

Late Cretaceous (Campanian) leaf and palynoflora from southern Skåne, Sweden

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Abstract: A Late Cretaceous (Campanian) leaf megaf flora from the Vomb Trough in southern Skåne, Sweden, has been investigated on the basis of collections held at the Swedish Museum of Natural History. The main plant-bearing locality is Köpinge, but single specimens originate from Högestad, Ingelstorp, Rödmölla, Svenstorps mölla and Tosterup. The fossil flora is dominated by the angiosperm (eudicot) *Debeya* (*Dewalquea*) *haldemiana* (Debey *ex de* Saporta & Marion) Halamski. Other dicots are cf. *Dryophyllum* sp., *Ettingshausenia* sp., *Rarykinia*? sp., *Dicotyphyllum* *friesii* (Nilsson) comb. nov. and *Salicites* *wahlbergii* (Nilsson) Hisinger. Conifers are represented by cf. *Aachenia* sp. (cone scales), *Pagiophyllum* sp. and *Cyparissidium* sp. (leaves). Single poorly preserved specimens of ferns and monocots have also been identified. The terrestrial palynomorphs (the focus herein) clearly link to the megaf flora, although with different relative abundances. The fern spore *Cyathidites* dominates along with the conifer pollen *Perinopollenites* *elatoides* and *Classopollis*. Angiosperm pollen comprise up to 15% of the assemblage, represented by monocolpate, tricolpate and periporate pollen and the extinct Normapolles group. The spores in the kerogen residue show a thermal alteration index (TAI) of 2+.

The flora probably represents mainly a coastal lowland *Debeya*/conifer forest, and is similar to approximately coeval assemblages from analogous palaeo-communities described from eastern Poland, western Ukraine and Westphalia.



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Late Cretaceous terrestrial to shallow-marine rocks of Skåne, southern Sweden yield plant micro-, meso- and megafossils. The micro- and mesoflora have been the subject of several studies over the past three decades (mostly from northern Skåne: see the review by Friis *et al.* (2011, pp. 70–72)). The wood remains and fossil cones were described by Conwentz (1892), Nykvist (1957), Srinivasan & Friis (1989) and Herendeen (1991). However, the leaf megaf flora has only been reported and briefly described in a few publications from the first half of the nineteenth century (Nilsson 1824, 1832; Hisinger 1837), and no palynological analyses have been performed on the Campanian successions from the Vomb Trough. This paper aims to revise the Campanian leaf flora from the Vomb Trough in southern Skåne (Fig. 1) and to compare the megaf flora to the palynological assemblage recovered from the same strata. Santonian leaves and cones from the Kristianstad Basin in northern Skåne will be dealt with in a separate study.

History of research

Fossil plants from the Late Cretaceous deposits of Skåne were first mentioned and illustrated by Nilsson (1824). Sven Nilsson (1787–1883) began collecting objects of natural history in his youth, becoming Associate Professor in Natural History at Lund University by 1812. He took up the directorship of the Swedish Museum of Natural History in Stockholm (NRM) in 1828, but in 1832 he returned to Lund taking up a professorship in natural history until 1856. During his time at NRM, he assembled a collection that served as the basis for the first detailed study of Swedish Cretaceous plants, with the description of five new species from Köpinge (Nilsson 1832). Nilsson's palaeozoological collections were donated to the museum in Lund and have been used by subsequent researchers (e.g. Lundgren 1865, p. 1, 1874, p. 70, 1880, p. 23). Among the palaeobotanical collections available to the present authors, only two specimens (S084165 and Lund

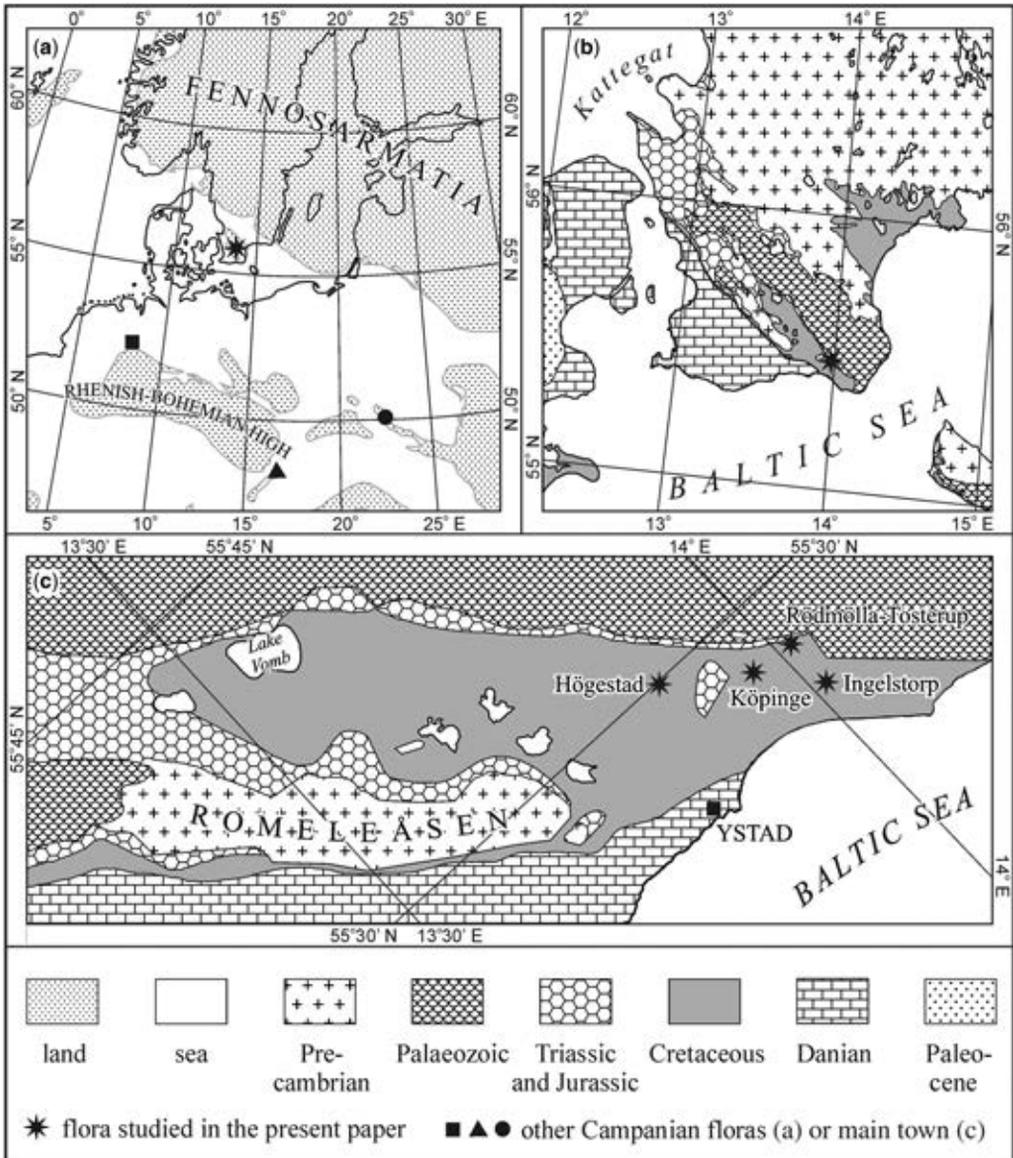


Fig. 1. Geographical and geological setting of the studied flora. (a) Present-day geography of northern and central Europe compared to Campanian palaeogeography (after Ron Blakey, from Csiki-Sava *et al.* (2015), modified after data in Chatziemmanouil (1982), Surlyk in Voigt *et al.* (2008) and Halamski (2013)), and the presumed location of the studied flora and of three other coeval palaeofloras (circle, Poland–Ukraine; square, Haldem in Westphalia; triangle, Grünbach in Austria). (b) Bedrock geological map of Skåne (Scania) and adjacent regions after Koistinen *et al.* (2001), Vajda & Gravesen (2008) and references therein. (c) Solid geological map of the Vomb Trough in southern Skåne showing the localities that have yielded the fossil flora studied, after Christensen (1986).

s.n. (*s.n.*, *sine numero*)), however, can be attributed unambiguously to the Nilsson collection. Some of his plant fossils are, perhaps, present amongst a collection of material originating from Lund but now

(2015) registered at the NRM, but the documents detailing the collector(s) and transfer are lacking. This concerns, in particular, type and figured specimens that could not be traced for the purpose of the

present study. Nilsson's specific descriptions were repeated by Hisinger (1837), who moreover introduced four new genera based on these species. He later relisted the four dicotyledonous species from Köpings in a synoptic table of fossils from Skåne (Hisinger 1840, p. 58).

Another major collection from the studied area (available to the present authors) was assembled by a collector named Gustaf von Schmalensée (1842–1919), and was deposited in the NRM during the years 1879, 1880 and 1903. It partly derives from the Swedish Geological Survey (Sveriges Geologiska Undersökning) collections, as testified by a letter of Edvard Erdmann to Alfred Gabriel Nathorst, a professor at the NRM, dated 5 November 1902. Nathorst (1881) had already published a short nomenclatural remark on the most abundant species at Köpings and apparently planned to undertake a more extensive study of this flora, based on the names attributed to him occurring on collection labels. However, these names have never been published.

