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Acta Palaeobotanica 59(2): 351–365, 2019
DOI: 10.2478/acpa-2019-0016

e-ISSN 2082-0259
ISSN 0001-6594

Nomenclatural novelties in the fossil genus *Spinopalmoxylon* (Arecaceae) from the Central European Oligocene and Miocene: A whole-plant concept for *Spinopalmoxylon daemonorops*

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Received 27 May 2019; accepted for publication 4 September 2019

ABSTRACT. The fossil genus *Spinopalmoxylon* from the Central European Oligocene and Miocene comprises three species: *S. daemonorops*, *S. parvifructum* sp. nov. and *S. cicatricosum* sp. nov. Here the species *S. daemonorops* is amended and its name is proposed as nomen conservandum against *S. teutonicum*. A series of synonyms is provided. In addition, two new species are described from late Oligocene deposits of Niederpleis: *S. parvifructum* sp. nov. (pistillate inflorescence, fruits, and seeds) and *S. cicatricosum* sp. nov. (staminate inflorescence and pollen). These three *Spinopalmoxylon* species together are proposed as a whole plant.

Floras with the *Spinopalmoxylon* palm reflect the vegetation of the near-shore fluvial floodplain and backswamp environments of the late Oligocene (Chattian) Köln Formation (Clay 1) and early Miocene (Burdigalian) Ville Formation (Seam 6A) in the northern foreland of the Siebengebirge Volcanic Field near Bonn, at the southeastern margin of the Lower Rhine Basin.

KEYWORDS: fossil Arecaceae, *Spinopalmoxylon*, whole plant, Oligocene, Miocene, Lower Rhine Basin

INTRODUCTION

The here-treated calamoid palm fossil genus *Spinopalmoxylon* was introduced by Weyland et al. (1966) for morphologically and anatomically preserved stems with attached spines from the Lower Rhenish brown coal. Weyland et al. (1966: 88) designated *Palaeospathe daemonorops* Unger (1860: 9) as the type of *Spinopalmoxylon* and introduced the species *S. rhenanum* for the spiny stems. These palm remains were first mentioned in the palaeobotanical literature by Ludwig (1860, as *Chamaerops teutonica*) and by Unger (1860, as *Palaeospathe daemonorops*), who described spines and spiny leaf sheaths from Miocene brown coal deposits in Wetterau in western Germany.

MATERIAL AND METHODS

The specimens examined and described herein come from the following localities (Figs 1, 2):

1. Spines of "*Chamaerops teutonica*" (Ludwig 1860).

Locality. Germany, Hesse, Hessenbrücken at Laubach near Giessen in Wetterau.

Stratigraphy. Middle Miocene (Langhian), brown coal of intravolcanic sediment deposits.

Repository. Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (MfN), Alexander Braun collection.

2. Spiny leaf sheaths of "*Palaeospathe daemonorops*" (Unger 1860).

Locality. Germany, Hesse, Hessenbrücken at Laubach near Giessen and Bad Salzhausen near Nidda in Wetterau.

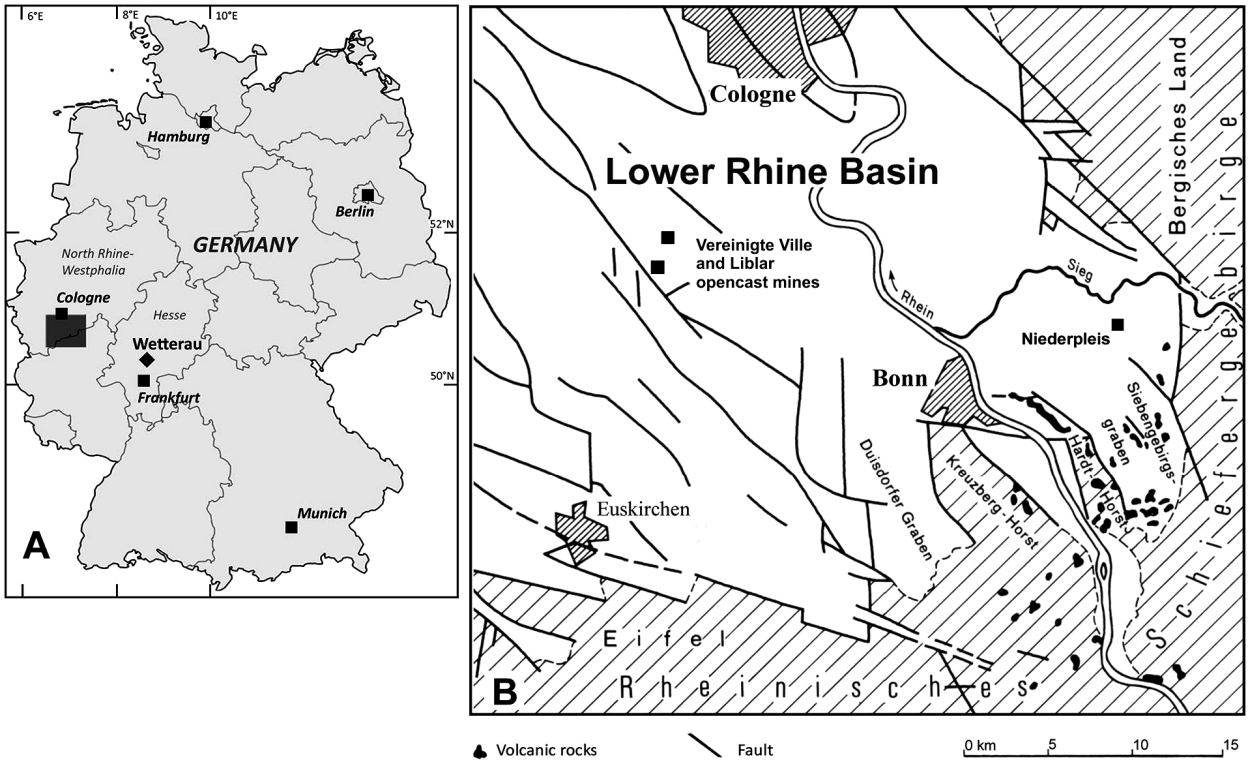

Fig. 1. Location of the study area in Germany with Wetterau in Hesse (**A**) and in the south-eastern Lower Rhine Basin in North Rhine-Westphalia (**B**)

CHRONOSTRATIGRAPHY		LITHOSTRATIGRAPHY Lower Rhine Basin		Localities
Miocene	Tortonian	**Inden Fm**	7A–7E	
	Serravallian	**Ville Formation**	6E – Garzweiler Seam	
			6D – Neurath Sand	
	Langhian		6C – Frimmersdorf Seam	
			6B – Frimmersdorf Sand	
	Burdigalian		**6A – Morken I Seam**	► **Vereinigte Ville and Liblar**
		Köln Formation	5D – Morken Sand	
			5C – Morken II Seam	
	Aquitanian		5B – Kerpen Sand	
			5A – Kerpen Seam	
		23,03 Ma	4 – Sand 4	
			3 – Clay 3 (*Unterflöz I*)	
			2 – Sand 2	
Oligocene	Chattian		**1 – Clay 1 (*Unterflöz II*)**	► **Niederpleis**
			Sand 09	
			Clay 08 (*Unterflöz III*)	
			Sand 07	
			Clay 06 (*Unterflöz IV*)	
			Sand 05	
		~~ *erosional unconformity* ~~		
		marine **Grafenberg Formation**		

Fig. 2. Stratigraphic position of the Niederpleis and Vereinigte Ville localities

Stratigraphy. Middle Miocene (Langhian), brown coal of intravolcanic sediment deposits.
Repository. Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (MfN), Rudolph Ludwig collection.

