



Angiosperm tree leaf as a bryozoan substrate: a case study from the Cretaceous and its taphonomic consequences

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LETHAIA



Apart from seagrasses, angiosperm leaves are rare substrates for marine bryozoans today and in the geological past. Here we describe two leaflets of a compound angiosperm tree leaf overgrown by bryozoan colonies from the Coniacian Wartowice beds in the upper part of the Rakowice Wielkie Formation in Lower Silesia. The bryozoans are preserved as moulds and cannot be precisely identified but are evidently membraniporimorph cheilostomes. By comparison with similar modern cheilostomes, the colonies are estimated to have taken a week or more to grow to their preserved sizes. From this it can be inferred that the encrusted leaves remained intact and may potentially have been transported several kilometres from the site of origin. Without other evidence, the presence of articulated compound leaves is an insufficient criterion for inferring the autochthonous or parautochthonous nature of plant megafossil assemblages. □ *Bryozoa, Cretaceous, Taphonomy, Lower Silesia, Poland, Europe, Angiosperms.*

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It is commonplace in palaeobotany to say that multicellular fossil plants are seldom preserved in their entirety. Organs are usually found separately and not infrequently in different sedimentary settings (e.g. Locatelli 2014 and references therein): for example, roots or rootlets may be preserved *in situ*, whereas leaves can be transported by water. Whole-plant reconstructions are thus often difficult to prepare, and taphonomic data is essential for biological interpretations (Gastaldo 2001) and palaeoclimatological reconstructions (Greenwood 1992).

In this short report we describe a specimen of a compound leaf of a Late Cretaceous flowering plant (angiosperm) overgrown by cheilostome bryozoan colonies. This unusual occurrence has no fossil and few Recent analogues. Bryozoans are common epiphytes of seagrass blades (see Di Martino & Taylor 2014; Taylor 2020) but excluding the unmineralized, freshwater phylactolaemates (e.g. Vorstman 1928), they are seldom found growing on angiosperm leaves: a rare exception is the amphibious gymnolaemate *Amphibiobeania*, a specialized epiphyte of mangrove leaves capable of surviving long periods of desiccation (Metcalf *et al.* 2007). We conclude that the Cretaceous leaf must have been submerged (either floating or sunken to the seabed) for a sufficiently long period of time to allow the development of the bryozoan colonies, remaining intact and potentially

transportable over a significant distance. As a consequence, the presence of articulated compound leaves should not be taken alone as sufficient evidence for either the autochthonous or parautochthonous nature of plant megafossil assemblages, contrary to proposals advanced in previous studies (Spicer *et al.* 2002; Halamski 2013).

It is worth noting that co-occurrences of terrestrial angiosperm leaves and marine faunas are rare, although reports from the Upper Cretaceous of Central and Northern Europe do exist. Bivalves and *Ophiomorpha* traces co-occurring with flowering plant leaves are known from the Coniacian of south-western Poland (Halamski 2015, pl. 1, figs 1, 2), whereas marine bivalves and leaves were noted to be present simultaneously in the Campanian of southern Sweden (Halamski *et al.* 2016, fig. 2c). Co-occurrence of a scaphitid ammonite with angiosperms was reported from the upper Campanian of western Ukraine (Halamski 2013, fig. 2a). However, attachment of marine epibionts onto terrestrial angiosperm leaves is an apparently unique phenomenon in the fossil record. The only analogy we were able to find is that of Permian to Triassic microconchids (probably an extinct clade of lophophorates, often wrongly identified as spirorbid polychaetes; Taylor *et al.* 2010) attached to terrestrial plant fragments. The analogy, however, is a relatively distant one, insofar as

