

## Seagrass foliage from the Maastrichtian type area (Maastrichtian, Danian, NE Belgium, SE Netherlands)

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Received 17 November 2005; received in revised form 3 July 2006; accepted 5 July 2006

Available online 18 September 2006

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### Abstract

Seagrasses are the only angiosperms that have invaded the marine environment. Fossil seagrasses are rare and received only little attention to date. However, among the scarce plant fossils in the marine deposits of the Maastrichtian type area, remains of seagrasses are relatively common. The present paper provides a detailed description of the morphology and anatomy of the leaves. Maastrichtian and Danian material is considered here as a single species: *Thalassotaenia debeyi* gen. nov., sp. nov. Campanian material is assigned to *Zosterites*, but this is not necessarily a seagrass. *Thalassotaenia* includes the oldest anatomically preserved material of seagrass leaves. Comparison with extant seagrasses shows that there is not an easy match with any of the extant genera or families. *Amphibolis* and *Thalassodendron* (Cymodoceaceae) and *Posidonia* (Posidoniaceae) show the greatest resemblance. Possibly, *Thalassotaenia* represents the leaves of an ancestor of the Cymodoceaceae–Posidoniaceae (–Ruppiaceae) clade found in several phylogenetic analyses. Because *Thalassotaenia* also shows some features not found in extant seagrasses, it might also represent an extinct clade of seagrasses. © 2006 Elsevier B.V. All rights reserved.

**Keywords:** seagrass leaves; Cymodoceaceae; Posidoniaceae; *Thalassocharis*; Maastrichtian

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### 1. Introduction

Worldwide, seagrass communities are important ecosystems in relatively warm, shallow seas (Green and Short, 2003). They are well-known for their high biodiversity and over the last decades there has been a lot of research into many aspects of seagrass biology and ecology (e.g. Brasier, 1975; Larkum et al., 1989, 2006). Seagrasses are the only angiosperms that have successfully invaded the marine environment. They make up an ecological, polyphyletic group rather than a single taxonomical, monophyletic group, three different clades within the subclass Alisma-

tidae (Monocotyledonae) having been recognised in a rbcL study by Les et al. (1997). Considerable monocot diversification took place during the Early Cretaceous, and seagrasses probably evolved from freshwater monocots during the Late Cretaceous (Janssen and Bremer, 2004).

Fossil seagrasses are rare. The oldest record is from the Early Campanian of the Netherlands: *Thalassocharis mülleri* (Debey, 1848; Pomel, 1849; Debey, 1851), which represents the stem of a seagrass. Voigt and Domke (1955) published an extensive paper on *Thalassocharis bosquetii* Debey ex Miquel from the Late Maastrichtian of the Netherlands, in which they analysed anatomically preserved stems and attached roots, considering these related to those of the extant genus *Cymodocea*. A description of the leaves is lacking so far. They are always found detached

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and incomplete, without base and apex, represented by fragments mostly not longer than a few centimeters, and usually poorly preserved, showing only a faint imprint with indistinct venation. Recently, however, several leaf fragments with remarkable details were discovered by one of us (LJ). These include isolated fragments in chert, showing venation, fiber strands and even cell patterns, as well as the remains of amassed fragments in chert suited for thin-sectioning. This material allows detailed description and statements about the affinity of the seagrass foliage from the Maastrichtian type area (NE Belgium, SE Netherlands).

The present paper is part of the ongoing study of fossil plants from the Maastrichtian type area. Earlier papers dealt with conifers and associated fungi (Van der Ham and Dortangs, 2005, and references therein).

## 2. Material, localities and stratigraphy

The material studied (c. 200 specimens; see Section 4. Systematics and descriptions) was collected in

different parts of the Maastrichtian type area (Fig. 1) and originates from the Early Campanian to Early Danian time interval (Fig. 2).

Two Early Campanian specimens are from the Vaals Formation (*Inoceramus lingua*/*Gonioteuthis quadrata* Zone) of Hallembaye in the southwestern part of the area (Fig. 1: locality 1).

