



Naiadita lanceolata (Marchantiophyta) from the Middle Triassic (Ladinian) of Germany: a new reconstruction attempt and considerations on taphonomy

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Received: 12 November 2018 / Accepted: 27 July 2019

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Abstract

The fossil liverwort *Naiadita lanceolata* is described here from lacustrine deposits occurring intercalated in the Albertibank complex of the Lower Keuper, Erfurt Formation (Ladinian, Middle Triassic) of Schleierieth, northern Bavaria, Germany. The specimens represent the stratigraphically oldest records of this taxon so far. Leafy gametophytic plants are preserved as impression-compression fossils and include four specimens also showing the terminal or subterminal sporophyte in situ, as well as four leafy stems bearing conical gemma cups with lobed margins. Based on the new material, a refined reconstruction of *N. lanceolata* is proposed. The new found specimens also shed light on some plant taphonomic processes. The mono-specific *N. lanceolata* assemblages comprise mostly leafy gametophytic stems, often still showing the three-dimensional orientation of the foliage. Another peculiar characteristic is the mass accumulation of isolated sporophyte capsules, which are partially surrounded by perianth leaves, probably a useful propagule mechanism for the cleistocarpous capsules.

Keywords *Naiadita* · Marchantiophyta · Fossil bryophyte · Plant taphonomy · Keuper · Albertibank · Germanotype Triassic

Introduction

Bryophytes have been widely recognised as an important component of the Mesozoic vegetation (e.g. Anderson 1976; Schuster 1981; Pant and Bhowmik 1998; Moisan et al. 2012; Bomfleur et al. 2014; Kustatscher et al. 2017; Tomescu et al. 2018). Among the innumerable bryophyte fossils that have been described to date, the leafy liverwort *Naiadita lanceolata* is certainly one of the best understood forms, due to the completeness of many of the specimens.

Although known for more than 170 years, this fossil has only rarely been documented photographically. For example, Sollas (1901: pl. 13) provided six photographs, Harris (1938: pls. 1–5) 17, and Gothan and Weyland (1964: fig. 31a) five, and Thomas et al. (2004: fig. 2a) included a single microphotograph of a fragmented leaflet. In addition

to the photographic documentation, Harris (1938) presented numerous outline drawings based on painstaking microscopic observations. His detailed examination and description demonstrate a complement of features that makes *N. lanceolata* the prime example of bryophytes from the Mesozoic (Stewart 1983; Taylor et al. 2009). However, all *Naiadita* fossils known to date come from the British Rhaetian, with one exception. A single conference abstract briefly mentions the occurrence of isolated leaves from sediments in Germany (Wilde and Heunisch 1990). Eighty years after Harris's iconic descriptions (Harris 1938, 1939), new minute *Naiadita* fossils have been excavated from Lower Keuper strata (Ladinian, Triassic) exposed at Schleierieth in southern Germany (Fig. 1).

History of discovery of the Lower Keuper specimens. First discoveries of small-sized and enigmatic plant fossils from the Schleierieth quarry were reported by Mr. Jürgen Sell, Museum Triassica Euerdorf, during his searches for fossil insects. He donated three slabs to the author, who recognised the traits of *Naiadita lanceolata* and immediately launched a more extensive and successful search campaign. The sample set that forms the basis for this study comprises 148 tiny slabs showing almost exclusively *N. lanceolata* parts preserved in various states and quantities.

Handling Editor: Benjamin Bomfleur.

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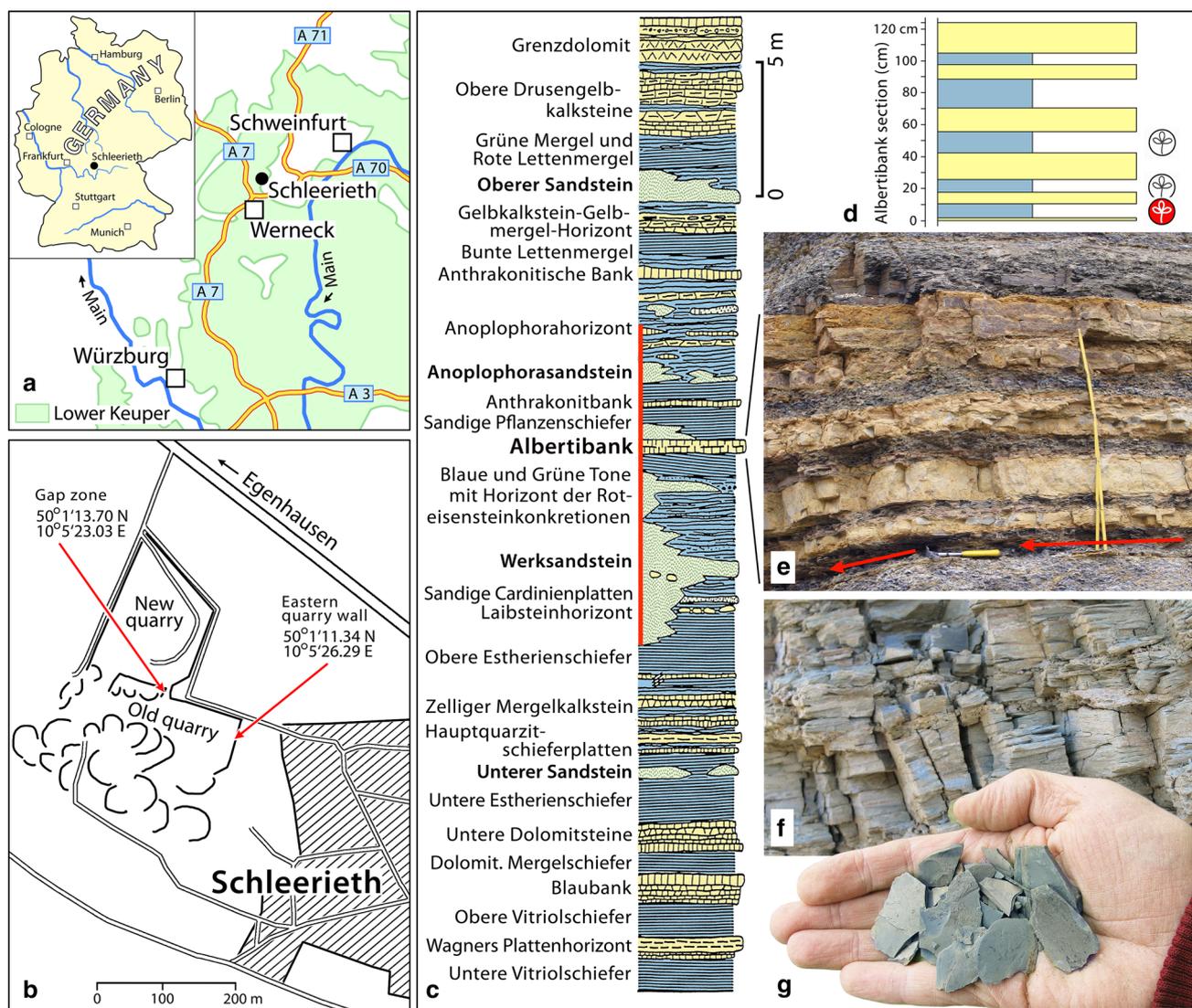


Fig. 1 Geographic and lithostratigraphic setting of the Lower Keuper quarry near Schleierieth, northern Bavaria, Germany. **a** Maps showing the geographic location of Schleierieth. **b** Sketch map of the Lower Keuper quarry NW of Schleierieth. **c** Generalized vertical section through Lower Keuper units of Frankonia, northern Bavaria (after Hoffmann 1967, modified). Red vertical bar indicates exposed strata in the quarry. **d** A detailed section showing the Albertibank divided into six carbonate beds (yellow) and argillaceous intercalations (blue grey), some containing *Naiadita lanceolata* (plant symbols).

These new specimens now permit a more accurate understanding of the overall morphology of *N. lanceolata* and its main diagnostic traits. They also provide a basis for detailed considerations on both taphonomy and palaeoecology and hence refine our knowledge of the Early Keuper ecosystem in which this plant lived. The current paper complements a preliminary account on these specimens by Kelber (2015).

e Outcrop image showing thin shared mudstone interbeds in the Albertibank lime- and dolostones (image taken from the outcrop “Gap zone”). Red arrows indicate the basal bryophyte bearing layer. **f** Close-up of a weathered shale and mudstone intercalation from the “Gap zone” outcrop, showing the splitting into thin clay chips. Perpendicular fissures often cause sub-rectangular columns of stacked flakes. **g** Only the horizontally weathered clayey chips provide easy access to the minute *Naiadita lanceolata* fossils

Geological setting, materials and methods

The new *Naiadita* fossils come from a sandstone quarry near Schleierieth, northern Bavaria, Germany (Fig. 1a, b), where the so-called Werksandstein was periodically quarried for building restoration purposes. Continued fossil excavation in the uppermost Werksandstein of Schleierieth over the past decades has yielded a rich and diverse assemblage of plant macrofossils (Kelber 1990, 2015; Kelber

and Hansch 1995), as well as animal feeding traces on plants, insect eggs and fossil insect remains (Geyer and Kelber 1987; Kelber 1988; Brauckmann and Schlüter 1993; Hagdorn et al. 2015a). The quarry near Schleiereth exposes the lithological Lower Keuper section, ranging from the Werksandstein to the Anoplophorasandstein (Fig. 1c), and showing a repetitive change between fluvial, lacustrine and pedogenic associations, as well as lime- and dolostones formed under restricted marine conditions.

