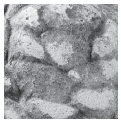
From animal to plant kingdom: the alleged sponge *Siphonia bovista* Geinitz from the Cretaceous of Saxony (Germany) in fact represents internal moulds of the cone-like plant fossil *Dammarites albens* Presl *in* Sternberg

Birgit Niebuhr



The smooth *Siphonia bovista* Gein. from the Saxonian Cretaceous Basin, introduced as a siliceous sponge by Hanns Bruno Geinitz in 1871, is interpreted as the simple internal mould of the cone-like plant fossil *Dammarites albens* Presl *in* Sternberg, 1838, representing the composite mould of the same organism, just in different preservation. Apart from the globular to egg-shaped outline, the size ratios and the same laterally flattened compaction, especially the basal area around the short stalk which is arched inwardly forms a characteristic feature of the taxon. Cone-like plant bodies and leaves of the salt-tolerant dwarf gymnosperm *D. albens* are always found in the lowermost marine sandstones of the Bohemian and Intrasudetic Cretaceous basins (Middle–Upper Cenomanian), overlying fluviatile to brackish strata. The same is true for "*S. bovista*": all Saxonian specimens were found in the lower Upper Cenomanian Unterquader of the Oberhäslich Formation, overlying the brackish Wurmsandstein of the uppermost Niederschöna Formation. Environment, sedimentary conditions and stratigraphic position of the smooth preservation form *Siphonia bovista* Gein. and the cone-like plant bodies of *Dammarites albens* Presl *in* Sternberg of Germany, the Czech Republic and Poland are thus identical. The species name *Siphonia bovista* Geinitz, 1871 is a rejected name and, therefore, replaced by *Dammarites albens* Presl *in* Sternberg, 1838 herein. The reinterpretation of "*Siphonia bovista* Gein." from Saxony provides the first proof of *Dammarites albens* Presl *in* Sternberg for Germany. • Key words: Upper Cretaceous, Saxonian, Bohemian and Intrasudetic Cretaceous basins, brackish environment, fossil conifer, *Dammarites albens*.

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Sponge? Ichnofossil? Fruit? There are findings that stubbornly defy a determination and interpretation for a long time – in this case an enigmatic fossil from the Upper Cretaceous of Saxony (Germany) that has been known for 150 years. In the first "Elbthal-Monographie" of Hanns Bruno Geinitz, a siliceous sponge named *Siphonia bovista* was figured for the first time (Geinitz 1871, pl. I.10, figs 5, 6; refigured here in Fig. 1). The species is "spherical compressed, partly from the top, partly from the side, about 2 inch in size and petiolate, consisting of fine, loose mesh, in which one also finds large, irregular furrows and larger depressions. The short, cylindrical stalk was inserted into the body, because the surface is slightly indented around the stalk" [in German: theils von oben, theils von der Seite zusammengedrückt-kugelig, circa 2″ grozs und gestielt, aus feinem, lockerem Netzgeweben bestehend, in welchem man auch grozse, unregelmäzsige Furchen und grözsere Vertiefungen findet. Der kurze walzige Stiel ist gleichsam in den Körper eingesetzt, denn es vertieft sich die Fläche etwas rings um den Stiel (Geinitz 1842, p. 96)]; it "forms obliquely or laterally compressed spherical bulps, which are without a stalk or very short stalked and have a flat depression at their crest or to the side" [in German: bildet schief- oder seitlich zusammengedrückt kugelige Knollen, welche ungestielt oder sehr kurz gestielt sind und an ihrem, oben oder auch seitlich liegenden Scheitel eine flache Aushöhlung besitzen (Geinitz 1871, p. I.40)]. Both the descriptions (Geinitz 1842, 1871) and the illustration (Geinitz 1871, pl. I.10, figs 5, 6) clearly indicate a sponge; nobody was able to link it to the cone-like plant bodies of

Figure 1. *Dammarites albens* Presl *in* Sternberg = reproduction of the first illustration of *Siphonia bovista* Gein. of Geinitz (1871, pl. I.10, figs 5, 6); a – "Scheitelvertiefung" (crest depression), b – "Befestigungsstelle" (attachment area). Original see Fig. 2A.

the genus *Dammarites*. Also Geinitz did not, even though he knew the typical specimens from Králův Dvůr, Czech Republic (in German: Königshof; MMG: PB-CsK 221; Fig. 5A, B) and Mieroszów-Łączna, Poland (in German: Raspenau; MMG: PB-PnK 45; Fig. 5D, E) from the Dresden "Petrefacten-Sammlung" (Geinitz 1849, p. 274; 1895, p. 367).

Siphonia bovista Gein. was found in the lowermost of the thick-bedded Saxonian quartz sandstones ("Quadersandsteine") southwestern of Dresden, the lower Upper Cenomanian Unterquader of the Oberhäslich Formation. The total of sixteen known specimens, hosted in the palaeozoological collection of the Museum of Mineralogy and Geology (MMG) in Dresden, are very characteristic for the Unterquader, and even today they have only been found in this horizon. In Cenomanian strata of Saxony, sponges are abundant in individuals and species; however, spicules are not preserved in the quartz sandstones.

In the year 2015, Radek Vodrážka (Prague) initiated the revision of the Saxonian Cretaceous sponges of the MMG, and quickly a heated discussion ensued: he didn't like the fossils as sponges at all, mainly because they are distinctly different to the Bohemian *Siphonia bovista* (*cf.* Počta 1884). He suggested that they may be trace fossils, but the authors of the ichnofossil revision (Niebuhr & Wilmsen 2016) declined this idea. One specimen (MMG: PZ-SaK 653a) was cut vertically to clarify the facts – with a sobering result: internally, *S. bovista* proved to be completely structure-less, only consisting of fine-grained sandstone (Fig. 3B). For the time being, the sixteen *Siphonia bovista* specimens disappeared again in the drawers.

The palaeontological collections of the MMG emerged from the former "Petrefacten-Sammlung" of H.B. Geinitz. In the mid-1990s it was systematically separated and assigned to the sections palaeozoology (PZ) and palaeobotany (PB) as distinct collections. Therefore, the Cretaceous macrofloras were kept separately from the large collection of palaeozoological objects. As part of a future exhibition project, the author first evaluated the macrofloras of the Saxonian Cretaceous in summer 2017 – and found a well-known object: a supposed *Siphonia bovista* Gein., designated by H.B. Geinitz himself as "?*Dammarites albens* Presl" (Fig. 4). Specimen MMG: PB-SaK 47 comes from the same sandstone quarry of the Oberhäslich Formation in Bannewitz-Welschhufe (Geinitz 1849) as nine of the in total sixteen *Siphonia bovista* specimens of the PZ-collection. The answer to the riddle related to *Siphonia bosvista* has come closer.