A single Late Maastrichtian specimen is from the Lixhe I Member of the Gulpen Formation (*Belemnitella junior* Zone) of Loën in the southwestern part (Fig. 1: locality 2), while all other Late Maastrichtian material is from several members of the Maastricht Formation (*Belemnitella junior* Zone and *Belemnella kasimiroviensis* Zone) in both the southwestern and the northeastern part of the area. The material from the southwestern part (Fig. 1: localities 1, 3–6) is from the fully marine facies of the Maastricht Formation (Valkenburg to Meerssen Members), while specimens from the northeastern part (Fig. 1: localities 8–20) originate from the Kunrade Chalk, which is the more coastal facies of the Maastricht Formation (Fig. 2). The

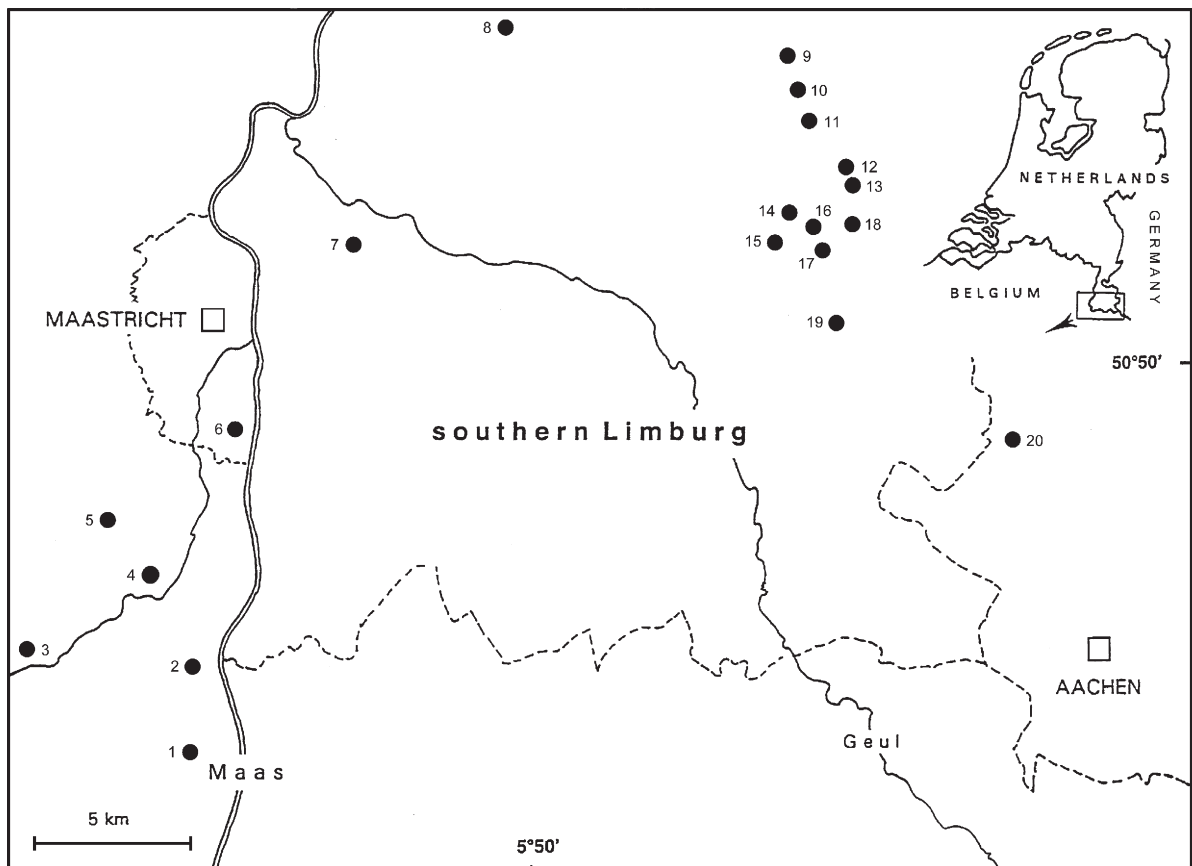


Fig. 1. Map of the Maastrichtian type area, showing the localities where *Thalassotaenia debeyi* has been collected: 1. Hallembaye, 2. Loën, 3. Sluizen, 4. Romontbos, 5. Zichen, 6. ENCI, 7. Geulhem, 8. boring XVI, 9. boring S.M. XIX, 10. Emma I, 11. Oranje Nassau III, 12. boring 634, 13. boring 1291, 14. Kunrade, 15. Winthagen, 16. Welterberg, 17. Daelhoeve, 18. Benzenrade, 19. Simpelveld, 20. Vetschau. Locality 1 (Hallembaye) also provided the material of *Zosterites* sp.