The mixed siliciclastic, mudstone and carbonate sediments of the Lower Keuper (“Lettenkeuper”, Erfurt Formation) were deposited in the semi-enclosed intracratonic German Basin during the Late Ladinian, Triassic. Fluvial siliciclastic sediment input from the Fennoscandian high alternates with transgressive marine incursions from the south (Pöppelreiter 1999; Nitsch 2015). Alberti- and Anthrakonitbank as prominent marker beds (Etzold and Schweizer 2005) often contain marine to brackish marine faunas (Hagdorn and Mutter 2011; Böttcher 2015; Hagdorn et al. 2015b).

All new *Naiadita* fossils have been unearthed from argillaceous intercalations of two Albertibank outcrops in the quarry. One spot is situated in the gap zone between older and newer quarry parts (Fig. 1b, “gap zone”), coordinates 50° 1'13.70 N, 10° 5'23.03 E. Nevertheless, only one area of approximately 2–3 m width provided *Naiadita* fossils. The second spot containing *Naiadita* occurs some 100 m away, on the eastern wall (Fig. 1b, “eastern quarry wall”), coordinates 50° 1'11.34 N, 10° 5'26.29 E. This location has yielded fossil bryophytes in a line of approx. 5 m width.

The monospecific *Naiadita* assemblages from Schleiereth are cleavage impressions, except the compression preservation of the sporophyte capsules. Most *Naiadita* fossils are derived from the bottommost clayey intercalation (Fig. 1e, red arrows), which rests above the 2–3 cm-thick, first Albertibank carbonate layer. The Albertibank mudstones are not uniform across the entire site; rather, they resulted from different sedimentary events which are reflected in many thin layers, often homogenous without a bedding plane inside.

Significantly fewer *Naiadita* remains often intermixed with poorly preserved plant debris, have also been discovered from the next two upsection mudstone interlayers (Fig. 1d). Invertebrate and arthropod zooclasts occur rarely among the bryophyte accumulations. To mention are also the occurrence of a dotted elytron impression of a polyphagan coleopteran, fragments of Spinicaudata (“Conchostraca”) and some darwinulid ostracods and lingulid brachiopods, the latter representing excellent proxy indicators of palaeosalinity (Hagdorn et al. 2015a).

The studied material is deposited in the collection K. P. Kelber, Würzburg, Germany. All slabs are catalogued by a locality code (SCHL-N-) and according to collecting

numbers. Images have been captured with a digital Leica photomicroscope at the University of Würzburg, Department of Botany II, Julius-von-Sachs-Institute for Biological Sciences, Würzburg, Germany; images in Fig. 2b–c were taken by G. Geyer using the Keyence photomicroscope VHX of the Department of Palaeontology, TU Bergakademie Freiberg, Germany.

Systematic palaeontology

Phylum **Marchantiophyta**

Class **Marchantiopsida**

Subclass **Marchantiidae**

Order **Naiaditales**

Family **Naiaditaceae**

Genus *Naiadita* Brodie 1845

Naiadita lanceolata Buckman 1850

Figures 2, 3, 4, 5, 7

Description of the new material. The new Schleiereth specimens are not as complete as Harris’s original material from England. Plant parts not yet discovered from the Schleiereth material include rhizoid-bearing stems, isolated short elliptical stalked gemmae, the asexual propagules, as well as stemborne archegonia.

Leaf description.—Leaves are helically attached to an unbranched axis (e.g. Figs. 3d; 4h; 5i), and often incompletely preserved. Leaf laminae frequently seem to be folded, conjugated or twisted (Figs. 3c, f; 5h), which makes it difficult to recognize the shape and leaf proportions, particularly the delineation of leaf margins. Sharply defined impressions show ecostate leaves (leaves without a costa), with leaf cells forming longitudinal and obliquely transverse rows (Fig. 3a, e, g, h).

Two main leaf phenotypes are distinguished: (1) Elongate, obovate leaves (Figs. 4f; 5a–c, f, j) with an obtuse or rounded apex (Fig. 3g). These leaves even occur in the terminal part of the plant (Fig. 5h). Several of these leaves seem to be distinctly larger than normal leaves (Fig. 3f). Notably, the perianth leaves show a somewhat broader leaf base (Fig. 5b); they can be typified as lingulate with a rounded blade tip (Fig. 5f). (2) Other leaves give the impression of being oblong or just slightly obovate, with a rounded apex (Fig. 3a, b, e), and, as far as visible, all have a decurrent base (Fig. 3a, b, e). Rather exceptional is the occurrence of abnormal orbicular leaves or leaf-like appendages, occasionally attached to the stem (Fig. 5e), or embedded detached (Fig. 5j, lower part of image). Such structures probably belong to leaves just below a terminal gemma cup or might belong to the perianth of a terminal or subterminal

Fig. 2 Configuration of *Naiadita lanceolata* debris on a thin clayey chip, exemplary for all new specimens from Schleerieth. SCHL-N-65c. **a** Overview of slab, showing a monospecific accumulation of *N. lanceolata* parts. Note uneven cleavage plane. Scale bar 10 mm. **b** Close up, showing fragmented leafy gametophytes, a sporophyte capsule and a gemma cup attached to an axis. Scale bar 1 mm. **c** Detail of the gemma cup. Scale bar 1 mm

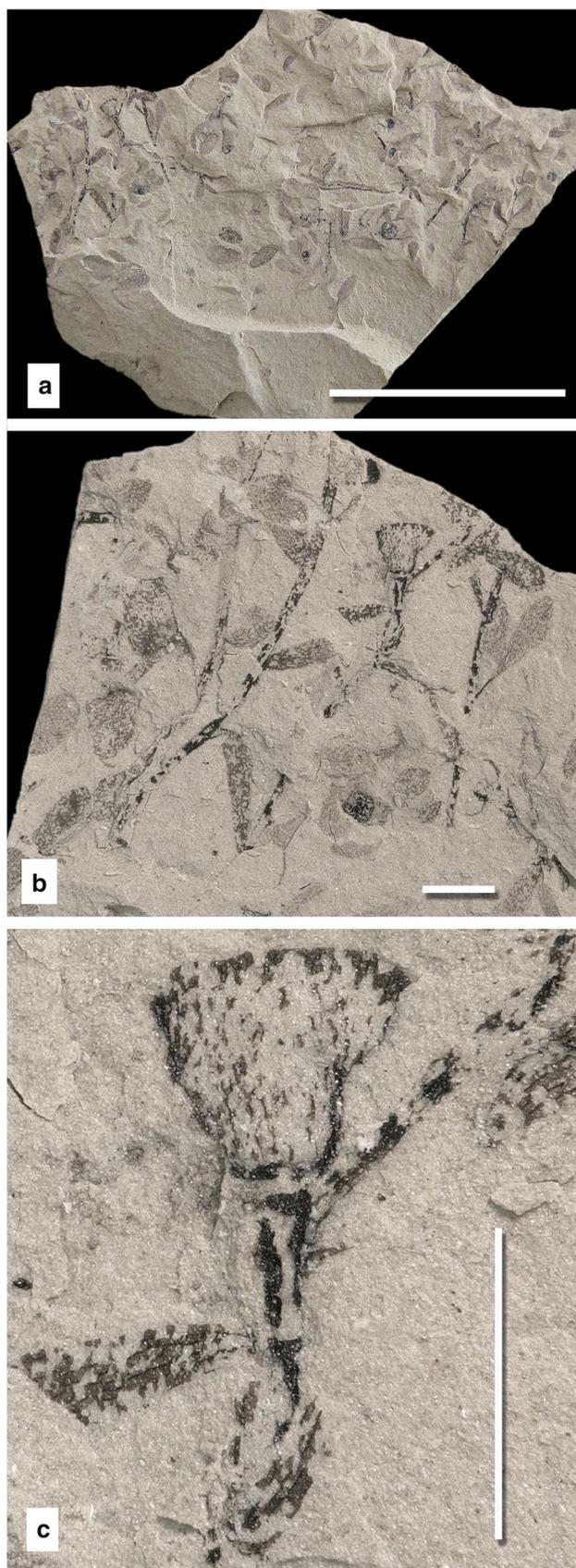
sporophyte (Fig. 5h). No evidence has been found to date of lanceolate leaves with an acute apex, or almost linear leaves similar to those described by Harris (1939). Leaf outlines of Schleerieth fossils that resemble leaves seen in Harris's description (e.g. Fig. 3c arrows; Figs. 4d; 5g) are the result of taphonomic processes.

Gemma cups.—Four leafy gametophytes bear gemma cups attached to the stem. Two of these specimens are compressed in lateral view (Figs. 2c; 4e; 5d), the others are preserved in a more oblique view and show the lobed mouth of the cup (Fig. 5f, j). According to Harris's depictions (Harris 1938: fig. 13), three cups are attached on short (Fig. 5d) or slightly longer stout branches along the stem (Figs. 2c; 5j), but no fragments of a surrounding rosette of leaves remained fossil preserved on a cup. *N. lanceolata* provides the oldest unequivocal evidence of liverwort gemmae and gemma cups in the fossil record (Bippus et al. 2017).

