **(a, b)** and *M. ubaghsi* **(e)** appeared during the Chattian peaks in sea level curve (e.g. Miller et al., 2020) and global SST (e.g. Westerhold et al., 2020). The occurrence of *Miogypsinella borodinensis* in the Chattian of eastern Mexico **(b)** is interpreted as the result of Pacific migrants likely following an eastward path to Central America. *Miogypsinella bermudezi* **(d)** descended from *M. borodinensis* (1). *Miogypsinella borodinensis* **(c)** and *M. ubaghsi* **(f)** disappear near the Aquitanian–Burdigalian eustatic rise, which nearly coincides with the initiation of the Indonesian Seaway restriction and the abrupt deposition of deeper-marine clays in Southeast Asia (ca. 23–20 Ma; 2). See text and Table 3 for details; a: Cole (1954), BouDagher-Fadel (2018), BouDagher-Fadel et al. (2000a), BouDagher-Fadel and Price (2013), Hanzawa (1940, 1957), and Raju (1974); b: Barker and Grimsdale (1937), Cole (1967), Hanzawa (1940); c: Hanzawa (1965); d: Drooger (1951); e: Mohler (1949), Cole (1957b), Hanzawa (1962), Matsumaru (1996, 2012), BouDagher-Fadel et al. (2000a), Mohiuddin et al. (2000), Sharaf et al. (2005); f: BouDagher-Fadel (2018), BouDagher-Fadel and Price (2013), Cole (1954), Tan (1936a, b). Timescale after Cohen et al. (2025).

form protoconch; asymmetrical equatorial chamberlets; septal flap, intraseptal interlocular space with cover, vertical canals extended to both sides of the shell; distinctively lamellar, thick lateral walls.

Miogypsinoides lateralis Hanzawa, 1940
Figures 8 and 9.

1940 *Miogypsinoides lateralis* n. sp. Hanzawa, p. 783, pl. 39, figs. 10–14.

1953 *Miogypsinoides formosensis* Yabe and Hanzawa; Cole et al., pl. 14, fig. 8.

1957 *Miogypsinoides lateralis* Hanzawa; Hanzawa, pp. 92–93.

1957 *Miogypsinoides dehaartii* (Van der Vlerk); Cole, pl. 111, figs. 6, 11.

1957 *Miogypsinoides bantamensis* Tan; Cole, pl. 110, fig. 15.

1962 *Miogypsinoides lateralis* Hanzawa; Hanzawa, pl. 7, figs. 9, 13.

1969 *Miogypsinoides dehaartii* (van der Vlerk) (with "*M. lateralis*" kind of embryonic apparatus"); Cole, pl. 1, figs. 5–6, 9, 11–12, 20.

1974 *Miogypsina* (*Miogypsinoides*) *bantamensis* Tan Sin Hok; Adams and Belford, p. 496, pl. 73, figs. 8–11.

Type reference and figures. *Miogypsinoides lateralis* Hanzawa, 1940, p. 783, pl. 39, figs. 10–11 (isolated specimens), 12 (axial section), 13 (equatorial section), 14 (equatorial section, detail of the nepionic stage).

Repository data. Thin sections labelled "*Miogypsinoides lateralis* Hanzawa, Kutadaito Jima Boring core 363.76–371.83 m, a" (Fig. 8a) and isolated specimens in cell slide labelled "AQUITANIAN Kita-Daito-jima Deep well. 331.52–338.57 Deep Hypotype *Miogypsinoides lateralis* Hanzawa IGPS. Coll. Cat. No. 21491" and "*Miogypsinoides lateralis* Hanzawa n. sp. Hypotype 351.52–338.57 m IGPS Cat. 21491" (Fig. 8d); housed at the IGPS, Tohoku University, Sendai, Japan.