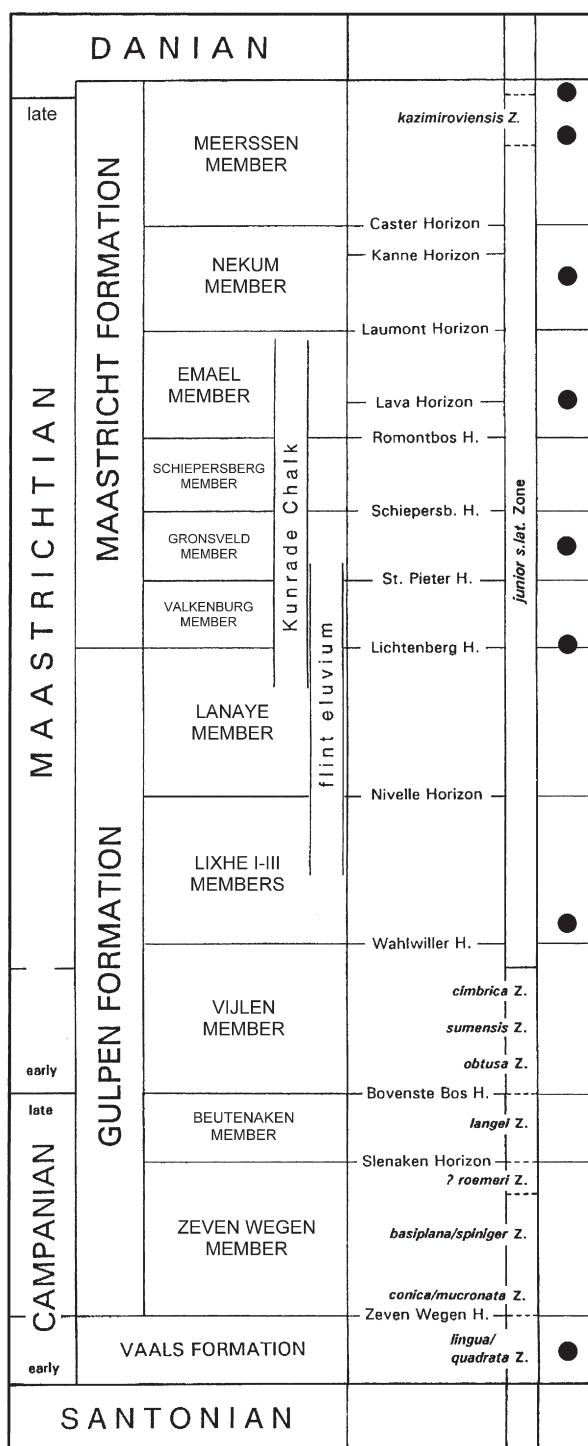


Fig. 2. Stratigraphy of the Cretaceous deposits in the Maastrichtian type area, showing the origin of the material of *Thalassotaenia debeyi* (Gulpen and Maastricht Formations) and *Zosterites* sp. (Vaals Formation). See Jagt (1999) for further stratigraphical details. The dot at the level of the Lichtenberg Horizon represents the specimens from the residual chert deposit ('flint eluvium') of Hallembaye (including the type material) as well as those from the Valkenburg Member, and the dot at the Gronsveld Member, besides those of the Gronsveld Member, also the specimens from the Kunrade Chalk. Besides the residual chert deposit derived from the top of the Lanaye Member and base of the Maastricht Formation (indicated in scheme as 'flint eluvium'), a younger residual chert deposit exists (not indicated in scheme) derived from a part of the Nekum Member.