3. Spiny stems of "*Spinopalmoxylon rhenanum*" (Weyland et al. 1966).

Locality. Germany, North Rhine-Westphalia, Rhein-Erft-Kreis, former Vereinigte Ville open-cast lignite mine near Hürth-Knapsack. Geographic coordinates: 50°51′06.0″N, 6°50′12″E.

Stratigraphy. Early Miocene (Burdigalian) Ville Formation (layer Seam 6A).

This locality is the now-closed Vereinigte Ville open-cast lignite mine of the former Rheinischen Braunkohlenwerke AG mining company near Hürth, ~10 km south of Cologne. The flora of the Vereinigte Ville mine was described by Weyland et al. (1966) and Kempf (1971: 51; 1993: 570–572).

Repository. Palaeobotanical collections of the Goldfuss Museum of the Institut für Geowissenschaften at the Rheinische Friedrich-Wilhelms-Universität Bonn (inventory numbers starting with STIPB, Hermann Weyland collection). Part of the Hermann Weyland collection is stored in the palaeobotanical collection of the Institut für Geologie und Mineralogie der Universität zu Köln [GMIK].

4. Spiny stems of "*Spinopalmoxylon rhenanum*" (Weyland et al. 1966), pistillate flowers, fruits and seeds of *S. parvifructum* sp. nov., staminate flowers of *S. cicatricosum* sp. nov., and pollen.

Locality. Germany, North Rhine-Westphalia, Rhein-Sieg-Kreis, former Niederpleis clay pit near Sankt Augustin-Niederpleis. Geographic coordinates: 50°46′12.1″N, 7°13′40.5″E.

Stratigraphy. Late Oligocene (Chattian) Köln Formation (layer Clay 1).

The Niederpleis clay pit was operated in the 1960s and 1970s by the Großpeter, Lindemann & Co. mining company. The flora was described by Weyland et al. (1966: 75, 76), Kempf (1971: 49, 50; 1993: 562–566), Gregor (1986: 19–21), and Winterscheid (2006: 36, 37, 402). In 2007 the clay pit was re-opened by the Rhein-Sieg-Abfallgesellschaft company at the eastern side of the former Tonwerk Großpeter, Lindemann & Co. works, and clay was only mined for a limited time because of the sealing of a waste disposal site near Sankt Augustin-Niederpleis. The new samples were collected in June and September 2008, and in May 2009, in a clayey and coaly horizon in the upper part of the layering sequence of the pit.

Repository. The specimens described here are deposited in the palaeobotanical collections of the Goldfuss Museum of the Institut für Geowissenschaften at the Rheinischen Friedrich-Wilhelms-Universität zu Bonn (inventory numbers starting with STIPB; Maria Pingen and Heinrich Winterscheid collections). This material was collected by H.W. in the 1970s and from the mine dump by H.W. and Maria Pingen in 2008.

PHOTOGRAPHIC RECORD

SEM micrographs were taken with a CamScan MV 2300 scanning electron microscope. Morphological traits were studied and photographed using a ZEISS AXIO Zoom.V16 Digital Microscope, with the AxioCam HR R3-ZEN2pro program. Macroscopic images were made using a Nikon D3X camera (AF-S Nikkor Micro objective).

TAXONOMIC TREATMENT

Subclass MAGNOLIIDAE
Novák ex Takht. (1967: 51)

MONOCOTS (APG IV)

Order ARECALES Bromhead (1840: 333)

Family ARECACEAE
Berchtold & Presl (1820: 266), nom. cons.

Subfamily CALAMOIDEAE
Beilschmid (1833: Beil. 2, 55)

Tribus CALAMEAE
Kunth ex Lecoq & Juillet (1831: 98)

Fossil genus ***Spinopalmoxylon***
Weyland, Kilpper & Berendt (1966: 88)

Type. *Spinopalmoxylon daemonorops* (Unger) Weyland et al. (≡ *Palaeospathe daemonorops* Unger, nom. cons. prop.).

Diagnosis in protologue. "Achsen von Palmen oder Teile von ihnen, die durch ansitzende Stacheln gekennzeichnet sind." [Axes of palms or parts of them, characterized by bearing spines.] (Weyland et al. 1966: 89–90).

Emended diagnosis. Calamoid fossil palm genus with thin spiny stems, spathaceous bracts, and leaf sheaths; spines single or in groups; pistillate flowers, fruits, seeds, and staminate flowers with pollen of *Dicolpopollis kockelii* type.

Nomenclatural notes. The earlier designation of *Palaeospathe daemonorops* Unger (1860: 9–10; pl. 2, figs 9–12) as the generic type of *Spinopalmoxylon* by Weyland et al. (1966: 88) was revised by Winterscheid (2018: 224–226), because *Chamaerops teutonica* R.Ludw. (date of publication: April 1860; date reference: *Palaeontographica*, vol. 8, part 3) is the first validly published name and has priority over the later heterotypic synonym *Palaeospathe daemonorops* Unger (date of publication: September

01–10 1860; date reference: *Oesterreichische Buchhändler-Correspondenz*, no. 26, p. 145). Thus, *Chamaerops teutonica* had to be designated as the generic type of *Spinopalmoxylon*. For precise publication dates, bibliographic records and nomenclatural notes regarding the generic names *Palaeospathe* (Unger 1860), *Calamus* (Chandler 1957) and *Spinophyllum* (Huard 1967) for *Spinopalmoxylon teutonicum*, see Winterscheid (2018: 224–226). Although some later authors knew that *C. teutonica* is the older name with priority over *P. daemonorops*, they used the epithet "*daemonorops*": cf. Heer (1862), Beck (1882), Reid & Reid (1910), Kirchheimer (1931, 1933, 1937, 1938) and Kräusel & Weyland (1954). The affiliation of the palm *Palaeospathe daemonorops* to the extant genus *Calamus* L. by Chandler (1957: 88–89) is questioned by Chandler herself (cf. Winterscheid 2018: 225). Winterscheid & Doweld (2019, in press) proposed *Palaeospathe daemonorops* (*S. daemonorops*) as nomen conservandum against *Chamaerops teutonica* (*S. teutonicum*), nom. rej. prop., because the epithet "*teutonica*" has been used only twice in the palaeobotanical literature, "whereas the epithet '*daemonorops*' has been widely applied in all major works on European Cenozoic palaeofloras" (see Winterscheid & Doweld 2019, in press).

Spinopalmoxylon now contains three fossil species: *S. daemonorops* (Unger) Weyland et al. with vegetative organs, as well as *S. parvifructum* sp. nov. and *S. cicatricosum* sp. nov. for female and male reproductive organs respectively. Presumably, the species *S. daemonorops*, *S. parvifructum* and *S. cicatricosum*, described below, may form one natural species, but the different organs have not been found in organic connection.

Spinopalmoxylon daemonorops

(Unger) Weyland, Kilpper & Berendt (1966: 88), **nom. cons. prop.**, **emend**. Winterscheid, **emend. nov.**

Pl. 1, figs 1–6; Pl. 2, figs 1–6; Pl. 3, figs 1–6

Basionym. *Palaeospathe daemonorops* Unger (1860: 9, 10; pl. 2, figs 9–12), **nom. cons. prop.** – Neotype (designated by Winterscheid 2018: 227). MB.Pb.1980/0296 [illustrated in Winterscheid (2018: fig. 2A)], Pl. 1, fig. 1.