Sporophytes.—Four longer leafy shoot fragments bearing terminal or subterminal sporophytes in situ (Figs. 3c; 4a; 5f; 7h) have been discovered. These fossils contradict Harris's (1939: 58) interpretation that *Naiadita* axes terminate in a conical gemma cup, but rather suggest that they more often bear a terminal (or subterminal) sporophyte. Five leaves with broader leaf bases attached opposite the equator form the perianth that covered the sporophyte capsule (Figs. 4c; 5b). The lower capsule part is sunken into the widened pedicel of the gametophore (Fig. 5a), but apart from that only rarely discoverable in a few laterally embedded specimens (Figs. 4b; 5a, c).

Disarticulated capsules, partly preserved with remnants of perianth leaves (Figs. 4b, c; 7c–e, g), but also some lacking evidence of perianth leaves (Figs. 4g; 7f), are found more frequently. The globose sporophyte is typically preserved as a lenticular fossil compression and, as already stated in Solias (1901) and Harris (1938), its wrinkled surface seems to be composed of small rectangular cells (Fig. 7f, upper right corner). Capsules lack evidence of an apiculus and a line of dehiscence, and thus were most probably cleistocarpous. Entire and fragmented capsules are a constituent feature of monospecific *Naiadita* lakeball structures (Fig. 7a, b).

Comparison and classification. Harris (1938: 17) listed early nomenclatorial views and misguided assignments of *N. lanceolata*. Eighty-eight years after its initial description by Buckman (1850), he recognised the bryophytic affinity of the plant and tentatively referred the taxon to the family Riellaceae of



the Sphaerocarpaceae, primarily because of exceptional features such as a radial organisation and the leaf-like form of the perianth (Harris 1938, 1939). Townrow (1959) pointed out that *N. lanceolata* would have been easier to classify if the rhizoids were not preserved. Without the rhizoids, the plant could be readily assigned to the Calobryales. Several of the vegetative features seen in *N. lanceolata* are also present in modern liverworts, including Calobryales (today Haplomitriales), which has been demonstrated in Schuster (1966) and Taylor et al. (2009). Watson (1971) stated that important morphological features of the fossil are reminiscent of the modern genus *Corsinia* (Marchantiales), but all in all, he found that *Naiadita* is fairly unique.

Stewart (1983) also argued in favour of affinities of *N. lanceolata* the Sphaerocarpaceae, but the unusual combination of characteristics makes it impossible to assign to a family, let alone a genus, of extant Hepaticae. The absence of elaters prompted Krassilov and Schuster (1984) to tentatively place *N. lanceolata* into the Sphaerocarpaceae, but Krassilov favoured calobryalean affinities based on the erect, radial gametophytes. The latter author (Krassilov 1987) subsequently concluded that *Naiadita* is an order of its own that can be provisionally placed near the node where the Calobryales and Sphaerocarpaceae diverge. Hemsley (1989) examined the exine ultrastructure of the *N. lanceolata* spores, and found a resemblance to *Geothalpus* (Sphaerocarpaceae) and *Riccia* (Marchantiales), but no clear affinity between these plants.

In their morpho-molecular classification scheme, Frey and Stech (2005) placed *N. lanceolata* either in the Haplomitriopsida or the Marchantiopsida subclass Sphaerocarpaceae. Heinrichs et al. (2011), in a synopsis of Mesozoic bryophyte fossils, emphasized the outstanding position of *N. lanceolata*, and point out that it is better preserved than other bryophytes and therefore should not be described only as a form-genus. However, the unusual shoot architecture of *N. lanceolata* renders assignment to any order of extant liverworts ambiguous (Heinrichs et al. 2007; Villarreal et al. 2015). Katagiri and Hagborg (2015) underlined that the morphology of *Naiadita* justifies placement in a separate order rather than in a suborder of Sphaerocarpaceae, and validated the ordinal and family names.

Discussion

Implications for the prospection of bryophyte fossils

Experienced fossil hunters usually try to obtain large slabs of unweathered rocks for subsequent splitting with chisel-tip rock hammers (Rowe and Jones 1999). The larger the area of the cleavage surface, the better the chance for yielding rare plant fossils or plant organs still organically connected to each other. Nonetheless, this approach widely

fails with all fresh Albertbank shales and mudstones due to the dense structure of these sediments. Rather, splitting of fresh mudstone material nearly always results in fragmentations because of the lack of prominent bedding planes. Only prolonged weathering frees the delicate bryophyte fossils on surfaces of subparallel flakes of mudstones (Fig. 1f), and then they can be easily collected (Figs. 1g; 8d). The need for this peculiar fossil prospection and screening of small weathered clay chips might be the simple reason why evidence of *N. lanceolata* from the Lower Keuper beds of the germanotype Triassic has remained virtually absent hitherto.

Ignatov (1990) and Hübers and Kerp (2013) have successfully taken a new path to obtain larger quantities of fossil bryophytes by bulk maceration. Greater observance and a survey conducted among weathered mudstone chips might also be a successful means for new fossil discovery, more particularly for minute bryophytes.

Terminal vs subterminal and lateral position of the sporophyte

Harris (1939: 60, fig. f; reproduced here in Fig. 6b) provided a detail reconstruction of the *Naiadita lanceolata* sporophyte borne on a lateral pedicel, which allegedly is 0.25 mm thick and up to 2 mm long (Harris 1938: 39). Harris (1938, 1939) hypothesized that the sporophytes developed from a naked archegonium in a lateral position that was then enveloped by a ring of perianth leaves.

Four specimens of leafy gametophores from Schleerith show a globose sporophyte capsule terminally or perhaps subterminally attached to the stem (Figs. 3c; 4a, j; 5f; 7h). Based on these specimens, the new reconstruction now has the sporophyte at the tip of the plant, surrounded by five perianth leaves (Fig. 6c). In Figs. 3c and 5f, the sporophyte capsule gives the impression of being slightly displaced from its central terminal position by compaction of the sediment. Likewise, the condition in the specimen in Fig. 4a, j, cannot be determined beyond doubt. Limited by insufficient preservation, it remains unclear whether the impression of the elongate plant part (arrow in Fig. 4j) belongs to a fragmented perianth leaf, then indicating a terminal sporophyte position, or represents the fragmented impression of the shoot.

As a matter of principle, it cannot be ruled out that a tiny pedicel once existed but has not been fossilized in recognizable form or is perhaps hidden in the sediment behind the capsule. But then again, more than 20 Schleerith specimens in different preservation stages show the sporophyte capsule attached to axis portions centrally and terminally (e.g. Figs. 4i; 5a, c). The axis widths in these specimens correspond perfectly with those seen in normal