Material and methods

Twenty specimens, pending this revision all belonging to *Dammarites albens* Presl *in* Sternberg, 1838. The different names are related to different preservation forms and are thus treated separately below.

Sixteen specimens of the smooth preservation form *Siphonia bovista* Gein. (acc. to Geinitz) (MMG: PZ-SaK 196; PZ-SaK 529a–d; PZ-SaK 545a, b; PZ-SaK 651; PZ-SaK 652; PZ-SaK 653a–e; PZ-SaK 5659a, b); all of them were found in the lower Upper Cenomanian Unterquader of the Oberhäslich Formation at Bannewitz southwest of Dresden, Saxony (sandstone quarries Welschhufe, Prinzenhöhe, Goldene Höhe); labels of H.B. Geinitz, see Figs 2B; 3I, J.

One specimen of ?*Dammarites albens* Presl (acc. to Geinitz); MMG: PB-Sak 47 was found in the lower Upper Cenomanian Unterquader of the Oberhäslich Formation at Bannewitz, southwest of Dresden, Saxony (sandstone quarry Welschhufe); label of H.B. Geinitz from 1858, see Fig. 4B.

Two specimens of cone-like plant bodies of *Dammarites crassipes* Göpp. (acc. to Geinitz). Specimen MMG: PB-CzK 221 was found in the lower Upper Cenomanian Korycany Member of the Peruc-Korycany Formation at Králův Dvůr (in German: Königshof), Czech Republic; label of H.B. Geinitz from 1896, see Fig. 5B. Specimen MMG: PB-PnK 45 is a gypsum cast, the original was found in the Middle–Upper Cenomanian Glauconitic Sandstone overlying alluvial sediments at Mieroszów-Łączna (in German: Raspenau), Poland; label of H.B. Geinitz from 1869, see Fig. 5E.

One imprint of an outer surface of a cone-like plant body of *Dammarites albens* Presl *in* Sternberg; MWL: III 4497 was found in the lower Upper Cenomanian Unterquader of the Oberhäslich Formation of the Lusatian Massif, Saxony (Niebuhr 2018).

Smooth internal sandstone moulds (preservation form *Siphonia bovista*), ?*Dammarites albens* Presl (acc. to Geinitz) and cone-like composite sandstone moulds of *Dammarites albens* were measured to be able to compare their size ratios (Tabs 1–3).

Collections. – Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie (MMG), palaeozoological section (PZ) and palaeobotany section (PB), Königsbrücker Landstr. 159, 01109 Dresden, Germany; Museum der Westlausitz (MWL), geological section (III), Sammelsurium, Macherstr. 140, 01917 Kamenz, Germany.

Systematic palaeontology

The systematic position of the genus *Dammarites* is poorly constrained. In terms of higher rank systematic categories, it can safely only be assigned to the Pinophyta (conifers) within the Gymnospermae. Hluštík (1974) places *Dammarites* in the family Kranneriaceae Corda *in* Renger, 1866 (syn. Dammaritaceae Knobloch, 1973). According to Barale (1992), the genus may be assigned to the family Araucariaceae (class Pinopsida, order Pinales).

Genus *Dammarites* Presl *in* Sternberg, 1838

***Dammarites albens* Presl *in* Sternberg, 1838**
[syn. smooth and cone-like plant bodies as well as leaves of *D. albens*]
Figures 1–5, 7

*1838 *Dammarites albens* Presl; Sternberg, p. 203, pl. 52, figs 11, 12.
1842 *Dammarites crassipes* Goepp.; Göppert, p. 122, pl. 53, fig. 3.
1842 *Achilleum fungiforme* Goldf. – Geinitz, p. 96.
1846 *Dammara albens* Presl. – Reuss, p. 92, pl. 49, figs 6–8.
1847 *Dammarites albens* Presl. – Göppert, p. 365.
1847 *Dammarites crassipes* Göpp. – Göppert, p. 365.
1849 *Achilleum fungiforme* Goldf. – Geinitz, p. 264.
1849 *Dammarites albens* Presl, Sternb. – Geinitz, p. 274.
1849 *Dammarites crassipes* Göpp. – Geinitz, p. 274.
1871 *Siphonia bovista* Gein.; Geinitz, p. I.40, pl. I.10, figs 5, 6.
1878 *Siphonia bovista* Gein. – Zittel, p. 143.
1885 *Krannera mirabilis* Corda in lit. – Velenovský, p. 1 (*partim*), pl. 1, figs 1–7, pl. 4, figs 1, 2, 4, 7–9 [*non* pl. 1, figs 10–13, 18, ?pl. 3, fig. 13].
1895 *Siphonia bovista* Gein. – Geinitz, p. 353.
1895 ?*Dammarites albens* Presl. – Geinitz, p. 367.
1895 *Dammarites crassipes* Göpp. – Geinitz, p. 367.
1900 *Carpolithes vyšerovicensis* m. – Bayer, p. 47, fig. 15.
1974 *Dammarites albens* Presl. – Hluštík, p. 50, pl. 1, figs 1–4, pls 2–8.
1981 *Dammarites albens* Presl *in* Sternberg 1838. – Givulescu, p. 159, pls 1, 2.
2010 *Dammarites albens* Presl *in* Sternberg. – Kvaček & Lobitzer, p. 131, figs 1–4.
2018 *Dammarites albens*. – Niebuhr, pl. 1, fig. a.

Type. – The holotype of *Dammarites albens* was first described as a female conifer cone (Presl *in* Sternberg 1838). Velenovský (1885) saw actually leave bases and interpreted it as a dwarf stem. Knobloch (1973) was of the same opinion. Hluštík (1974) proved the connection of the stem and leaves earlier described as *Krannera mirabilis* Velenovský, 1885. These facts were clarified by Kvaček (*e.g*. in Uličný *et al*. 1997, Kvaček 1998, Kvaček & Lobitzer 2010).

Preservation form *Siphonia bovista* Gein. (acc. to Geinitz)
[syn. smooth plant bodies of *D. albens*]
Figures 1–3

non 1826 *Achilleum fungiforme* nobis. – Goldfuss, p. 1, pl. 1,fig. 3.
1842 *Achilleum fungiforme* Goldf. – Geinitz, p. 96.
1849 *Achilleum fungiforme* Goldf. – Geinitz, p. 264.
*1871 *Siphonia bovista* Gein.; Geinitz, p. I.40, pl. I.10, figs 5, 6.
1878 *Siphonia bovista* Gein. – Zittel, p. 143 [= Geinitz 1871, pl. I.10, figs 5, 6].
non 1884 ?*Siphonia bovista* Gein. – Počta, p. 33, fig. 18.
1895 *Siphonia bovista* Gein. – Geinitz, p. 353.
non 1911 *Siphonia bovista* Gein. – Frič, p. 81, fig. 352 [= Počta 1884, fig. 18].