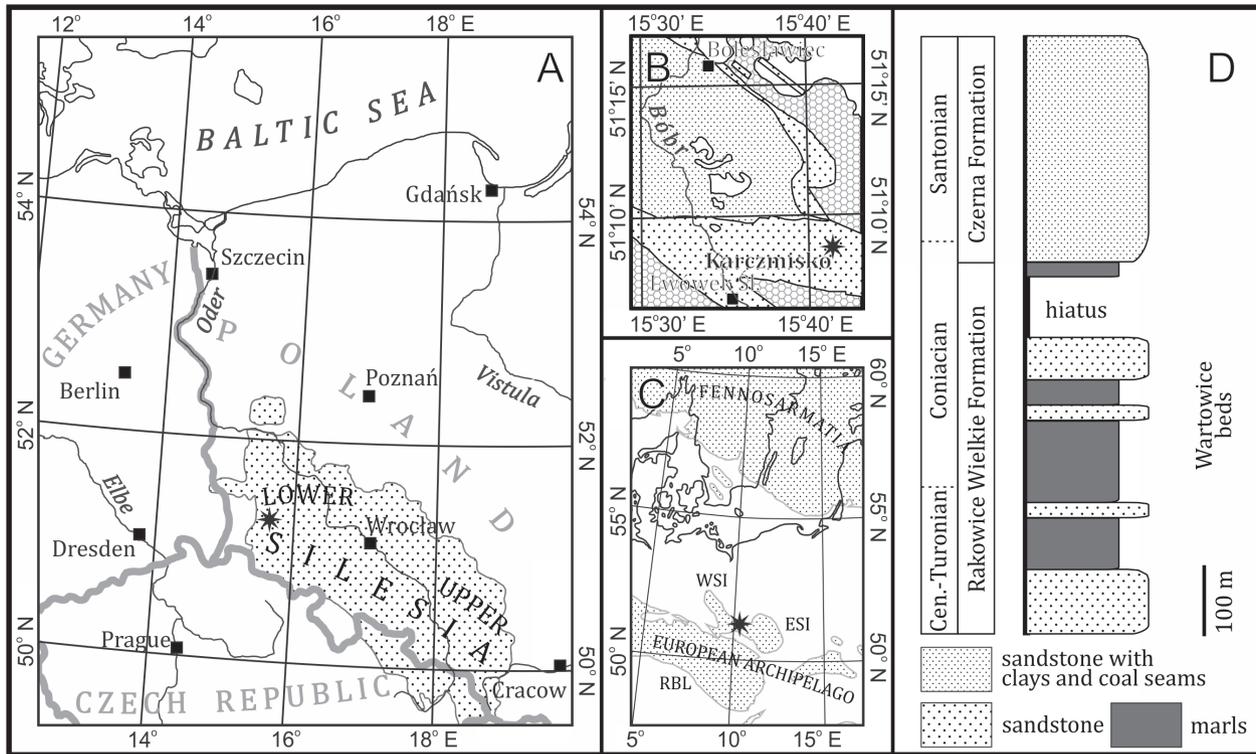


Fig. 1. Geographical, palaeogeographical, and geological context of the described specimen. A, geography of Central Europe. Present-day political boundaries in light grey, historical territory of Silesia (as approximated by administrative divisions of 1741) stippled. B, simplified bedrock map of the central part of the North Sudetic Basin. Pre-Cretaceous represented by hexagonal infill, lower Upper Cretaceous (Rakowice Wielkie Fm., Cenomanian to Coniacian) by dense stippling, upper Upper Cretaceous (Czerna Fm., upper Coniacian? to Santonian) by light stippling, post-Cretaceous white (mainly after Sawicki 1966, from Heřmanová *et al.* 2020). C, Late Cretaceous palaeogeography of Central Europe (after Ron Blakey from Csiki-Sava *et al.* 2015, modified after data in Chatziemmanouil 1982, Surlyk in Voigt *et al.* 2008, Janetschke and Wilmsen 2014). Present-day coastlines in black; Cretaceous coastlines in grey, land stippled, sea in white. ESI, East Sudetic Island; RBL, Rhenish-Bohemian Land; WSI, West Sudetic Island. D, generalized lithostratigraphy of the central-eastern part of the North Sudetic Basin (after Milewicz 1985, 1997, as modified by Walaszczyk 2008). Wartowice beds represent an informal unit, so precise limits cannot be given. The exact position of the specimen within the Wartowice beds is unknown. Asterisks denote the study locality.

microconchids were euryhaline organisms and these reports mostly originate from lacustrine and fluvial settings (Shcherbakov *et al.* 2021), although there is at least one case from a marginal marine environment (a Carboniferous lagoon: DiMichele *et al.* 2006).

