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Spongeliomorpha in nonmarine settings: an ichnotaxonomic approach

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ABSTRACT: The authors revise the occurrences of burrow networks with striated walls having dominantly transverse to oblique striae, which have been assigned to the ichnogenera *Spongeliomorpha* Saporta, 1887, and *Steinichnus* Bromley & Asgaard, 1979. The taxonomic status of the ichnogenus *Steinichnus* Bromley & Asgaard, 1979 is examined and it is suggested that this ichnogenus is a subjective junior synonym of *Spongeliomorpha* Saporta, 1887. *Spongeliomorpha* is best reserved for an unlined network of burrows having distinct surface ridges or grooves of different orientation and massive filling. The diagnosis of *Spongeliomorpha* is emended accordingly and the proposed ichnospecies revised for consistency with the diagnostic features of the ichnogenus. *Spongeliomorpha milfordensis* Metz, 1993a is considered a subjective junior synonym of *Spongeliomorpha carlsbergi* (Bromley & Asgaard, 1979) after a visual comparison and statistical analysis of the angle of striation with respect to the burrow midline in the type material. Nevertheless, the use of statistical techniques is not advocated for distinction of ichnotaxa, but may support observations. *Spongeliomorpha carlsbergi* is considered as an indicator of nonmarine settings and was probably produced by burrowing insects. Proposed ichnospecies of *Spongeliomorpha* that fit the emended diagnosis include *S. sudolica* (Zaręczny, 1878); *S. iberica* Saporta, 1887; *S. sicula* D'Alessandro & Bromley, 1995; *S. chevronensis* Muñiz & Mayoral, 2001; and *Spongeliomorpha* isp. nov. aff. *sicula* Lewy & Goldring, 2006.

KEY WORDS: continental, ichnology, ichnotaxonomy, striated burrow network

The distinctive features of the ichnogenus *Spongeliomorpha* Saporta, 1887 are a dominantly horizontal, unlined burrow system showing Y- and T-bifurcations and ornamented with scratch traces showing various orientations. The ornament is incuse as viewed from the burrow lumen, and thus stands as a pattern of ridges as viewed on the outer surface of the trace fossil. The specimens of *Spongeliomorpha* commonly found in nonmarine settings display a pattern of striae that is consistently oblique to transverse to the burrow axis. Similar striated burrow networks have also been compared with the ichnogenus *Steinichnus* Bromley & Asgaard, 1979.

Bromley & Asgaard (1979) proposed the ichnogenus *Steinichnus* for a dominantly horizontal burrow system having T-shaped branching and characterised by fine and deep striations transverse to the axis of the burrow. Their material is derived from the Triassic Fleming Fjord Formation of East Greenland. After the revision of Saporta's (1887) Spanish Miocene topotype material of *Spongeliomorpha* by Calzada (1981), it became clear that *Steinichnus* was a junior synonym of *Spongeliomorpha*. Ekdale *et al*. (1984) used *Spongeliomorpha* instead of *Steinichnus* when describing the ichnofauna from the Fleming Fjord Formation. Bromley (1990, 1996), Bromley & Asgaard (1991) and Pickerill (1992) adopted this position, although no formal proposal has been published to date. Subsequently, different authors have used both *Steinichnus* (Gand *et al*. 1997; Bailey 2000; Hasiotis 2004; Gillette *et al*. 2003; Bohacs *et al*. 2007) and *Spongeliomorpha* (Metz 1993a, b; D'Alessandro & Bromley 1995; Muñiz & Mayoral 2001; Melchor *et al*. 2006) to refer to burrow systems with bioglyphic striae transverse or oblique to the burrow axis. Burrow systems having a pattern of striations that is consistently oblique to transverse to the burrow axis have been recognised under *Steinichnus carlsbergi* Bromley & Asgaard, 1979 and *Spongeliomorpha milfordensis* Metz, 1993a.

Saporta (1887) considered *Spongeliomorpha iberica* to be a sponge, an opinion also shared with other authors (e.g., de Laubenfels 1955; Häntzschel 1962). Boscá (1917) considered it to be an alga. The first identification as a burrow was by Reis (1910), although Saporta (1893) already considered the possible inclusion of *Spongeliomorpha* among the traces of animals.

The purpose of this present paper is to compare the ichnogenus *Steinichnus* Bromley & Asgaard, 1979 with *Spongeliomorpha* Saporta, 1887 and to assess the status of the ichnospecies *Steinichnus carlsbergi* Bromley & Asgaard, 1979 and *Spongeliomorpha milfordensis* Metz, 1993a. These ichnotaxa have only been recorded in nonmarine settings.