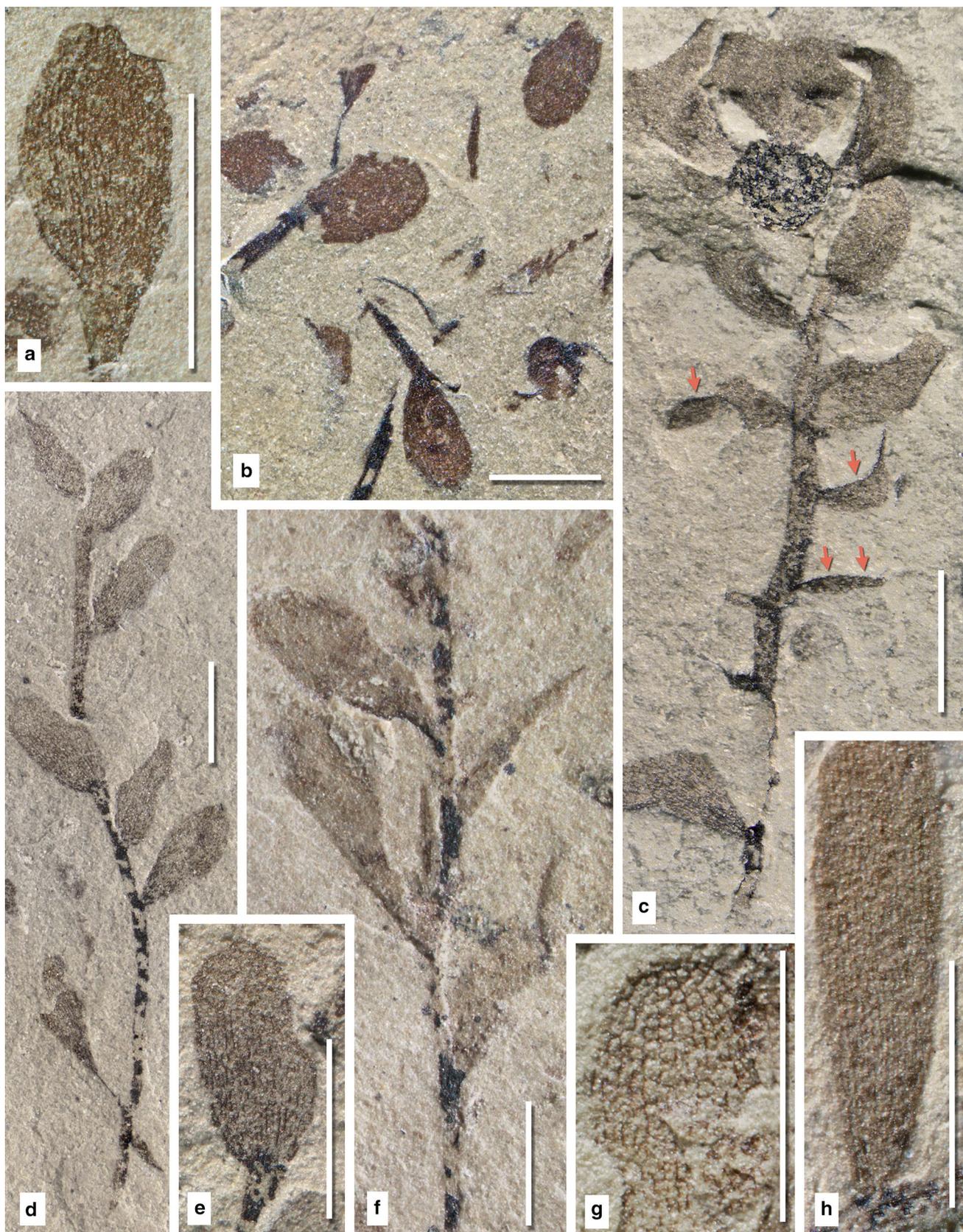


Fig. 3 Isolated leaflets, leafy shoots and a leafy shoot with a capsule in situ of *Naiadita lanceolata* from the Lower Keuper of Schleerieth. Scale bars 1 mm. **a** Isolated leaf with decurrent base. SCHL-N-18a. **b** Isolated leaflets. SCHL-N-70. **c** Gametophore with terminal (or subterminal) sporophyte. Capsule position probably slightly displaced by sediment compaction. Arrows point to transversely embedded leaves. SCHL-N-65a. **d** Leafy shoot with chiefly obovate and ovate leaves, revealing their arrangement spirally around the axis. SCHL-N-121. **e** Detail of Fig. 3d. **f** Leafy shoot with large, partially folded leaves, spirally arranged around the axis. Leaf edges only faintly visible. SCHL-N-46b. **g** Upper portion of a leaf. SCHL-N-144. **h** Attached obovate leaf. SCHL-N-144

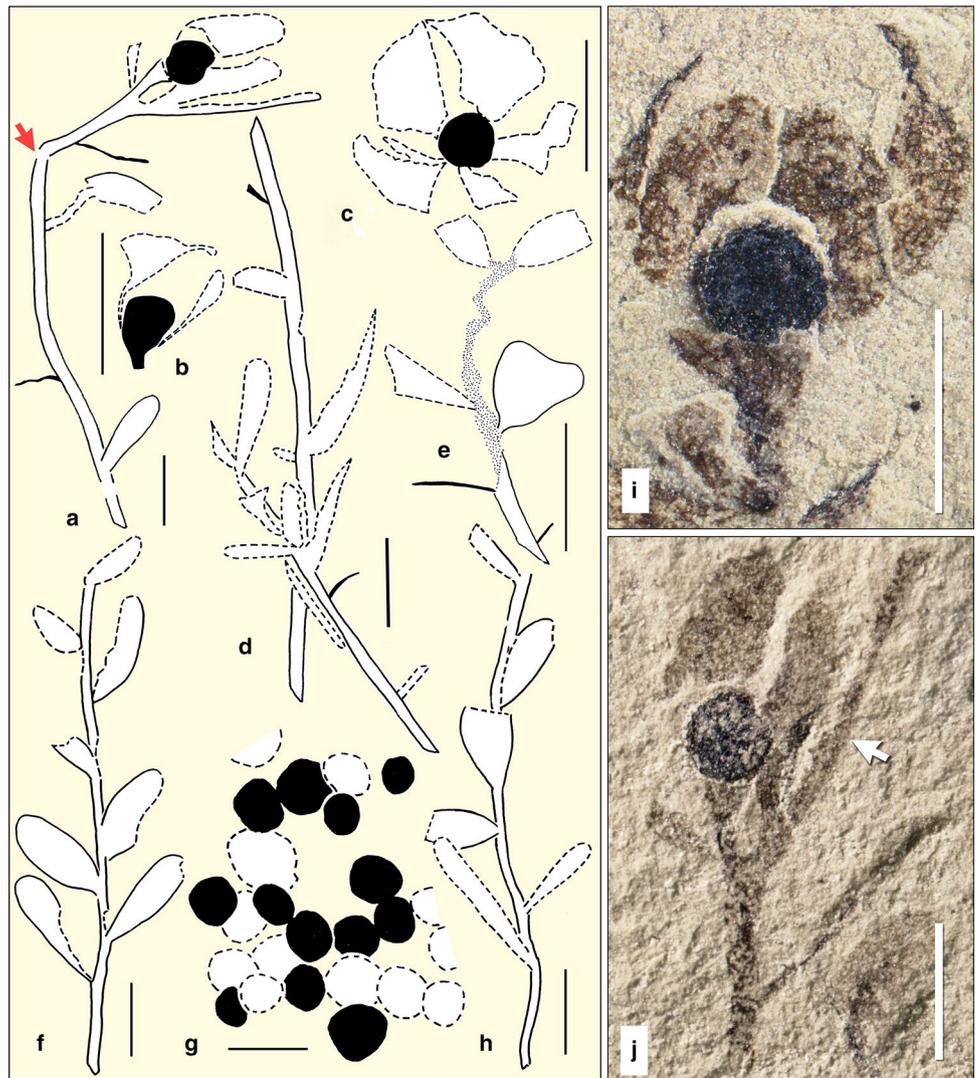
leafy shoots. However, according to Harris, all these fossil plant parts have to be interpreted as sporophytes attached to a fragmented pedicel. Despite intensive screening, evidence of antheridia, developing antheridia, and the branching off of the suggested pedicel from the shoot has not been found in the Schleerieth *Naiadita* material.

On the other hand, already Sollas (1901: pl. 13, fig. 1) has shown—as far as observable from her photograph—the

central terminal position of the sporophyte capsule surrounded by perianth leaves and positioned on the leafy shoot. Harris presented two photographs (1938: pl. 4, figs. 3, 4) together with eight line drawings of the sporophyte capsule attached to fragments of short axes (1938: fig. 18), which he interpreted as pedicels. His drawings of these fossils are strikingly similar to some of the Schleerieth specimens, including those presented in Figs. 4b, i; 5a, c. But only one of Harris's drawings (1938: fig. 18d) vaguely indicates the pedicel branching from the shoot. And even a structure interpreted as an archegonium in subterminal position has been indicated by Harris (1938: fig. 5a). If this interpretation is correct, then it would corroborate a subterminal sporophyte position as has also been indicated in the new reconstruction provided in this study (Fig. 6c).

Because of the anacrogynous features in Sphaerocarpaceae and Marchantiales (i.e. production of archegonia from the lateral cells of a shoot, rather than from the apical cell), the

Fig. 4 Outline drawings and photographs of *Naiadita lanceolata* from the Lower Keuper of Schleerieth. Scale bars 1 mm. **a** A leafy shoot with a sporophyte in situ. Note the kink point in the terminal part (arrow). SCHL-N-144b. **b** Apical axis or pedicel fragment showing the basis of the sporophyte. SCHL-N-12. **c** Apical axis or perianth fragment showing the sporophyte capsule surrounded by fragmented leaves of the perianth. SCHL-N-66. **d** Two overlapping gametophyte fragments showing leaves partially torn in longitudinal direction. Close-up in Fig. 5g. SCHL-N-32. **e** Leafy shoot bearing a gemma cup. SCHL-N-49. Close-up in Fig. 5d. **f** Leafy shoot. SCHL-N-144b. **g** Accumulation of thick-walled capsules, preserved as compressions (black) and impressions (white circles). SCHL-N-41b. **h** Leafy shoot. SCHL-N-53b. **i** Apical axis or pedicel fragment, lateral view. SCHL-N-53a. **j** Close-up of Fig. a. Arrow points to the impression of the poorly preserved shoot or a fragmented attached leaf