Geological setting

The specimen described here originates from Lower Silesia (Dolny Śląsk, Niederschlesien; Fig. 1A), a region in south-western Poland with extensive outcrops of Upper Cretaceous rocks (Voigt *et al.* 2008). More precisely, it comes from the North Sudetic Synclinorium (Walaszczyk 2008), a syncline exposing Cenomanian to Santonian sedimentary rocks (Fig. 1B) deposited in varying environments, for the most part marine from the Cenomanian to Coniacian but predominantly brackish, limnic, or

fluvial from the Coniacian to Santonian (Leszczyński 2010, 2018).

The Cenomanian to Santonian palaeogeographical setting of Lower Silesia comprised islands of varying size located in the seaway between the Tethys and the northern ocean. These islands, termed the European Archipelago (Fig. 1C), hosted a diverse flora consisting mostly of angiosperms, conifers and ferns (Heřmanová *et al.* 2019, 2020; Halamski *et al.* 2020), the remains of which are found in rocks deposited in marine to freshwater environments (see Halamski *et al.* 2020 for an extensive summary of regional geology and palaeogeography, with a description of localities).

The described specimen, which is registered as MB.Pb.2008/336 in the Museum für Naturkunde, Berlin, Germany, was collected by W. Zimmer in February 1918 on Karczmysko hill near Zbylutów (51°09'N 15°41'E; at the time Kretschamberg bei Deutmannsdorf). Its stratigraphical provenance is