1. Material and methods

This study compares the holotype (MGUH 14373, Fig. 1A) and paratype material (MGUH 14374, 14376, 14377; Fig. 1E, B, C, respectively) of *Steinichnus carlsbergi* Bromley & Asgaard, 1979 and photographs of the holotype (NJSM 15469) and paratype (NJSM 15470) of *Spongeliomorpha milfordensis* published by Metz (1993a), as well as specimens of the paratype series (GHUNLPam 4324, 4325;

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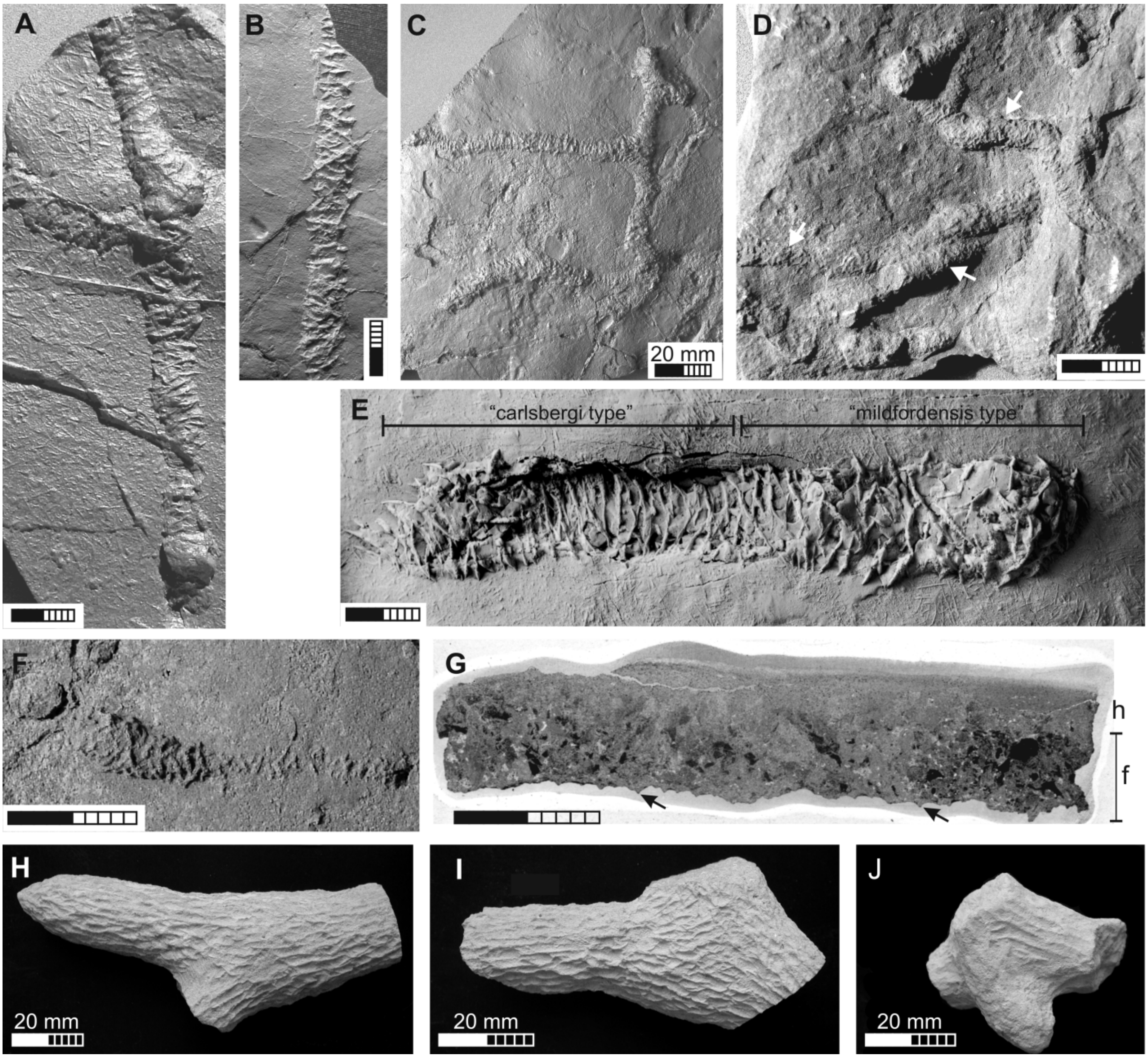