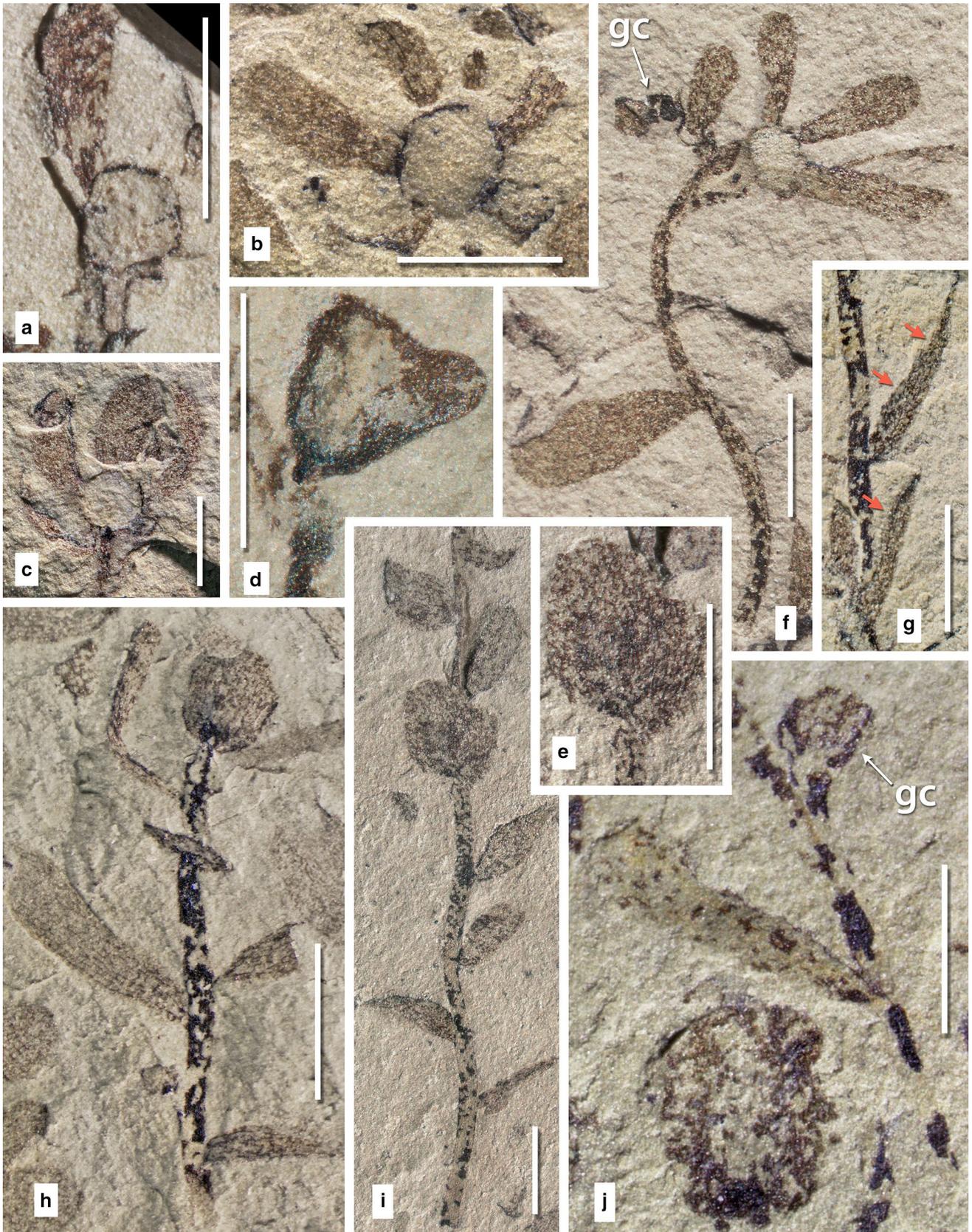


Fig. 5 Leafy shoots of *Naiadita lanceolata*, partially with inserted gemma cups and sporophyte capsules from the Lower Keuper of Schleieth. Scale bars 1 mm. **a** Impression of the terminal (or subterminal) sporophyte capsule. Note the hollowed-out top at the capsule basis. SCHL-N-42a. **b** Impression of the sporophyte, surrounded by a pentamerous perianth. SCHL-N-54a. **c** Terminal (or subterminal) sporophyte impression in lateral view. The front perianth leaves are broken off, revealing the uppermost part of the gametophyte stem. SCHL-N-65c. **d** Short-stalked gemma cup attached to a leafy shoot, close-up of Fig. 4e. SCHL-N-49. **e** Abnormal subcircular structure, close-up of Fig. 4i. **f** Gametophore bearing a terminal (or subterminal?) sporophyte and a subterminal gemma cup (arrow gc). SCHL-N-117. **g** Close-up of Fig. 4d. Transversely embedded leaves, lengthwise torn along the cleavage plane (arrows). SCHL-N-32. **h** Terminal gametophyte shoot bearing what appears to be a gemma cup (according to Harris 1938, 1939) or terminal (or subterminal?) sporophyte capsule enclosed by a perianth. SCHL-N-65a. **i** Leafy gametophyte shoot, showing helically arranged leaves and an abnormal subcircular structure. SCHL-N-144b. **j** Portion of a leafy shoot with an attached gemma cup (arrow gc). SCHL-N-57b

reconstruction of a terminal sporophyte has to be considered generally problematic. Better-preserved specimens need to be discovered and examined in future research to determine whether the sporophyte position is subterminal or terminal.

Harris's reconstruction of *Naiadita lanceolata* and a fresh reconstruction attempt based on the new Schleieth specimens

Harris (1938) restored two leafy shoots bearing exclusively elongate leaves (Harris 1938: figs. 4b; 6b). Another restoration shows a leafy gametophyte bearing a gemma cup and an archegonium, both surrounded by terminal leaves (Harris 1938: fig. 5b). These drawings were reproduced in Gothan and Weyland (1964), as well as in slightly altered form, in Taylor and Taylor (1993), and Taylor et al. (2009), but mistakenly, in the last-mentioned depictions the leaves are sketched with a costa. Another suggested reconstruction was provided in Harris (1939: 60, fig. a; reproduced in Fig. 6a); it shows a leafy shoot bearing rhizoids, archegonia and gemma cups, the latter surrounded by leaves. This iconic outline drawing has been widely reproduced in textbooks, e.g. in Stewart 1983 (three-dimensionally enhanced by dots); Schofield 1985 (together with the reconstruction from Harris 1938: fig. 6b); Oostendorp 1987; Pant and Bhowmik 1998; van Konijnenburg-van Cittert 2008.

The Schleieth material provides additional insights into the morphology of the *N. lanceolata* plant, and hence necessitates refining of the overall view reconstruction (Fig. 6c). Key aspects of this modification are as follows: intact linear or extreme linear-lanceolate leaves basally attached to the stem have not been found among the new material so far; therefore they have been omitted in the new drawing.

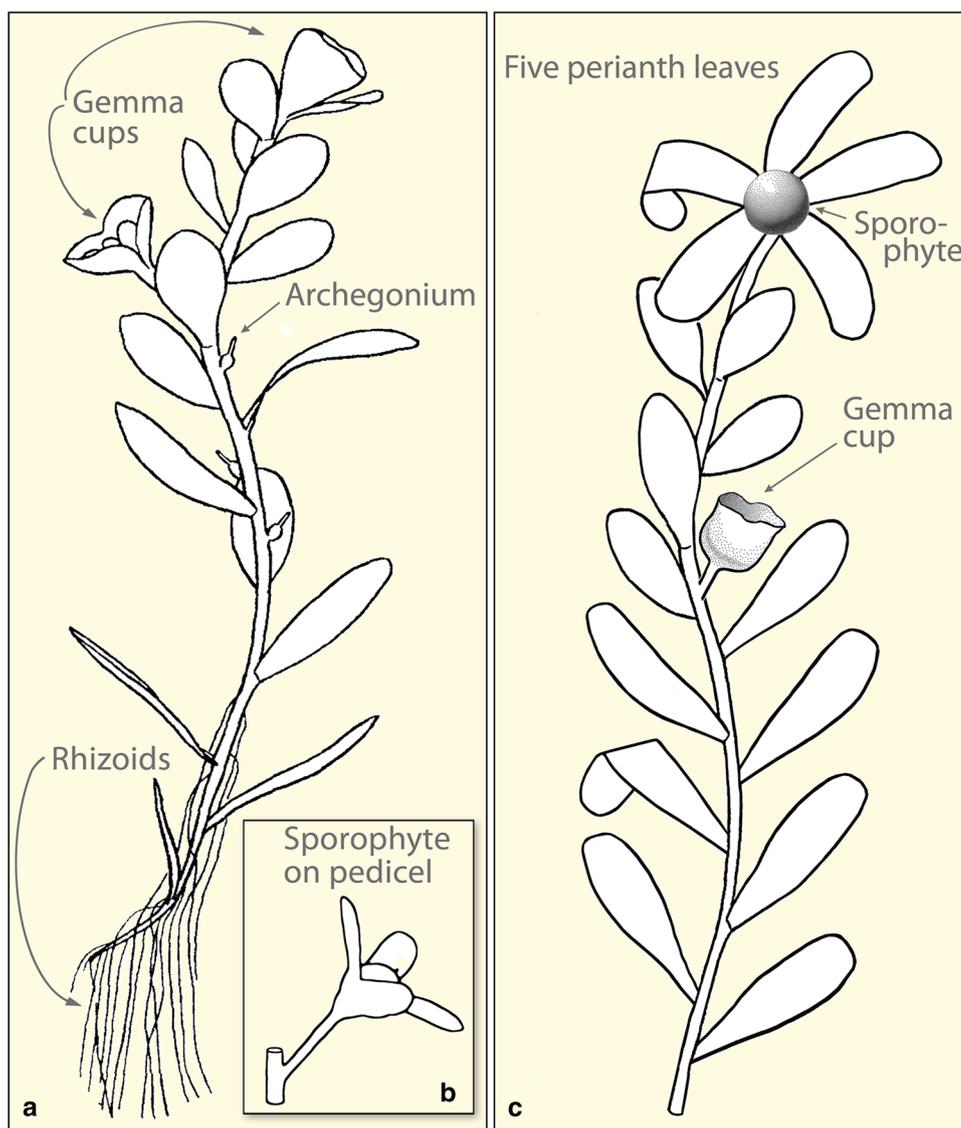
As already described, and terminologically in accordance with leaf typifying standards (Ash et al. 1999; Malcom and Malcolm 2006), most Schleieth leaves are either elongate obovate, lingulate, or oblong or slightly obovate. Lanceolate leaves (termed in Harris 1938, 1939) in their strict sense (i.e. lanceolate leaves being widest below the middle) do not occur, either in Harris's leaf depictions or in the *Naiadita* fossils from Schleieth. The misleading description "leaves typically lanceolate" should therefore be omitted.