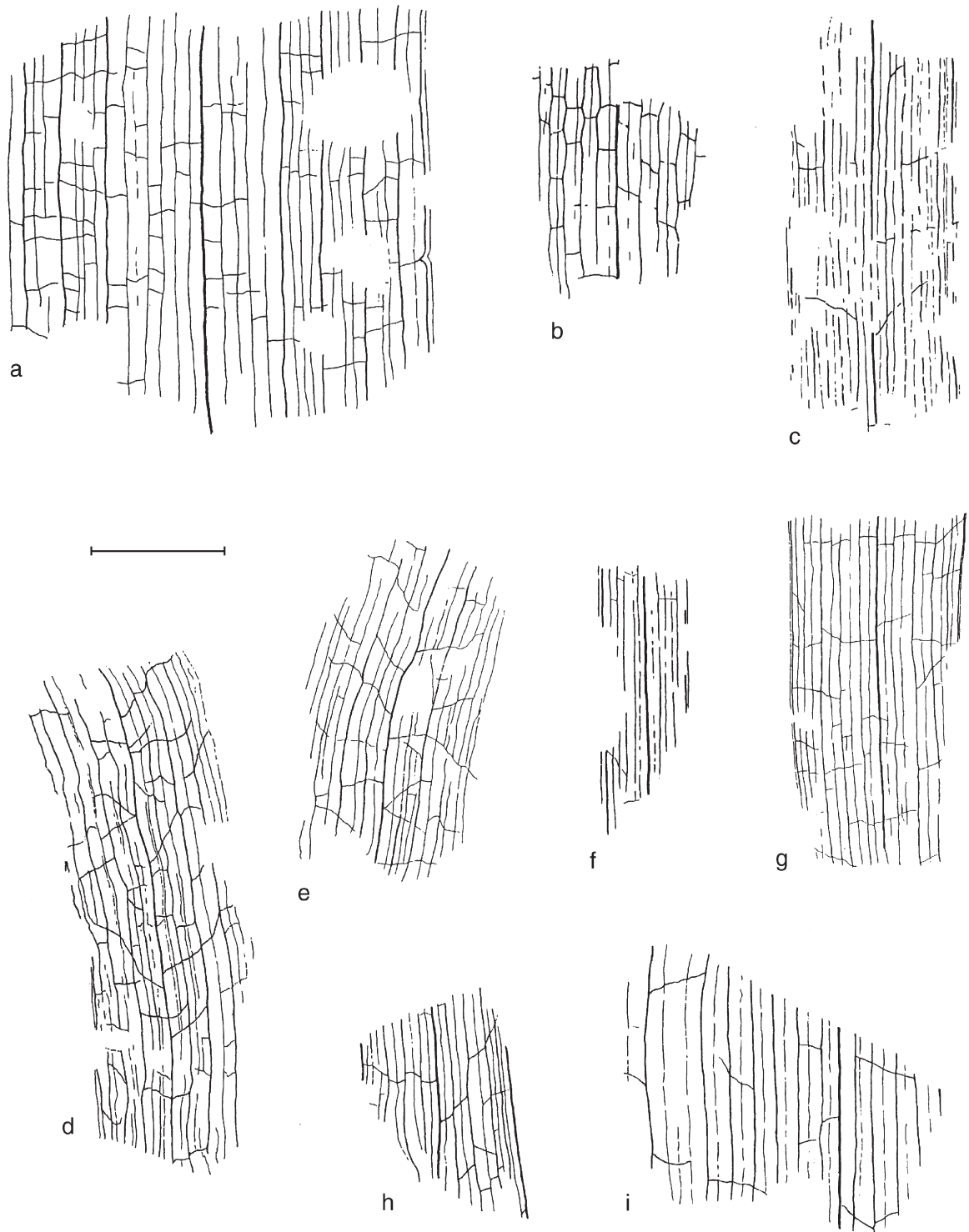


Fig. 3. Selected specimens of *Thalassotaenia debeyi*, gen. et sp. nov., showing veins, alternating fiber strands and cross-veins. a–c. Kunrade Chalk, Emma I, a. JMS 52006 (see also [Plate III](#), 3), b, c. JMS 52067 (see also [Plate III](#), 1). d–e. Residual chert deposit ('flint eluvium'), Hallembaye, NHMM LI 451 and 452, respectively (part and counterpart; type material; see also [Plate I](#), 3, 4); note adaxial and abaxial fiber strands close together in Fig. 3d, immediately right of the midrib. f–g. Kunrade Chalk, Benzenrade, f. JMS 52027 (see also [Plate II](#), 2), g. JMS 52045. h. Nekum Member, residual chert deposit, Sluizen, NHMM LI 4606 (see also [Plate I](#), 2). i. Early Danian part of Meerssen Member, Geulhem, NHMM RH 808. Bar=10 mm (a–e, g–i) or 20 mm (f).

anatomically preserved leaves were found in residual chert deposits ('flint eluvium'), which originated by dissolution of the chalky matrix from the top of the Lanaye Member of the Gulpen Formation and the base of the Maastricht Formation (Hallembaye; Fig. 1: locality 1) and from the Nekum Member (Romontbos quarry and Sluizen; Fig. 1: localities 3, 4).

Early Danian fossils are from the uppermost part of the Meerssen Member of the Maastricht Formation (E clay sensu Smit and Brinkhuis, 1996) of Geulhem (Fig. 1: locality 7).

The following abbreviations are used to denote the locations of the specimens: IRSNB: Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; JMS: Jongmans collection, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; MB.PB.: Museum für Naturkunde der Humboldt Universität, Berlin, Germany; NHMM: Natuurhistorisch Museum Maastricht, The Netherlands (LI: collection Ludo Indeherberge, RD: collection Rudi Dortangs, RH: collection Raymond van der Ham); RGM: Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; U: Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands.