Syntypes (designated by Winterscheid 2018: 228). MB.Pb.2016/1652 [illustrated in Winterscheid (2018: fig. 2B)], MB.Pb.2016/1653, MB.Pb.2016/1654 [illustrated in Winterscheid (2018: fig. 2C)], MB.Pb.2016/1655, MB.Pb.2016/1657.

Repository. Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (MfN); Alexander Braun collection.

Locus typicus. Germany. Hesse: Hessenbrücken at Laubach near Giessen in Wetterau ["In geanthrace ad Laubach Wetteraviae", Unger (1860: 9)].

Stratum typicum. Middle Miocene (Langhian), brown coal of intravolcanic sediment deposits.

Diagnosis in protologue. "*P. Daemonorops*, spatha? plures pollices longa lataque conacea, longitudinaliter striata, aculeata, aculeis crebris seriatim in lineis oblique transversis conjunctis, compressis subulatis rectis semipollicem longis brevioribusque, simplicibus geminisque vel utplurimum trigeminis subconiventibus sursum adpressis, e cellulis pachytiehis exterioribus angustioribus interioribus latioribus conflatis saepius substantia rubra impletis.", Unger (1860: 9).

Emended diagnosis. Vegetative fossil plant parts of palms including spiny stems, spathaceous bracts, and leaf sheaths, with spines single or in groups, suggesting a relationship with genera of tribus Calameae Lecoq & Juill.

Synonymy.

≡ *Palaeospathe daemonorops* Unger; Ettingshausen (1868: 824); Engelhardt (1870: 30, 31; pl. 9, figs 2, 3).

≡ *Palmacites daemonorops* (Unger) Heer (1862: 1056–1058; pl. 55, figs 7–15; pl. 60, figs 50–53; pl. 62, figs 1–11; comb. nov.); Beck (1882: 757–760; pl. 31, figs 10–13); Reid & Reid (1910: 172; pl. 16, figs 44–49); Kirchheimer (1931: 307–311); Weyland et al. (1954: 101); Kräusel & Weyland (1954: 115–117; pl. 20, figs 5, 6).

≡ *Palmoxylon daemonorops* (Unger) Kirchheimer (1933: 139; comb. nov.); Kirchheimer (1937: 916; 1938: 357, 358).

≡ *Calamus daemonorops* (Unger) M.Chandler (1957: 88, 89; pl. 12, figs 24–42; comb. nov.); M.Chandler (1962: 55, 56); Mai (1998: 62); Meller (1998: 102, 103; pl. 6, figs 5–9); Teodoridis (2003: 26; pl. 7, figs 17, 18); Kvaček & Wilde (2006: 146).

≡ *Spinophyllum daemonorops* (Unger) Huard (1967: 332; comb. nov.); Czeczott & Juchniewicz (1980: 26–28; pls 4, 5, 7), Holý et al. (2012: 65; pl. 5, fig. 13).

= *Spinopalmoxylon teutonicum* (R.Ludw.) Winterscheid (2018: 226–228; figs 2A–D), **syn. nov.**

Basionym. *Chamaerops teutonica* R.Ludw. (1860:

Plate 1. **1–6**. *Spinopalmoxylon daemonorops* (Unger) Weyland et al.; Laubach near Giessen (Germany); middle Miocene (Langhian) brown coal of intravolcanic sediment deposits. **1–4**. Groups of spines on spathaceous bracts (1, 2, 4) and leaf sheaths (3). **1**. Neotype of *Palaeospathe daemonorops* [MB.Pb.1980/0296]. **2**. Syntype [MB.Pb.2016/1652]. **3**. Syntype [MB.Pb.2016/1654]. **4**. Syntype [MB.Pb.2016/1653]. **5**, **6**. Isolated groups of spines. **5**. Lectotype of *Chamaerops teutonica* [MB.Pb.2005/0214.1] (left), **6**. syntype [MB.Pb.2005/0214.2]. Scale bars = 20 mm

86, 87; pl. 20, figs 2, 3), **nom. rej. prop.** – Lectotype (designated by Winterscheid 2018: 226). MB.Pb.2005/0214.1 [illustrated in Ludwig (1860: pl. 20, fig. 3a) and Winterscheid (2018: fig. 2D, left)], Pl. 1, fig. 5. Syntypes (designated by Winterscheid 2018: 226). MB.Pb.2005/0214.2 [illustrated in Winterscheid (2018: fig. 2D, right)], MB.Pb.2005/0213. Repository. Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (MfN); R. Ludwig collection. Locus typicus. Germany. Hesse: Hessenbrücken at Laubach near Giessen in Wetterau. Stratum typicum. Middle Miocene (Langhian), brown coal of intravolcanic sediment deposits.

= *Spinopalmoxylon rhenanum* Weyland, Kilpper & Berendt (1966: 89, 90; pls 12–19), **syn. nov.**

Holotype (designated by Weyland et al. 1966: 89). 33904(1-2) [illustrated in Weyland et al. (1966: pl. 12, fig. 1; pl. 13, figs 9, 10, stem with spines)]; pl. 2, figs 1, 2. Paratypes. 33544(1) [illustrated in Weyland