Harris (1938), like Sollas (1901), possibly took Buckman's line drawing of a leafy stem fragment into account (Buckman 1850: fig. 1). This drawing shows a stem fragment bearing four leaves, two of which are damaged, but two others indeed are truly lanceolate in shape. But then again, in his fig. 3, Buckman portrays a stem fragment with ovate leaves somewhat blunt at the apex and named it *N. obtusa*, and the leafy stem fragment shown in his fig. 4 possesses ovate leaves on short petioles, a form he named *N. petiolata*. Harris (1938: 49) took the epithet *lanceolata* from the fact that it was so-called first in an earlier publication. As already mentioned, the leaf forms originally referred to as "*N. obtusa*" and "*N. petiolata*" are typical also in the Schleieth material.

Harris (1938: fig. 16c) provided a line drawing showing a feature-poor terminal bulbous, which is thought to represent a gemma cup surrounded by two leaf fragments. Three of the four newly found gemma cups from Schleieth are laterally attached to the stem (Figs. 2c; 4e; 5d, j) and only one is suggestive of a subterminal position, adjacent to the terminal (or possibly also subterminal) globose sporophyte (Fig. 5f). The attached gemma cup in the new reconstruction is therefore placed sideways, growing on a short stalk without perianth leaves, similar to what is recognizable in Figs. 2c; 5j.

It should be emphasized that both reconstructions (Fig. 6a, c) are somewhat artificial in the way of presenting all characteristic features of *N. lanceolata*. In his exemplary reconstruction, Harris (1939: 60, fig. a; reproduced in Fig. 6a) shows attached leaves that differ in size and shape, i.e. three leaves are extremely thin and linear, one is elliptical with a rounded apex, one is oblong (behind the stem), and three are elongate obovate with acute blade tips. The leaves in the distal portion of the plant are obovate-ovate and possess rounded apices. This heterophyllous foliage might be the result of considerations made on a synthesised reconstruction. Harris, however, documented already two larger plant parts with slender, isophyllous leaves (Harris 1938: figs. 5, 6), two configurations which differ from his overall reconstruction (Harris 1939). It is clear, therefore, that not all characteristics might have been observed on a single individual plant at a given time, not to mention being preserved in one fossil plant fragment.

Fig. 6 Suggested morphology of *Naiadita lanceolata*. **a** Overall reconstruction. **b** Reconstruction of a pedicel with sporogonium and perianth. **a, b** Reproduced from Harris (1939: 60). **c** Refined tentative reconstruction based on the new specimens from the Lower Keuper of Schleerieth, in the style of Harris (1939: 60). Sporophyte possibly subterminal, attached via a short pedicel



Plant taphonomic features of *Naiadita lanceolata*

Although the Schleerieth fossils are approximately 37 million years older than Harris's material of *Naiadita lanceolata* from the Rhaetian of the West- and Midlands of England, both fossil assemblages interestingly consist mainly of monospecific aggregates of leafy gametophytes, in part with attached gemma cups and sporophytes (e.g. Fig. 2a, b), while detached leaves are generally rare (Fig. 3a, b). On the other hand, the depositional environments (and thus the rock matrices) preserving the two assemblages of fossils are quite different. While the British material has accumulated in limestone sediments and is preserved as compactions or cellular permineralizations (Harris 1938), the Schleerieth specimens occur in mudstones and are therefore preserved as impressions or compressions.

With regard to whole-plant concepts (Bateman and Hilton 2009), the Schleerieth fossils are unique because they easily allow faithful reconstruction of the morphology and habit of *N. lanceolata*. However, the monospecific *Naiadita* assemblages from England and Schleerieth raise several interesting taphonomic questions, in particular because they are so similar with regard to the detachment of leafy shoots, sporophyte capsule abscission, and transportation to the final deposition.

Basic principles of plant taphonomy have been reviewed by many authors, including Ferguson (1985), Gastaldo (1988), Greenwood (1991), Spicer (1991) and Locatelli (2014). Special attention has been given to lacustrine taphofacies by Birks (1980) and Rich (1989). The preservation potential of bryophytes and their peculiar taphonomy was discussed in Hemsley (2001), and more recently in Tomescu et al. (2018). Nevertheless, the Schleerieth fossils provide

an extraordinary first-hand insight into fossil bryophyte taphonomy and therefore deserve attention.

Plant taphonomic features concerning the leafy shoot. The *Naiadita* shoot fragments provide evidence of rapid entombment. Prevalent is the simple pattern of horizontal burial, yielding two corresponding impressions (part and counterpart) of isolated leaves (Fig. 3a, b) or leafy shoots (e.g. Fig. 3d). This common plant taphonomic pathway is outlined in Fig. 8: floating bryophyte debris (Fig. 8a) sinks to the bottom of a lake or pond, or is washed ashore and becomes buried. The weight of overlying sediments causes the cylindrical stems to collapse and to become preserved as compression-impression fossils in the same way as the leaves (Fig. 8b, e).

Many other *Naiadita* impressions are suggestive of a different taphonomic process. Fossilized shoots often show attached leaves still in their twisted-protruding natural orientation (Fig. 8f, g), probably due to the rigidity of the *Naiadita* leaves, and possibly also to a decelerated sink rate of the tiny bryophyte fragments similar to clay particles in the suspended load (Fig. 8c). These half-twisted, distant leaves are seen in Fig. 3c (arrows). Here, as already pointed out by Rex and Chaloner (1983) and Chaloner (1999), the pathway taken by the fracture through the matrix changed from one cleavage plane of weakness to another (Fig. 8f), thus generating fragmented leaf impressions longitudinally torn to their length (Figs. 4d; 5g, arrows).

Even strongly skewed and distorted leaves, embedded nearly vertical to the bedding plane, can commonly be observed (Fig. 7h). In such cases, instead of a fragmented leaf impression, just a coalified narrow line is visible on the cleavage plane. Differences in leaf preservation, ranging gradually from horizontal to half- and steep vertical embedding, are also ascertainable in compression fossils of isolated capsules with surrounding perianth leaves (Fig. 7d, e, g). This taphonomic pattern provides a means of inferring the relative stiffness of *N. lanceolata* leaves.

Mass accumulations of sporangiophores with and without attached perianth leaves. Bryophyte gametophytes consist of shoots and leaves, while the capsule and subtending seta represent the sporophyte. Capsules with attached perianth form a remarkably stable unit in the *Naiadita* assemblages from Schleierth. In all likelihood resulting from a synchronous abscission or detachment process, the details of which are entirely unknown, many isolated capsules with adherent leaves entered the water body simultaneously. A small hint at the existence of a predetermined fracture zone is visible in Fig. 3a (arrow); the terminal portion of the gametophyte is strongly, but still organically, connected with perianth and capsule.

Furthermore, several present-day bryophytes (e.g. *Sphagnum*) demonstrate a peculiar feature of decomposition. They decay proximally while the distal portions of the shoots are vital, green, and continue to grow (Glime 2017b). If capsule abscission was not a natural process in *N. lanceolata*, then desiccation could possibly have caused mass detachment of sporangia. Glime (2011) refers to aquatic bryophytes in stream beds with lowered water levels, resulting from higher temperatures and reduced rainfall. Such incidents cause dying away by desiccation of susceptible bryophytes on rock surfaces located too far above the water level.

After remaining in the water for some time (Fig. 9a), the free-floating *Naiadita* capsules, still with attached perianth leaves, stranded in close proximity to one another and were finally embedded (Fig. 9b). Taking the relatively complete preservation into account (Fig. 7c), it may be concluded that the individual elements of such assemblages, which in fact resemble “flower carpets”, were only transported for relatively short distances.

Isolated sporophyte capsules with attached leaves also occur singly and scattered on some bedding planes or cleavage surfaces, showing often only two leaves of the perianth in plane position (Fig. 7d), slightly tilted, or even in a strongly twisted position, respectively (Fig. 7e, g). Likewise, hydraulically sorted and concentrated clusters of leafless capsules occur on some of the bedding planes (Figs. 4g; 7f).

Lake ball structures. Some of the small mudstone chips show subcircular debris patches of 1–1.3 cm diameter (Fig. 7a) that consist exclusively of poorly preserved portions of *N. lanceolata* leafy shoots, isolated leaves and capsules (Fig. 7a, b). These accumulations are interpreted as lake- or sea-ball structures, being buried and preserved in an initial phase of formation. Partially decayed *Naiadita* portions in shallow water agglomerated to form loosely interwoven spherical aggregates (Fig. 9c). These aggregates then were washed ashore and dried out (Fig. 9d), and subsequently became embedded. After sediment compaction, the highly fragmented flabby patches of plant material became the more or less two-dimensional structures that are found as fossils on some bedding planes.