Diagnosis. Nepionic stage with seven to eight chambers in a planispiral whorl. Sub-spheroidal proloculus ca. 160 µm in diameter followed by reniform deuteroconch, ca. 175 µm wide (Fig. 9b, d and e). Arc length of nepionic spiral whorl starting from embryonic chambers and ending at the apical point of test of ca. 90°. Nepionic chambers are connected by a primary spiral canal (Fig. 9b, d and e). Intraseptal interlocular space formed between the posterior bilamellar wall of a chamber and the distal bilamellar wall of the preceding one as a result of a deeply sunken suture (Fig. 9c–e). Intraseptal space is open to the exterior along its margins either continuously or through openings between points of marginal adherence of consecutive lateral chamber walls (Fig. 9c–e). Toothplates develop from an intercameral foramen to an aperture and are attached to both (Fig. 9d). These toothplates

are shaped to form a single fold with a free distal end and distally protruding into the aperture. Septal flaps are part of the inner lamella covering the preceding septal face. By its adherence to the septal face, the septal flap produces a trilamellar septum (Fig. 9d).

Lectotype. Hanzawa (1940) did not designate a type. The original material illustrated by Hanzawa (1940) occurs in one thin section (Fig. 8a). In accordance with Art. 74 of ICZN (1999), we hereby designate as lectotype the specimen in thin section "*Miogypsinoides lateralis* Hanzawa, Kutadaito Jima Boring core 363.76–371.83 m, a" (Fig. 8a–c), originally illustrated by Hanzawa (1940, pl. 39, figs. 13–14), with the purpose of clarifying the application of this name. The isolated specimens in cell slides thus become paralectotypes (Fig. 8d).

Remarks. The specimens illustrated in pl. 39, figs. 12–14 (Hanzawa, 1940) show the thickness of the lateral wall and the ventral canal system to either side of the shell, which are characters diagnostic for *Miogypsinoides* (Table 1). The occurrence of nepionic chambers in a single planispiral whorl, intraseptal interlocular space, thickened lateral walls with vertical and lateral canal systems to both sides, and equatorial ogival chambers confirms that the type specimens belong to the genus *Miogypsinoides* (de Bock, 1976; Loeblich and Tappan, 1987; Drooger, 1993; Table 1).

Although considered a junior synonym of *Miogypsinoides bantamensis* (Cole, 1957c, p. 339; Drooger, 1963, p. 346), *M. lateralis* differs from *M. bantamensis* in having fewer nepionic chambers (6–7 versus 11–14). Based on specimens from Saipan, Cole (1967) reconsidered *Miogypsinoides lateralis* to be a distinct species, with the "*lateralis* kind of specimens" occurring with the "*bantamensis*" and "*dehaartii*" "kinds". Cole (1969) identified *Miogypsinoides lateralis* along with *M. bantamensis*, *M. dehaartii*, and *M. mauretanicus* in deep drill cores in the Midway Atoll. Despite stating that *Miogypsinoides lateralis* is easily distinguishable from *M. bantamensis*, Cole (1969, p. C11) proposed to group both species into *M. dehaarti* (p. C12) because they were found "constituting a continuous series" in one part of the studied region. This proposal is not supported by any morphologic characters, which clearly differentiate *Miogypsinoides lateralis* from the other species. Adams and Belford (1974) considered *Miogypsinoides lateralis* to be a synonym of *M. bantamensis* with no discussion on systematic remarks.

Based on Aquitanian specimens from Shikoku (Japan), Matsumaru et al. (1993) considered *Miogypsinoides lateralis* to be a synonym of *Miogypsinoides dehaartii*. However, the illustrated axial sections do not show specific diagnostic characters, and the ascription of specimens is uncertain. Later, Matsumaru et al. (2010, p. 454) and Matsumaru (2017, p. 166) also regarded *Miogypsinoides lateralis* as a synonym of *M. bantamensis*. The described and illustrated specimens clearly do not belong to *Miogypsinoides lateralis* as they show 10–14 nepionic chambers and an angle γ of ca. 150°. Raju (1974) described *Miogypsinoides indica* from the lower Burdigalian of Kutch and Saurastra in India. This species is comparable to *Miogypsinoides lateralis* in the number of nepionic chambers (five to eight versus seven to eight) and the protoconch diameter (ca. 193 µm versus 175 µm) (Fig. 10a). However, the angle γ (17° versus 90°) clearly separates the two species.