Table 1. Dimensions of smooth plant bodies of *Dammarites albens* Presl *in* Sternberg, 1838 = preservation form *Siphonia bovista* Gein. (acc. to Geinitz).

MMG specimen	plant body / **height** (mm)	stalk opening / **length** (mm)	peculiarities	locality
PZ-SaK 651 (Figs 1, 2A)	52 × 38 = ⌀ 45 / 50	22 × 16 = ⌀ 19 / 3	depression in opposite to the stalk, imprints of organic tissue on surface	Bannewitz-Welschhufe
PZ-SaK 652 (Fig. 3G)	44 × 30 = ⌀ 37 / 37	18 × 13 = ⌀ 15.5 / 2		Bannewitz-Welschhufe
PZ-SaK 653a (Fig. 3B)	50 × 34 = ⌀ 42 / 50	20 × 18 = ⌀ 19 / –	vertically cut, imprints of organic tissue on surface	Bannewitz-Welschhufe
PZ-SaK 653b (Fig. 3D)	44 × 29 = ⌀ 36.5 / 49	18 × 16 = ⌀ 17 / 5		Bannewitz-Welschhufe
PZ-SaK 653c	62 × 50 = ⌀ 56 / 45	20 × 17 = ⌀ 18.5 / 1	imprints of organic tissue on surface	Bannewitz-Welschhufe
PZ-SaK 653d (Fig. 3H)	53 × 27= ⌀ 40 / 51	18 × 10 = ⌀ 14 / 2	with furrows and grooves, coal matter on surface	Bannewitz-Welschhufe
PZ-SaK 653e	65 × 64 = ⌀ 64.5 / 30	–	strong compressed vertically, not typical	Bannewitz-Welschhufe
PZ-SaK 5659a (Fig. 2F)	60 × 37 = ⌀ 48.5 / 60	22 × 12 = ⌀ 17 / –	imprints of organic tissue on surface	Bannewitz-Welschhufe
PZ-SaK 5659b (Fig. 2C)	>47 × 41 = ⌀ <44 / 30	18 × 15 = ⌀ 16.5 / 1	imprints of organic tissue on surface	Bannewitz-Prinzenhöhe
PZ-SaK 545a (Fig. 3E)	53 × 40 = ⌀ 46.5 / 42	21 × 16 = ⌀ 18.5 / 5		Bannewitz-Prinzenhöhe
PZ-SaK 545b (Fig. 2G)	43 × 26 = ⌀ 34.5 / 3	16 × 12 = ⌀ 14 / 3	with furrows and grooves	Bannewitz-Prinzenhöhe
PZ-SaK 529a (Fig. 2D)	61 × 44 = ⌀ 52.5 / 60	22 × 19 = ⌀ 20.5 / 3	largest specimen, very well preserved and typical	Bannewitz-Goldene Höhe
PZ-SaK 529b (Fig. 2E)	50 × 37 = ⌀ 39 / 52	17 × 16 = ⌀ 16.5 / 6		Bannewitz-Goldene Höhe
PZ-SaK 529c (Fig. 3F)	59 × 38 = ⌀ 48.5 / 62	20 × 14 = ⌀ 17 / 3	imprints of organic tissue on surface	Bannewitz-Goldene Höhe
PZ-SaK 529d (Fig. 3C)	48 × 30 = ⌀ 39 / 61	18 × 10 = ⌀ 14 / 1		Bannewitz-Goldene Höhe
PZ-SaK 196 (Fig. 3A)	54 × 32 = ⌀ 43 / 45	18 × 14 = ⌀ 16 / 8	with furrows and grooves, large stalk	Bannewitz

Dimensions. – See Tab. 1.

Description. – Preserved as sandstone casts (Fig. 3B1), mostly laterally flattened to different degrees. The outline is globular (Figs 2A, E, F; 3B, G, H) to egg-shaped with the largest diameter related in the lower third of the specimens (Figs 2D; 3D, F). Assuming that the specimens primary have had a round cross-section before compaction the maximum diameter is 52.5 mm, the maximum height is 62 mm, and the maximum diameter of the stalk opening

Figure 2. Smooth plant bodies of *Dammarites albens* Presl *in* Sternberg = preservation form *Siphonia bovista* Gein. (acc. to Geinitz), lower Upper Cenomanian Unterquader of the Oberhäslich Formation, Saxony; ×1; A – MMG: PZ-SaK 651, two lateral (A1, A2), top (A3) and stalk (A4) views, the only specimen with a depression opposite to the stalk, Bannewitz-Welschhufe, original of Geinitz (1871, pl. I.10, figs 5, 6) and holotype of this species name; B – original label of H.B. Geinitz for MMG: PZ-SaK 651; C – MMG: PZ-SaK 5659b, stalk view with deep furrows, Bannewitz-Prinzenhöhe; D – MMG: PZ-SaK 529a, two lateral (D2, D3) and stalk (D1) views, Bannewitz-Goldene Höhe; E – MMG: PZ-SaK 529b, lateral (E2) and stalk (E1) views, Bannewitz-Prinzenhöhe; F – MMG: PZ-SaK 5659a, lateral view, stalk not preserved, Bannewitz-Welschhufe; G – MMG: PZ-SaK 545b, lateral view with bulges and grooves on the surface, Bannewitz-Goldene Höhe.


A1
A2
A3
A4
10 mm
Siphonia bervista
(Orig. v. Gein.) Gein.
Unt. Qu. Welschhufa
N. 1.
B
C
D1
D2
D3
E1
E2
F
G

is 20.5 mm (Tab. 1). In general, the specimens have smooth surfaces (Figs 2D2, D3, E2; 3B2, C, D1, F, G1). However, some of them bear some weak furrows and grooves (Figs 2A2, F, G; 3A, H), MMG: PZ-SaK 545b (Fig. 2G) additionally has unequal bulges. The stalk is short (maximal 8 mm long), rounded and weakly conical, and appears from a deep depression. The edge around the stalk depression is bent inwards and folded (Figs 2A4, C, D1; 3A2, D2, E, G2). This basal indented area around the short stalk distinguishes "*Siphonia bovista* Gein." from all Cretaceous sponges of Saxony.