Although “moss balls” are also known to occur among certain extant bryophytes living unattached and movable in terrestrial as well as in submerged habitats (Glime 2013), the fossil spheroidal *Naiadita* structures correspond much better with the so-called lake- or sea-balls that are sometimes washed ashore. Most widely known are sea-balls consisting of filamentous green algae (aegagropilae), mainly *Aegagropila linnaei* (Tsutsui et al. 2015; Bryant and Irvine 2016), and others comprising fibrous, felt aggregates of the widgeon grass *Ruppia maritima* (Olson et al. 2005), and the seagrass *Posidonia oceanica* (Cannon 1979; Pietrelli et al. 2017; Verhille et al. 2017). Such structures form as a result

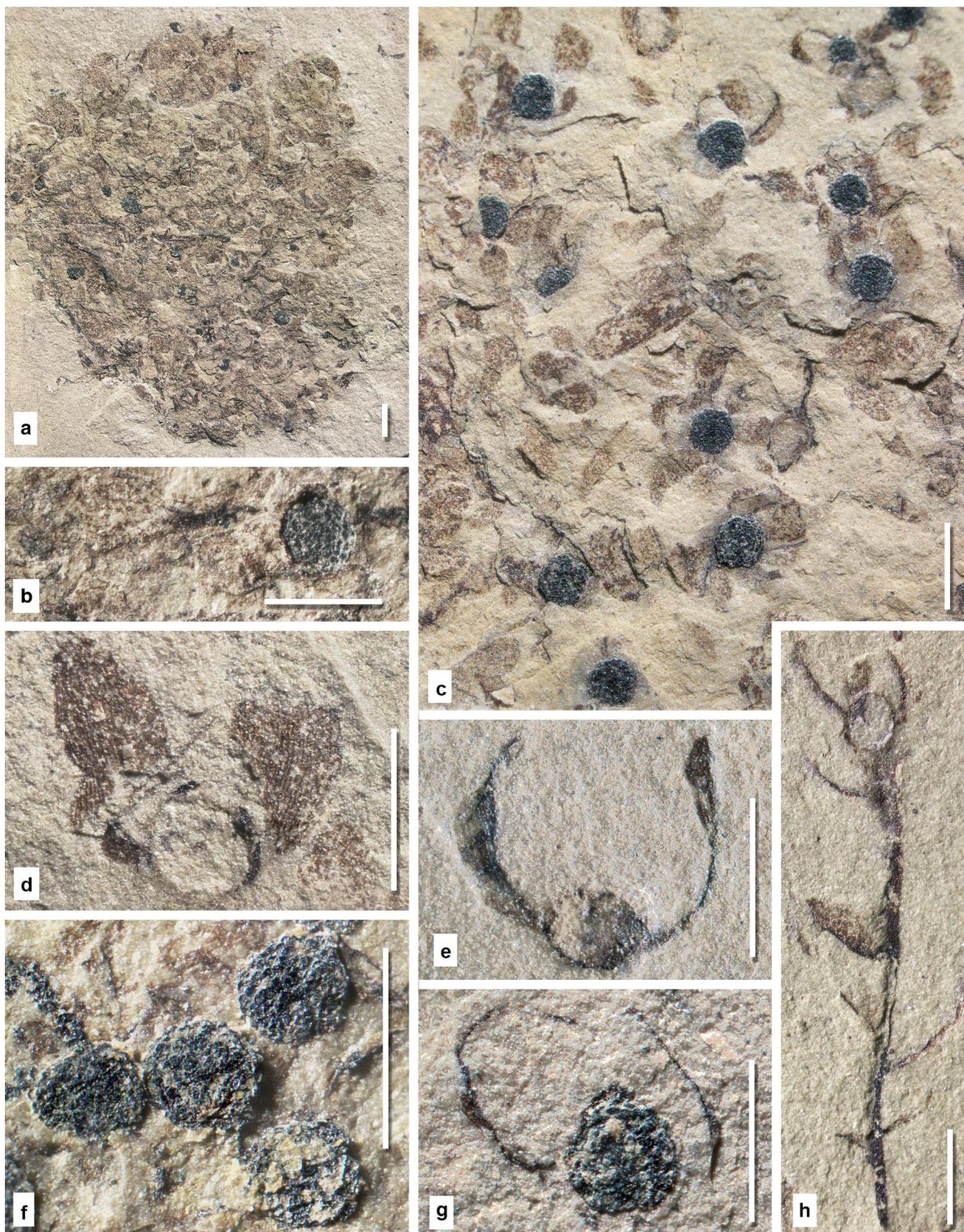


Fig. 7 Taphonomically relevant specimens of *Naiadita lanceolata* from the Lower Keuper of Schleerieth. Scale bars 1 mm. **a** A formerly flabby formed spheroidal structure consisting of ill-preserved *N. lanceolata* remains, now collapsed and flattened on a bedding plane. SCHL-N-51b. **b** Close-up of Fig. 5a (from the counterpart SCHL-N-51a), showing a leafy branch and sporophytic capsule. **c** Mass occurrence of isolated capsules bearing perianth leaves. SCHL-N-61. **d** Isolated sporophyte capsule impression with two attached leaves, embedded horizontally. SCHL-N-57a. **e** Isolated sporophyte capsule impression with two attached leaves, obliquely embedded. SCHL-N-12. **f** Isolated capsules preserved as compression fossils, detail of Fig. 4g. SCHL-N-41b. **g** Isolated sporophyte capsule with two attached leaves, embedded nearly perpendicular to the bedding plane. SCHL-N-52. **h** A leafy shoot with the impression of the sporophyte in situ. Leaves embedded perpendicular to the bedding plane. SCHL-N-112b

of the rotation effect of water, and are held together solely by friction between the fibres. Mass occurrences at beach sites are described in Mathieson and Dawes (2002), Kumar (2014) and Cooke et al. (2015).

Did *Naiadita lanceolata* live in an aquatic habitat?

Harris (1938, 1939) suggested that *N. lanceolata* was probably a submerged freshwater plant. His interpretation is widely accepted (e.g. see Watson 1971; Schuster 1981, 1984; Collinson 1988; Martín-Closas 2003; van Konijnenburg-van Cittert 2008). Harris bases his argumentation on some anatomical and reproductive features of the plant, including the presence of rhizoids that differ from those seen in terrestrial liverworts, a stem that is too delicate to support the weight of the plant body on land, the unusual free archegonia, and especially the abundance of gemmae that are all in the beginning stages of germination.

In addition, Harris regarded the assemblage of fossils co-occurring with his *Naiadita* specimens (i.e. *Darwinula*, insect larvae, and remains of an alga) as strong evidence of what one might expect to find in a freshwater or brackish lake deposit (Harris 1938: 52). The situation in the Schleerieth *Naiadita* beds is quite similar. Rarely associated with

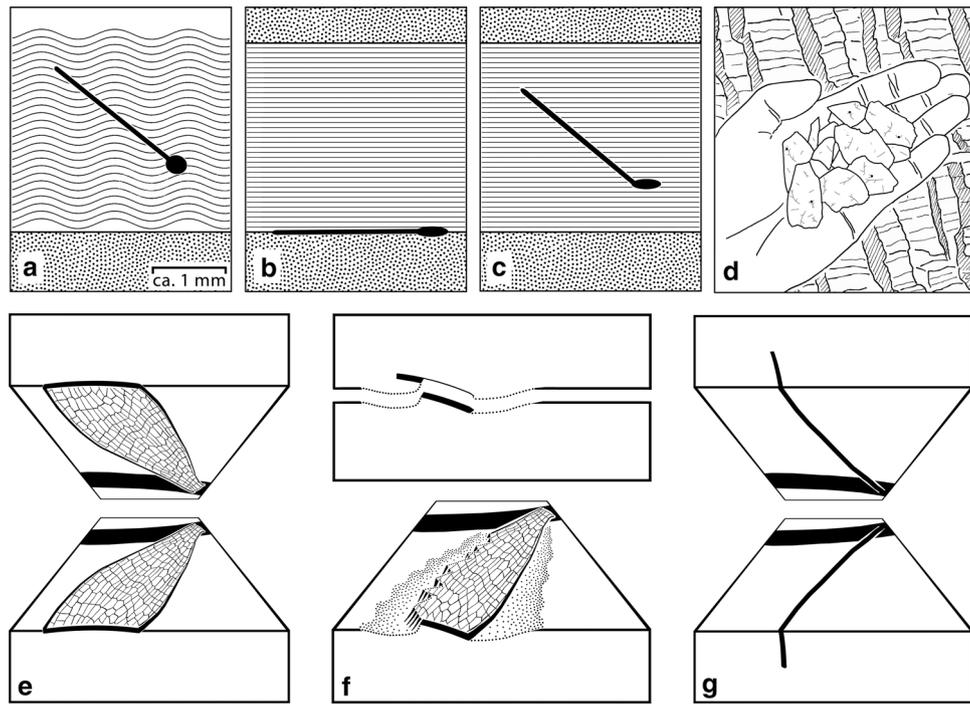
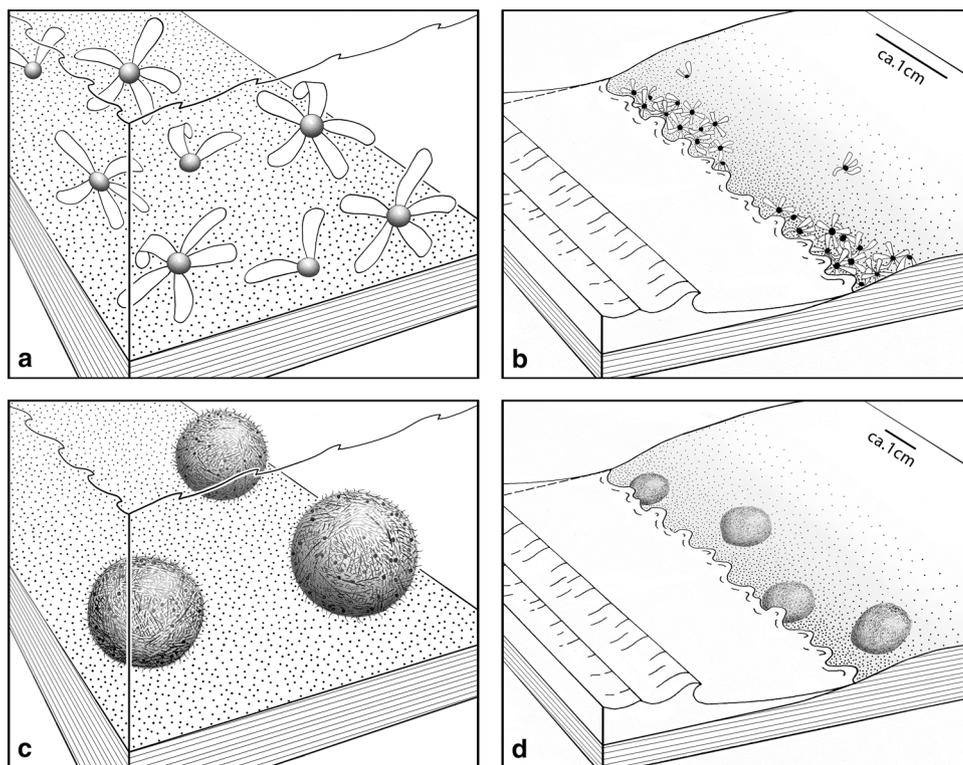