Stratigraphical distribution. The genus *Miogypsinoides* ranges from the Rupelian to the Chattian in America (Drooger, 1993; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018), from the Chattian to the Burdigalian in the Mediterranean (Drooger and Laagland, 1986; Cahuzac and Poignant, 1997; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018), and from the Chattian to the Langhian in the Indo-Pacific (Drooger, 1993; BouDagher-Fadel and Price, 2013; BouDagher-Fadel, 2018; Lunt and Allan, 2004; Lunt and Luan, 2022) (Fig. 10b).

Miogypsinoides lateralis appears in the Aquitanian in Kitadaito Jima (Hanzawa, 1940, 1962), Saipan (Cole, 1957c), and the Midway Atoll (Cole, 1969).

The single record of *Miogypsinoides lateralis* in the western Tethys is from the Chattian of southern Aquitaine (France; Cahuzac, 1984, pl. 1, fig. 8). The specimen shows six to seven nepionic chambers, a proloculus diameter of ca. 110 µm, and an angle γ of ca. 90°. This proloculus is smaller than that of *M. lateralis* (i.e. ca. 160 µm in diameter). Sztrákos and Steurbaut (2017) mentioned *M. lateralis* from the Chattian (P22 biozone) of western Aquitaine with no illustration. These records require further study.

4 Discussion

4.1 Palaeobiogeographical patterns

Miogypsinella borodinensis and *M. ubaghsi* occur in the Chattian of Kitadaito Jima, Chichi Jima, north-eastern Borneo, Eniwetok, and Saipan (Fig. 6, Table 3). The single record of *Miogypsinella borodinensis* from the Chattian of India (Kutch; Raju, 1974) is the westernmost record of this species from the central Indo-Pacific, whereas its easternmost occurrence is in eastern Mexico (Fig. 6).

Considering that this species has never been identified in the western Tethys (Mediterranean), the occurrence of *Miogypsinella borodinensis* in the Chattian of eastern Mexico (Barker and Grimsdale, 1937; Hanzawa, 1940; Cole, 1967) is probably the result of Pacific migrants following an eastward path to Central America. The eastward Pacific currents were ways to the propagation of various shallow-water benthic species (e.g. Langer and Hottinger, 2000; Yasuhara et al., 2022). Central Indo-Pacific and eastern Pacific coral faunas show strong affinities, and numerous reef-associated species from both areas have a high genetic similarity (Glynn and Ault, 2000; López-Pérez, 2005; Lessios and Robertson, 2006; Wood et al., 2013). It is widely accepted that Indo-Pacific immigrants constitute approximately 66 % of the eastern Pacific fauna (Reyes-Bonilla, 2002;