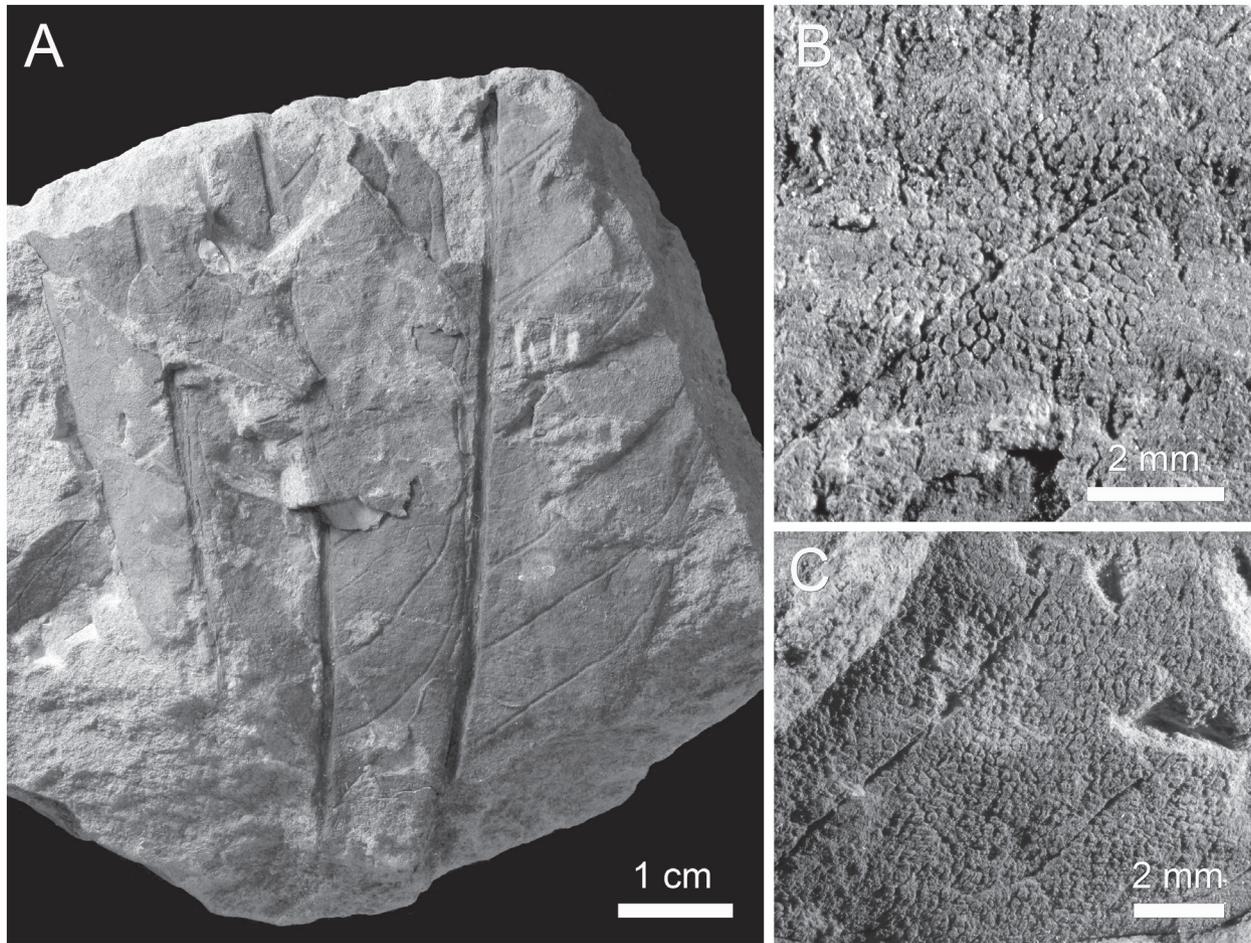


Fig. 2. *Dewalquea?* sp., incompletely preserved compound angiosperm leaf overgrown by colonies of membraniporimorph cheilostome bryozoans. Upper Cretaceous, Coniacian, Rakowice Wielkie Formation, Wartowice beds; Karczmysko hill near Zbylutów, Lower Silesia, Poland. Specimen MB.Pb.2008/336, collected by W. Zimmer, 1918. A, general view. B, C, enlargements of bryozoan colonies.

described as ‘Neuwarthauer Schichten’ (Wartowice beds), an informal stratigraphical unit (Williger 1882) corresponding to the upper part of the Rakowice Wielkie Formation (Fig. 1D) in the current lithostratigraphical scheme (Milewicz 1985, 1997). The exact age of this unit is difficult to establish, but it falls within the lower part of the Coniacian stage. The fauna from the Wartowice beds (Scupin 1913, pp. 44–46, with corrections by Andert 1934, p. 27) is diverse and dominated by bivalves (48 species according to Scupin 1913; 44 species after Andert 1934). The fauna also includes two crustacean species, three ammonites (*Placenticerus orbignyianum*, *Scaphites kieslingwaldensis*, *Baculites bohemicus*), one nautiloid, 14 gastropods and two echinoid species. The only bryozoan recorded by these authors was identified questionably as a *Sparsicavea dichotoma* (Goldfuss, 1827), but was said by Andert (1934, pp. 28, 79) to be poorly preserved and unworthy of description. Redescribed

by Canu & Bassler (1922) and made the type species of their new genus *Grammascosoecia*, *S. dichotoma* is a cyclostome with erect, ramose colonies, quite unlike the cheilostome with encrusting colonies described in the present paper.

The vascular flora of the Wartowice beds is scarce and consists of nine specimens representing six species (including the two described herein, not treated in Halamski *et al.* 2020). The most common plant species is the platanoid *Ettingshausenia* cf. *superstes* (Velenovský, 1882) Kvaček & Halamski in Halamski & Kvaček, 2015 (five specimens from the Wartowice beds). During recent work on the Cretaceous flora from Lower Silesia (Halamski *et al.* 2020), no new plant material from the Wartowice beds was recovered.

The depositional environment of the Wartowice beds may thus be tentatively described as marginal marine (fauna with relatively poorly diverse

cephalopod assemblage) with moderate terrestrial influence (rare land plants).