### 3. Methods

Most of the material consists of imprints and silicified leaf fragments in surface views, which did not need any further preparation. One chert specimen (NHMM LI 4171), including the remains of amassed leaf fragments, was thin-sectioned according to the techniques described by Taylor and Taylor (1993, p.19). Light micrographs were taken with a Nikon Coolpix 5200 digital camera on a Leitz Dialux 20 microscope. The scanning electron micrographs were produced with a Jeol JSM-5300, using a Bal-Tec SCD 005 sputter coater and the programme SemAfore (Jeol).

### 4. Systematics and descriptions

There are two different kinds of leaves, the most common type, from the Maastrichtian and Danian, accommodated here in a new genus and species, *Thalassotaenia debeyi*, and leaves from the Early Campanian Vaals Formation, assigned here to *Zosterites*.

#### *Thalassotaenia* Van der Ham et Van Konijnenburg-Van Cittert, gen. nov.

**Generic diagnosis:** Morphotaxon including (fragments of) detached strap-shaped leaves with parallel, longitudinal veins and alternating fiber strands; longitudinal veins connected by cross-veins; middle longitudinal

vein thicker than the others; stomata absent; hypodermis present.

**Etymology:** From Greek *thalassa* (sea) and *tainia* (strap), referring to the shape of the leaves and the environment in which they grew.

**Type:** *Thalassotaenia debeyi* sp. nov.

**Affinity:** Monocotyledonae, ?Cymodoceaceae/Posidoniaceae (see: Section 6. Affinities).

#### *Thalassotaenia debeyi* Van der Ham et Van Konijnenburg-Van Cittert, sp. nov. (Fig. 3; Plates I, 2–4; II; III; IV, 1–3; V, 1–3;)

- 1849 Abdrücke eines najadeenartigen Blattes — Debey, p. 285, 286
- 1851 Najadeenblätter (*Thalassocharis/Zosterites*) — Debey, p. 568
- 1853 ? *phyllitae monocotylei*, 1. — Miquel, p. 53
- 1853 non *phyllitae monocotylei*, 2. — Miquel, p. 53, pl. 1, fig. 3
- 1853 ? *phyllitae monocotylei*, 3. — Miquel, p. 54
- 1859 *Phyllites monocot.* sp. Miquel — Binkhorst van den Binkhorst, p. 61
- 1860 *Phyllites monocotyleus* Miquel — Bosquet, p. 417
- 1885 *Phyllites monocotyleus* Miquel — Ubaghs, p. 28
- 1926 *Phyllites monocotyleus* Miquel — Umbgrove, p. 266
- 1937 lintvormige bladeren — Jongmans and Van Rummelen, p. 33
- 1947 *Phyllites monocotyleus* Miquel — Francken, p. 38–40, 43, 96, 101, 118, 119, 132
- 1981a *Thalassocharis bosqueti* Debey ex Miquel — Voigt, p. 282 (excl. fig. 2A, 2B)
- 1998 *Thalassocharis bosqueti* Debey ex Miquel — Dortangs, p. 100, pl. 3, fig. 5

**Specific diagnosis:** *Thalassotaenia* leaves with 9–15 longitudinal veins; epidermis without distinctly larger or smaller cells; hypodermis cells larger than the epidermis cells, smaller than the underlying parenchyma cells, arranged in a single layer of longitudinal rows.

**Etymology:** Named after Matthias Dominikus Hubert Maria Debey (1817–1884), physician and palaeobotanist at Aachen (Stafleu and Mennega, 1998), who was the first to recognise seagrass foliage in the Maastrichtian type area.

**Type locality:** Former CPL SA quarry near Hallembaye (NE Belgium; Fig. 1: locality 1).

**Type stratum:** The residual chert deposit ('flint eluvium') that originated by dissolution of the chalky matrix from the top of the Lanaye Member and the base of the Maastricht Formation (Late Maastrichtian, *Belemnitella junior* Zone; Fig. 2).