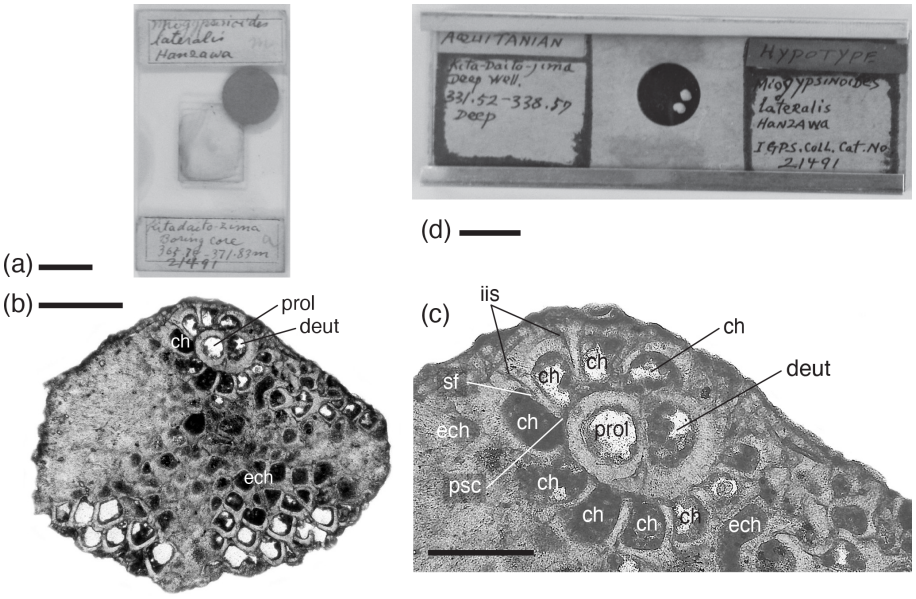

Figure 8. *Miogypsinoides lateralis* Hanzawa, 1940, thin section of types **(a–c)** and isolated specimens **(d)**; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. **(a)** "*Miogypsinoides lateralis* Hanzawa, Kitadaito-zima Boring core 363.76–371.83 m, 21491". **(b, c)** Equatorial section of an isolated specimen (Hanzawa, 1940, pl. 39, figs. 13–14. **(d)** "*Miogypsinoides lateralis* Hanzawa, IGPS. Coll. Cat. No. 21491, Kita-daito-jima, Deep well, 331.52–338.57, deep, Aquitanian". Scale bar represents 1 cm in **(a)** and **(d)**, 0.500 mm in **(b)**, and 0.250 mm in **(c)**. For abbreviations, see Fig. 2.

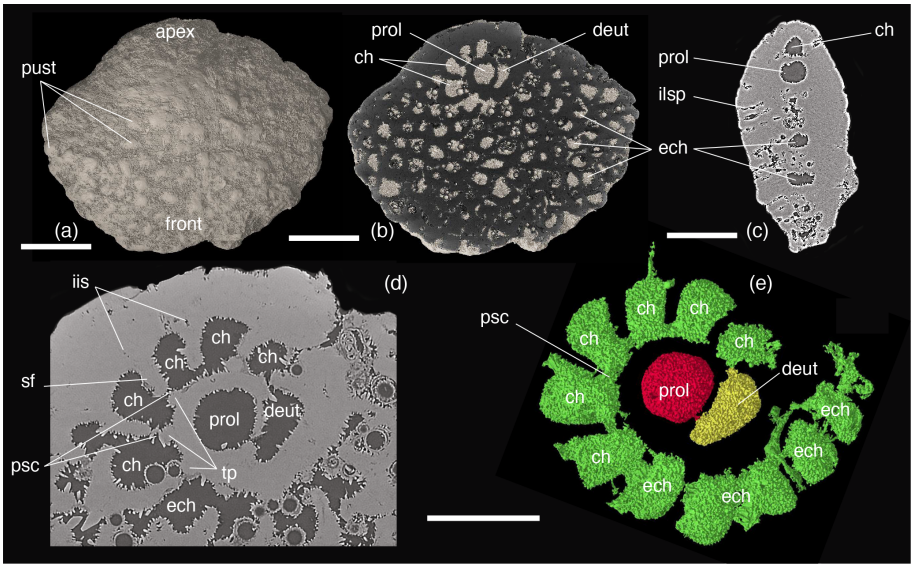

Figure 9. *Miogypsinoides lateralis* Hanzawa, 1940; Hanzawa's collection; IGPS, Tohoku University, Sendai, Japan. Micro-computed tomographic analysis of megalospheric specimens showing outer shell morphology **(a)** and equatorial **(b)** and axial **(c)** sections. **(d, e)** Micro-computed tomographic scanning 3D-rendered models with shell removed (rendering by Shunichi Kinoshita). Scale bar represents 0.500 mm in **(a)**–**(c)** and 0.250 mm in **(d)** and **(e)**. For abbreviations, see Fig. 2.