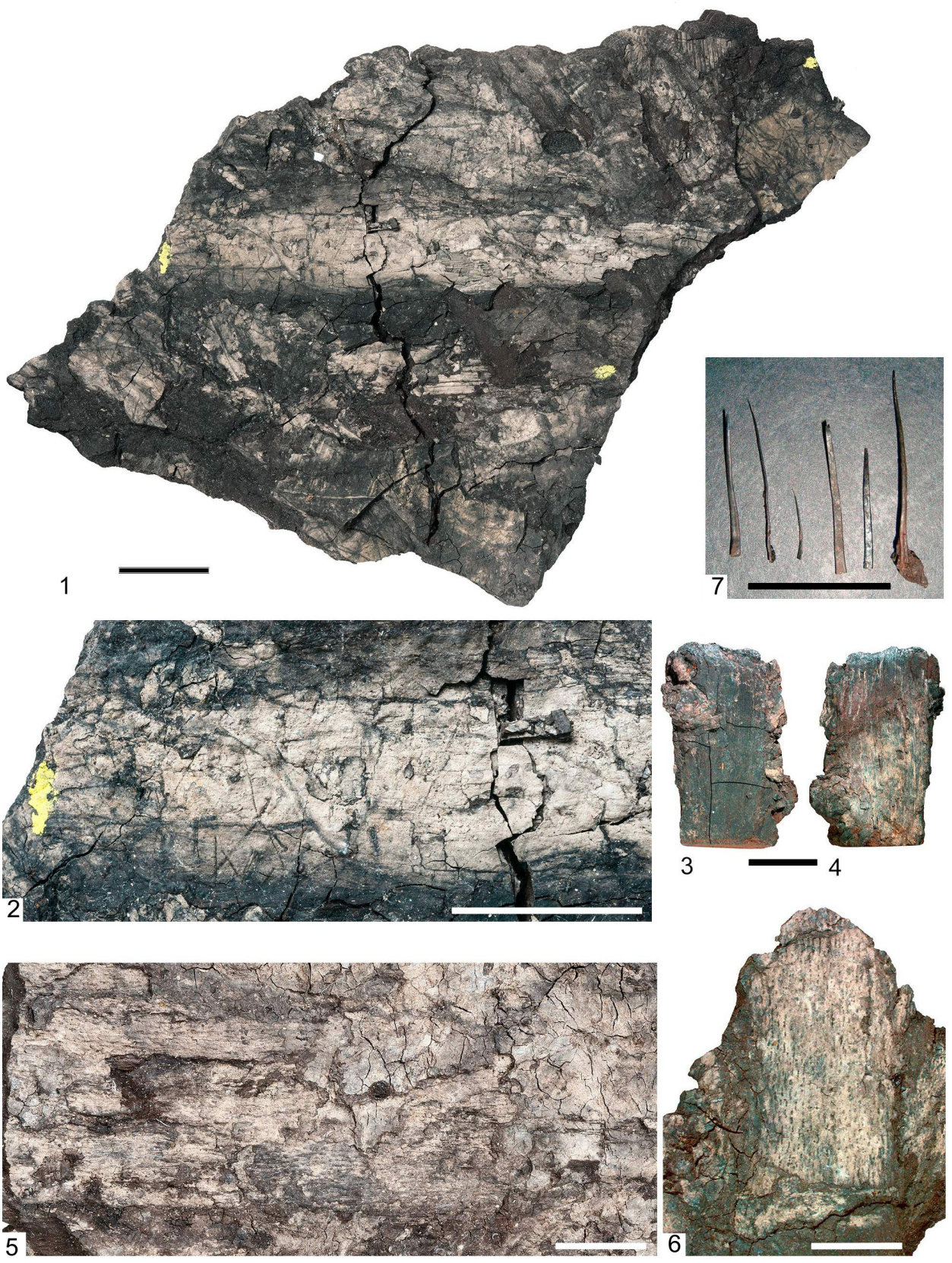

Plate 2. **1–7**. *Spinopalmoxylon daemonorops* (Unger) Weyland et al.; former Vereinigte Ville open-cast lignite mine near Cologne (Germany), lower Miocene (Burdigalian) Ville Formation. **1**, **2**. Holotype [STIPB 33904(1-2)]. **1**. Shoot axis with spines. **2**. Higher magnification of shoot axis in figure 1, with impressions of scars and spines. **3**, **4**. Decorticated shoot axis seen from both sides, with two scars of large spines [specimen STIPB 33544(1)]. **5**. Decorticated shoot axis with visible vascular bundles [specimen STIPB 33906(1)]. **6**. Shoot axis with bark and parallel rows of small scars of spines [STIPB 33544(3)]. **7**. Isolated spines [STIPB 33910(1-6)]. Scale bars: 1–2, 7 = 20 mm; 3–6 = 5 mm

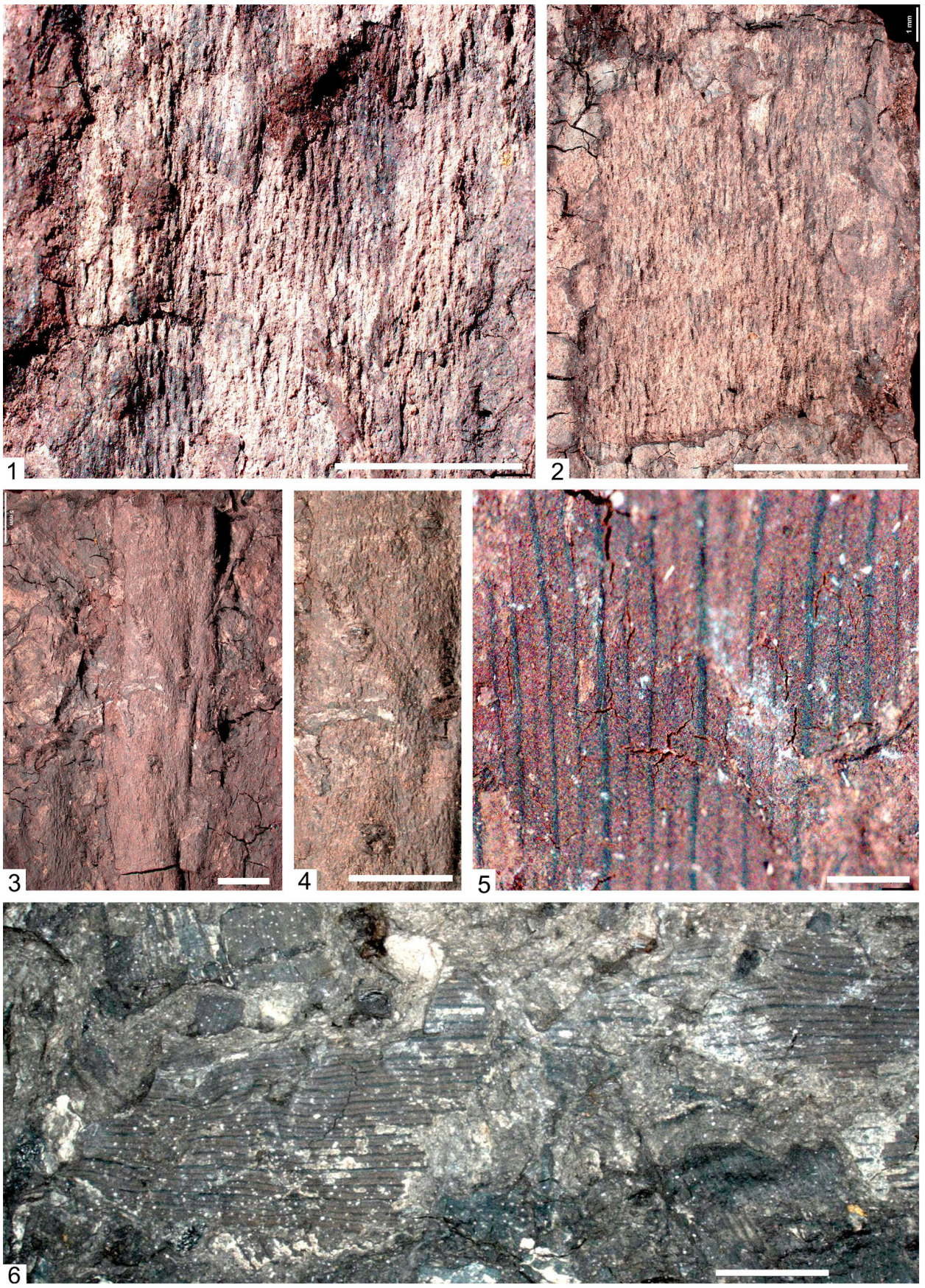

Plate 3. **1–6**. *Spinopalmoxylon daemonorops* (Unger) Weyland et al. **1–2**. Decorticated shoot axis with visible vascular bundles; clay pit at Niederpleis [STIPB 33906(1)]. **3**, **4**. Corticated shoot axis with scars of spines; former Vereinigte Ville open-cast lignite mine [STIPB 33544(2)]. **3**. Spine on edge of shoot, top right. **4**. Higher magnification of shoot axis, with impressions of scars of spines. **5–6**. Leaf; clay pit at Niederpleis [STIPB 33907(1)]. **5**. Magnification of figure 6. Scale bars: 1–4 = 5 mm, 5 = 0.5 mm, 6 = 5 mm