Figure 1 Selected specimens from the type series of *Spongeliomorpha carlsbergi* (Bromley & Asgaard, 1979) and *Spongeliomorpha milfordensis* Metz, 1993a, and topotype material of *Spongeliomorpha iberica* Saporta, 1887: (A) Holotype of *Spongeliomorpha carlsbergi* (MGUH 14373); (B, C) Paratypes of *Spongeliomorpha carlsbergi* (MGUH 14376, 14377). Note T- and Y-bifurcation in MGUH 14377; (D) Paratype material of *Spongeliomorpha milfordensis*, burrows indicated by white arrows (GHUNLPam 4235); (E) Paratype of *Spongeliomorpha carlsbergi* (MGUH 14374) showing a burrow interval with dominantly transverse striations ('*carlsbergi* type') and an adjacent portion with dominantly oblique striations ('*milfordensis* type'). See text for discussion; (F) Paratype material of *Spongeliomorpha milfordensis* (GHUNLPam 4234); (G) Scanned longitudinal thin section of unnumbered paratype material of *Spongeliomorpha carlsbergi*. f=burrow fill, h=host rock. Arrows point to some cross-sections of striae in the sole of the burrow fill; (H–J) Topotype material of *Spongeliomorpha iberica* (MGUH 28777, 28776, 28778) showing dominantly longitudinal pattern of striae, burrow termination (H), burrow bifurcation (H, I) and enlargement at burrow intersection (J). Scale bars=10 mm, except otherwise indicated.

Fig. 1D, F), provided by Robert Metz. The specimens of *Steinichnus carlsbergi* were obtained from the Fleming Fjord Formation (Triassic), Carlsberg Fjord, Jameson Land, East Greenland. The material of *Spongeliomorpha milfordensis* comes from the Perkasie Member of the Passaic Formation (Late Triassic), Smith Clark Quarry, Milford, New Jersey, USA. The authors also examined topotype material of *Spongeliomorpha iberica* Saporta, 1887 from the Miocene of Alcoy (Spain), collected by Sebastián Calzada and presented to RB (MGUH 28777, 28776, 28778; Fig. 1H, I, J). The measurements of the angle between individual burrow striations were made by drafting the striations and burrow outline using a camera lucida and then measuring the angles from the drawing. The mean and standard deviation of the readings of the angle of orientation were obtained and the mean was used to compare ichnospecies using a hypothesis test for two populations' mean of independent and normal samples with proven equal variances (Weiss 2002). The test was performed using the software Statistica 6.0 (StatSoft, Inc).

Institutional abbreviations: MGUH: Geological Museum, University of Copenhagen, Denmark; NJSM: New Jersey State Museum, Trenton, New Jersey, USA; GHUNLPam: Paleontology Collection, Universidad Nacional de La Pampa, Santa Rosa, Argentina.

2. Systematic ichnology

Ichnogenus *Spongeliomorpha* Saporta, 1887
Type ichnospecies: *Spongeliomorpha iberica* Saporta, 1887

1887 *Spongeliomorpha*; Saporta, p. 289
1917 *Spongiliomorpha*; Boscá, p. 267
1922 *Spongeliomorpha*; Reis, pp. 231–236
1962 *Spongeliomorpha*; Häntzschel, p. W 216, fig. 134.2a, 2b
non 1969 Type 3 *Ophiomorpha*; Kennedy & MacDougall, pp. 460–464, fig. 1.C, plate 88.1
partim 1973 *Spongeliomorpha*; Fürsich, pp. 729–730
non 1975 *Spongeliomorpha*; Chiplonkar & Ghare, p. 77, figs 2E, 3
1975 *Spongeliomorpha*; Häntzschel, p. W 109, figs 67.2a, 2b
1975 *Thalassinoides*; Marcinowski & Wierzbowski, pp. 400–403, text-figs 1, 2, plates 1, 2
non? 1977 *Planolites*; Gand, p. 12–15, plates 1, A.1, B.1, B.2, B.3
v 1979 *Steinichnus*; Bromley & Asgaard, pp. 57–59, figs 11–12
v 1981 *Spongeliomorpha*; Calzada, pp. 190–192, plates I–II
partim 1981 *Thalassinoides*; Pollard, pp. 581–584, plate 90
1981 *Spongeliomorpha*; Fürsich, p. 154
1981 *Spongeliomorpha*; Fürsich *et al.*, pp. 539, 545–547, 549–550, plates 1, 3, text-fig 3, table 3
1984 *Spongeliomorpha*; Ekdale *et al.*, pp. 162, 165, fig. 13-4
1984a *Spongeliomorpha*; Frey *et al.*, p. 342, table 2
1990 *Spongeliomorpha*; Bromley, p. 186, fig. 11.5
1993a *Spongeliomorpha*; Metz, pp. 259–262, figs 2–6
1993b *Spongeliomorpha*; Metz, p. 171, fig. 4
1995 *Spongeliomorpha*; Metz, p. 47, fig. 3E–F
1995 *Spongeliomorpha*; D'Alessandro & Bromley, pp. 393–397, figs 3–7
1996 *Spongeliomorpha*; Bromley, p. 214, fig. 10.5
1996 *Spongeliomorpha*; Metz, p. 123, fig. 4D
non? 1998 *Spongeliomorpha*; Uchman, pp. 129–130, fig. 29
partim 2000 *Spongeliomorpha*; Schlirf, pp. 158–160
2000 *Spongeliomorpha*; Uchman & Álvaro, p. 210, figs 4A–B
partim 2001 *Spongeliomorpha*; Muñiz & Mayoral, pp. 119–126, figs. 4, 5, 7, tables 1, 2, 3
? 2003 *Steinichnus*; Gillette *et al.*, p. 142, figs 3, 4B, 5A
? 2004 *Steinichnus*; Hasiotis, p. 197, fig. 9A–B
2005 *Spongeliomorpha*; Gibert & Robles, pp. 299–301, fig. 5
2006 *Alezichnus*; Gobetz, pp. 121–124, 132–133, figs 3, 4, 5, 7, 8, 9, 10, 11, 12, 13C
2006 *Spongeliomorpha*; Melchor *et al.*, p. 265, fig. 7A, B, C
2006 *Spongeliomorpha*; Mikuláš, p. 81, figs 5.1, 5.4, 5.8
2007 *Spongeliomorpha*; Neto de Carvalho & Rodrigues, pp. 298–303, fig. 5A, B
partim 2007 *Steinichnus*; Bohacs *et al.*, pp. 87–88, figs 6, 7
? 2008 *Spongeliomorpha*; Leonowicz, pp. 93–94, figs 6D, 6G, 6H
non 2009 *Steinichnus*; Smith *et al.*, p. 17656 and p. 21 (suppl. mat.), fig. S3D–S3E