Specimen MMG: PZ-SaK 651 (Fig. 2A), the original von "*Siphonia bovista* Gein." of Geinitz (1871, pl. 10, figs 5, 6; refigured here in Fig. 1), is the only specimen with a depression in opposite position to the stalk (Fig. 2A2, A3), and very likely the reason for Geinitz' determination as a sponge. However, none of the specimens have an opening at the top, which could interpret as an osculum of a sponge; furthermore, a large central cavity (spongocoel), eponymous for the genus *Siphonia* Goldfuss, was not found. The depression in opposite of the stalk is not a characteristical feature of the specimens lumped in the species name "*Siphonia bovista* Gein."; the figured specimen of Geinitz (1871) is unique.

The networks on the surface of some specimens (Figs 2A2, F; 3A1, B2, F) are either imprints of organic tissue or probably the result of wood borings in the sheltered inner parts of the cone-like plant bodies. Specimen MG: PZ-SaK 653d (Fig. 3H) has preserved coal matter on its surface which is typical for drift wood found in quader sandstones (see Niebuhr & Wilmsen 2016, fig. 23i, j).

Remarks. – Taxonomic comments on the species name *Siphonia bovista* Gein.: Zittel (1878) only noted the figured specimen of Geinitz (1871, pl. I.10, figs 5, 6). Počta (1884) placed a question mark before the species name, because his single *Siphonia bovista* Gein. from the Upper Cenomanian Peruc-Korycany Formation of Bohemia (refigured by Frič 1911, fig. 352) differs from the Geinitz' specimens "by smaller dimensions, peculiar nature of the surface and by the absence of the flat hollow at the vertex" [in German: durch kleinere Dimensionen, eigenthümliche Beschaffenheit der Oberfläche und durch das Fehlen der flachen Aushöhlung am Scheitel (Počta 1884, p. 34, fig. 18)]. A stalk is also missing in the Bohemian specimen, it is "grown with short, thin roots" [in German: unten mit kurzen, dünnen Wurzeln angewachsen]. According to Počta's description (1884), the Bohemian specimen is not "*S. bovista*" in the sense of Geinitz (1871), but a "real" lithistid sponge probably of the genus *Siphonia* Goldfuss (which now needs a new species name).

Furthermore, Geinitz (1843, pl. 6, figs 14, 15; 1871, pl. I.6, fig. 2) figured a single find from the Ratssteinbruch in Dresden-Dölzschen [*Tragos stellatum* Goldf. = *Stellispongia* (*Asterospongia*) *Michelini* Gein. from the *plenus* Pläner of the upper Upper Cenomanian Dölzschen Formation] which looks similar to "*S. bovista*". However, the original in the palaeozoological collection (MMG: PZ-SaK 776) likewise misses the characteristic inwardly arched area around the short stalk. Thus, the Dresden specimen is in fact closely related to the Czech sponge specimen of Počta (1884).

After introduction by Geinitz (1871), the species name *Siphonia bovista* Gein. was no longer mentioned in the literature, and further findings were not made public. The species name *S. bovista,* introduced for a siliceous sponge, got lost (*nomen oblitum*, acc. Chapter 6, Article 23.9.1.1 of the ICZN 2012) and the Saxonian specimens disappeared from the focus of interest for nearly 150 years.

Preservation form ?*Dammarites albens* Presl (acc. to Geinitz)
[syn. transition between smooth and cone-like plant bodies of *D. albens*]
Figure 4

1849 ?*Dammarites albens* Presl, Sternb. – Geinitz, p. 274.
1895 ?*Dammarites albens* Presl – Geinitz, p. 367.

Dimensions. – See Tab. 2.

Description. – Preserved as sandstone cast (Fig. 4A), flattened laterally. The outline is rounded. At one side, remains of rhombic flat scale-like projections, 3 × 5 mm in size, are poorly preserved, maybe representing the leaf bases (Fig. 4A1). At the other side, some small aligned pits, *ca*. 3 mm in diameter, are visible (Fig. 4A3, A4), similar to those in the specimen figured by Hluštík (1974, pl. 6, fig. 1).

Figure 3. Smooth plant bodies of *Dammarites albens* Presl *in* Sternberg = preservation form *Siphonia bovista* Gein. (acc. to Geinitz), Upper Cenomanian Unterquader of the Oberhäslich Formation, Saxony; ×1; A – MMG: PZ-SaK 196, lateral (A1) and stalk (A2) views, Bannewitz; B – MMG: PZ-SaK 653a, vertically sawed, lateral (B2) and internal (B1) views, Bannewitz-Welschhufe; C – MMG: PZ-SaK 529d, lateral view with stalk visible, Bannewitz-Goldene Höhe; D – MMG: PZ-SaK 653b, lateral (C1) and stalk (C2) views, Bannewitz-Welschhufe; E – MMG: PZ-SaK 545a, stalk view¸ Bannewitz-Prinzenhöhe; F – MMG: PZ-SaK 529c, lateral view with network on the surface, Bannewitz-Goldene Höhe; G – MMG: PZ-SaK 652, lateral (G1) and stalk (G2) views, Bannewitz-Welschhufe; H – MMG: PZ-653d, lateral view with coal matter at the surface, Bannewitz-Welschhufe; I – original label of H.B. Geinitz for MMG: PZ-SaK 5659a, b; J – original label of H.B. Geinitz for MMG: PZ-SaK 545a, b.


A1
B1
B2
A2
C
D1
E
D2
G1
F
G2
H
Siphonia bovista
Quin.
U. Qu.
Wilschhusa
N. 3.
u. Cunnersdorf.
10 mm
I
J
Siphonia bovista
Quin.
U. Qu.
Cunnersdorf
N. 2.
a. d. Primkenhöhe

Figure 4. *Dammarites albens* Presl *in* Sternberg = preservation form ?*Dammarites albens* Presl (acc. to Geinitz), lower Upper Cenomanian Unterquader of the Oberhäslich Formation at Bannewitz-Welschhufe, Saxony; A – MMG: PB-SaK 47, two lateral (A1, A3) and stalk (A2) views, ×1, A4 detail of the pits, width 25 mm; B – original label of H.B. Geinitz for MMG: PB-SaK 47.

Table 2. Dimensions of *Dammarites albens* Presl *in* Sternberg, 1838 = preservation form ?*Dammarites albens* Presl (acc. to Geinitz).