Description of the specimen

Specimen MB.Pb.2008/336 is a small sandstone slab about 75 mm long by 85 mm wide (Fig. 2A). Most of the rock surface is occupied by incomplete leaf imprints. There is also a small fragment of another leaf on the left-hand side. The laminae of these leaves differ from the surrounding rock owing to their brownish coloration. Such a preservation, previously reported in terrestrial angiosperm leaves from marine Cretaceous rocks of Central Europe (Halamski 2013; Halamski & Kvaček 2015), Northern Europe (Halamski *et al.* 2016) and North America (Spicer 1977), is suggestive of bacterially mediated deposition of iron oxides (Dunn *et al.* 1997) or biologically precipitated clays (Locatelli *et al.* 2017), but detailed microscopic investigations on the Central European material have not been conducted.

The larger leaf is interpreted as consisting of three leaflets (Fig. 3). This interpretation is plausible given the similarity of shape and decreasing size of the presumed leaflets as well as venation asymmetry in the basal part of a presumed lateral leaflet (the middle one in the specimen), but the physical connection of leaflets is not preserved. See Halamski *et al.* (2020, figs 8C, 9B, C) for an analogous interpretation of similarly preserved trifoliolate compound leaves of *Dryophyllum westerhausianum* (Richter, 1904) from the Santonian of Lower Silesia. The leaflet on the right-hand side is thus most probably the median one, and the other leaflets are lateral. The general organization of the leaf is probably pedate (see Halamski *et al.* 2020, fig. 15A for a reconstruction of such a leaf from slightly younger strata in Lower Silesia), but a palmate arrangement cannot be excluded.

The leaflets are petiolulate, probably elliptical in shape but too poorly preserved to be sure, and may originally have been up to 10 cm long by 5 cm wide. The venation pattern is pinnate (camptodromous?). It is uncertain whether the margin was entire or toothed. This leaf is suggestive of the genus *Dewalquea* (probably a basal eudicot), three species of which are present in the Santonian of Lower Silesia (Halamski *et al.* 2020), but too poorly preserved to be reliably identified, all the more so because it is the only one of its kind in the Coniacian of the investigated area. The smaller leaf fragment might be the apical part of *'Dryandroides' quercinea* Velenovský, 1883.

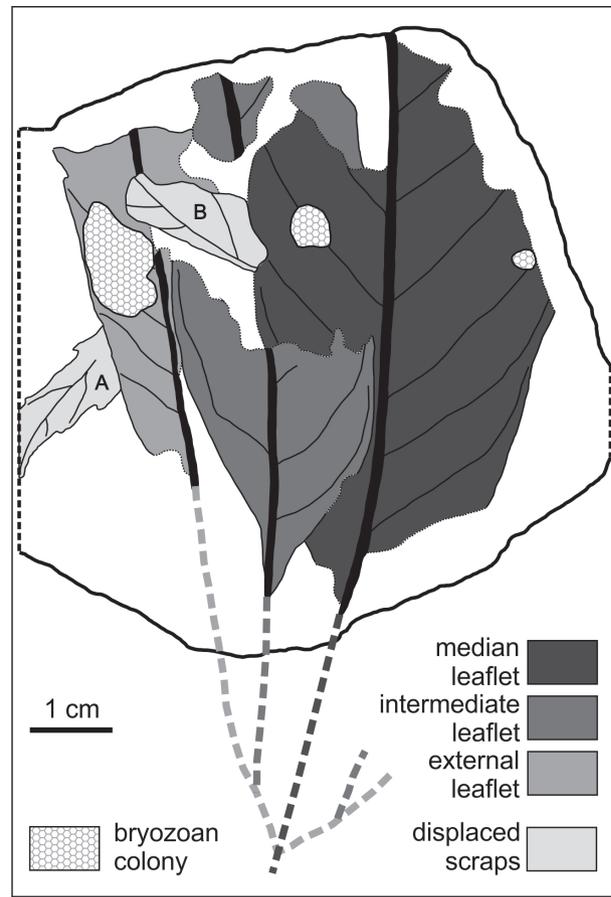


Fig. 3. Interpretive drawing of specimen MB.Pb.2008/336. The compound leaf of *Dewalquea?* sp. is shown with leaflets indicated in different shades of grey (median, darkest; external, lightest); the presumed course of petiolules is shown with interrupted lines of corresponding shades. Displaced leaf scraps are in very light grey and comprise: A, *'Dryandroides' quercinea*; B, probably originating from the compound leaf of *Dewalquea?* sp. Compare with Figure 1A.