**Type material:** NHMM LI 451 and 452 (part and counterpart, anatomically preserved; Fig. 3d, e; Plate I, 3, 4).

**Additional material:** Late Maastrichtian, Gulpen Formation, Lixhe I Member, Loën: NHMM RH 811. Gulpen or Maastricht Formation, residual chert deposit ('flint eluvium'), Hallembaye: NHMM RH 220. Maastricht Formation, Lichtenberg Horizon, ENCI: NHMM RH 809; Valkenburg Member, ENCI: NHMM 1996103;

Gronsveld Member, ENCI: NHMM RH 810, 812; Kunrade Chalk, boring S.M. XIX: JMS 52005; Emma I: RGM 21679, JMS 52006–52009, 52012, 52062–52078; Kunrade area (Benzenrade, Daelhoeve, Kunrade, Welterberg, Winthagen): JMS 52000–52004, 52014–52061, 52079–52115, 52119–52129, 52139–52167, MB.PB. (Binkhorst collection) 1980/324, NHMM 003634, 004591, 1984136, NHMM RD 30, NHMM RH 783, 805, RGM 21373, 21376b, 21403, 21405, U 462, 1123, 1125; Emael Member, Lava Horizon, Romontbos: NHMM RD 41; Nekum Member, residual chert deposit, Romontbos: NHMM LI 30606-1, 2 (anatomically preserved); Sluizen: NHMM LI 4606, 4174 (both anatomically preserved); Meerssen Member, ENCI: Renkens 52105; member unknown, Maastricht: IRSNB Ubaghs 385, 387, 390, RGM 27764; Zichen: IRSNB Ubaghs 386. Early Danian, Maastricht Formation, Meerssen Member, Geulhem: NHMM RH 807, 808. *Literature records*: Vetschau (Debey, 1849), Oranje Nassau III (Umbgrove, 1926), borings 634, 1291 and XVI, and Simpelveld (Francken, 1947), probably all from Kunrade Chalk.

*Stratigraphical range*: Late Maastrichtian to Early Danian.

*Morphology*: Leaf fragments (imprints) strap-shaped, with parallel margins. Length of fragments up to 16.6 cm, though leaves up to 1 m, without base and apex, are

known from field observations (Jongmans and Van Rummelen, 1937); width 3.5–32 mm (Figs. 3a, f, and 4). Margins entire. Several specimens show a tapering leaf fragment that might represent a near-basal part (Plate II, 3). Apex unknown. Veins (9–)11(–15), parallel, connected by perpendicular to oblique cross-veins (Fig. 3). Middle vein, and usually both marginal veins (e.g. Plate I, 2), relatively distinct. Narrow leaves (up to c. 20 mm) seem to have relatively thick marginal veins and about oblique cross-veins (e.g. Fig. 3c–e, h, Plate III, 3, 4), and wide leaves (c. 20–32 mm) indistinct marginal veins and about perpendicular cross-veins (e.g. Fig. 3a, b, i, Plate IV, 1). Fiber strands parallel to and alternating with the veins, often hard to discern from the veins. There are usually two superposed fiber strands between each two adjacent veins (Fig. 3d), one adaxial and one abaxial. In wide leaves there seem to be more than two fiber strands between adjacent veins, but possibly some of them are minor veins. Several of the anatomically preserved leaf fragments show more details of the venation and fiber strands:

NHMM LI 4606 (Fig. 3h; Plate I, 2): leaf fragment 10 mm wide, with 11 veins of which the middle one and both marginal veins are relatively thick, c. 140 µm and c. 125 µm, respectively, while the others are 60–90 µm thick; between each two adjacent veins there is a 40–50 µm thick fiber strand in a lower plane. One side of the blade is

Plate I (see plate on page 307). Bar=1 cm (1, 3, 4) or 0.5 cm (2).

1. *Phyllites monocotyleus* N°. 2 Miquel, type (U 1123, Kunrade Chalk, Kunrade).
- 2–4. *Thalassotaenia debeyi*, gen. et sp. nov.
2. Leaf fragment with 11 veins (middle and both marginal veins relatively thick), alternating fiber strands and cross-veins (NHMM LI 4606, Nekum Member, residual chert deposit, Sluizen; see also Fig. 3h).
- 3, 4. Leaf fragment with 11 veins (right marginal vein not preserved), alternating fiber strands, and cross-veins (NHMM LI 451 and 452, respectively, part and counterpart, type material, Gulpen or Maastricht Formation, residual chert deposit ('flint eluvium'), Hallembaye; see also Fig. 3d, e); note the cast fragment of the echinoid *Cardiaster granulatus* (Goldfuss, 1829) at the left.

Plate II *Thalassotaenia debeyi*, gen. et sp. nov. (see plate on page 308). Bar=1 cm.