'*Dewalquea nilssonii*' was listed among fossils from Köpings by Moberg (1884). The flora of 'Köpings Sandstone' was then briefly mentioned by Hartz (1909, p. 2), who described it as consisting of: 'fragmentary rests of ferns, conifers, and angiosperm trees; the most common leaf being that of *Dewalquea Nilssonii* (*Helleborea?*)'. A similarly laconic remark was made by Ross (1949, p. 38), who stated: 'a few dubious dicotyledonous fossils [*Acerites*, *Alnites*, *Cycadites* (*Dewalquea*), *Salicites*] from the Upper Cretaceous of Scania'. Unlike the floras from the Kristianstad Basin, Cretaceous plants from southern Skåne have not been studied for more than a century.

Geological setting

Skåne (also known as Scania) is a province of southern Sweden that incorporates the geological transition (Sorgenfrei–Tornquist Zone) between the Baltic (Fennoscandian) Shield and the Danish Basin within the Northwest European Craton. Mesozoic strata are known in Skåne from both outcrops and borings. Cretaceous deposits are known from several areas (Fig. 1b), the most important from a palaeobotanical perspective being the Kristianstad Basin, situated on the southernmost part of the Fennoscandian Shield, and the Vomb Trough, situated in the Fennoscandian Border Zone (Christensen 1984; Larsson *et al.* 2000). The Late Cretaceous landscape of Skåne consisted of several elongate islands and peninsulas (Fig. 1a) formed of basement (Precambrian–Palaeozoic) rocks surrounded by shallow-marine areas (Surlyk in Voigt *et al.* 2008, p. 940). Åsen, a well-known fossil site

within the Kristianstad Basin, hosts charcoaled flowers within Santonian–lower Campanian fluvial deposits (Skarby 1968; Friis 1984; Friis *et al.* 2011). Within the Kristianstad Basin, the fluvial successions are overlain by marine glauconitic calcareous sandstones hosting a rich fossil biota, including a range of invertebrates (Einarsson *et al.* 2016), but also vertebrates including sharks and fish (Bazzi *et al.* 2015; Siverson *et al.* 2015), mosasaurs, plesiosaurs (Einarsson *et al.* 2010) and even non-avian dinosaurs (Poropat *et al.* 2015). Oysters were described from Åsen showing heteromorphic ornamentation interpreted as attachment *in vivo* to arborescent plants (presumably mangroves: Friis & Skarby (1981)).

The Vomb Trough (Fig. 1c) is a graben extending for about 55 km northwestwards and 25 km southeastwards from Ystad (Norling 1982). It is bordered by the Precambrian Romeleåsen Horst to the SW and by a lower Palaeozoic plateau to the NE: both were also areas of elevation in the Cretaceous (Chatziemmanouil 1982) and, thus, may be assumed to be the source of the flora described from the localities situated in that region. The Upper Cretaceous stratigraphy of the Vomb Trough was elaborated by Christensen (1986) on the basis of belemnites.

The richest Late Cretaceous megafloreal assemblage in Skåne derives from Köpings. The name of this locality (also Köpings mölla) situated approximately 10 km NE of Ystad (not to be confused with Köpings 10 km SE from Kristianstad) denotes a large number of small outcrops (see detailed description by Hägg (1954, pp. 11–13): most of them described as already inaccessible by Christensen (1986) of a yellow calcareous sandstone rich in glauconite, the so-called 'Köpings sandstone'. Besides plants, the 'Köpings sandstone' has yielded foraminifera (Brotzen 1938), molluscs (Schlüter 1870), brachiopods (Dalman 1828; Hägg 1954) and vertebrates (Nilsson (1835): see the list published by Moberg (1884, p. 35) and the bibliography in Christensen (1986, p. 9)). The rock is sufficiently characteristic to also be recognized among erratic boulders (Foth *et al.* 2011). The age of the 'Köpings sandstone' (Christensen 1986) is latest early Campanian and middle late Campanian (strata of earliest late Campanian age are apparently absent). The locality Svenstorp (or Svenstorps mölla) is situated in the greater Köpings area (Hägg 1954, pp. 11–12). Ingelstorp is situated immediately SE of Köpings and the sandstone exposed in this parish is about the same age as that from the latter locality (Hägg 1954, p. 15). Högestad is situated about 10 km NW of Köpings and strata exposed there belong to the middle part of the Campanian (Mucronatenkreide *sensu* Hägg (1954, pp. 11, 15); see also Christensen (1976, pp. 16–17)).

The localities Röd mölla and Tosterup, situated approximately 2 km east of Köpings, require a slightly more detailed comment. A series of outcrops formerly existing in that area exposed several Upper Cretaceous beds (Christensen 1976, pp. 11–12; see also Moberg 1884, pp. 31–34). Some of them belong to strata older than the succession at Köpings (Mamillatenkreide *sensu* Hägg 1954, p. 4); however, it may be assumed that the plant material comes from the Tosterup conglomerate dated to the latest early Campanian on the basis of belemnites (Christensen 1976, p. 13).

Material and methods

Megaflora

The studied material consists of 160 specimens, 147 of them (92%) derived from Köpings. The absolute and relative abundances of the various taxa identified in this collection are summarized in Table 1. Plant fossils were studied entirely from historical

collections, as the outcrops are long since inaccessible. Most of the name-bearing specimens (types) of Nilsson (1832) could not be found and are probably lost. This is particularly unfortunate because taxonomic interpretations of the relevant taxa will necessarily be hypothetical. Taxa that could not be identified due to a lack of specimens are *Acerites cretaceus* (Nilsson, 1832) Hisinger, 1837, *Comptonites antiquus* (Nilsson, 1832) Hisinger, 1837 and *Cannophyllites septentrionalis* Nilsson, 1832. The studied collection of 159 specimens is housed in the NRM in Stockholm. A single specimen is housed in the type collection at the Department of Geology, Lund University, Sweden.

The plant fossils are fragmentary or incomplete leaves preserved as imprints in calcareous sandstone (Figs 2–7) and many are curved (i.e. not preserved along a single plane): this suggests high-energy sedimentation or bioturbation. The leaves are distinguished from the surrounding rock owing to their brownish coloration (Fig. 2a, c–f), likely to be a result of bacterially mediated ferric-oxide

Table 1. Absolute and relative abundances of individual leaf taxa divided by locality

Species	Locality/outcrops						Total	
	Köpings	Svenstorps mölla	Ingelstorp	Högstad	Röd mölla	Tosterup		
Ferns	1 <1%	–	–	–	–	–	1 <1%	
Conifers	cf. <i>Aachenia</i> sp.	2 1%	–	–	–	–	2 1%	
	<i>Pagiophyllum</i> sp.	31 21%	–	–	–	1 20%	31	
	<i>Cyparissidium</i> sp.	–	1 100%	–	–	–	1 <1%	
	Dicots	<i>Debeya haldemiana</i>	99 67%	–	3 100%	–	1 33%	103 64%
	cf. <i>Dryophyllum</i> sp.	1 <1%	–	–	–	–	1 <1%	
	<i>Ettingshausenia</i> sp.	1 <1%	–	–	1 100%	4 80%	2 5%	8 5%
	<i>Rarytkinia?</i> sp.	4 3%	–	–	–	–	4 2%	
	<i>Dicotylophyllum friesii</i>	2 1%	–	–	–	–	2 1%	
	<i>Salicites wahlbergii</i>	5 3%	–	–	–	–	5 3%	
Monocots	1 <1%	–	–	–	–	–	1 <1%	
Total	147 92%	1 <1%	3 2%	1 <1%	5 3%	3 2%	160 100%	

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Fig. 2. Taphonomy of the studied flora: (a) *Rarytkinia?* sp. co-occurring with a fragmentary leaf of *Debeya* (*Dewalquea*) *haldemiana*, specimen S085093, Köpinge; (b) three twigs of the conifer *Pagiophyllum* sp., specimen S083932, Köpinge; (c) the terrestrial angiosperm *Salicites wahlbergii* S084155 (neotype) co-occurring with a marine bivalve, Köpinge; (d) *Pagiophyllum* sp., a conifer twig, Lund *s.n.* (original of Nilsson 1832, pl. 2, fig. 7), Köpinge; (e) cf. *Aachenia* sp., a conifer cone scale, specimen S084113, Köpinge; (f) subcomplete compound leaf S166107 of *Debeya* (*Dewalquea*) *haldemiana*; and (g) fragmentary leaflets of *Debeya* (*Dewalquea*) *haldemiana*, the arrangement of which suggests that they come from a single compound leaf, specimen S084187, Köpinge.