The bryozoan colonies are present on the median leaflet and on the external lateral leaflet (Fig. 2B, C). They are decalcified and preserved as moulds, which compromises identification because the taxonomy of post-Palaeozoic bryozoans relies on characters from adequately preserved colony surfaces. Similar mouldic preservation has been described as ‘Type 3 preservation’ by Dick *et al.* (2009) in Cretaceous bryozoans from Japan that encrusted mollusc shells. While these authors were able to replicate key taxonomic characters by making artificial casts from the natural moulds, this procedure was precluded in the case of the Silesian bryozoans because of the likelihood of damaging the fossil leaves. In addition, the sediment from the Polish locality is relatively coarse and the moulding of the bryozoans appears to be of low fidelity, suggesting that casts would be uninformative. Despite these limitations, the leaf-encrusting

bryozoans are evidently cheilostomes with multiserial, sheet-like colonies comprising zooids of generally hexagonal outline each approximately 0.3 mm in length. The fact that the zooidal chambers became infilled by sediment completely, or almost so, suggests the presence of a broad surface opening rather than a restricted opening in a calcified frontal wall which tends to impede entry of sediment, resulting in incomplete filling of the zooidal chambers. Therefore, the bryozoans can be tentatively identified as ‘membraniporimorph’ cheilostomes, i.e., anascan cheilostomes having *Membranipora*-like zooids with extensive open opesia and little or no frontal calcification. This morphotype is common among Cretaceous bryozoans. It is found among non-brooding malacostegines such as *Conopeum*, *Charixa* and *Iyarisipora* (e.g. Martha *et al.* 2019; Taylor & Rogers 2021) and also in ovicell-bearing, brooding neocheilostomes such as *Wilbertopora*, *Flustrellaria* and *Pyriporella* (e.g. Taylor & McKinney 2006) (note that in older publications, such bryozoans are often identified incorrectly as *Membranipora*).

Interpretation

Compound leaves are those consisting of two or more leaflets, the laminae not being interconnected by laminar tissue (Ellis *et al.* 2009). Such leaf forms (as opposed to simple leaves with a single lamina) are present in many groups of ferns, gymnosperms, and angiosperms; within the latter group their presence is a significant taxonomic character (Halamski 2013). Usually whole compound leaves (i.e., not disarticulated into individual leaflets) are shed from their mother plants.

Preservation of terrestrial plant megafossil in sediments deposited in the sea is an exception rather than a rule (Florjan & Worobiec 2016). Plant taphonomy is thus much better studied in freshwater than in marine environments, as fluvial or lacustrine milieu are regarded as ‘default’ conditions for land plant megafossil assemblages, whereas marine sedimentary rocks may even not be considered at all in earlier overviews of the discipline (e.g. Greenwood 1991; Gastaldo 1992). Actinopalaeontological experiments have shown differences between decay in freshwater and marine environments (Gupta & Pancost 2004), but a key factor of taphonomic processes in seawater was shown to consist in the presence of diatoms. This is not necessarily applicable to the situation in the Cretaceous, when coccolithophores and dinoflagellates were the dominant primary producers in the sea rather than diatoms (Falkowski *et al.* 2004).

The question is thus whether disarticulation of compound leaves into individual leaflets can occur sufficiently rapidly to be considered a good taphonomic indicator of (sub)autochthonous character of plant assemblages. Gastaldo (1994) concluded that leaves can be transported far, but few of them remain intact. Spicer *et al.* (2002, p. 84) interpreted the presence of compound leaves with intact leaflets as indicating ‘minimal transport prior to deposition’. Halamski (2013, p. 409) was more cautious, inferring that ‘the transport of the plant material must have been relatively short’ on account of the presence of subcomplete compound leaves. In reality such interpretations are rather speculative in view of the scant experimental data concerning marine settings, while studies of decay processes (e.g. Steart *et al.* 2009; Gastaldo & Demko 2011) have not included disarticulation of compound leaves into leaflets.