MMG specimen	**plant body / height** (mm)	**stalk opening / length** (mm)	**peculiarities**	**locality**
PB-Sak 47 (Fig. 4)	46 × 31 = ⌀ 38.5 / 44	16 × >10 = ⌀ >12 / 6	leaf bases and small pits on parts of the surface	Bannewitz-Welschhufe

Dammarites albens Presl *in* Sternberg, 1838
[syn. cone-like plant bodies and leaves of *D. albens*]
Figure 5

*1838 *Dammarites albens* Presl; Sternberg, p. 203, pl. 52, figs 11, 12.
1842 *Dammarites crassipes* Goepp.; Göppert, p. 122, pl. 53, fig. 3.
1846 *Dammara albens* Presl. – Reuss, p. 92, pl. 49, figs 6–8.
1847 *Dammarites albens* Presl. – Göppert, p. 365.
1847 *Dammarites crassipes* Göpp. – Göppert, p. 365.
1849 *Dammarites albens* Presl, Sternb. – Geinitz, p. 274.
1849 *Dammarites crassipes* Göpp. – Geinitz, p. 274.
1885 *Krannera mirabilis* Corda in lit. – Velenovský, p. 1 (*partim*), pl. 1, figs 1–7; pl. 4, figs 1, 2, 4, 7–9 [*non* pl. 1, figs 10–13, 18, ?pl. 3, fig. 13].
1895 *Dammarites crassipes* Göpp. – Geinitz, p. 367.
1900 *Carpolithes vyšerovicensis* m. – Bayer, p. 47, fig. 15.
1974 *Dammarites albens* Presl. – Hluštík, p. 50, pl. 1, figs 1–4, pls 2–8 [with full synonymy and taxonomic discussion].
1981 *Dammarites albens* Presl *in* Sternberg 1838. – Givulescu, p. 159, pls 1, 2.
2010 *Dammarites albens* Presl *in* Sternberg. – Kvaček & Lobitzer, p. 131, figs 1–4.
2018 *Dammarites albens*. – Niebuhr, pl. 1, fig. a.

Dimensions. – See Tab. 3.

Table 3. Dimensions of cone-like plant bodies of *Dammarites albens* Presl *in* Sternberg, 1838.

MMG specimen	**plant body / height** (mm)	**stalk opening / length** (mm)	**peculiarities**	**locality**
PB-CsK 221 (Fig. 5A)	75 × 40 = ⌀ 57.5 / 40	22 × 13 = ⌀ 17.5 / 3	very well preserved and typical	Králův Dvůr, CZ
PB-PnK 45 (Fig. 5D)	56 × 50 = ⌀ 53 / 28	17 × 16 = ⌀ 16.5 / 10	gypsum cast of a typical specimen	Mieroszów-Łączna, PN

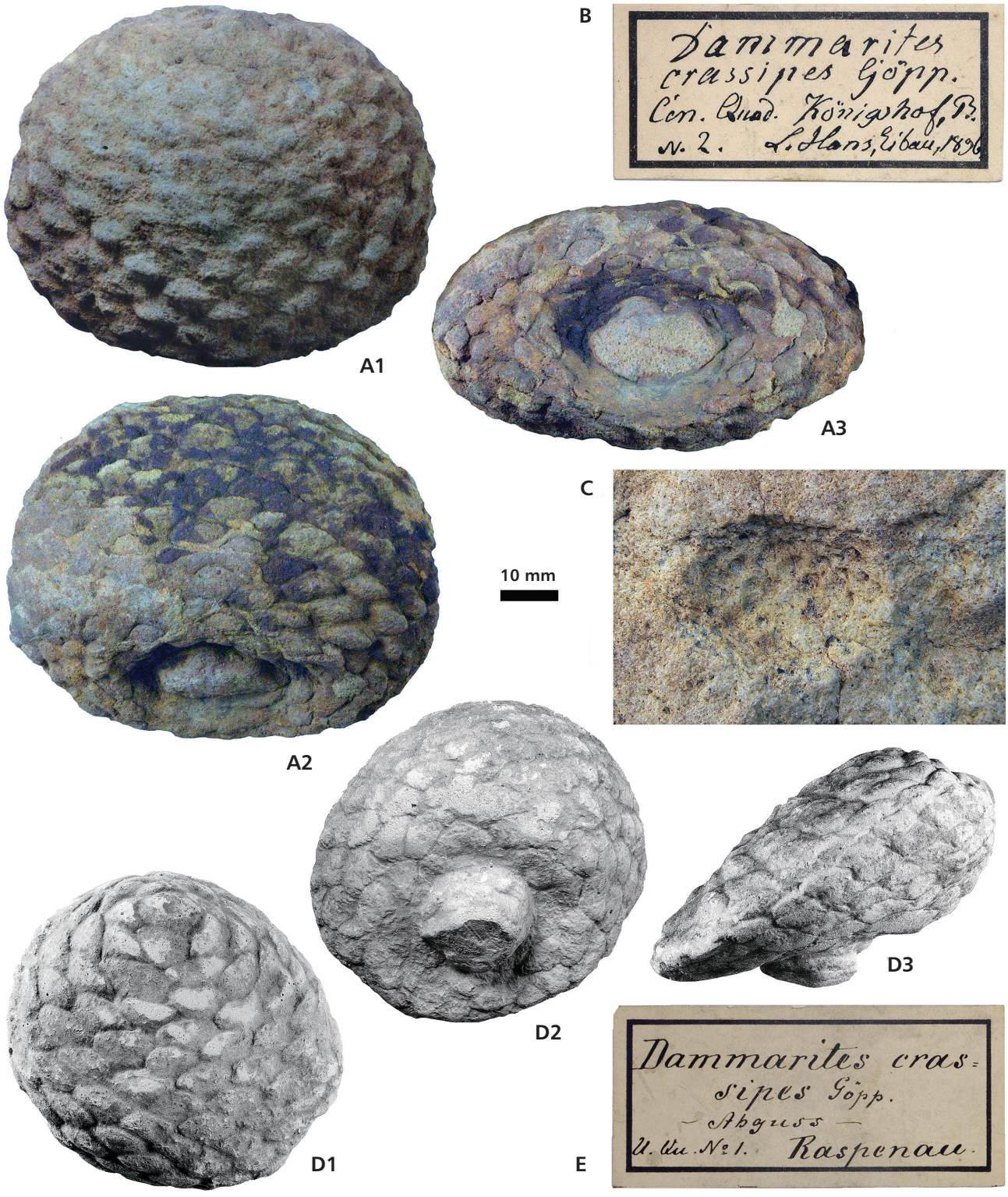

Figure 5. Cone-like plant bodies of *Dammarites albens* Presl *in* Sternberg; ×1; A – MMG: PB-CsK 221, two lateral (A1, A2) and stalk (A3) views, Korycany Member of the lower Upper Cenomanian Peruc-Korycany Formation at Králův Dvůr (in German: "Königshof"), Czech Republic; B – original label of H.B. Geinitz for MMG: PB-CzK 221; C – MWL: III 4497, imprint of the outer surface, lower Upper Cenomanian Unterquader of the Oberhäslich Formation, boulder in Cenozoic river gravels on the Lusatian Massif, Saxony, original of Niebuhr (2018); D – MMG: PB-PnK 45, gypsum cast; top (D1), stalk (D2) and lateral (D3) views, original from the Middle–Upper Cenomanian Glauconitic Sandstone at Mieroszów-Łączna (in German: Raspenau), Poland; E – original label of H.B. Geinitz for MMG: PB-PnK 45.