Remarks. After a careful analysis of the morphological features of potential ichnotaxonomic value for *Ophiomorpha*, *Thalassinoides* and *Spongeliomorpha*, Fürsich (1973) considered that orientation of burrows, presence or absence of pelletal lining and the general branching pattern and burrow outline are only valid for the ichnospecific distinction of these burrow systems. In consequence, this author proposed to synonymise the mentioned ichnogenera under the first named ichnotaxon, *Spongeliomorpha* (see also Schlirf 2000). Regarding ornamentation on burrow walls (longitudinal scratch traces), Fürsich (1973) considered that its preservation depends mainly on grain size and consistency of the substrate and that these traces do not form any distinctive pattern. Fürsich (1973) and Schlirf (2000) believed that surface ornament can only be used as a taxobase at the ichnospecific level (see also Bertling *et al.* 2006) because of its purported low potential of preservation and lack of definite patterns of ornamentation. The preservation of striae on burrow surfaces is commonly taken as indicative of burrowing in a firm or desiccated substrate. The association between firmgrounds and burrows with surface texture is common in marine settings, although there are indications that surface ornament can be formed and likely preserved in unconsolidated sediments, both marine and non-marine. The formation of clear and distinctive bioglyphs in Heteroceridae and Gryllotalpidae burrows formed in mud has been demonstrated (Clark & Ratcliffe 1989; Metz 1990). Seike & Nara (2007) also found that modern *Ocypode* burrows formed in a firm substrate show bioglyphs over the entire burrow surface, whereas those excavated in loose sand (softground) preserved bioglyphs in part of the burrow surface (side, roof and terminus). Modern freshwater crab burrows from the Parque Nacional Río Pilcomayo (Formosa province, Argentina) found in unconsolidated cohesive and water-saturated sandy mud preserve strong wall ornamentation over the entire burrow surface, even underwater. These freshwater crab bioglyphs occur in a repeated pattern of parallel sets of 3–4 grooves arranged obliquely to the burrow axis (Melchor *et al.* 2010). In consequence, the assumption that ornamented burrows indicate firm or desiccated substrates should be contrasted with independent evidence in each case study (Melchor *et al.* 2006).

The second issue against the validity of surface ornament as a generic ichnotaxobase, raised by Fürsich (1973), is the lack of a repetitive pattern. A number of authors have argued that burrow ornamentation is a diagnostic feature and that the surface sculpture on burrow walls can be distinctive and recurring (e.g. Martin & Bennet 1977; Frey *et al.* 1984a, b; Smith 1987; Hasiotis & Mitchel 1993; Muñiz & Mayoral 2001; Genise 2004; Gobetz 2005, 2006; Gobetz & Martin 2006; Gastaldo & Rolerson 2008; Bedatou *et al.* 2008). Schlirf (2000) further argued that surface ornament is an ephemeral feature that can be lost under continued burrow occupation (see also Asgaard *et al.* 1997). Although it is possible that surface ornament can be lost by repeated passage of the occupant, the present authors argue that surface ornament is not an ephemeral feature and that it can also give clues on the history of burrow usage (behaviour) and occupation (e.g. occupant different from original excavator).