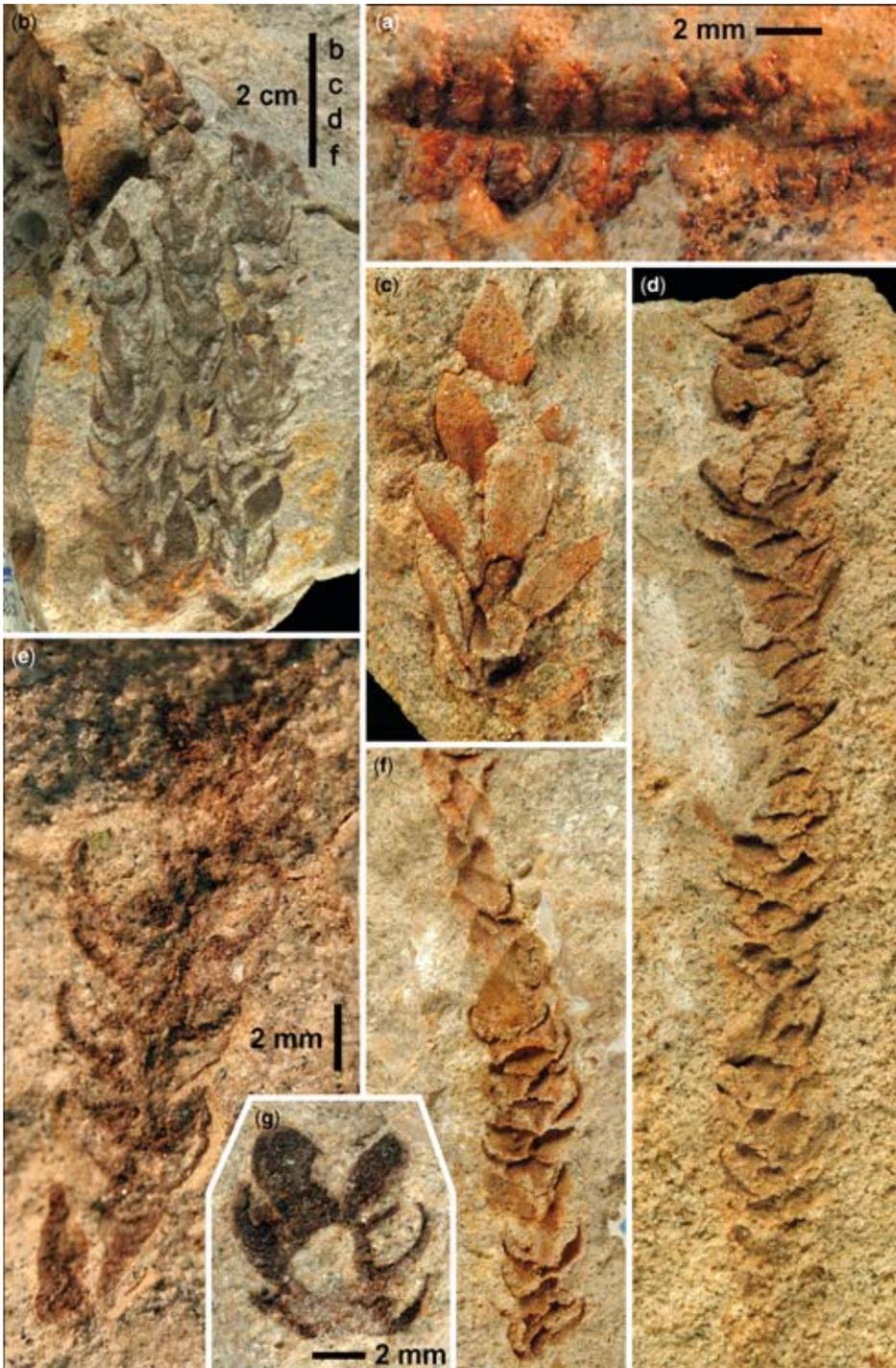


Fig. 3. (a) Ferns and (b)–(g) conifers from the studied flora. (a) *Korallipteris* sp., fragmentary twig S084170, Köpinge. (b)–(g) *Pagiophyllum* sp.: (b) twigs S083936, Köpinge; (c) twig S084212, Rödmölla; (d) twig S166168, Köpinge; (e) twig S166108, Köpinge; (f) twig S083929, Köpinge; (g) twig S166150 cut transversely, Köpinge.



Fig. 4. Conifer *Cyparissidium* sp. Twig S084219, Svenstorps mölla.

precipitation. Such preservation is rather similar to that of the coeval flora from eastern Poland and western Ukraine (Halamski 2013). Rare specimens are blackish (Figs 2b & 5c), suggesting a different type of preservation, but this has not been investigated in detail. Concerning the venation, in all leaves belonging to *Ettingshausenia* sp. tertiaries and quaternaries are preserved, and in *Debeya haldemiana*, two specimens bear faint traces of tertiaries (Fig. 5h), whereas in all other leaves only the midvein and the secondaries can be observed. Overall, the preservational state of the megafloora may be described as rather poor. Uncoated specimens were photographed under oblique and most often polarized light, using a Canon 350D digital camera either with a Canon EFS 17–85 mm lens or, if required, with a Canon EF 100 mm macro lens.

Palynology

Two rock samples from the Köpinge locality (NRM-S089754 and NRM-S089755), each yielding leaf macrofossils, were selected for palynological analysis. Around 10 g of beige, fine-grained sandstone were processed according to standard palynological procedures at Global Geolab Ltd, Canada (e.g. see Vajda *et al.* 2013). The organic residue was sieved using a 5 µm mesh and mounted in epoxy resin on two microscopic slides. Three hundred pollen and spores were identified per sample and the percentage of each palynomorph taxon was calculated (Table 2). In addition, one kerogen slide was prepared from each sample (i.e. where the residue did not go through the oxidation or sieving processes) in order to estimate the thermal alteration index (TAI) of the palynomorphs.

Palynofacies analysis involved counting the relative abundance of organic particles based on 500 counts per slide. Classification of the palynological matter was based on the scheme developed by Batten (1996), and the groups identified were: (I) palynomorphs (pollen, spores, dinoflagellates and

algae); (II) wood; (III) charcoal; (IV) plant cuticle; and (V) amorphous organic matter (AOM). The slides and residues are deposited in the palaeobiology collections of the NRM, Stockholm, and light micrographs of selected pollen and spores from the two studied samples are illustrated in Figure 8 and are identified by NRM numbers and England-finder coordinates.

Systematic palaeontology (megafloora)

Infrakingdom **Cormophyta** (Endlicher, 1836)

Cavalier-Smith, 1988

Division **Tracheophyta** Sinnott *ex*

Cavalier-Smith, 1988

Subdivision **Euphyllophytina** auct.

Infradivision **Moniliformopses** auct.

Class **Leptosporangiales** von Goebel, 1881

Order and family unknown

Genus *Korallipteris* Vera & Passalia, 2012

Type species. *Korallipteris argentinica* (Berry) Vera & Passalia (2012, p. 423, figs 1A–D, 2) ≡ *Gleichenia argentinica* Berry (1924, p. 18, pl. 1, figs 1–5). Meseta Baqueró, Santa Cruz Province, Argentina; Baqueró Group (Aptian).

Korallipteris sp.

(Fig. 3a)

Material. Köpinge: S084170.

Description. The single available specimen is a frond fragment approximately 25 mm long. The pinnules are 2–2.5 mm long and of about the same width, alternate to subopposite, pectopteroid, integrimarginate, with a main vein perpendicular to the rachis and a few secondary veins branching at high angles therefrom.

Remarks. Fern frond fragments reported herein under *Korallipteris* are very similar (although not



Fig. 5. Eudicot *Debeya* (*Dewalquea*) *haldemiana* (all figured specimens from Köpinge), the most common plant in the studied flora: (a) leaf fragment S084189, showing incomplete petiole and seven incomplete petiolules in pedate arrangement; (b) S084032, one of the largest leaflets in the material studied; (c) apical parts of two leaflets, specimen S084201; (d) incomplete compound leaf S083957, with a complete petiole and basal parts of five leaflets; (e) & (f) fragmentary compound leaves, S083948 and S083947; (g) accumulation of probably juvenile leaflets, specimen S084188; and (h) leaflet S084058, with preserved secondary brochidromous venation.