Description. – MMG: PB-CzK 221 is preserved as a composite sandstone cast (Fig. 5A), the cone-like plant body is flattened laterally. The surface is covered by spirally arranged rhombic flat scale-like projections. The stalk is situated in a rounded depression. Specimen MMG: PB-CsK 221 resembles the holotype of *Dammarites albens* Presl *in* Sternberg, refigured by Reuss (1846, pl. 49, figs 6–8) and Hluštík (1974, pl. 1, figs 1, 2). Specimen MMG: PB-PnK 45 is a gypsum cast of a small, typical cone-like plant body. It was transferred to the "Petrefacten-Sammlung" in 1869 by "Oberamtmann Lachmann" (Geinitz 1895, p. 367).

In the Museum of West Lusatia (MWL) in Kamenz, Saxony, an imprint of a cone-like plant body from the Oberhäslich Formation is housed (MWL: III 4497) which resembles the outer surface of *D. albens* found in Bohemia (Fig. 5C). This proves that the preservation form as cone-like plant body also occurred in the Saxonian Cretaceous.

Discussion

The dwarf gymnosperm *Dammarites albens* Presl *in* Sternberg, probably assigned to the family Araucariaceae (*cf*. Barale 1992), is considered as a salt-tolerant (halophytic) plant (Uličný *et al.* 1997, Kvaček & Lobitzer 2010). Possible habitats of the living plant are discussed and shown by Hluštík (1977, p. 361, fig. 2). The cone-like plant bodies are known from several localities of the Bohemian and Intrasudetic Cretaceous basins (BCB and ICB on Fig. 6A, B), always associated with or embedded in marine sediments. The up to 150 mm long lanceolate leaves, first described as *Krannera mirabilis* (Velenovský 1885) and figured by Hluštík (1974, pl. 6, fig. 1) in natural position at the clinging leaf bases of a cone-like plant body of *D. albens*, are found usually in marine sandstones (Frič & Bayer 1901, Givulescu 1981, Kvaček & Lobitzer 2010). All *Dammarites albens* Presl *in* Sternberg, 1838 of the Czech Republic (cone-like plant bodies as well as leaves) were found in lowermost marine sandstones of the BCB, the time-equivalent Korycany Member of the Peruc-Korycany Formation, overlying the fluviatile to brackish Peruc Member. The *D. albens* specimens from the ISCB in Poland near Chełmsko Śląskie (in German: Schömberg) – *Dammarites crassipes* Goepp. found by Ernst von Otto (Göppert 1842) – as well as the original of MMG: PnK 45 from Mieroszów-Łączna (in German: Raspenau; Geinitz 1895, p. 367), only *ca*. 3 km apart, likewise appear in the lowermost marine sandstone of Middle–Upper Cenomanian age (Glauconitic Sandstone), overlying alluvial sediments (Radwański 1975, Walaszczyk 2008). The same is true for the "sponge *S. bovista*" from Saxony (Geinitz 1871): all "*Siphonia bovista* Gein." were found in the lowermost marine strata of the Saxonian Cretaceous Basin (SCB on Fig. 6A, B), the lower Upper Cenomanian Unterquader of the Oberhäslich Formation, overlying the brackish Wurmsandstein of the uppermost Niederschöna Formation (1 in Fig. 6B). Environment and sedimentary conditions as well as stratigraphic positions of the preservation form *Siphonia bovista* Gein. and *Dammarites albens* Presl *in* Sternberg of the Saxonian, Bohemian and Intrasudetic Cretaceous basins of Saxony, the Czech Republic and Poland (Fig. 6A, B) are thus identical.

In Austria, lanceolate leaves of *D. albens* appear in the Upper Turonian shallow marine Streiteck Formation of the lower Gosau Group, likewise overlying continental strata (Wagreich 2003, Kvaček & Lobitzer 2010), and in the eastern Carpathians of Romania they were found in Mid-Cenomanian marls (Givulescu 1981). The minimum stratigraphic and palaeogeographic range of the dwarf gymnosperm, therefore, is (Middle) Cenomanian up to the Turonian–Coniacian boundary interval of Central Europe (Poland, Czech Republic, eastern Romania, Austria, and – formerly described as "*S. bovista*" – Saxony in eastern Germany; Göppert 1842, Geinitz 1895, Hluštík 1974, Givulescu 1981, Kvaček & Lobitzer 2010, Niebuhr 2018, this paper) between the 32 and 40 degree of northern palaeo-latitudes (acc. Philip & Floquet 2000). Northern Bavaria was located during Cenomanian–Turonian times within these palaeo-latitudes, too, but no smooth or cone-like plant bodies of *Dammarites albens* have been found yet in the lower Upper Cretaceous strata of the Danubian Cretaceous Basin (DCB on Fig. 6A) (written messages 03/2018, M. Krings and M. Nose, Bavarian State Collection of Palaeontology and Geology, Munich) although the same environments were present there (Niebuhr *et al.* 2009).

Most specimens of the smooth preservation form *S. bovista* are smaller than those of the cone-like plant bodies (comp. Tabs 1–3); likewise, smooth and cone-like plant bodies have the same proportions, supporting their interpretation as simple inner and composite moulds of the same organism *Dammarites albens*. Apart from the globular to egg-shape outline, the size ratios and similar lateral flattening due to compaction, for a specific feature of the preservation form *Siphonia bovista* Gein. and ?*Dammarites albens* Presl (acc. to Geinitz) is the conspicuous inward-arching of the basal area around the at maximum 10 mm short stalk (*e.g.* Figs 2A4, D1; 3E, D2 comp. 4A2). Specimen MMG: PB-SaK 47 (Fig. 4A) is here, so to speak, the missing link: parts of its surface saved remains of (poorly preserved) rhombic flat scale-like projections of *D. albens*, representing woody leaf bases, and a few mm-sized pits; other parts of the surface are smooth, and the basal area around the stalk which is arched inwardly is similar as in "*S. bovista*". Hluštík (1974, pl. 4, fig. 5, pl. 5, fig. 3) shows the same arrangement of the basal area around the stalk in *Dammarites albens* Presl

in Sternberg, also visible in MMG: PB-CzK 221 (Fig. 5A2, A3) and MMG: PB-PnK 45 (Fig. 5D2, D3).