In summary, it is proposed to use the taxobases suggested by Fürsich (1973) to distinguish ichnospecies for burrow networks of *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides* (orientation of burrows, presence or absence of pelletal lining and the general branching pattern and burrow outline), but at the ichnogeneric level. It is also suggested that surface ornament or sculpture should be added to the ichnotaxobases of generic value for this group of trace fossils. This position is in agreement with those accepted by Fürsich (1981). The present authors also concur with Bertling *et al.* (2006), who recognised that surface features may become more important in the ichnotaxonomy of some groups as knowledge about modern producers increases. The suggested procedures are in agreement with the suggestion by Bertling *et al.* (2006) regarding the ichnotaxonomical treatment of compound trace fossils. In addition, *Spongeliomorpha*, *Ophiomorpha* and *Thalassinoides* are distinct ichnotaxa that have been widely used in the literature. *Spongeliomorpha*, *Thalassinoides* and *Ophiomorpha* are considered as preservational variants included within 'ophiomorphids' by Seilacher (2007, p. 54). *Spongia sudolica* Zaręczny, 1878 was considered as belonging to *Spongeliomorpha* by Raciborski (1890), a form akin to *Thalassinoides* by Kennedy (1967), and recently as a senior synonym of *Spongeliomorpha iberica* Saporta, 1887 by Schlirf (2000). After examination of the material figured by Marcinowski & Wierzbowski (1975), including the original specimens of Zaręczny (1878) and syntypes of *Spongia sudolica*, and the neotype and lectotype of that ichnospecies figured by Uchman (2008, p. 19), the present authors are not certain about the synonymy of *Spongeliomorpha iberica* under *Spongeliomorpha sudolica* as proposed by Schlirf (2000). The pointed burrow terminations typical of *S. iberica* (see Calzada 1981; Gibert & Ekdale 2008, fig. 2H) are not clearly identified in the scarce material available of *S. sudolica*, which also does not show a sharp surface ornament.

Kennedy & MacDougall (1969) considered tunnels with surface ridges or striae from the Weald Clay (England) to represent a variation of the pelleted surface ornament in *Ophiomorpha nodosa* Lundgren, 1891. However, these trace fossils were later assigned to the ichnogenus *Scoyenia*, on the basis of meniscated filling and a particular surface texture (Goldring & Pollard 1995).

Bromley & Asgaard (1979) proposed the ichnogenus *Steinichnus* and its type ichnospecies *Steinichnus carlsbergi* because at that time *Spongeliomorpha* was considered a *nomen dubium* (Bromley & Frey 1974; Marcinowski & Wierzbowski 1975). The revision of additional material of *Spongeliomorpha* by Calzada (1981) rendered the ichnogenus valid.

The ichnogenus *Spongeliomorpha* was recently reviewed by Muñiz & Mayoral (2001). These authors included an ichnospecies comprising lined burrows (*S. sinuostriata* Muñiz & Mayoral, 2001), whereas *Spongeliomorpha* is commonly referred to unlined burrow networks.

Spongeliomorpha reticulata Chiplonkar & Ghare, 1975 was erected on the basis of a single specimen from the Cretaceous Bagh Beds of India. This specimen is a cylindrical structure that does not form a network, which is considered an essential feature of *Spongeliomorpha*. *Planolites cullesensis* Gand, 1977 was proposed for burrows having a horizontal and a vertical component, with rare bifurcations, absence of wall, and showing a striated or granular surface. Although further examination is necessary, some of these burrows have the basic distinguishing features of *Spongeliomorpha*, and are considered as potentially assignable to that ichnogenus. The material assigned by Gand *et al.* (1997, figs 11-2, 11-3) to cf. *Steinichnus* is comparable with *Spongeliomorpha*. Uchman (1998) proposed to include *Halymenites sublumbricoides* Azpeitia Moros, 1933 under *Spongeliomorpha*. However, the type material of *H. sublumbricoides* is a burrow lacking bifurcation and showing a poorly developed ornamentation (Azpeitia Moros 1933). In consequence, its inclusion under *Spongeliomorpha* is questionable. Bailey (2000) mentioned the presence of cf. *Steinichnus carlsbergi* from the Permian Abo Formation (USA). However, this material seems to lack the characteristic striations and bifurcations of *Spongeliomorpha* and displays a meniscate backfill (as judged from the illustration and description). The material described by Hasiotis (2004) as *Steinichnus* isp. from the Upper Jurassic Morrison Formation is partially comparable with *Spongeliomorpha*, although this author also included forms having a knobbly surface under *Steinichnus* (Bromley *et al.* 2007). The assignment of the burrows described by Gillette *et al.* (2003) and Sandau (2005) to *Steinichnus* is uncertain because no description was provided and the illustrations do not allow clear distinction of striations in the specimens. Part of the burrows described by Bohacs *et al.* (2007) as *Steinichnus* may be comparable with *Spongeliomorpha*, as these authors included forms with and without branching and the available illustrations are not detailed enough. The specimens described as *Steinichnus* isp. by Smith *et al.* (2009) are unbranched and are thus not included under *Spongeliomorpha*. Metz (1993a) suggested that retaining the ichnogenus *Steinichnus* for nonmarine forms of *Spongeliomorpha*, would help to emphasise the potential environmental–biostratigraphic significance of these ichnotaxa (a suggestion followed by Gillette *et al.* 2003). However, this procedure is not considered acceptable, as the inferred palaeoenvironment or facies is not judged as a valid ichnotaxobase (e.g. Bromley 1990, 1996; Pickerill 1994; Bertling *et al.* 2006). Lewy & Goldring (2006) described Campanian bifurcated burrow systems from Israel, showing chambers and surface scratch traces, which were tentatively assigned to the ichnogenus *Spongeliomorpha*. The ichnogenus *Alezichnus* Gobetz, 2006 was proposed for a branched network of nearly horizontal and strongly ornamented burrows from the Miocene of Colorado, which are interpreted as rodent burrows. This ichnogenus shares the essential features of *Spongeliomorpha* and it is considered a junior synonym. Portions of *Glyphichnus* Bromley & Goldring, 1992, a striated burrow with an arcuate or U form, may be confused with *Spongeliomorpha*, although the former is unbranched. The main distinctive features of *Spongeliomorpha* are a predominantly horizontal burrow network with unlined, striated walls.