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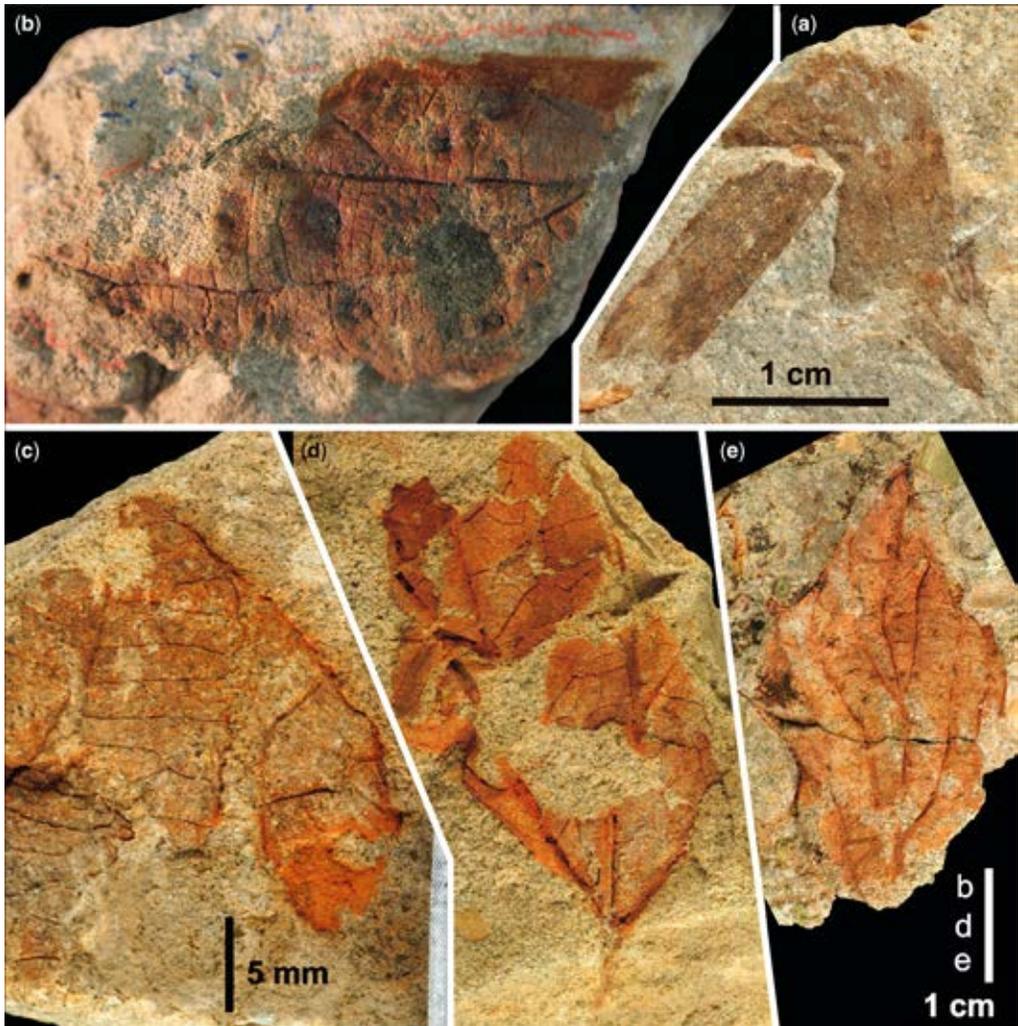


Fig. 6. (a) Monocots and (b)–(f) platanoid *Ettingshausenia* sp. from the studied flora: (a) Monocotyledoneae ord., fam., gen. et sp. indet., leaf fragment S084048, Köpinge; (b) leaf fragment S166202 showing venation, Tosterup; (c) leaf fragment S084207 showing the margin, Rödmölla; (d) incomplete leaf S166203, Tosterup; and (e) leaf fragment S166204, Högstad.

identical) to those reported as *Microphylopteris* by Halamski (2013).

Infradivision **Radiatopses** auct.
 Subinfradivision **Gymnospermae** (Lindley, 1830)
 Prantl, 1874
 Class **Coniferae** (Jussieu, 1789) Engler, 1892
 Order **Pinales** Gorožankin, 1904
 Family unknown

Genus *Achenia* Knobloch, 1972

Type species. *Achenia debeyi* Knobloch (1972, p. 401, figs 1–10). Aachen, Germany; lower Campanian.

cf. *Achenia* sp.
 (Fig. 2d)

Material. Köpinge: S083930, 084113.

Description. Ovuliferous cone scale 14 mm long and 12 mm wide, triangular in outline, with an attenuate apex and an inconspicuous keel. The basal region of the scale bears three impressed depressions

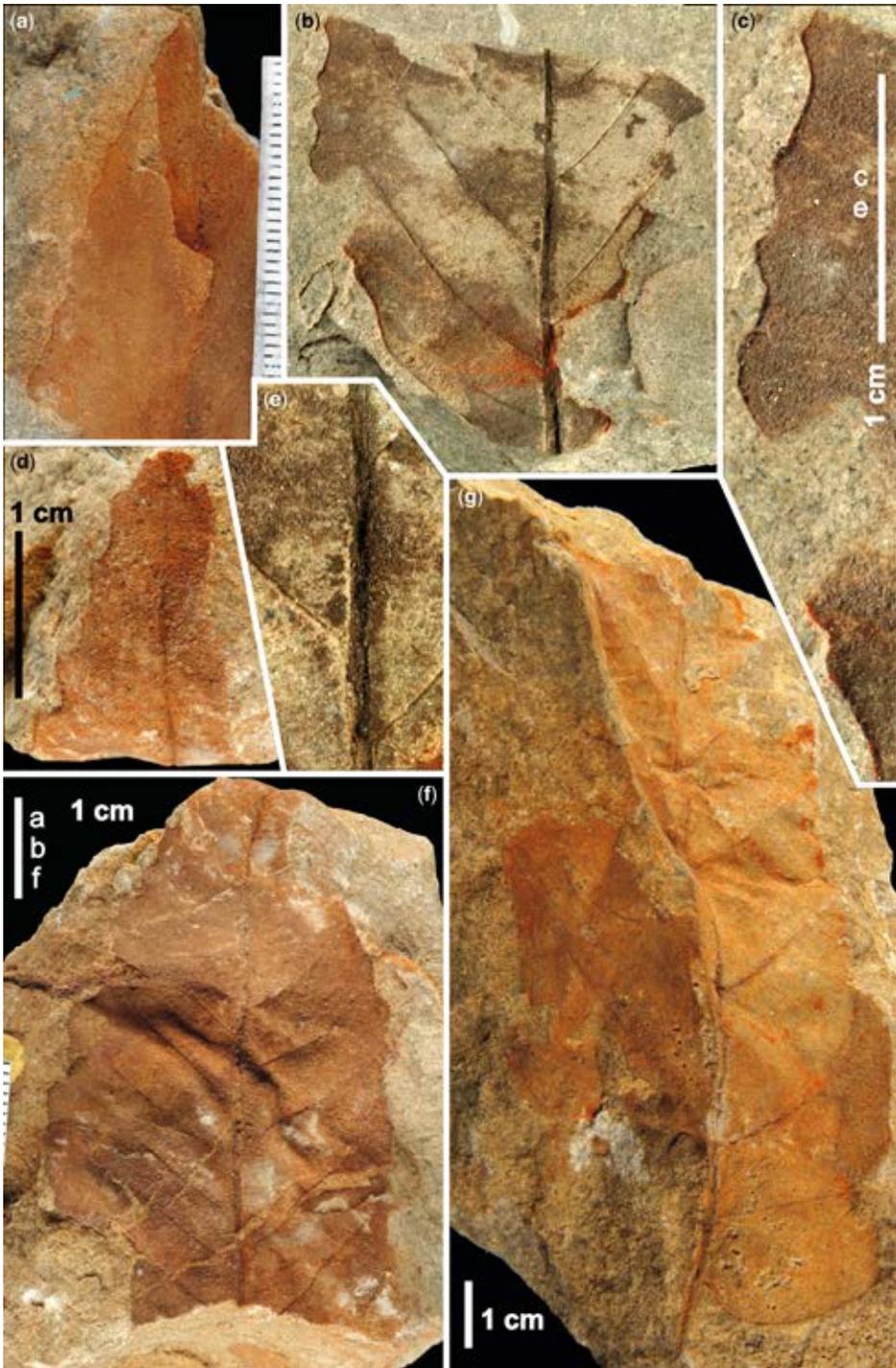


Fig. 7. Dicots from the Campanian of Köpings: (a) *Dicotylophyllum friesii*, leaf fragment S083980 showing margin; (b), (c) & (e) *Dicotylophyllum friesii*, leaf S084030 (neotype), general view and enlargements of the margin and of the decurrent departure of secondaries; (d) & (f) cf. *Dryophyllum* sp., incomplete leaf S084140, apical part and general view; (g) *Rarytkinia?* sp., incomplete leaf S083990.

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probably representing seeds attached at the base of the scale. The seeds are ovoid, 4–5 mm long and 2–3 mm wide. It is unclear whether the lack of a basal stalk characteristic of *Aachenia* is a preservation artefact or if the stalk was originally missing.

Remarks. This ovuliferous scale is broadly similar to scales described as *Aachenia debeyi* from the Late Cretaceous of Aachen (Knobloch 1972) and *A. knoblochii* Wagner from the Maastrichtian of Mexico (Weber 1985). However, a basal stalk diagnostic of *Aachenia* is missing in the studied specimens: hence, the material is reported under open nomenclature.

Genus *Pagiophyllum* Heer, 1881

Type species. *Pagiophyllum circinicum* Heer (1881, p. 11, pl. 10, fig. 6); Portugal; Upper Jurassic.

Pagiophyllum sp.
(Figs 2c & 3b–g)

1832 fructification af en Cycadit – Nilsson: 8; pl. 2, figs 4–7.

Material. Köpings: S083923, 083925–083929, 083931, 083932–083936, 084122, 084169, 084173–084177, 084203, 084204, 084217, 084222 (cast), 085088, 085089, 085102, 166108–166111, 166113, 166150, 166151, 166168, Lund *s.n.* (original to Nilsson 1832, pl. 2, fig. 7). Röd-mölla: S084212.