Velenovský (1885, pl. 1, figs 10–13, 18) figured two specimens which have smooth surfaces such as "*Siphonia bovista* Gein.", but the characteristic depression of the stalk opening is missing at his "fruit remains". Even Hluštík (1974) did not considered their taxonomic position to be secure and, therefore, excluded them from the synonymy of *Dammarites albens* Presl *in* Sternberg. However, he pointed out that hardly anything is known about the internal structures of the cone-like plant bodies.

The cone-like plant body was at least partly woody (Hluštík 1974), especially the spirally arranged rhombic, flat, scale-like projections on the outer surface of

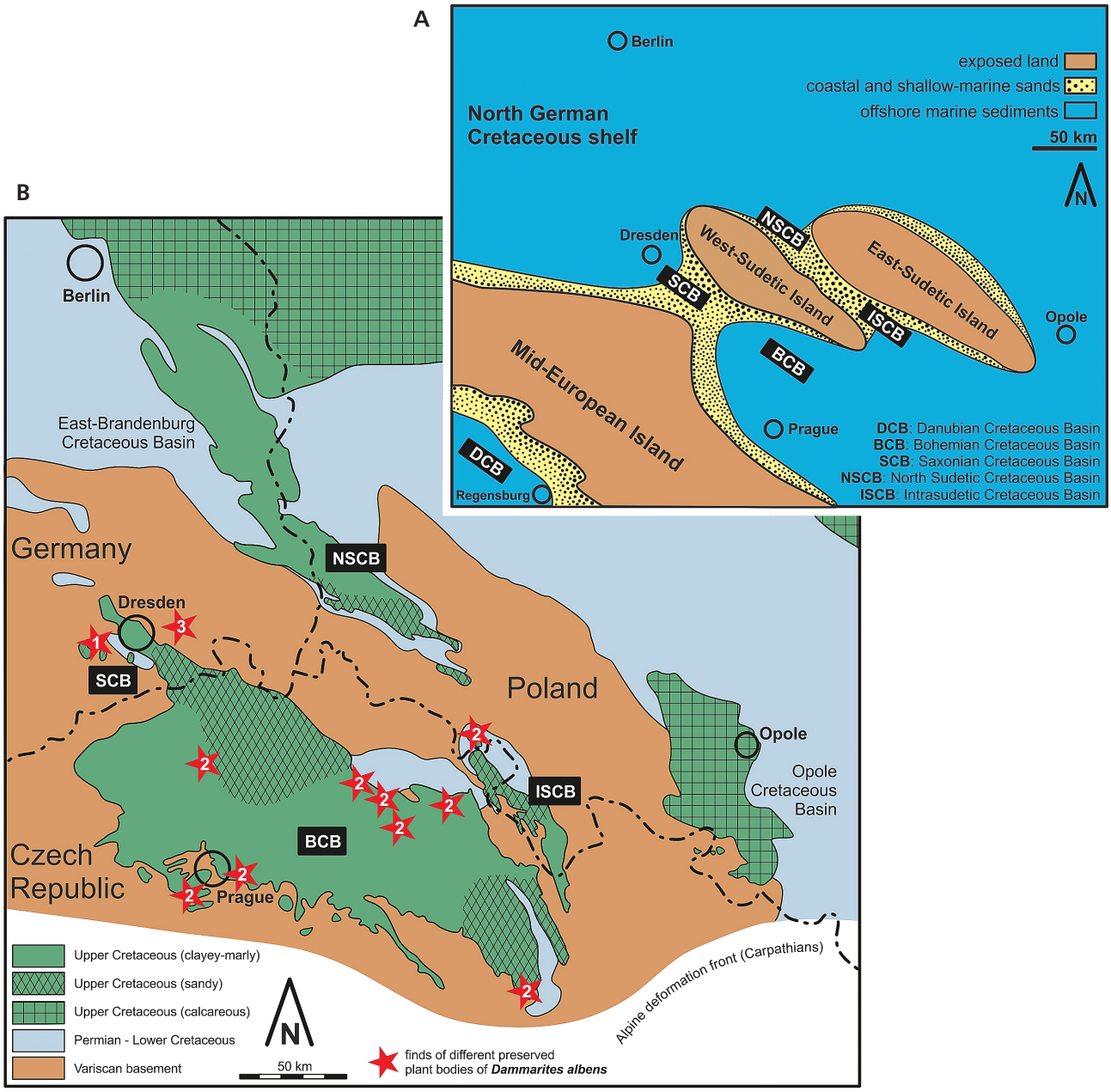

Figure 6. A – Upper Cenomanian to Lower Coniacian palaeogeography with position of subbasins around the Mid-European Island (modified after Voigt 1994); B – uncovered geological map of the border triangle of Germany, Poland and the Czech Republic (simplified after Uličný *et al.* 2008; Voigt 2009, 2015); asterisks mark occurrences of differently preserved plant bodies of *Dammarites albens* Presl *in* Sternberg as (1) smooth internal and (2) cone-like composite sandstone moulds as well as (3) external imprints in Upper Cenomanian strata (acc. Göppert 1842; Geinitz 1871, 1895; Hluštík 1974; Niebuhr 2018; this paper).