López-Pérez, 2005). In fact, eastward (from the Pacific to the Atlantic) current flow at the Oligocene–Miocene boundary is documented by planktonic foraminifera (Fraass et al., 2019), by the coralline red algal *Lithophyllum pustulatum* species group (Bassi et al., 2009), and by the larger porcelaneous benthic foraminifer *Borelis pulchra* (Bassi et al., 2021). The prevailing hypothesis proposes that many LBF groups dispersed eastward from the Caribbean to western Africa and subsequently spread northward into the Mediterranean region before reaching the Middle East, India, and

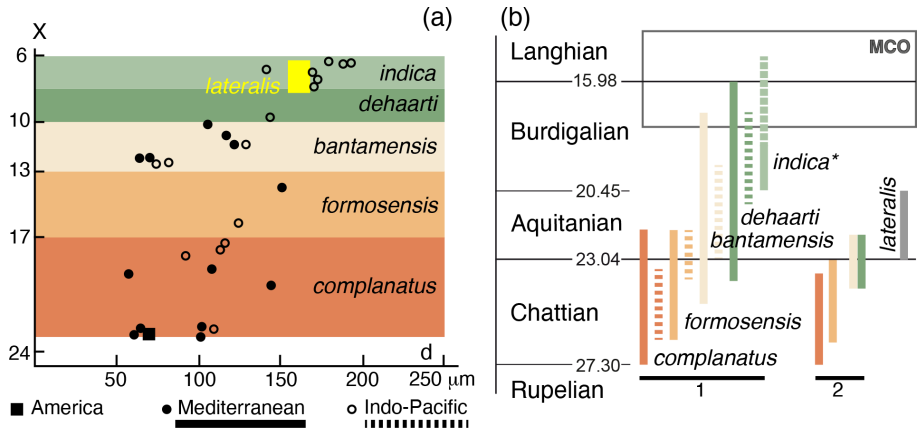

Figure 10. **(a)** Plot of mean protoconch diameter (d) and number of nepionic chambers (X) for the *Miogypsinoides* species from American, Mediterranean, and Indo-Pacific areas (Drooger and Raju, 1973; Drooger, 1993). Although values of $d - X$ of *Miogypsinoides lateralis* fall into the lower Burdigalian *M. indica* range, *M. lateralis* clearly differs from *M. indica* in having a larger angle γ (90° versus 17°). The Aquitanian *Miogypsinoides lateralis* likely represents an exception to the nepionic acceleration trend. **(b)** Stratigraphical distributions of *Miogypsinoides* species and location of *M. lateralis* from the Aquitanian of Kitadaito Jima. 1: Lunt and Allan (2004), BouDagher-Fadel and Price (2013), BouDagher-Fadel (2018). 2: Drooger and Laagland (1986), Cahuzac and Poignant (1987; as to *bantamensis–dehaarti*), Özcan et al. (2009). * Raju (1974, fig. 38) localized *M. indica* in the lower Burdigalian, whereas BouDagher-Fadel (2018, fig. 7.16) considered the species to be upper Burdigalian–lower Langhian in age. MCO, Miocene Climatic Optimum. Timescale after Cohen et al. (2025).

ultimately Southeast Asia (Adams, 1967; Butterlin, 1987; Mello e Sousa et al., 2003; BouDagher-Fadel and Price, 2010, 2013; BouDagher-Fadel, 2018; Özcan et al., 2022). In this regard, the eastward migration of *Miogypsinella borodinensis* from the Indo-Pacific into the Caribbean region is not exceptional. Because the shallow clockwise India-to-Indonesia current (and seasonally reversing monsoon currents) that flowed off the modern Andaman Sea coasts and finally mixed with western Pacific Ocean waters (Gourlan et al., 2008; Van der Stocken et al., 2019; Sosdian and Lear, 2020), it is unlikely that *Miogypsinella* could migrate westwards (i.e. to the western Tethys) and from there to eastern Mexico. Our hypothesis of an eastward dispersion route for *Miogypsinella borodinensis* agrees with the hypothesis of Drooger (1993, p. 104) that the first miogypsinids did cross the "Pacific barrier following some sweepstake road which the group presumably did not practice very often afterwards".