Description. Fragments of isolated branches with helically arranged leaves. Leaves obovate, typically 0.5–2 × 1–5 mm. A perpendicularly broken specimen (Fig. 3g) has a quite flat obovate lamina without a pronounced keel. Branch diameter ranges from 7 mm (S84217) to 12 mm (S84212).

Remarks. Leaves are longer than wide, a characteristic feature of *Pagiophyllum* as reintroduced by Harris (1969). There are numerous similar fragmentary sterile branches described from several Cretaceous deposits globally (e.g. from the Campanian of Grünbach: Herman & Kvaček (2010); Campanian of James Ross Island, Antarctica: Kvaček & Sakala (2012), Kvaček & Vodrážka (2016)). The studied material has leaves similar in shape to *Brachyphyllum patens* (Miquel, 1853) (van der Ham & van Konijnenburg-van Cittert in van der Ham *et al.* 2003), and *Brachyphyllum* sp. 1 and sp. 2 (van der Ham & van Konijnenburg-van Cittert in van der Ham *et al.* 2003) from the Maastrichtian of The Netherlands and Belgium.

Genus *Cyparissidium* (Heer, 1874) Harris, 1969

Type species. *Widdringtonites gracilis* Heer, 1868; West Greenland; Cretaceous (Heer 1868, p. 83).

Remarks. We employ this genus in the sense of its emendation by Harris (1969, pp. 248–249; see also Harris 1979, p. 77).

Cyparissidium? sp.
(Fig. 4)

Material. Svenstorps mölla: S084219.

Description. The single available specimen represents a fragment of a leafy twig 23 mm long with numerous, dense, helically arranged, needle-like leaves. The leaves are 0.7 × 3 mm and appressed to the axis, forming a branch 3 mm in diameter.

Discussion. The studied material is similar to *Cyparissidium bohemicum* Bayer and *Cyparissidium minimum* Vel. from the Cenomanian of the Bohemian Cretaceous Basin (Velenovský 1885; Bayer 1914, 1920; Kvaček 1999). It is particularly similar to *C. minimum* based on its very delicate needles. However, both mentioned species have epidermal features preserved, so these names are inappropriate for the Skåne specimen.

Subinfradivision **Angiospermae** A. Brown & Doell
ex Doell, 1857

Class **Dicotyledoneae** de Candolle, 1817

Supersubclass **Eudicotyledoneae** Doyle & Hotton *ex*
Halamski, 2013

Order and family unknown

Group ***Debeya*** *sensu* Krassilov *et al.* 2005

Genus *Debeya* Miquel, 1853

Type species. *Debeya serrata* Miquel, 1853; Maastrichtian, Kunrade, Limburg, The Netherlands

Subgenus *Debeya* (*Dewalquea*) (de Saporta &
Marion, 1873) Halamski, 2013

Type species. *Dewalquea haldemiana* Debey *ex de*
Saporta & Marion, 1873; Late Cretaceous, Haldem,
Westphalia.

Debeya (*Dewalquea*) *haldemiana* (Debey *ex de*
Saporta & Marion, 1873) Halamski, 2013
(Figs 2a, e, f & 5)

1824 en bladform – Nilsson: 147; pl. 2,
figs 4, 6.

non 1825 *Cycadites nilsonii* Sternberg: XXXII; pl.
47, fig. 1.

1828 *Cycadites Nilsonii* Brongniart, 204. [*nomen*
nudum]

1832 *Cycadites Nilssonii* Brongn. – Nilsson: 8; pl. 2,
figs 1–3. [*nom. illegit.*]

1873 *Dewalquea haldemiana* (*Araliophyllum*
haldemianum Deb. Ms.) – de Saporta &
Marion: 60–61; pl. 7, 1–2.

v* 1880 *Dewalquea haldemiana* Sap. & Mar. var.
latifolia; Hosius & von der Marck 1880:
173; pls 35: 114, 34: 115.

Table 2. Absolute and relative abundances of individual pollen and spore taxa from samples NRM S089754 and NRM S089755

	Köpinge 23 (absolute numbers)	Köpinge 23 (%)	Köpinge 41 (absolute numbers)	Köpinge 41 (%)
BRYOPHYTA (mosses)				
<i>Cingtriletes scanicus</i>	1	0.3	0	0
<i>Stereisporites psilatus</i>	0	0.0	1	0.3
Total Bryophyta	1	0.3	1	0.3
LYCOPHYTA (club-mosses)				
<i>Camazonosporites</i> sp.	1	0.3	0	0.0
<i>Echinosporis</i> sp.	2	0.7	4	1.3
<i>Retitriletes semimuris</i>	1	0.3	2	0.7
<i>Retitriletes austroclavatifidites</i>	0	0.0	4	1.3
<i>Retitriletes clavatooides</i>	0	0.0	1	0.3
<i>Retitriletes rosewoodensis</i>	0	0.0	2	0.7
Total Lycophyta	4	1.3	13	4.3
FILICOPHYTA (ferns)				
<i>Cibotiumspora juriensis</i>	0	0.0	4	1.3
<i>Cyathidites australis</i>	27	9.0	52	17.3
<i>Cyathidites minor</i>	40	13.3	42	14.0
<i>Concavisporites</i> sp.	1	0.3	0	0.0
<i>Deltoidospora toralis</i>	12	4.0	21	7.0
<i>Gleichenidiites senonicus</i>	6	2.0	13	4.3
<i>Laevigatosporites ovatus</i>	3	1.0	4	1.3
<i>Marattiasporites scabratus</i>	0	0.0	1	0.3
<i>Osmundacidites wellmanii</i>	1	0.3	0	0.0
<i>Pilosporites</i> sp.	1	0.3	0	0.0
Total Filicophyta	91	30.3	137	45.7
Total spores	96	32	151	50
GYMNOSPERMS				
<i>Alisporites thomasi</i>	8	2.7	10	3.3
<i>Araucariacites australis</i>	2	0.7	10	3.3
Bisaccate pollen spp.	7	2.3	12	4.0
<i>Callialasporites dampieri</i>	0	0.0	1	0.3
<i>Cedripites</i> sp.	13	4.3	4	1.3
<i>Chasmatosporites apertus</i>	4	1.3	0	0.0
<i>Circulina parva</i>	5	1.7	0	0.0
<i>Classopollis</i> sp.	22	7.3	11	3.7
<i>Eucommiidites troedsonii</i>	0	0.0	6	2.0
<i>Ginkgo/Cycadopites</i>	5	1.7	2	0.7
<i>Parvisaccites radiatus</i>	0	0.0	5	1.7
<i>Perinopollenites elatoides</i>	27	9.0	31	10.3
<i>Pinuspollenites minimus</i>	10	3.3	4	1.3
<i>Podocarpidites ellipticus</i>	7	2.3	5	1.7
<i>Quadraeculina anellaeformis</i>	9	3.0	2	0.7
<i>Sciadopitipollenites megaorbiculus</i>	12	4.0	2	0.7
<i>Spheripollenites subgranulatus</i>	2	0.7	0	0.0
<i>Vitreisporites bjuvensis</i>	3	1.0	6	2.0
Total gymnosperms	136	45.3	111	37.0
ANGIOSPERMS				
<i>Alnipollenites verus</i>	0	0.0	1	0.3
<i>Comptoniapollenites</i> sp.	0	0.0	1	0.3
<i>Ilexpollenites</i> sp.	1	0.3	0	0.0
<i>Liliacidites variegatus</i>	4	1.3	2	0.7
<i>Monocolpites</i> sp.	5	1.7	0	0.0
Normapollens – <i>Extremipollis caminus</i>	6	2.0	7	2.3

(Continued)

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Table 2. Continued.

	Köpinge 23 (absolute numbers)	Köpinge 23 (%)	Köpinge 41 (absolute numbers)	Köpinge 41 (%)
Normapollens – <i>Trudopollis variabilis</i>	4	1.5	7	2.3
Normapollens – <i>Trudopollis</i> sp.	2	0.5	0	0
<i>Platanuspollenites</i> sp.	1	0.3	0	0
<i>Tricolpites psilatus</i>	9	3.0	11	3.7
<i>Tricolpites reticulatus</i>	12	4.0	6	2.0
Total angiosperms	44	14.7	35	11.6
ALGAE				
<i>Botryococcus braunii</i>	21	7.0	2	0.7
<i>Michrhystridium</i> sp.	3	1.0	0	0.0
Other	0	0.0	1	0.3
Total algae	24	8.0	3	1.0
Total counts	300	100%	300	100%

- v. 1880 *Dewalquea haldemiana* Sap. & Mar. var. *angustifolia*; Hosius & von der Marck 1880: 173; pls 33: 116–117, 34: 118–121.
- 1881 *Dewalquea nilssonii* (Brongniart) Nathorst: 84 [*nom. illegit.*]
- ? 1883 *Dewalquea haldemiana* Sap. et Mar. – Heer: 37; pl. 55, figs 19a, 20; pl. 62, figs 2–4.
- 1884 *Dewalquea Nilssonii* – Moberg: 35.
- v. 1907 *Dewalquea haldemiana* Sap. et Mar.; Nowak 1907: 53; pl. 1, figs 7, 13.
- v. 2013 *Debeya haldemiana* (Debey ex de Saporta & Marion, 1873) Knobloch, 1964 – Halamski: 422, figs 7B, G, 8, 9C, D, E, 10C.
- v. 2013 *Debeya* (*Dewalquea haldemiana*) (Debey ex de Saporta & Marion, 1873) Halamski 2013 – Halamski & Kvaček: 83, text-fig. 1.