et al. (1966: pl. 12, figs 2, 3)], 33544(3) [illustrated in Weyland et al. (1966: pl. 12, fig. 4, 7)], 33906(1) [SEM stub 029] [illustrated in Weyland et al. (1966: pl. 12, figs 5, 6)], 33910(1) [illustrated in Weyland et al. (1966: pl. 12, fig. 8)], 33947 (LM-prep. 13)–33959 (LM-prep. 1). Repository. Institut für Geowissenschaften, Abteilung Paläontologie, Universität Bonn (STIPB), Hermann Weyland collection. Locus typicus. Germany. North Rhine-Westphalia: former Vereinigte Ville open-cast lignite mine near Hürth south of Cologne. Stratum typicum. Early Miocene (Burdigalian) Ville Formation (layer Seam 6A). Additional paratypes. Germany. North Rhine-Westphalia: former clay pit of Tonwerk Großpeter, Lindemann & Co. in Niederpleis near Sankt Augustin; late Oligocene (Chattian) Köln Formation (layer Clay 1): STIPB, Weyland coll.: 33544(2) [illustrated in Weyland et al. (1966: pl. 13, figs 12–14)], 33914 (LM-prep. 47)–33946 (LM-prep. 15) [illustrated in Weyland et al. (1966: pl. 15, figs 26, 27, 29–32; pl. 16, figs 35, 37–39; pl. 17, 40–42, fig. 43)], 33925 (LM-prep. 36) [illustrated in Weyland et al. (1966: pl. 17, fig. 43)], as "*Spinopalmoxylon rhenanum*".

= *Spinophyllum lepidocaryoides* Huard (1967: 332, 333; text-figs 1–4; pls 1–3), **syn. nov.**

Holotype (designated by Huard 1967: 333). Huard série A, n° 150. Isotypes (designated by Huard 1967: 333). Huard série A, n° 141, 145, 162. Repository. Muséum National d'Histoire Naturelle, Paris, France (MNHN); Jean Huard collection. Locus typicus. France. Landes: Arjuzanx ["Mine de lignite d'Arjuzanx (près de Morcenx, …), gisement de Beylongue Nord (1964-1966).", Huard (1967: 333)]. Stratum typicum. Middle–late Miocene ["Parties inférieure et moyenne de la couche de lignite.", Huard (1967: 333)].

Additional specimens examined. [1] Germany. Hesse: Bad Salzhausen in Wetterau; middle Miocene (Langhian) brown coal of intravolcanic sediment deposits ("Carpolithen-Kohle"): MfN: MB.Pb.2016/1656, MB.Pb.2016/1658, as "*Palaeospathe daemonorops*". [2] Germany. North Rhine-Westphalia: former clay pit of Tonwerk Großpeter, Lindemann & Co. in Niederpleis near Sankt Augustin; late Oligocene (Chattian) Köln Formation (layer Clay 1): STIPB, H.Winterscheid coll.: NDPL-001, NDPL-002, NDPL-003, NDPL-004. STIPB, M.Pingen coll.: NDPL-005 (sample no. 381b), NDPL-006 (sample no. 381c), NDPL-007 (sample no. 381c), NDPL-024 (sample no. 399-6), NDPL-156 (sample no. 426 [SEM stub 024]), NDPL-157 (sample no. 399-7), NDPL-158 (sample no. 399-6), NDPL-159 (sample no. 381b), NDPL-160 (sample no. 399-2), as "*Spinopalmoxylon rhenanum*". [3] Germany. North Rhine-Westphalia: former Gruhlwerk II open-cast mine near Hürth south of Cologne; early Miocene (Burdigalian) Ville Formation (layer Seam 6A): STIPB, Weyland coll.: 31762(1) [SEM stub 027], as "*Palmacites daemonorops*" (Kirchheimer 1931).

Description. The preserved palm remains show the morphological growth habit of a climbing palm with spiny shoots. **Spines** solitary, isolated or arranged in groups, up to 4.0 cm long, largely preserved in their form, thin and awl-shaped, apically tapered, occasionally compressed, adaxially with central longitudinal furrow; spines parallel or divergent oriented, but mostly straight and ± parallel-oriented to plant axis, spines adaxial carinate, dark to light brown with smooth shiny surface. Small compressed spines in dried condition oriented in all directions. **Stems** without sheaths 0.75–3.0 cm wide, densely covered with small scars for insertion of spines. Scars arranged in lines parallel to longitudinal axis of stems. **Leaf sheaths** basally abruptly cut and curved, up to 10 cm wide, surface striated by through-printing of rigid epidermal fibres, or rather fibres in tissue below epidermis of petiole. Leaf sheaths covered with 0.3–4.0 cm long spines arranged in groups parallel to striation, with maximum number of spine groups eight, and spines up to 1 mm broad at the base. **Spathaceous bracts** with smooth glossy surface and groups of spines arranged in rows. Also see description of **stems** (*Achsenteile*) and **haustoria** (*Saugwurzeln*) in Weyland et al. (1966: 76–82, 85). **Leaf remains** in brown coal layers associated with stems and bark of *S. daemonorops*. Leaves fragmentary, lamina shape oblong, strap-shaped, margin not preserved. Venation parallelodromous, between two strong and ~0.5 mm broad veins and with 0.6 to 0.8 mm spacing, one narrower vein in middle of the two broad veins. One narrower vein between these vein types (see Pl. 3, fig. 5, 6).

Notes. The holotype and paratypes of "*S. rhenanum*" from the Weyland collection (macroscopic type material and prepared microscope slides) and the newly collected specimens were reinvestigated. A comprehensive description of the morphological and anatomical characteristics of the vegetative organs (stems, shoots, haustoria) was made by Weyland et al. (1966). After the reexamination, no further comments are necessary at this time.

On the basis of the morphological and anatomical description by Weyland, the

fragmentary leaf remains should be designated *Spinopalmoxylon daemonorops*. Leaf remains of "*Calamus*" are described under different names from early Miocene deposits, such as Engelswies near Meßkirch, southern Germany (Schweigert 1992) and Ipolytarnóc (Tarnóc), Hungary (Jablonszky 1915, Rásky 1964), as impressions of "feather palm leaves" of *C. noszkyi*, as well as from Santa Giustina, northern Italy (Meschinelli & Squinabol 1893), as *C. beccarii* and *C. nervosus*. All of these records are doubtful.

Spinopalmoxylon parvifructum Winterscheid, **sp. nov.**

Pl. 4, figs 1–8

Holotype. NDPL-008 (sample no. 381c, SEM stub 018)!, leg. M. Pingen, 1 May 2009; Pl. 4, fig. 2.

Paratypes. NDPL-009 (sample no. 381c, SEM stub 019)!, NDPL-011 (sample no. 399-4, SEM stubs 017, 023)!, NDPL-012 (sample no. 399-4, SEM stub 019)!, NDPL-151 (sample no. 381c, SEM stub 021)!, NDPL-152 (sample no. 381c)!, NDPL-161 (sample no. 381c)!.

Repository. Institut für Geowissenschaften, Abteilung Paläontologie, Universität Bonn, Germany (STIPB), M.Pingen collection.

Locus typicus. Germany. North Rhine-Westphalia: former Tonwerk Großpeter, Lindemann & Co. clay pit at Niederpleis near Sankt Augustin [50°46′12.1″N, 7°13′44.3″E], May 2009.

Stratum typicum. Late Oligocene (Chattian) Köln Formation (layer Clay 1).

Derivatio nominis. The epithet "parvifructum" refers to the size of the fruits, derived from the Latin words "parvus" (small) and "fructus" (fruit).