Emended diagnosis. Cylindrical to subcylindrical burrow systems comprising predominantly horizontal elements, showing Y-, T-shaped or multiple branching and massive filling. Burrow terminations are conical, tapered or hemispherical but uninflated. Burrow walls are unlined and ornamented with deep ridges, which are longitudinal, oblique or transverse to the main axis of the trace. Individual ridges usually intersect, composing different patterns (modified after Calzada 1981 and Muñiz & Mayoral 2001).

Spongeliomorpha carlsbergi (Bromley & Asgaard, 1979)

v 1979 *Steinichnus carlsbergi*; Bromley & Asgaard, pp. 57–59, figs 11–12
1990 *Spongeliomorpha carlsbergi*; Bromley, p. 186, fig. 11.5
1993a *Spongeliomorpha milfordensis*; Metz, pp. 259–262, figs 2–6 (*syn. nov.*)
1993b *Spongeliomorpha milfordensis*; Metz, p. 171, fig. 4
1996 *Spongeliomorpha carlsbergi*; Bromley, p. 214, fig. 10.5
1996 *Spongeliomorpha milfordensis*; Metz, p. 123, fig. 4-D
? 2003 *Steinichnus milfordensis*; Gillette *et al.*, p. 142, figs 3, 4B, 5A
2006 *Spongeliomorpha carlsbergi*; Melchor *et al.*, p. 265, fig. 7A, B, C

Remarks. Calzada (1981) considered that the dominantly horizontal development of the burrow network, the pattern of ornamentation of the burrow surface and the form of the burrow bifurcation were the main ichnospecific taxobases for *Spongeliomorpha*. In their revision of *Spongeliomorpha*, Muñiz & Mayoral (2001, p. 126) followed the ichnotaxobases proposed by Calzada (1981), although they recognised the orientation of the scratch traces with respect to the burrow axis as

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Table 1 Summary of the average orientation, standard deviation, and number of readings of striations for the type series of *Spongeliomorpha carlsbergi* and *Spongeliomorpha milfordensis*.

Specimens	Mean angle (degrees)	Standard deviation	Number of readings
S. carlsbergi holotype (MGUH 14373)	71·1	14·0	49
S. milfordensis holotype (NJSM 15469)	67·3	14·3	37
S. carlsbergi type series	71·4	13·4	293
S. milfordensis type series	67·4	14·1	126
S. carlsbergi paratype (MGUH 14374) '*carlsbergi* type' portion	77·5	9·0	38
S. carlsbergi paratype (MGUH 14374) '*milfordensis* type' portion	66·9	17·9	39

the more important criterion for distinction of ichnospecies of *Spongeliomorpha*. Muñiz & Mayoral (2001) also used other features (regularity of surface ornamentation, shape of ramification, and burrow cross-section) as ichnotaxobases in a less consistent manner. In addition to *S. reticulata* Chiplonkar & Ghare, 1975 and *S. sublumbricoides* (Azpeitia Moros, 1933), which are not considered herein as belonging to the ichnogenus, Muñiz & Mayoral (2001) distinguished nine ichnospecies under *Spongeliomorpha*. Among these ichnospecies there are four that do not fit the diagnostic features of the ichnogenus. These are *Spongeliomorpha annulatum* Kennedy, 1967 and *Spongeliomorpha sinuostriata* Muñiz & Mayoral, 2001 which are lined burrows, and thus do not belong to the ichnogenus. *S. oraviense* (Książkiewicz, 1961) and *Spongeliomorpha* ichnosp. indet. Muñiz & Mayoral, 2001 do not form a network or display bifurcations and are also excluded from the ichnogenus (see also Uchman 1998, 2008).