The Chattian FAD of *Miogypsinella borodinensis* and *M. ubaghsi* took place during a eustatic peak and sea-surface temperature rise (Miller et al., 2020; Westerhold et al., 2020; Fig. 7), coeval with the increase in shallow-water carbonate areas likely associated with the collision of the Australia–New Guinea plate with SE Eurasia (Williams and Duda, 2008). Southern and eastern Sundaland recorded a widespread transgression from ca. 24 to 20 Ma, which resulted in the deposition of attached carbonate shelves and isolated carbonate platforms (Lunt and Woodroof, 2023). These platforms represent the thickest carbonates in SEA, often reaching over 2 km of stacked deposits (Wilson, 2002). They survived until near the end of the early Miocene (Yasuhara et al., 2022; Lunt and Woodroof, 2023; Gallagher et al., 2024). From ca. 23 Ma the collision of Australia with Southeast Asia and the Philippine Sea Plate initiated the Indonesian Seaway restriction, which likely led to limited shallow-water connectivity between the Indian Ocean and North and South Pacific source waters (Zeiza et al., 2012; Hall, 2013; Sosdian and Lear, 2020; Gallagher et al., 2024, p. 21.11). Southeast Asian shallow-water deposits show an abrupt interruption near the top of Letter Stage Te, at ca. 20 Ma, when they are overlain by deeper marine clays (Hutchison, 2005; Lunt and Woodroof, 2023). These events probably constrained the westward dispersion of *Miogypsinella borodinensis* and *M. ubaghsi* to the western Indo-Pacific (Fig. 6). *Miogypsinella bermudezi* is restricted to the lower Miocene deposits of Cuba (Drooger, 1951, 1952, 1993), likely deriving from the Chattian ancestor *M. borodinensis* (Fig. 6). Drooger (1951) proposed *Miogypsinella bermudezi* as the most primitive member of the *Miogypsina* lineage, considering the Central America type material to be Oligocene in age. However, this type material is in fact Aquitanian (see "Systematic palaeontology"). In western India, Raju (1974) successively found specimens with a number of nepionic chambers comparable to those of *bermudezi* in the same biostratigraphical position, preceding *Miogypsinoides complanatus*. Drooger (1993) questioned that *Miogypsinella bermudezi* ($X =$ ca. 12 in India) was ancestral to *Miogypsinoides complanatus* ($X = 17$–21) if considering nepionic acceleration. Further confusion was added by Drooger (1993, p. 84), stating that "the primitive *M. bermudezi* of the *Miogypsinoides* group fits better to the *Miogypsina sensu stricto* $d - X$ regression line (d, diameter of the proloculus) than to that of the other *Miogypsinoides* species". Since *Mio-*

gypsinella bermudezi was found stratigraphically below *Miogypsinoides complanatus*, Drooger (1993) questioned retaining *bermudezi* in the *bermudezi–complanatus–formosensis–bantamensis–dehaarti–indica* lineage (Drooger and Raju, 1973; Raju, 1974; BouDagher-Fadel, 2018). This lineage is not based on the diagnostic characters that separate the three genera *Miogypsinella*, *Miogypsinoides*, and *Miogypsina* and, therefore, is not supported by morphological traits (see also Table 1).

The occurrence of similar shell characters in *Miogypsinella borodinensis* and *Neorotalia mexicana* (Nuttall) from the upper Eocene of Mexico (Hanzawa, 1965; Drooger, 1952) is probably due to an independent origin of the cover on interlocular space, intraseptal interlocular space, apertural lip, septal flap, primary spiral canal, and toothplate (Hottinger et al., 1991) shown by both forms (Tables 1 and 2).