Diagnosis. Female reproductive organs of *Spinopalmoxylon* on rachillae, pistillate flowers tubular, petals and sepals with striated surface; fruits globular to oval, chalaza basally pre-bulging, calyx two opposite whorls; seeds oval, smooth, not ruminated, dorsally with poor radial striation, ventrally flattened, raphe aligned laterally.

Description. Pistillate inflorescences on up to 11 mm long fragments of rachillae, partly with scars interpreted as involucrophores on which bracts are inserted, partly with basal portions of bracts. Pistillate flowers in immature buds prior to anthesis, on rachillae, tubular, ~0.5–0.7 mm × 1.0–1.2 mm. **Fruits** globular, chalaza basally pre-bulging, calyx with two opposite whorls, with three petals and three sepals, surface of epicarp with vertical rows of imbricate scales. Dimensions: ~2.5–3.5 mm × ~2.0–2.8 mm. **Seeds** oval in outline, smooth, not ruminated; dorsally with poor radial striation, ventrally flattened, raphe aligned laterally. Position and morphology of hilum and micropyle not visible. Dimensions: 3.0–3.2 mm × 2.2–2.4 mm.

Notes. Weyland et al. (1966: 82–84; pl. 19, figs 60–66 from Vereinigte Ville, and figs 67, 68 from Niederpleis) described and illustrated fruits and seeds in brown coal (*Unreife Früchtchen und Samen im Gestein*) that are not the remains of fossil palms and thus do not belong to this taxon. Instead, the seed in fig. 60 (STIPB Weyland collection: 33911) described as "*Samen einer* (*?*) *Palme*" pertains to *Symplocos* Jacq. (Symplocaceae); the others on pl. 19, figs 61–65 [STIPB Weyland collection: 33909, 33912] and figs 66–68 [STIPB Weyland collection: 33907 (2–9)] described as "*unreife Früchtchen und Samen*" are fruits of Cyperaceae, cf. the genera *Caricoidea* M.Chandler, *Mapania* Aubl., and *Scleria* P.J.Bergius (Mai 1998).

Table 1. Comparison of the fruit dimensions described as different calamoid fruit remains

Author	Locality	Stratigraphy	fruit dimensions
Mai & Walther (1985)	Weißelster Basin/Germany	late Eocene	"wenige Millimeter bis haselnußgroß im Durchmesser"
Heer (1862)	Bovey Tracey Basin/ England	early Oligocene	13 mm length and 10 mm width
Reid & Reid (1910)			full-grown specimens 6 or 7 mm
Chandler (1957)			oval, 1.6–3.3 mm × 1.5–2.7 mm
Meller (1998)	Korneuburg Basin/Austria	early Miocene	2.5–4.0 mm in diameter
S. parvifructum Winterscheid, sp. nov.	Lower Rhine Basin/ Germany	late Oligocene/ early Miocene	oval, ~2.5–3.5 mm × ~2.0–2.8 mm

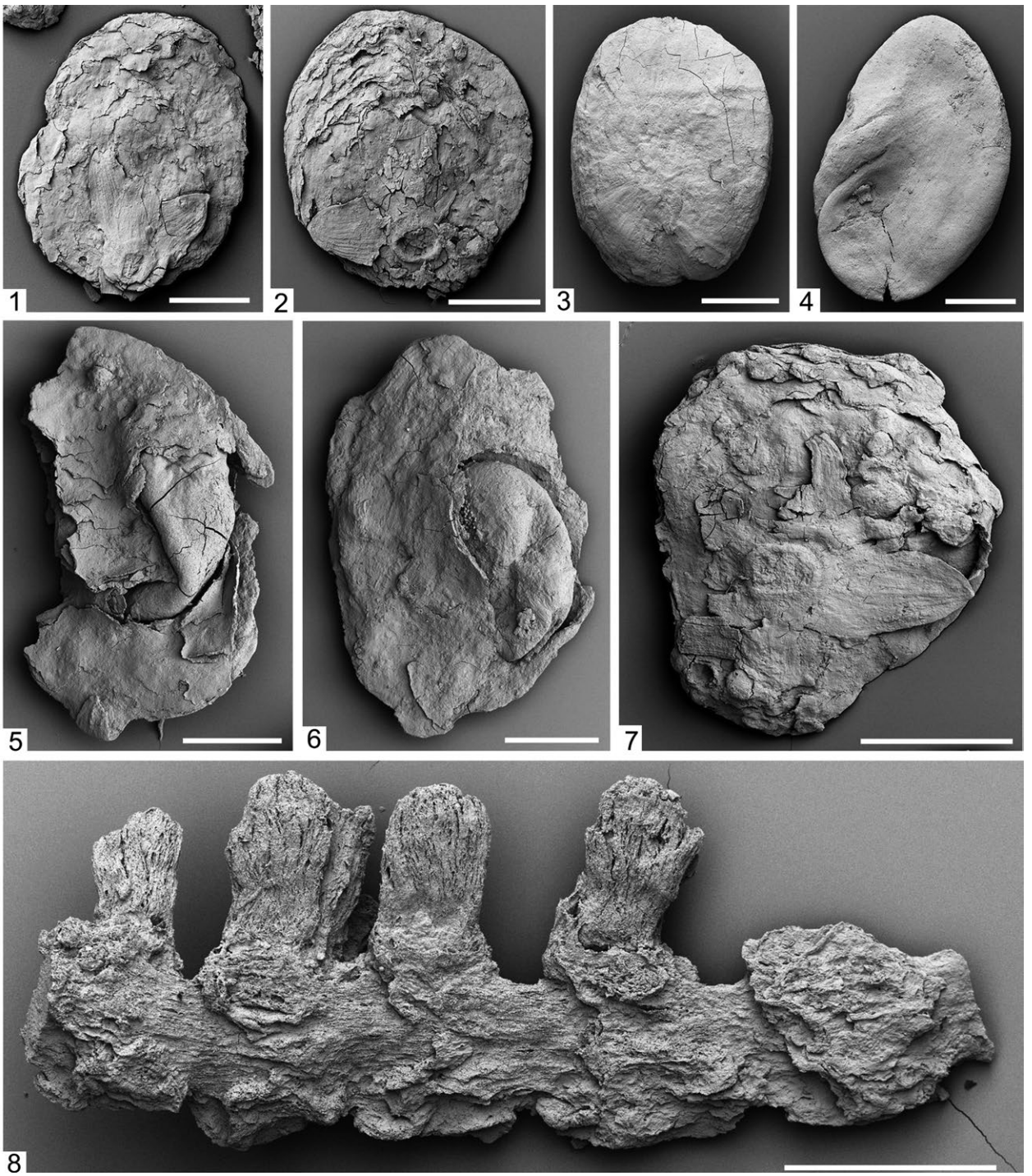

Plate 4. **1–8**. *Spinopalmoxylon parvifructum* Winterscheid, sp. nov.; former clay pit at Niederpleis near Sankt Augustin; late Oligocene (Chattian) Köln Formation (layer Clay 1). **1–7**. Fruits and Seeds. **1**, **2**. Fruits from basal view. **2**. Holotype [specimen STIPB NDPL-008]. **3**, **4**. Seeds. **3**. Dorsal view with poor radial striation. **4**. Ventral view with raphe. **5**, **6**. Fruits with exposed seed in ventral view. **7**. Fruit from basal view. **8**. Pistillate flower buts prior to anthesis on rachilla. Scale bars = 1 mm