The ichnospecies that belong to *Spongeliomorpha* following the diagnostic features discussed above are as follows: *S. iberica* Saporta, 1887, with striae forming a reticulate or plaited pattern; *S. chevronensis* Muñiz & Mayoral, 2001 exhibiting ear-shaped ridges oblique to the main axis of the burrow, although the holotype is unbranched; *S. sicula* D'Alessandro & Bromley, 1995, characterised by longitudinal ridges and striated, vertical chambers (also consider *Spongeliomorpha* isp. nov. aff. *sicula* described by Lewy & Goldring 2006); and *S. carlsbergi* (Bromley & Asgaard 1979), which shows dominantly oblique to transverse surface ridges. A potential additional ichnospecies is *S. sudolica* (Zaręczny, 1878), although a detailed comparison is out of the scope of this work. *Thalassinoides paradoxicus* (Woodward, 1830) emended by Kennedy (1967), shows somewhat clumsy scratch ornaments locally. But the silicification of the material is rather crude and requires closer investigation.

The ichnospecies *S. carlsbergi* and *S. milfordensis* display striations oblique to transverse to the burrow axis, forming a fairly similar pattern. Metz (1993a) recognised the similarity between *S. carlsbergi* and *S. milfordensis* and indicated that the main differences are thicker striae and striae that form an average oblique angle with the axis of the burrow in the latter, while *S. carlsbergi* displays transverse striations. A visual comparison of the type material of both ichnospecies suggests a close affinity in the pattern of striae. This subjective impression is further supported by a hypothesis test for the mean of the two populations of striae, performed to compare the average orientation of scratch ornament between the holotype material of *S. carlsbergi* and *S. milfordensis*. This test suggests ($p=0{\cdot}22$) that both values are statistically similar (Table 1).

The comparison was also extended to the type series of both ichnotaxa. A plot of the orientation of the scratch ornament of the type series (holotype and paratype material) of *Steinichnus carlsbergi* and *Spongeliomorpha milfordensis* (Fig. 2) suggests that both ichnospecies show a marked overlap in the range 30–90°, although *S. milfordensis* has more readings than *S.*

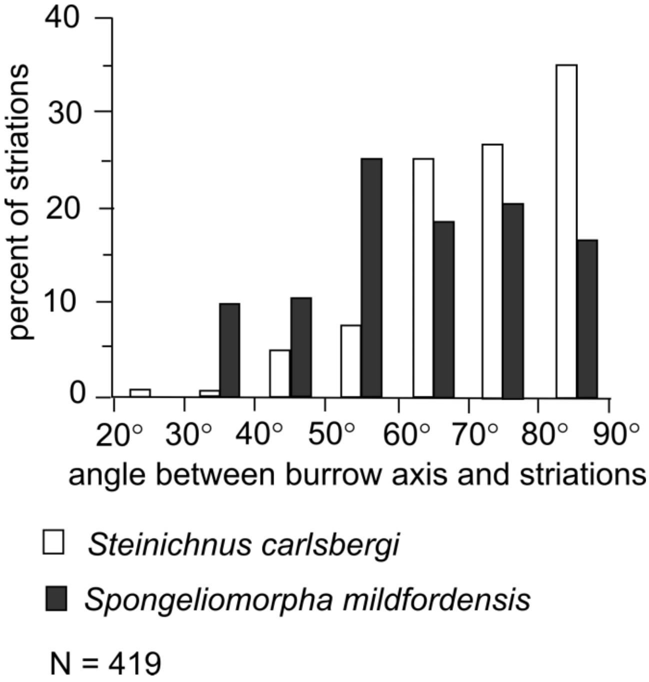

Figure 2 Histogram of the orientation of surface striation with respect to the burrow axis for the holotype and paratypes of *Steinichnus carlsbergi* and *Spongeliomorpha milfordensis*. See summary of data in Table 1.