1. Typical leaf fragment from the Kunrade area, showing veins and fiber strands, which are hard to distinguish (NHMM RH 783, Kunrade Chalk, Benzenrade).
2. Narrow leaf fragment, 3.5 mm wide (JMS 52027, Kunrade Chalk, Benzenrade; see also Fig. 3f).
3. Tapering leaf fragment that might represent a near-basal part (NHMM RH 805, Kunrade Chalk, Benzenrade).
4. Leaf fragment with imprints of three bryozoan colonies and traces of an unknown organism, with veins in/below imprints (JMS 52007, Kunrade Chalk, Emma I; see also Plate II, 5).
5. Detail of counterpart (upside-down) of specimen shown in Plate II, 4, showing the lower sides of the three bryozoan colonies and two unidentified other organisms.

Plate III *Thalassotaenia debeyi*, gen. et sp. nov., (see plate on page 309) specimens from the Kunrade Chalk of the Emma I. Bar=0.5 cm (2) or 1 cm (1, 3, 4).

1. Specimen showing narrow leaf type (at the left; see also Fig. 3c) and wide leaf type (at the right; see also Fig. 3b).
2. Same specimen as in Plate III, 1, showing at the left the continuation of the leaf at the right in Plate III, 1; the other leaf is also of the wide type.
- 3, 4. Wide leaf fragments with veins, alternating fiber strands and ± perpendicular cross-veins (JMS 52006 and 52071, respectively; part of specimen in Plate III, 3 also illustrated in Fig. 3a).

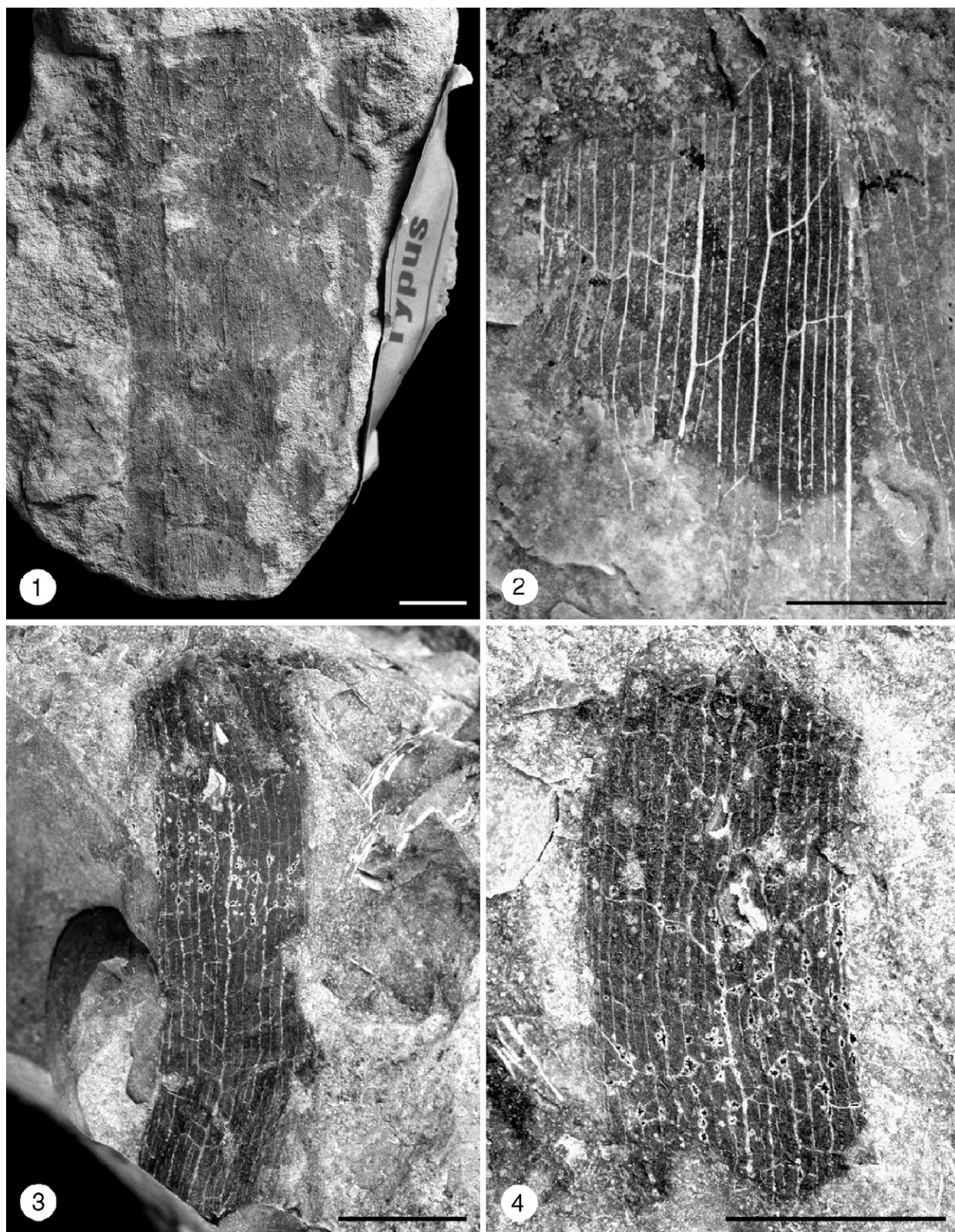


Plate I (caption on page 306).