Fossil fruiting-organs (fruiting axis, fruits, and seeds) are also described from other localities, mostly referred to as "*Calamus daemonorops*": Mai & Walther (1985: 135, 136; pl. 32, figs 33–38, "*wenige Millimeter bis haselnußgroß im Durchmesser*") from Weißelster Basin/Germany, late Eocene; Heer (1862: 1056–1058; pl. 60, figs 50–53, the fruit is "*13 millims. in length and 10 millims. in breadth, and covered with scales*", as *Palmacites daemonorops*), Reid & Reid (1910: 172; pl. 16, figs 44–48, "*The length of our full-grown specimens is 6 or 7 mm*") and Chandler (1957: pl. 12, figs 30, 31, 37, fruits of 1.75 mm × 1.5 mm, 1.6 × 1.7 mm and 3.3 × 2.7 mm in dimensions) from Heathfield and Bovey Tracey in the Bovey Tracey Lake Basin in Devonshire/England, early Oligocene; and Meller (1998: 102, 103;

pl. 6, figs 5–7, "*Früchte rund und diskusartig abgeflacht*, *2.5–4.0 mm im Durchmesser*") from the Korneuburg Basin/Austria, early Miocene. The described fruits are of different size, and therefore they cannot be attributed to the here-treated new species.

Spinopalmoxylon cicatricosum
Winterscheid, **sp. nov.**

Pl. 5, figs 1–5

Holotype. NDPL-010 (sample no. 399-4, SEM stub 016)!, leg. M.Pingen, 1 May 2009; Pl. 5, figs 1–5.

Paratypes. NDPL-010 (sample no. 399-4, SEM stubs 016, 022)!, NDPL-025 (sample no. 381c)!, NDPL-147 (sample no. 402-3, SEM stub 016)!, NDPL-150 (sample no. 381b, SEM stub 020)!, NDPL-153 (sample no. 381b)!, NDPL-154 (sample no. 381b)!, NDPL-155 (sample no. 399-6, SEM stub 023, 025, 026)!.

Repository. Institut für Geowissenschaften, Abteilung Paläontologie, Universität Bonn, Germany (STIPB), M.Pingen collection.

Locus typicus. Germany. North Rhine-Westphalia: former Tonwerk Großpeter, Lindemann & Co. clay pit at Niederpleis near Sankt Augustin [50°46′12.1″N, 7°13′44.3″E], May 2009.

Stratum typicum. Late Oligocene (Chattian) Köln Formation (layer Clay 1).

Derivatio nominis. The epithet "cicatricosum" refers to the scarred filaments of the staminate flowers and is derived from the Latin word "cicatricosus" (full of scars).

Diagnosis. Male generative organs of *Spinopalmoxylon* on rachillae with fractional fibrous split and closed petals, abaxially covered with crater-like scars, with pollen of *Dicolpopollis kockelii* type.

Description. Staminate flowers prior to anthesis on up to 12 mm long fragments of rachillae, ~1.0–1.2 mm × 0.9–1.0 mm; bracts 3, oblong-ovate, in two whorls laterally overlapping. Petals closed, covered with crater-like scars, petals longitudinally split, whereby anthers with adherent pollen became visible; stamina and filaments not visible. Pollen of the type of *Dicolpopollis kockelii* Pflanzl (1956: 241; pl. 16, figs 9–12).

Note. For full description of the pollen *Dicolpopollis kockelii* see Pflanzl (1956: 241; pl. 16, figs 9–12), Takahashi & Jux (1986: 127; pl. 22, figs 6–14) and Konzalová & Ziembińska-Tworzydło (2008: 151; pl. 3, figs 2, 3).

DISCUSSION

OCCURRENCE AND HABITAT

Lower Rhine Basin (North Rhine-Westphalia). Fossil remains of vegetative organs of this fossil palm occur in the Lower Rhine Basin and in the limited chrono- and lithostratigraphic interval between the late Oligocene (Chattian) Köln Formation and the early Miocene (Burdigalian) basal layers of the Ville Formation. The remains from the Lower Rhine Basin are always from specific horizons in coaly clay or brown coal layers from the following localities: Niederpleis, late Oligocene (Chattian): Kirchheimer (1937, 1938, as *Palmoxylon daemonorops*), Weyland et al. (1966, as *S. rhenanum*), Kvaček & Wilde (2006, Niederpleis, as *Calamus daemonorops*); Ville, early Miocene (Burdigalian): Kirchheimer (1931, Gruhlwerk, as *Palmacites daemonorops*); Weyland et al. (1954, Liblar, as *Palmacites daemonorops*), Kräusel & Weyland (1954, Liblar, as *Palmacites daemonorops*), Weyland et al. (1966, Vereinigte Ville, as *S. rhenanum*), Kvaček & Wilde (2006, Vereinigte Ville, as *Calamus daemonorops*). The pistillate inflorescences with fruits and seeds of *S. parvifructum* and the staminate inflorescences of *S. cicatricosum* were, until now, only known from the late Oligocene type locality Niederpleis in the southern Lower Rhine Basin. At the end of the early Miocene (Burdigalian), in the middle part of the Morken Seam in the Ville Formation, the palm went extinct in the Lower Rhine Basin. The stratigraphic occurrence of the megafossils of *S. daemonorops* corresponds with that of the pollen described as *Dicolpopollis kockelii* Pflanzl (1956: 241) (Takahashi & Jux 1986: 127; Von der Brelie et al. 1981: 29, text-fig. 3, 4).

The co-occurrence of *Dicolpopollis kockelii*, *S. daemonorops*, and the accompanying flora with *Salvinia cerebrata* Nikitin ex Dorof., *Osmunda lignitum* (Giebel) Stur, *Glyptostrobus europaea* (Brongn.) Unger, *Nyssa ornithobroma* Unger, *Myrica pseudointegerrima* Weyland & Kilpper and *Spirematospermum*