carlsbergi for acute angles (30–60°), whereas the latter shows more readings at higher angles (60–90°). The difference in average orientation of scratches between both type series is only ten degrees (Table 1). A hypothesis test performed to compare the average orientation of scratch ornament between the type series of *S. carlsbergi* and *S. milfordensis* suggests that both values are different ($p=0{\cdot}006$). However, the apparent variability in the distribution of scratch ornament is easily accommodated if the specimen MGUH 14374, paratype of *Steinichnus carlsbergi* (Bromley & Asgaard 1979, fig. 11B), is considered (Table 1). This comparison indicates that the angles of striations in a part of the same burrow are dominantly transverse ('*carlsbergi* type') and dominantly oblique in another adjacent portion ('*milfordensis* type') (Fig. 1E). A hypothesis test between the '*carlsbergi* type' and the '*milfordensis* type' portions of specimen MGUH 14374 shows that they are different ($p=0{\cdot}002$). Both the '*carlsbergi* type' and '*milfordensis* type' portions were also tested against the *S. milfordensis* holotype specimen and its mean values were proven to be different ($p=0{\cdot}0004$) and equal ($p=0{\cdot}93$) respectively.

In consequence, it is considered that the morphological differences between both type specimens are minor and they should be included under a single ichnospecies. In this case, *Spongeliomorpha milfordensis* Metz, 1993a is proposed as

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junior synonym of *Spongeliomorpha carlsbergi* (Bromley & Asgaard, 1979). The type series of *Spongeliomorpha milfordensis* Metz, 1993a commonly displays scratch traces having a rounded cross-section, in comparison with the 'v'-shaped cross-section in *Steinichnus carlsbergi* Bromley & Asgaard, 1979 (Fig. 1B, F, G). This difference is not considered significant for ichnotaxonomy, although it may help to infer the producer.

Diagnosis. Network of cylindrical burrows, dominantly horizontal, showing T- or Y-branching, deeply striated and unlined walls and hemispherical uninflated terminations. Orientation of striae mostly ranging from transverse to oblique to the axis of the burrow (modified after Bromley & Asgaard 1979).

Comments. Further characterisation of *Spongeliomorpha carlsbergi* is obtained by study of a longitudinal thin section of an unnumbered specimen from the type locality and unit (Fig. 1G). The burrow displays a massive filling composed of calcareous siltstone and microsparite, similar to the host rock, with micritic, darker rip-up clasts.

The known records of *S. carlsbergi* range from Late Triassic to Miocene continental deposits (Bromley & Asgaard 1979; Metz 1993a, b, 1996; Gillette *et al*. 2003; Melchor *et al*. 2007).

Bromley & Asgaard (1979) proposed some terrestrial insect as trace makers and indicated the similarity with modern mole cricket surface burrows. Published observations on modern mole crickets indicate that the burrows display strong ornamentation (Metz 1990) and that herbivorous mole crickets construct shallow horizontal burrows with numerous branches in many directions (Endo 2007). Modern mud-loving beetles (Heteroceridae) also construct similar burrows (Clark & Ratcliffe 1989). Another author also consider that an insect, probably in larval stage, is responsible (Metz 1993a, 1996). In consequence, *S. carlsbergi* is regarded as a good indicator of nonmarine depositional environments and was likely produced by burrowing insects, mainly mole crickets and heterocerid beetles. Comparison of the bioglyphic pattern with those of modern burrows can help to elucidate the producer in each case study.

3. Conclusions

1. It is suggested that the ichnogenus *Spongeliomorpha* should be used for a network of dominantly horizontal unlined burrows with clear and deep surface ridges and massive filling.
2. The ichnogenus *Steinichnus* Bromley & Asgaard, 1979 is considered a subjective junior synonym of *Spongeliomorpha* Saporta, 1887 and the ichnospecies *Steinichnus carlsbergi* is transferred to *Spongeliomorpha carlsbergi*.
3. The ichnospecies *Spongeliomorpha milfordensis* Metz, 1993a is regarded as a synonym of *Spongeliomorpha carlsbergi* (Bromley & Asgaard, 1979), based on a similar range of orientation of striae (from transverse to oblique to the burrow axis).
4. The ichnospecies of *Spongeliomorpha* that agree with the diagnostic features of the ichnogenus includes *S. iberica* Saporta, 1887; *S. carlsbergi* (Bromley & Asgaard, 1979); *S. sicula* D'Alessandro & Bromley, 1995; *S. chevronensis* Muñiz & Mayoral, 2001; and *Spongeliomorpha* isp. nov. aff. *sicula* Lewy & Goldring, 2006. An ichnospecies of uncertain status is *S. sudolica* (Zaręczny, 1878).
5. The known occurrences of *Spongeliomorpha carlsbergi* (Bromley & Asgaard, 1979) are restricted to continental deposits, and the trace fossil was probably produced by burrowing insects.
6. This case illustrates that the distinction of ichnospecies should be based on clear morphological differences and not on subtle morphological contrasts that require statistical studies to define the assignment of new material.

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