Of key importance in the interpretation of the specimen from the Wartowice beds is the possibility of estimating the age of the bryozoan colonies. It is not possible to measure directly the growth rates of these Coniacian bryozoans, as is also true for better-preserved fossil cheilostomes, because they lack periodic growth banding. Therefore, growth rate has to be estimated by comparison with growth rates recorded in modern bryozoans. Linear growth rates among bryozoans vary enormously according to taxon, colony morphotype and latitude of occurrence (Kuklinski *et al.* 2012; Smith 2014; Taylor 2020). The majority of species grow from 0–5 mm per annum but the growth rate of some is an order of magnitude greater. Colonies of a membraniporimorph cheilostome – *Conopeum tenuissimum* – living in the brackish water of Chesapeake Bay are capable of budding at least 100 zooids within a week of recruitment (Dudley 1973). The smallest colony studied here from the Wartowice beds contains approximately 100 zooids, which by analogy with *C. tenuissimum* could indicate that it was as little as one week old. Some of the other colonies seem to be larger but their outlines are less well-defined.

Could the Coniacian specimen be interpreted as bryozoans overgrowing the leaves of a periodically submerged mangrove tree? This seems unlikely for two reasons. First, mangrove communities did not appear until the Maastrichtian (McLoughlin *et al.* 2018). Moreover, plants preserved in sandy marine facies are likely to have originated from riparian forests (this is in line with the flora of the Wartowice beds being dominated by a platanoid species), whereas any plants growing along the sea-coast might be preserved in the silty facies; this is at least the situation in the Coniacian of nearby Bohemia (Halamski *et al.* 2018, p. 137).

Given the estimate based on likely bryozoan growth rate that the leaf remained relatively unaltered and not covered by sediment (either floating or sunken to the seabed) for at least a week, one may ask how far such a leaf might be transported? Bottom current velocities in modern oceans usually range from 1 to 20 cm s⁻¹ (Hollister & Heezen 1972), equivalent to about 0.8 to 17 km per day, whereas surface currents velocities are usually 10–20 sea miles per day (c. 18–36 km per day), but values of 50–90 sea miles per day (c. 90–160 km per day) have been reported (Zagrodzki 1956). Taking even the lowest of these values means that transport of a nearly intact compound leaf for several kilometres (0.8 × 7 ≈ 6 km) is possible. If this is the case, the presence of articulated compound leaves is by itself insufficient evidence of a plant megafossil assemblage being autochthonous or parautochthonous.

This is in line with preliminary observations on controlled decay of compound leaves of the horse chestnut *Aesculus hippocastanum* L. in seawater that change colour and lose turgor, but do not disarticulate into individual leaflets (Z. Remin, pers. comm. 2020). Furthermore, decay of rather fragile fern pinnae was still incomplete after four months in a laboratory experiment (Iniesto *et al.* 2018).

Conclusions

A single specimen from the Coniacian Wartowice beds (an informal unit belonging to the upper part of the Rakowice Wielkie Formation) of Karczmisko (Kretschamberg) hill, Lower Silesia, shows two leaflets of a compound angiosperm tree leaf overgrown by cheilostome bryozoan colonies.

The minimum time for growth of a cheilostome bryozoan colony consisting of more than 100 zooids is likely to have been in the order of one week. To serve as a substrate for bryozoan colonies during this time the leaf must not have suffered excessive decay or have been covered by sediment; it may have either been floating or sunk to the seabed. Even slow currents (c. 1 cm/s) could result during a week in the possible transportation of the leaf over a distance of c. 6 km. Although the described material consists only of a single specimen and the bryozoans are poorly preserved, it points to survival of unburied terrestrial angiosperm leaves in seawater sufficient to allow significant transportation by currents. We conclude that presence of articulated compound leaves cannot be taken alone as unequivocal evidence for very short transport before burial, contrary to previous assumptions (Spicer *et al.* 2002, Halamski 2013).

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