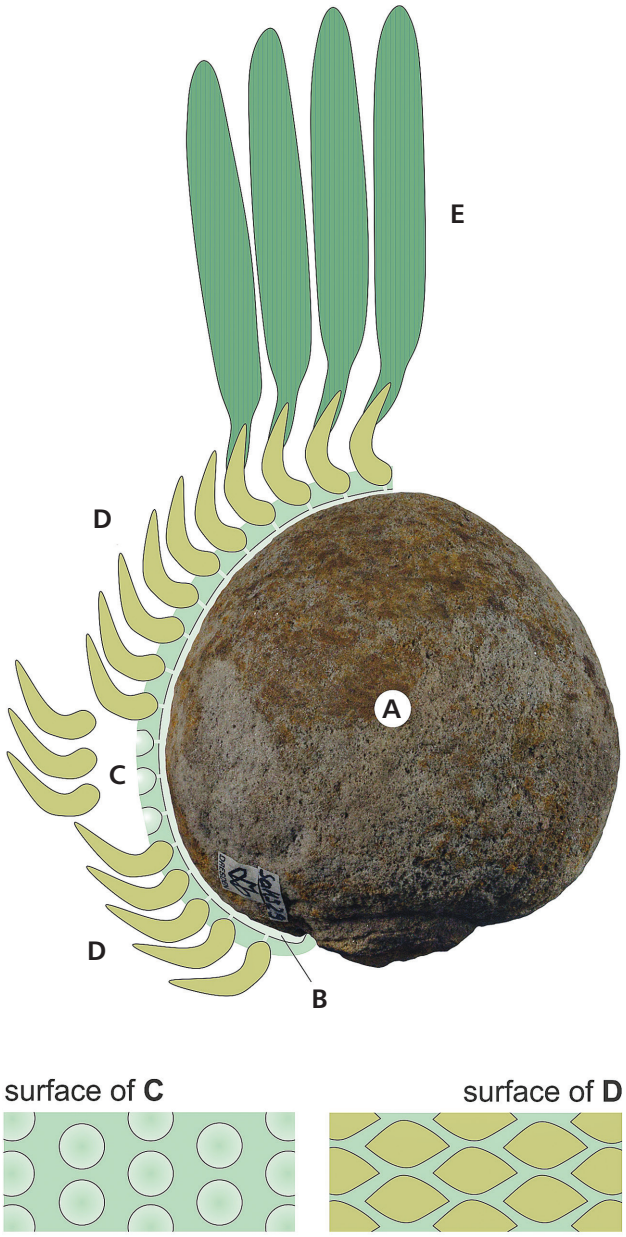

Figure 7. Different preservation types in *Dammarites albens* Presl *in* Sternberg, 1838 (not to scale); A – preservation form *Siphonia bovista* Gein. (acc. to Geinitz), simple internal mould with smooth surface, infilling of sand while hard, lignified tissues of the outer cortex are still preserved; B – soft, non-lignified layer; C – woody layer with pits remaining after leaf bases have fallen off, "sandstone cast with destroyed surface" (acc. to Hluštík 1974, pl. 6, fig. 1), resembles preservation form ?*Dammarites albens* Presl (acc. Geinitz; *e.g.* MMG: PB-SaK 47 of Fig. 4); D – classic preservation of the cone-like plant bodies in the Bohemian and Intrasudetic Cretaceous basins (*e.g.* MMG: PB-CsK 221 and MMG: PB-PnK 45 of Fig. 5), composite mould with clinging leaf bases, infilling of sand after nearly all of the organic matter decayed; E – completely preserved cone-like plant body with leaves in natural position at the clinging leaf bases (acc. Hluštík 1974, pl. 4, fig. 1); rarely realized.

D. albens and the layer with their basal attachments. After burial they formed a stable, slow-decaying cortex while the internal non-lignified, soft and moist organic fabric rapidly decayed and sand infilled the evolving cavity – "*Siphonia bovista* Gein." was formed as a smooth internal sandstone mould of the cone-like plant body (A in Fig. 7). It is likely that the small pits on the surface of ?*Dammarites albens* Presl (acc. to Geinitz) represent the basal braces of the fallen woody leaf bases rather than the area between them (*cf.* Hluštík 1974). The preservation without leaf bases but small pits on the surface (C in Fig. 7; "destroyed surface" of Hluštík 1974, pl. 6, fig. 1) is rare. Non-lignified organic tissues (B in Fig. 7) must have separated the typical appearance of "*S. bovista* Gein." from the woody attachment layer of the leaf bases, since all *bovista*-like internal moulds have primarily smooth surfaces without pits. The most common stage in preservation of *Dammarites albens* Presl *in* Sternberg are the classic cone-like plant bodies with fossilized leaf bases, representing the outer surface morphology superimposed onto the composite sandstone moulds (D in Fig. 7). However, Hluštík (1974, pl. 4, fig. 1) figured a specimen with some leaves preserved in natural position at the leaf bases (*e.g.* E in Fig. 7). *Dammarites albens* in these kinds of preservation were not found in Saxony and outer imprints in quartz sandstones (Fig. 5C) are very rare; neither in the palaeobotanical nor palaeozoological collection of the MMG, a single find exists.

The cone-like plant bodies of *Dammarites albens* look similar to those of the famous *Araucaria mirabilis* (Spegazzini) from the Upper Jurassic of Argentina. Both species have a globular to egg-shape outline, rhombic flat scale-like projections on the outer surface, and a basal indented area around the stalk. Furthermore, vertically sawed specimens of *A. mirabilis* show a central inner area well separated by soft tissues from the outer leaf bases that could correspond to the smooth inner fillings of *D. albens*, respectively, the "sponge *Siphonia bovista* Gein." of Geinitz (1871) (see for example: *www.fossilmuseum.net/plantfossils/Araucaria-mirabilis/Araucaria.htm; www.mineralienatlas.de/lexikon/index.php/FossilData?fossil=Araucaria%20mirabilis*). Whether the plant body of *D. albens* is a real cone or an independent plant is still unclear. However, that the preservation form *S. bovista* is the simple smooth internal sandstone mould of the cone-like *D. albens* (a composite sandstone mould), and therefore, the same organism in different preservation, is hardly to doubt. All specimens of the smooth preservation form *Siphonia bovista* Gein. are hereby integrated into the species concept of *Dammarites albens* Presl *in* Sternberg. The sponge species name *Siphonia bovista* Geinitz, 1871 is a rejected name (acc. Chapter 6, Article 23.12.1 of the ICZN 2012) and replaced by *Dammarites albens* Presl *in* Sternberg, 1838.

Conclusions

(1) Environment, sedimentary conditions and stratigraphic position of the preservation form *Siphonia bovista* Gein. and *Dammarites albens* Presl *in* Sternberg are identical.

(2) All "*S. bovista* Gein." of the Saxonian Cretaceous Basin (Germany) as well as all *D. albens* Presl *in* Sternberg of the Bohemian and Intrasudetic Cretaceous basins (Czech Republic and Poland), cone-like plant bodies as well as lanceolate leaves, were found in the lowermost Cretaceous marine sandstones (Middle–Upper Cenomanian), overlying fluvial to brackish strata.

(3) Typical for both, "*S. bovista*" and the cone-like plant bodies of *D. albens*, are the globular to egg-shape outline and the basal area which is indented around the stalk.

(4) "*S. bovista*" has smooth surfaces and represents the simple internal sandstone mould of the woody outer parts of *D. albens*, the cone-like plant bodies of which representing the composite sandstone moulds.

(5) The alleged sponge *S. bovista* Gein. and the cone-like plant fossil *D. albens* Presl *in* Sternberg belong to the same organism, just representing different preservational forms.

(6) The reinterpretation of "*S. bovista* Gein." provides the first proof of *D. albens* Presl *in* Sternberg for Germany.

(7) The species name *Siphonia bovista* Geinitz, 1871, introduced for a siliceous sponge, is a rejected name and hereby replaced by *Dammarites albens* Presl *in* Sternberg, 1838.

(8) The minimum stratigraphic and palaeogeographic range of the salt-tolerant (halophytic) dwarf gymnosperm *D. albens* (including smooth and cone-like plant bodies as well as leaves) is (Middle) Cenomanian up to the Turonian–Coniacian boundary interval of Europe between the 32 and 40 degree of northern palaeo-latitudes.

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