Fig. 8 Diagrammatic sketches and block diagrams of taphonomic features of leafy *Naiadita lanceolata* shoots. **a** Simplified section through a *N. lanceolata* shoot with an attached leaf (in black), floating in the water column. **b** The leafy shoot sunken to the bottom or stranded ashore, buried rapidly by sediment, and subsequently flattened by sediment compaction. **c** Entombment of the shoot into a clayey slurry layer. After the mud has settled and after sediment compaction, the former cylindrical stem has collapsed, but the laterally protruding leaf retained more or less its three-dimensional orientation. **d** Unweathered uniform mudstone layers today often split indiscriminately into horizontal cleavage planes. Only after a prolonged period of aerial weathering the *Naiadita* phytoclasts become easily detectable on sharp-edged clayey shards. **e** Horizontal embed-

ding of a leafy shoot according to Fig. 8b, then split alongside the bedding plane. Stem collapsed, leaves adpressed to the stem by compression. Slab and counter slab show two similar but mirror-inverted impression fossils or a compression faced by an impression. **f** Oblique embedding of a twisted leaf attached to the shoot. Because of its rigidity and/or the sedimentary conditions in the clayey slurry, the leaf more or less retained its three-dimensional position. The line of splitting depends on the fracturing of the matrix. Slab and counter-slab show torn leaf parts, respectively. **g** Embedding of a twisted leaf attached to a shoot near-perpendicularly to the bedding plane. The split surface of the rock shows torn leaf parts visible as thin coalified lines

Fig. 9 Block diagrams illustrating the forming of mass occurrences of isolated capsules bearing perianth leaves and the stranding of monospecific *Naiadita lanceolata* lake ball structures. **a** Sporophyte capsules with attached perianth leaves floating in the water. **b** The stranded capsules in close neighbourhood. This situation has been subsequently buried. **c** Floating portions of destroyed leafy shoots, isolated leaflets and capsules were loosely conglomerated to form flabby ball-like structures by water turbulence. **d** After stranding and water loss, the flabby lake-ball-like structures lack firmness, and hence remain as flattened subcircular clusters, followed by embedding and fossil diagenesis



Naiadita are darwinulid ostracods indicative of freshwater or brackish environments, and *Lingularia* sp. and *Euestheria* sp., which are both representatives of brackish-water palaeocommunities (Hagdorn et al. 2015a). The Schleerieth *Naiadita* assemblage itself also provides evidence of the place of growth of this interesting plant. The large amount of predominantly well-preserved leafy shoots, some even with reproductive structures in organic connection, suggest a habitat close to or in an aquatic environment. Delicate bryophyte remains would probably not be able to withstand longer periods of drought or long-distance transport.

Another argument in favour of aquatic conditions is the mass accumulation of sporangia surrounded by perianth leaves (Fig. 7c). It is hardly conceivable that these fragile plant parts were transported via terrestrial input, more or less at the same time, then arranged side by side in close proximity to one another and assembled in the place of final deposition. This could not happen outside the aquatic realm. Even the lake-ball structures composed of *Naiadita* fibrous material can be used to reason in this direction (Fig. 7a). All fibres comprising recent lake- or sea-balls derive from water plants or green algae. Based on the preceding considerations, it is highly likely that *Naiadita lanceolata* was an aquatic bryophyte.

Distribution of the cleistocarpous capsules

The taphonomic examination of the *Naiadita* material from Schleerieth has revealed different stages of preservation

of the sporophyte capsules, ranging from in situ on leafy stems (Figs. 3c; 4a; 5f), to parautochthonous assemblages of detached capsules surrounded by perianth leaves (Figs. 5b; 7c–e, g), to hydraulically sorted leafless capsule accumulations (Figs. 4g; 7f). These stages are suggestive of a particular pathway of transportation of the cleistocarpous sporophytes. Isolated *N. lanceolata* capsules partly surrounded by perianth leaves exposed on a bedding plane are strikingly similar in overall appearance to a winged seed, and hence might be used to suggest capsule dissemination by wind (e.g. Fig. 7d). Nevertheless, there remains hardly any doubt that *N. lanceolata* was a submerged-living plant. Perianth leaves and attached fragments of normal leaves likely improved the floating and hovering abilities of the capsules in the water column, and therefore were potentially important structures aiding the capsules to dislodge from the parent plant. During transport the capsules with perianth leaves probably underwent abrasion and biodegradation, resulting in only the most durable and thick-walled of the capsules to become preserved as fossils. Robust phytoclasts like the leafless capsules then behaved in their sediment environment like small seeds (for details on seed taphonomy, refer to Collinson 1983; Scott and Collinson 1983; Gee 2005). Finally, *Naiadita* was probably cleistocarpous, and thus required disintegration of the capsule/sporangium wall before the spores could be dispersed (Goffinet et al. 2009).

Reproduction of water mosses today typically occurs during intermittent periods when plants dry up; these plants cannot reproduce in running water (Frahm 2001).

It has been observed in *Riella* spp. thriving in arid habitats that after capsule decay, the large spores were transported into the soil via mud cracks, where they accumulated in the lower and moister depths and, in this way, were able to stay viable for years of desiccation. At some point when favourable conditions (i.e. when saline waters are diluted by fresh water) again prevail, they germinate (Espinar and Clemente 2007; Djamali et al. 2008).

The presence of large numbers of nutritious capsules in water also raises the question as to whether interactions with animals might also have played a role in the distribution of the spores. In extant bryophytes, spores are often distributed by animals, notably invertebrates and water fowl. It is interesting to note that in these latter cases the capsules must be ingested by the animal to release the spores (Proctor 1961; Frahm 2008; Vanderpoorten and Goffinet 2009; Glime 2017a).

Summary

The newly discovered *Naiadita lanceolata* fossils from the Lower Keuper of Schleerieth (Ladinian, Triassic) represent the only evidence outside the United Kingdom and the stratigraphically oldest fossils of this taxon worldwide. The specimens demonstrate that weathered mudstone chips deserve more attention as an eligible source of minute bryophyte fossils. *Naiadita lanceolata* is one of only a few fossil bryophyte taxa in the fossil record with sporophytes preserved in situ, as is documented by four leafy gametophytes showing the terminally or subterminally positioned sporophyte. Stems bear leaves of various shapes, and gemma cups arise singly on the stem.

The new Schleerieth fossils demonstrate that several different taphonomic pathways led to preservation of *Naiadita* at Schleerieth. Preservation of leafy gametophytes suggest little post-mortem transport and deposition in a low-energy sedimentary environment. Conclusions can be drawn on transport mechanisms of detached cleistocarpous sporophyte capsules. In a progressive stage, largely decayed remains formed loosely interwoven spherical lake-balls, exclusively consisting of *Naiadita* remains. The variously preserved capsules permit a glimpse of the attuned life strategy of *N. lanceolata* and testify that bryophytes were important constituents of the Lower Keuper ecosystem.

Acknowledgements I would like to thank Jürgen Sell, Museum Terra Triassica, Euerdorf, Germany, whose diligent fossil collecting has made this study possible. Many thanks to Gerd Geyer, Institute of Geography and Geology, University of Würzburg, for taking the photographs in Fig. 2b, c. I am also grateful to Gerd Vogg, Botanical Garden and Department of Botany 2, Julius-von-Sachs-Institute for Bioscience, University of Würzburg, who granted access to the photomicroscope. This manuscript was greatly improved by reviews from Benjamin Bomfleur, Michael Krings, Mihai Tomescu, an anonymous reviewer and the Editor-in-chief Mike Reich.

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