Material. Köpinge: S083947, 083948, 083957–083963, 083968–083971, 083975–083979, 084005, 084016, 084018, 084021–084027, 084031–084033, 084035, 084040, 084041, 084058, 084077, 084078, 084091, 084099, 0840101, 0840103, 0840115, 0840117, 0840123, 0840124, 0840126, 0840127, 0840129, 0840138, 0840139, 0840142, 0840143, 0840150, 0840151, 0840158, 084165, 084187–084195, 0840197–0840202, 0840205, 085090, 085091, 085098, 166107, 166297, 166123, 166124, 166126, 166128, 166114, 166116, 166121–166122, 166127, 166129, 166131, 166134–166136, 166139, 166140, 166142–166144, 166147, 166155–166158, 166163–166164, 166179, 166180, 166182.

Ingelstorp: S083913, 083914, 083920.

Tosterup: S166173.

Description. Leaves pedately compound, with presumably from five to nine leaflets. Petiole 20–25 mm long, relatively slender, weakly enlarged proximally. Leaflets subsessile, linear, usually 4–10 mm wide (maximum recorded width 16 mm), total length unknown (exceeding 9 cm in a leaflet 4 mm wide). Base cuneate, apex not preserved. Margin entire. Midvein straight, strong; secondaries generally not preserved, brochidodromous, subopposite, excurrent; tertiaries observed in two specimens (Fig. 5h), leaving the proximal side of secondaries at a right angle.

Remarks. *Debeya haldemiana* is by far the most common plant species in the material studied. The specimens are usually leaflets showing no organic connection, only rarely do they represent incomplete leaves (apical parts always lacking). In comparison to other localities from which this species was reported (Haldem, Potylicz), the striking feature of the Köpinge material is the common occurrence of small leaves (up to 4 mm in width compared with presumably adult leaves 10 mm or more wide).

Debeya from Köpinge was first mentioned and illustrated (without formal description) by Nilsson (1824). The name *Cycadites Nilsonii* was first published by Sternberg (1825, in 1820–38, p. XXXII; pl. 47, fig. 1) for a Late Triassic or Early Jurassic cycadophyte (holotype: S087452; correct name: *Nilssonia brevis* Brongn.; Brongniart (1824, p. 218); Sternberg's name is thus a *nomen illegitimum*, Kvaček & Straková (1997, p. 109)). The same name (spelt *Cycadites Nilsonii*) was then published by Brongniart (1828, p. 204) in a synoptic table of Cretaceous plants from various localities. An indication of the locality and the collector was



Fig. 8. Selected pollen and spores from samples SO89754 and SO89755 from the early Campanian Köpings mälla locality. Specimens listed as: taxa, sample number and slide number, and England Finder Reference (EFR), scale bars are 10 μm . (a) *Cingutrites scanicus*, NRM S089755-1, EFR-V32. (b) *Gleicheniidites senonicus*, NRM S089754-1, EFR-U28. (c) *Cyathidites australis*, NRM S089755-1, EFR-S32. (d) *Pilosisporites* sp., NRM S089754-1, EFR-T13. (e) *Vitreisporites bjuvensis*, NRM S089755-1, EFR-V34. (f) *Chasmatosporites apertus*, NRM S089755-2, EFR-S30. (g) *Perinopollenites elatoides*, NRM S089754-2, EFR-U32. (h) *Araucariacites australis*, NRM S089755-1, EFR-R33. (i) *Alisporites thomasi*, NRM S089754-2, EFR-O23. (j) Normapollens: *Trudopollis* sp. NRM S089754-2, EFR-V34. (k) Normapollens: *Trudopollis variabilis*, NRM S089755-1, EFR-X47. (l) *Comptoniapollenites* sp. NRM S089755-2, EFR-R32. (m) *Tricolpites reticulatus* NRM S089755-2, EFR-V36. (n) *Tricolpites reticulatus* NRM S089755-1, EFR-V34. (o) Normapollens: *Extremipollis caminus* NRM S089754-1, EFR-T28. (p) Normapollens: *Extremipollis caminus* (undeveloped), NRM S089754-1, EFR-U28. (q) Normapollens: *Trudopollis* sp. NRM 23-1, J32. (r:1) *Platanuspollenites*. (r:2) NRM S089754-1, EFR-T38.

given, but neither diagnosis nor description: it might be a matter of contention as to whether such a reference to a previous illustration is sufficient for this name to be valid, had it not been preoccupied by Sternberg's illegitimate name (Brongniart's name is, in any case, a homonym). The diagnosis and figure of the Cretaceous angiosperm described as *Cycadites Nilssonii* was first published by Nilsson

(1832), with authorship credited to Brongniart. The conclusion about the identity between *Cycadites nilssonii* and *Dewalquea haldemiana* was presented by Nathorst (1881, pp. 83–84), who also introduced the combination *Dewalquea nilssonii* (Nathorst, 1881, p. 84). Heer cited Nathorst's paper in an appendix to the second part of his Greenland flora monograph (Heer 1883, p. 274): in the

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main text, he used the name *D. haldemiana* (at least a large part of his material from Greenland being not conspecific with the plant from Köpings and Hal-dem). In the index to the aforementioned work, Heer (1883, p. 268) made a *lapsus calami*, misspelling the name as *D. nielsenii*. This error was repeated by van der Burgh (2008, p. 12), who moreover misattributed the authorship of the combination *Dewalquea nilssonii* to Heer. The name *Dewalquea nilssonii* was mentioned by Lundgren (1885, p. 84). In summary, the name *Cycadites nilssonii* Brongn. was preoccupied by *Cycadites nilssonii* Sternb. and thus is illegitimate, so the correct name for the discussed taxon is *Debeya* (*Dewalquea*) *haldemiana*.

Order **Fagales** Engler, 1892 *sensu lato*
Family unknown

Genus *Dryophyllum* (Debey *ex de* Saporta, 1865)
Jones, Manchester & Dilcher, 1988

Type species. Dryophyllum subcretaceum Debey *ex de* Saporta, 1865. Sézanne, France; Eocene.

cf. Dryophyllum sp.
(Fig. 7d, f)

Material. S084140, 085096 (part and counterpart).

Description. The single available specimen is an incomplete leaf (basal region lacking; preserved length *c.* 7 cm). Leaf size microphyll (estimated total length *c.* 10 cm, estimated total width *c.* 4 cm, thus a length to width ratio of *c.* 2.5), shape elliptical. Base not preserved, apex acute. Margin serrate, teeth regular, 2–3 per cm. Venation pattern pinnate; secondaries craspedodromous, spaced at approximately 5–9 mm, spacing irregular and asymmetric, departure angle 30°–60°.

Remarks. This specimen is compared to *Dryophyllum* (as emended by Halamski & Kvaček 2015) on account of its elliptical shape, pinnate craspedodromous venation and asymmetry of the secondaries, suggesting that it is, in fact, a leaflet of a pinnately compound leaf. However, interpretation of the single poorly preserved specimen is equivocal at best.

Supersubclass, subclass, order and family unknown
Form group **Platanofolia** Krassilov 1979

Genus *Ettingshausenia* Stiehler, 1857

Type species. Credneria cuneifolia Bronn, 1835–37; Upper Cretaceous, Cenomanian, Niederschöna, Saxony, Germany.

Ettingshausenia sp.
(Fig. 6b–e)

Material. Köpings: S084034.

Rödmölla: S084206, 084207, 084210, 084211.

Högestad: S166107.

Tosterup: S166202, 166203.

Description. Leaves entire-margined or with few teeth, trilobate with lobes poorly developed. The fragments vary in size, the smallest being 40 × 20 mm and the largest over 50 mm wide, suggesting that complete leaves were relatively small (*c.* 7 cm in width and length). Leaf lamina obovate. Apex acute (Fig. 6e); base probably cuneate as fragmentarily preserved (Fig. 6c). Lobes very small (Fig. 6e) or nearly absent (specimen S084207). Petiole preserved in a single specimen (Fig. 6d).

Venation palmately pinnate semibrochidromous. Midvein stout, terminating in the leaf apex. Two pairs of suprabasal secondary veins emerging obliquely from the midvein. No infrabasal secondary vein. Secondaries semibrochidromous (Fig. 6e). Tertiary veins prominent, straight or slightly curved, percurrent.

Remarks. The studied material is very similar in general venation style and size to *Ettingshausenia gruenbachiana* Herman & Kvaček, 2010 from the lower Campanian of Grünbach. It differs in its more angular leaf form and less pronounced lobes. The studied material differs from *Ettingshausenia? lublinensis* (Karczmarz & Popiel, 1971) Halamski, 2013 from the late Campanian of Poland in having an entire-margined lamina without any strongly pronounced lobes. *Ettingshausenia* sp. differs from *Ettingshausenia onomasta* (Bayer, 1896) Kvaček & Halamski in Halamski & Kvaček 2015 from the Coniacian of Idzików in having more pronounced tertiary venation and less pronounced lobes.