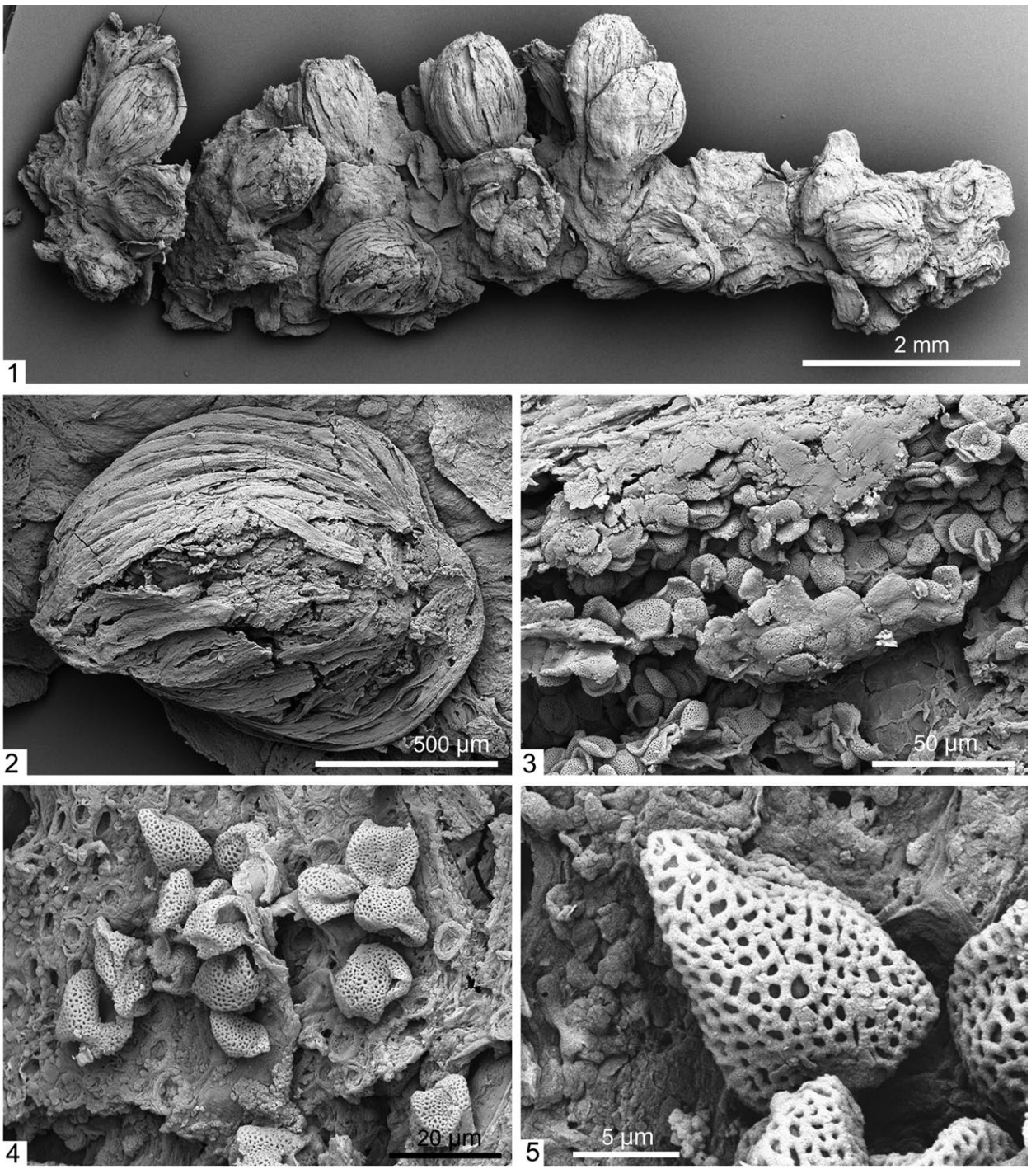

Plate 5. **1–5**. *Spinopalmoxylon cicatricosum* Winterscheid, sp. nov.; former clay pit at Niederpleis near Sankt Augustin; late Oligocene (Chattian) Köln Formation (layer Clay 1). Holotype [specimen STIPB NDPL-010], staminate flowers and pollen. **1**. Staminate flowers on rachilla. **2**. Closer view of figure 1 with single staminate flower. **3**. Closer view of figure 2 with pollen of *Dicolpopollis kockelii*. **4**. Abaxial view on stamen with group of pollen and crater-shaped scars. **5**. Single pollen grain

wetzleri (Heer) Chandler, indicate humid and swampy habitats with short-lived phases of stagnant groundwater and waterlogged soils that are found in swampy fluviatile floodplain and backswamp environments.

In the Lower Rhine Basin this palm is characteristic of coaly clay and brown coal layers in the late Oligocene to early Miocene Köln Formation and in the early Miocene brown coal of the basal Ville Formation. The sedimentological and floral composition of the type horizons in the former clay pit in Niederpleis and the former Vereinigte Ville open-cast lignite mine are typical of these habitats and ecological conditions.

Wetterau (Hesse). In Wetterau the palm *S. daemonorops* occurs in locally limited brown coal layers of intravolcanic deposits until the middle Miocene (Langhian) [Ludwig (1860, as

Chamaerops teutonica), Unger (1860, as *Palaeospathe daemonorops*), Ettingshausen (1868, as *Palaeospathe daemonorops*), Winterscheid (2018, as *S. teutonicum*)].

Further localities that yield this palm. Germany – Lower Saxony, Schöningen; Eocene: Riegel et al. (2012, as *Dicolpopollis kockelii*). Saxony, Weißelster Basin; late Eocene (Priabonian): Engelhardt (1870, as *Palaeospathe daemonorops*), Beck (1882, as *Palmacites daemonorops*), Mai & Walther (1985). Southern Brandenburg; "middle" Oligocene, Calau Beds: Mai (1998, as *Calamus daemonorops*). England – Devonshire, Bovey Tracey Lake Basin; early Oligocene (Rupelian): Heer (1862, as *Palmacites daemonorops*), Reid & Reid (1910), Chandler (1957, 1962, as *Calamus daemonorops*). France – Landes, Arjuzanx; middle–late Miocene: Huard (1967, as *Spinophyllum daemonorops*). Austria – Lower Austria, Korneuburg Basin; early Miocene (Burdigalian, Karpatian): Meller (1998, as *Calamus daemonorops*). Czech Republic – North Bohemia, Zittau Basin, Hrádek nad Nisou; early Miocene: Holý (1976), Holý et al. (2012, as *Spinophyllum daemonorops*), Teodoridis (2003, as *Calamus daemonorops*). Poland – Turów Basin; early Miocene: Czeczott & Juchniewicz (1980, as *Spinophyllum daemonorops*).

THE *SPINOPALMOXYLON DAEMONOROPS* WHOLE PLANT

The whole-plant concept for *Spinopalmoxylon daemonorops* is described here after specific consideration of the collections and type material from the Wetterau north of Frankfurt and from the Lower Rhine Basin in western Germany.

Plant parts of the *Spinopalmoxylon daemonorops* whole plant:

– Vegetative organs. *S. daemonorops* (Pl. 1, figs 1–6; Pl. 2, figs 1–7; Pl. 3, figs 1–6).

– Pistillate flowers, fruits and seeds. *S. parvifructum* (Pl. 4, figs 1–8).

– Staminate flowers. *S. cicatricosum* (Pl. 5, figs 1–3).

– Pollen. *Dicolpopollis kockelii* (Pl. 5, figs 4, 5).

– Stratigraphic range. Late Eocene (Priabonian) to middle Miocene (Langhian).

– Geographic occurrence. In Europe from south-west France (Landes, Arjuzanx), southern England (Devonshire, Bovey Tracey Lake Basin), Germany (Wetterau, Lower Rhine Basin, Weißelster Basin), Austria (Lower Austria, Korneuburg Basin), Czech Republic (North Bohemia, Zittau Basin) and Poland (Turów Basin).

– Habitat. Lowland forests, in fluviatile swampy floodplain and backswamp environments, lake basins and in lacustrine marshlands. Characteristic accompanying plant taxa are *Salvinia* spp., *Osmunda lignitum*, *Glyptostrobus europaea*, *Nyssa ornithobroma*, *Myrica* spp., *Spirematospermum wetzleri* and *Carpolithes mettenii*.

– Nearest living relative. East Asiatic species of the genus *Plectocomia* Mart. ex Schult. & Schult.f. with their habitats in tropical lowland and mountain rainforests (Weyland et al. 1966: 86).

ACKNOWLEDGMENTS

The author gratefully acknowledges Hans-Georg Herbig (Institut für Geologie und Mineralogie der Universität zu Köln) for permission to examine material of the palaebotanical Weyland collection for the present paper, and Maria Pingen (Hürtgenwald) for giving collection material from Niederpleis. The author also thanks Georg Oleschinsky for help with SEM and macrophotography, and Victoria McCoy for reviewing the English of the paper for submission. Special thanks are due to Dieter Uhl and Thomas Denk for their critical reviews and for valuable comments and suggestions to an earlier version of the manuscript.

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