The proposed Central American origin of the early miogypsinids in the Rupelian and their migration into the Mediterranean during the late Rupelian–early Chattian (BouDagher-Fadel and Price, 2013) was based on possible phylogenetic relationships between the Mediterranean *Paleomiogypsina* Matsumaru, 1996 and the central Indo-Pacific *Miogypsinella* (i.e. *M. cyprea* BouDagher-Fadel and Price, 2013). Both genera share the lack of "strong fissure around the apex of the test", which has been considered a characteristic of the American forms (BouDagher-Fadel and Price, 2013). No information about the apertural lip, subsutural canal, spiral canal, and vertical canal system is given in the description of *Miogypsinella cyprea*. Instead, the illustrated specimens (BouDagher-Fadel and Price, 2013, fig. A2d–h) are characterized by a thickened lateral shell wall, which suggests their reasonable assignment to *Miogypsinoides*. As remarked in the "Systematic palaeontology" section, the *Miogypsinella* records from the Mediterranean do not show the distinctive characters of this genus and have not been sufficiently described and illustrated to assess their status as separate species. *Miogypsinella* has never been confidently recorded in the Mediterranean upper Oligocene and lower Miocene carbonate deposits, thus discarding a possible origin of the taxon in the Mediterranean basin.

Since no evidence supports the proposed Central American origin of the early miogypsinids in the Rupelian, these LBF faunas were not isolated as previously thought (Adams, 1973), and genera and species arrived from other regions, as shown in this case study. In the Rupelian of Central America the early miogypsinids arrived from the Pacific, contradicting the supposed isolation of the LBF faunas of this area (Adams, 1973).

Miogypsinella borodinensis and *M. ubaghsi* occur in the Aquitanian in nearly the same areas where they appeared (Fig. 6). The LAD of *Miogypsinella borodinensis* in the Indo-Pacific is recorded in the Aquitanian of Kitadaito Jima and Bikini (Cole, 1954; Eames et al., 1962; Hanzawa, 1965; BouDagher-Fadel and Lokier, 2005), whereas the LAD of *M. bermudezi* is reported in the Aquitanian of Cuba (Drooger, 1951). Both LADs, along with that of *Miogypsinoides lateralis*, occur near the uppermost Aquitanian eustatic rise (ca. 20 Ma; Miller et al., 2020; Figs. 7 and 10) and near the termination of shallow-water carbonate sedimentation in Southeast Asia (upper Te limestone overlain by deep marine *Globigerina* deposits; Lunt and Woodroof, 2023). During this event, in Southeast Asia, Borneo became an important source of clastic sediments, which likely impacted on the extensive shallow-water carbonate shelves around Sundaland (Hallan, 2013; Lunt, 2023). In Indonesia the miogypsinid records are overprinted by regional tectonostratigraphical events and abrupt facies changes, and, therefore, they need further biostratigraphical assessment (Lunt and Allan, 2004; Lunt and Luan, 2022). In Central America, the lower Miocene delta systems in the north-western Gulf of Mexico have been associated with thick, sand-rich strandplain and barrier shore-zone systems with patchy, very thin carbonate accumulations (Galloway et al., 2000). These restricted shallow-water carbonate settings probably hampered the survival of miogypsinids.

Bassi et al. (2024) focused on comparing fossil LBF records from different regions within the western Tethys and the Indo-Pacific to track the Oligocene–Miocene migration patterns of these organisms. This helps to understand the connectivity between different marine basins during the Miocene, a period of important climatic and palaeoceanographic changes (e.g. Steinthorsdottir et al., 2021). Porcelaneous LBF underwent a decrease in species richness in the Burdigalian (Bassi et al., 2024), paralleling the global warming of the oceans (e.g. Steinthorsdottir et al., 2021). The disappearance of *Miogypsinella borodinensis*, *M. bermudezi*, and *M. ubaghsi* predates the decrease in porcelaneous LBF species richness. Considering that porcelaneous LBF thrived in proximal shallow-water carbonate settings mostly above the fair-weather wave base (e.g. Betzler and Chaproniere, 1993; Hottinger, 1997), in the central Indo-Pacific their lower Burdigalian crisis likely corresponds to the abrupt decrease in shallow-water carbonate areas at ca. 20 Ma that affected the *Miogypsinella* species (Lunt and Woodroof, 2023; Fig. 7).

By the end of the MCO, at ca. 15 Ma in the Sundaland area, widespread extensional episodes and a major and rapid subsidence event along with an eustatic rise led to the formation of new ocean basins, reducing the shallow-water carbonate shelves (Hall, 2013; Lunt and Woodroof, 2023; Gallagher et al., 2024). The disappearances of *Miogypsinoides bantamensis* and *M. dehaarti* in the late Burdigalian and *M. indica* in the early Langhian are likely related to the MCO (Fig. 10b).