Form group **Viburnifolia** Krassilov, 1979

Genus *Rarytkinia* Vassilevskaya & Golovneva in
Golovneva & Abramova 1990

Type species. Rarytkinia terehovae Vassilevskaya & Golovneva in Golovneva & Abramova 1990; Rarytkin Formation, upper Maastrichtian–Danian, Koryak Upland, NE Russia.

Rarytkinia? sp.
(Figs 1a & 7g)

Material. Köpings: S083988, 083990, 085092–085093 (part and counterpart), 085099.

Description. Blade attachment marginal, laminar size mesophyll (two fragmentary specimens are 10 cm long, the estimated total length is thus about 15 cm), estimated laminar length to width ratio of approximately 2.5, laminar shape unknown, possibly either elliptical or ovate. Base and apex unknown.

Primary venation pinnate, possibly craspedodromous. In the basal region, a secondary vein departing at 65° is evident; more distally, secondaries depart at 45°–55°, excurrent. Spacing of secondaries irregular, 1–2 cm between successive veins; intersecondaries absent. Margin not preserved.

Remarks. This leaf is tentatively ascribed to *Rarytkinia* on the basis of its large size and the departure angle of the secondary veins being significantly high in the basal region, but low and constant in the rest of the leaf. A coeval representative of the genus is the insufficiently known *Rarytkinia polonica* (Karczmarz & Popiel) Halamski from eastern Poland (Halamski 2013), which differs from the form described here in its wider shape and denser secondaries. Some leaves in the collection are labelled '*Protophyllum suecicum* Nath. mscr.', but this name has never been published and, thus, has no nomenclatural status; the available material is insufficient for a formal description.

Form group unknown

Genus *Dicotylrophyllum* auct.

Type species. Unknown (see Halamski 2013, pp. 429–430).

Remarks. *Alnites* Hisinger is a synonym of *Alnites* Goepfert (1836, p. 564, pl. 41, figs 1–7 – type *Alnites kefersteinii* Goepfert), which is recognized as a member of the genus *Alnus* – *Alnus kefersteinii* (Mai & Walther, 1978) and thus seems inappropriate for our material. *Alnites* Deane (1902) from the Tertiary of Australia is another synonym. The most appropriate genus to accommodate these Skåne leaves appears to be *Dicotylrophyllum*, based on their few generalized characters.

Dicotylrophyllum friesii (Nilsson, 1832) comb. nov. (Fig. 7a–c, e)

*1832 *Phyllites* (*Alnus*? *Friesii*) – Nilsson: 346; pl. 1, figs 7.

1837 *Alnites*? *Friesii* Nilss. – Hisinger: 112; pl. 34, fig. 8 [copy from Nilsson 1832]

Neotype. S084030 from Köpinge (selected herein).

Basionym. *Phyllites friesii* Nilsson, 1832, p. 346, pl. 1, figs 7.

Material. Köpinge: S083980.

Description. The available material consists of leaf fragments, one representing the basal and median regions of the lamina, and the other the apical region: the base and apex themselves, however, were not preserved. Leaf elliptical, estimated length of approximately 8–10 cm, estimated width approximately 2 cm. Midvein straight. Secondary

veins partly decurrent and partly excurrent (Fig. 7e), alternate, angle decreasing from c. 60° in the basal region through to c. 40° in the middle of the lamina to c. 30° in the apical region; spacing irregular. Margin serrate with one order of teeth and three teeth per cm; teeth short, proximal side convex, distal side weakly concave.

Remarks. In the absence of the holotype, the interpretation of the simple description and somewhat schematic figure given by Nilsson (1832) is not easy. However, the finely serrate ('*subcrenatus*') margin and the elliptical shape make the conspecificity of the material described here with Nilsson's species probable. A neotype is selected to fix the usage of the species name.

Genus *Salicites* Hisinger, 1837

Type species. *Phyllites wahlbergii* Nilss.; Köpinge, Skåne; Campanian.

Emended diagnosis. See Halamski & Kvaček (2015).

Salicites wahlbergii (Nilsson, 1832) Hisinger, 1837 (Fig. 1b)

*1832 *Phyllites* (*Salix*? *Wahlbergii*) – Nilsson: 345; pl. 1, figs 5, 6.

1837 *Salicites*? *Wahlbergii* Nilss. – Hisinger: 112; pl. 34, fig. 9 [copy from Nilsson 1832]

Neotype. S084155 from Köpinge (selected herein).

Material. Köpinge: S084000, 084001, 084011, 084185.

Description. Blade attachment marginal, leaf petiolate. Laminar size microphyll (maximum preserved length c. 60 mm). Laminar shape elliptical, asymmetrical. Base and apex weakly convex. Margin entire. Venation pattern pinnate, midvein straight; secondaries weak brochidodromous, excurrent, spacing slightly irregular, departure angle 40–60°; higher-order venation not preserved.

Remarks. Again, the interpretation of Nilsson's species in the absence of types is not easy. However, the absence of teeth and the irregular spacing of secondary veins is consistent with the figure in the protologue.

Class **Monocotyledoneae**

Monocotyledoneae ord., fam., gen. et sp. indet. (Fig. 6a)

Material. Köpinge: S084048, 084051 (part and counterpart).

Description. The single available specimen consists of two leaf fragments on a single rock sample, one fragment is approximately 17 mm long and 5.5 mm

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wide, and the other is approximately 15 mm long and 8 mm wide. The margins of the smaller fragment run parallel to each other; four parallel veins are present in the specimen. The larger fragment preserves only one margin and six parallel veins.

Remarks. The parallel venation allows a reasonably secure placement within monocots; no more detailed systematic analysis is possible given the fragmentary state of the specimen. Parallel veins without any forking distinguishes it from most cycad or bennettite foliage, which have forked veins.

Palynology

Well-preserved palynological assemblages were recovered from two samples: 47 miospore taxa were recorded, of which 18 taxa constitute spores, 18 gymnosperm pollen and 11 angiosperm pollen. In addition, the freshwater alga *Botryococcus* occurs in both samples. Most taxa in these samples are long ranging with a mix of typical Jurassic holdovers, such as representatives of *Cyathidites*, *Classopollis*, *Perinopollenites*, *Araucariacites* and *Alisporites*, together with typical Late Cretaceous angiosperm pollen. The relatively high abundance of tricolpate and periporate angiosperm pollen (up to 15%) including Normapolles and *Alnipollenites* sp. (Table 2) suggests an age not older than Campanian and not younger than Maastrichtian, which is consistent with previous age determinations.

Sample NRM S089754

Sample NRM S089754 derives from the Köpings locality and consists of fine-grained calcareous sandstone, and the organic residue yielded 32 species of pollen and spores (Table 2). The 11 spore taxa constitute 32% of the assemblage, the 15 gymnosperm pollen taxa represent 46% and the nine angiosperm pollen taxa embody 15%. In addition, the freshwater alga *Botryococcus* reaches 7% abundance. The spore component is highly dominated by the trilete fern spore *Cyathidites* (23%). Individual bryophyte and lycophyte taxa do not reach 1%. The gymnospermous component is represented by two important genera, *Perinopollenites elatoides* (9%) and *Classopollis* sp. (7%), but several other taxa reach significant levels (3–4% or above) (e.g. *Cedripites*, *Sciadopitys*, *Pinuspollenites*, *Araucariacites* and *Alisporites*) (Table 3).

Palynofacies. The microscopic organic matter in this sample is dominated (56%) by non-marine palynomorphs and phytoclasts (pollen, spores, wood remains, leaf cuticle and *Botryococcus*): the rest is represented by dinoflagellates (17%) and AOM

Table 3. *Palynofacies results, relative abundance expressed in % of the abundance of individual palynofacies groups calculated from samples NRM S089754 and NRM S089755*

Palynofacies groups	Köpinge NRM 23	Köpinge NRM 41
Spores	12	11
Pollen	15	27
Cuticle	2	2
<i>Botryococcus</i>	2	0
Wood	25	40
Dinoflagellates	17	4
AOM	27	16
Total	100%	100%

(27%: Table 3). No charcoal was identified. The kerogen sample indicates a thermal alteration index (TAI) of 2+, equivalent to 5 on the spore colour index (SCI) chart.

Sample NRM S089755

Sample NRM S089755 consists of fine-grained sandstone to siltstone. It yielded 33 pollen and spore taxa (Table 2). The spores are represented by 13 taxa and constitute 46% of the assemblage, gymnosperm pollen grains are represented by 15 taxa and attain 37%, and angiosperm pollen (c. 12%) are represented by seven taxa.

As in the previous sample, the spore assemblage is strongly dominated by *Cyathidites* (31%), followed by *Deltoidospora* and *Gleicheniidites senonicus* (Table 2). In this sample, lycophyte spores reach over 4% and are represented mainly by *Retitriletes*. The relative abundance of the various gymnosperm taxa is more evenly distributed in this sample compared to NRM S089754, and *Perinopollenites elatoides* dominates with 10%, followed by unidentified bisaccate pollen grains, *Classopollis*, *Alisporites* and *Araucariacites*: all reach relative abundances of about 3%.

Palynofacies. The organic matter in this sample is also dominated by non-marine palynomorphs, but at the significantly higher relative abundance of 80%. Dinoflagellates reach only 4% in this sample, and AOM typical of marine environments reaches only 16% (Table 3). The kerogen sample indicates a TAI of 2+, equivalent to 5 on the SCI chart.

Summary and discussion

Palaeoecology

The Köpings flora was unequivocally preserved in a near-shore marine environment, as evidenced by the

significant dinoflagellate component in the palynological assemblages and the co-occurrence of abundant marine invertebrates together with the leaf fossils (Fig. 2c). Despite the evidently allochthonous character of the described fossil flora, analogies to better-preserved fossil assemblages allow some general remarks on the Skåne Campanian plant communities. The angiosperm *Debeya haldemiana* dominates the macroflora in the available collection (Table 1). The apparent dominance of *Debeya haldemiana* may be biased by the fact that even small fragments of these distinctive leaves may be identified, whereas scraps of other angiosperm leaves cannot. However, even if the true percentage of fossils belonging to this species is perhaps lower, its dominance in the studied assemblage is undeniable. The abundance of *Debeya haldemiana* in marine sandstones at Köpinge suggests that this species dominated a coastal lowland forest similar to those described from the Cenomanian of Crimea and the Late Cretaceous 'Senonian' of Sakhalin by Krassilov (1979, 1984; *Debeyo-Dryophylletum sensu* Krassilov, 1997).

Within the palynoflora, however, the gymnosperm pollen grains and the fern spores dominate, which is to be expected as these are wind dispersed and have a much higher spore/pollen production compared to angiosperms, which commonly are insect pollinated. The angiosperm pollen is well represented in the palynoflora, but *Debeya* pollen is unknown, so no palynomorph can be linked to these megafossils. The fern component is visible in both the spore and the megafloral record.

The local abundance of *Perinopollenites elatoides* (pollen assigned to Cupressaceae) and *Classopollis* (pollen attributed to Cheirolepidiaceae) does not show an obvious link to the local megaflora. Although *Perinopollenites* might be affiliated with the relatively abundant *Pagiophyllum*, the producers of the *Classopollis* grains are uncertain. *Classopollis* derives from cheirolepidiacean conifers, particularly *Frenelopsis*, which typically occurs in Late Cretaceous marine-influenced habitats (Uličný *et al.* 1997). This type of conifer is characteristic of Late Cretaceous halophytic habitats (Uličný *et al.* 1997; Kvaček 2000). However, megafossils of *Frenelopsis* were not recorded in the Swedish assemblages. This could be due to their lower fossilization potential compared, for example, to *Pagiophyllum* (cf. Riera *et al.* 2010). Alternatively, *Classopollis* might be affiliated with non-frenelopsid cheirolepids, which could conceivably include some species of *Pagiophyllum* or similar awl-shaped coniferous foliage (e.g. *Otwayia* Pole, 2000) based on foliar anatomical characters and associated pollen from both the northern and southern hemispheres (Pole 2000; van der Ham *et al.* 2003; Tosolini *et al.* 2015).

By contrast, *Ettingshausenia* sp., known from a single leaf fragment at the richest locality of Köpinge and from more numerous specimens at Rödmölla and Tosterup (localities closer to the Palaeozoic plateau (Fig. 1c) and, arguably, to the Cretaceous shoreline), is best interpreted as a tree of riparian forests, as generally interpreted for platanoids (Doyle & Hickey 1976; Upchurch *et al.* 1994; Wing & Boucher 1998; Wing 2000; Coiffard *et al.* 2006).

It is problematic to link the angiosperm pollen taxa to the megaflora from the Köpinge site and currently we can only speculate. Monocolpate, reticulate *Liliacidites* pollen (monocotyledonous) is present in the palynoflora, but more abundant are representatives of the Normapolles Group, which make up 12–14% of the miospore assemblages yet are only represented by four taxa. Normapolles is a very diverse group with over 100 described species that had their greatest diversity during the Santonian and Campanian within the northern hemisphere (Skarby 1968; Friis *et al.* 2006, 2011), but were affected by the Cretaceous–Palaeogene mass extinction event, during which the group lost its diversity (Vajda & Bercovici 2014). The only extant plant-producing Normapolles-like pollen is *Rhoiptelea* (Friis *et al.* 2011) within Rhoipteleaceae, Fagales – an order that is represented within the megaflora at Köpinge.

Palaeobiogeography

The Campanian flora of southern Skåne may be compared with three approximately coeval floras: from eastern Poland and western Ukraine (mainly late Campanian: Halamski 2013); from Grünbach in Austria (early Campanian: Kvaček & Herman 2004; Herman & Kvaček 2010); and from Haldem in Westphalia (Hosius & von der Marck 1880), even if only the first two have been revised recently. *Debeya haldemiana* is a species shared between the floras of Skåne and Poland–Ukraine (although it is not so abundant in the latter regions). Other shared genera (but probably represented by different species) include *Ettingshausenia*, and probably also *Rarytkinia* and *Korallipteris*. *Debeya haldemiana* is also shared with the Haldem flora (see Halamski & Kvaček 2013), whereas cf. *Dryophyllum* sp. from Skåne is quite similar to the leaves reported by Hosius & von der Marck (1880) as species of *Quercus*. It is also notable that *Ettingshausenia* and probably *Korallipteris* occur at Haldem (Hosius & von der Marck 1880, pls 38–39, 42, fig. 176ff). Distinct similarities between these three floras (Skåne, Poland–Ukraine and Westphalia) reflect analogous palaeoecological settings within the same palaeoclimatic (palaeovegetation) zone. By contrast, the flora described herein is very different

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from that at Grünbach, which constitutes a thermophilic assemblage from a wet environment.

A comparison between the studied flora and an older (Coniacian) assemblage from the Sudetes (localities Idzików/Kieslingswalde and Nowy Waliszów/Neuwaltersdorf: Halamski & Kvaček 2015; Kvaček *et al.* 2015) shows that *Korallipteris* (earlier described as *Microphyllopteris*), *Debeya*, *Ettingshausenia*, *Dryophyllum* and *Salicites* are common to both floras, possibly reflecting similar palaeoecological conditions. *Ettingshausenia* is characteristic of Late Cretaceous floodplain vegetation (Kvaček & Herman 2004; Greguš & Kvaček 2015). The abundance of conifers in the Köpings assemblage favours a source from a floodplain swamp vegetation. The occurrence of *Classopollis* pollen reflects a contribution from halophytic vegetation in the region, although macrofossil elements of this community are not obviously represented in the Skåne megafloora.

Palaeoclimatic inferences based on six dicotyledonous angiosperm taxa can be only very general. However, the approximately equal abundance of entire-margined and serrate/dentate taxa in the studied flora (3:3 if *Ettingshausenia* sp. is counted as entire-margined and 2:4 if it has a dentate margin) suggests an intermediate character of the vegetation between thermophilic and polar floras. This aspect is consistent with the coeval assemblages from Poland and Ukraine (Halamski 2013, p. 435). The palaeovegetation of a broad transitional zone situated in the European archipelago between approximate palaeolatitudes of 40–45° N (Poland) and 45–50° N (Skåne) thus seems to have been relatively uniform.

Conclusions

- Campanian marine calcareous sandstones from the Vomb Trough in southern Skåne (main locality: Köpings) yielded a relatively low-diversity vascular flora with one fern, three conifer species (one cone scale and two foliage taxa), six dicotyledonous angiosperms and one monocot angiosperm.
- A well-preserved miospore assemblage was recovered from the same sediments as the megafloora, and 47 pollen and spore species were identified. In terms of abundance, the palynoflora is dominated by *Cyathidites* spores and gymnosperm pollen related to taxodiaceous Cupressaceae. Furthermore, angiosperm pollen is of relatively high diversity and, in terms of abundance, is mainly represented by pollen belonging to the Normapolles complex.
- The megafossil assemblage is quantitatively dominated by the angiosperm *Debeya* (*Dewalquea*) *haldemiana* (Deb. *ex Sap.* & Marion)

Halamski [= *D. nilssonii* (Brongn. *ex Nilsson*) Nath. non Sternberg, 1824], which constitutes up to 90% of the specimens. The conifer *Pagiophyllum* sp. is also a relatively abundant element of the flora.

- Neotypes of *Dicotylophyllum friesii* (Nilsson, 1832) comb. nov. and *Salicites wahlbergii* (Nilsson, 1832) Hisinger, 1837 are selected.
- The palaeoenvironment is interpreted on the basis of the mega- and palynoflora to represent a nearshore, possibly lagoonal, setting. This is more specifically corroborated by the relatively high abundance of dinoflagellates, together with the freshwater to brackish-water alga *Botryococcus* (which favours calm environments). The angiosperm *Debeya haldemiana* is interpreted as having formed coastal lowland forests.
- The described flora is broadly similar to the approximately coeval assemblages from analogous palaeocommunities described from eastern Poland and western Ukraine (Halamski 2013) and Westphalia (Hosius & von der Marck 1880).

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