4.2 Age of *Miogypsinoides lateralis*

The hypothesis of nepionic acceleration has been widely used as a biostratigraphical key for Oligocene–Miocene *Miogypsinoides* species (Drooger, 1963, 1993; Raju, 1974;

Schiavinotto, 1985; Özcan et al., 2009; Schiavinotto and Benedetti, 2021). Values of the proloculus diameter and *X* show that *Miogypsinoides lateralis* falls within the *M. indica* range, just succeeding *M. dehaarti* (Fig. 10a). This occurrence within the *complanatus–formosensis–bantamensis–dehaarti–indica* lineage (Drooger and Raju, 1973; Raju, 1974) repeatedly questioned the taxonomic validity of *Miogypsinoides lateralis* (Cole, 1957, 1969). In the *complanatus–formosensis–bantamensis–dehaarti–indica* lineage, *Miogypsinoides lateralis* likely represents an exception to the nepionic acceleration trend, with morphological values comparable to those of the Burdigalian–Langhian *M. indica* but occurring earlier in the Aquitanian (Fig. 10b).

5 Conclusions

- Species of *Miogypsinella* are delimited by the proloculus diameter, the number of nepionic chambers, the inclination of the planispiral whorl in relation to the equatorial chamber plane, and the arc length of the nepionic spiral from embryonic chambers and to the apical point of test.
- Two *Miogypsinella* species (*M. borodinensis*, *M. ubaghsi*) are widespread in the central Indo-Pacific from the Chattian to the Aquitanian. In Central America a single species occurred, respectively, in the Chattian (*M. borodinensis*) and in the Aquitanian (*M. bermudezi*).
- *Miogypsinella boninensis* Matsumaru, 1996 (see also Sharaf et al., 2014), *Miogypsinella bornea* BouDagher-Fadel and Price, 2013, *Miogypsinella cyprea* BouDagher-Fadel and Price, 2013, *Miogypsinella elongata* BouDagher-Fadel and Price, 2010, and *Miogypsinella matsumaria* BouDagher-Fadel and Price, 2010 have not been sufficiently described and illustrated to assess their status as separate species. The occurrence of a thickened lateral shell wall in these species suggests that they probably belong to *Miogypsinoides*.
- The Aquitanian *Miogypsinoides lateralis* is a distinct species that represents an exception in the Oligocene–middle Miocene temporal trend of the nepionic acceleration in miogypsinids.
- *Miogypsinella borodinensis* appeared in the Chattian in the central Indo-Pacific and reached Central America following an eastward path in the Chattian, where its descendant *M. bermudezi* occurred until the Aquitanian. *Miogypsinella* disappeared in the Aquitanian in both areas.
- The American Oligocene LBF faunas were not largely isolated as previously thought.
- The LADs of *Miogypsinella borodinensis*, *M. bermudezi*, *M. ubaghsi*, and *Miogypsinoides lateralis* near the latest Aquitanian eustatic rise coincide with the initiation of the Indonesian Seaway restriction and the subsequent sudden deposition of deeper-water *Globigerina* sediments.
- In the Indo-Pacific, the beginning of the MCO likely brought about the extinction of *Miogypsinoides bantamensis*, *M. dehaarti*, and *M. indica*.

Data availability. Studied materials are preserved both as thin sections and isolated specimens of Hanzawa's (1940) collection deposited in the Tohoku University Museum (Sendai, Japan). Oriented sections of LBF specimens of Hanzawa's (1940) collection from Kitadaito Jima were housed at the Institute of Geology and Paleontology (IGPS), Faculty of Science (currently Department of Earth Science, Graduate School of Science).

Author contributions. DB and YI conceived the project. JCB developed micro-CT scanning analyses. SK performed 3D-rendered models. Interpretation of data, discussion of the results, and writing of the manuscript were done by all authors.

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