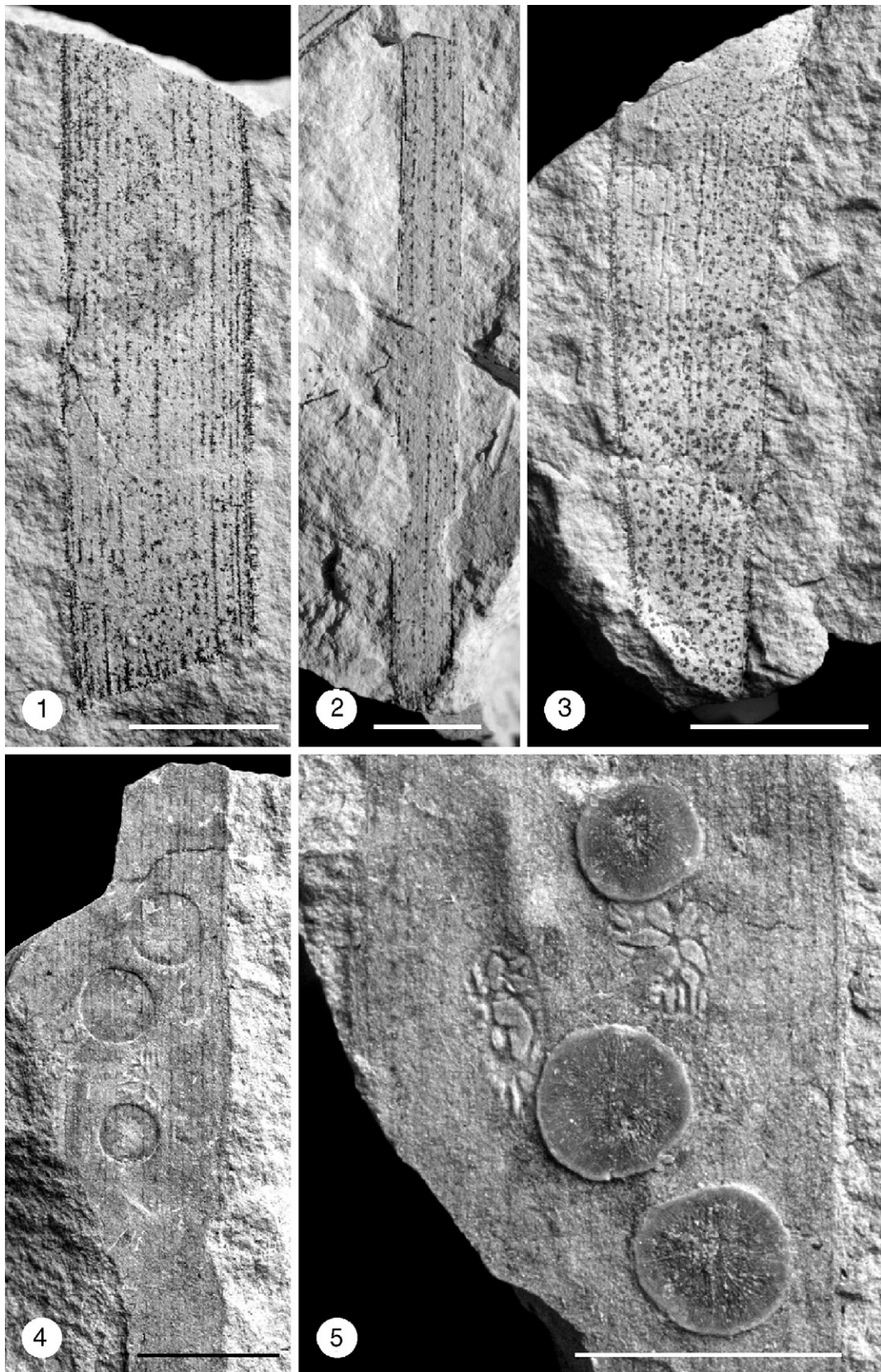


Plate II (caption on page 306).

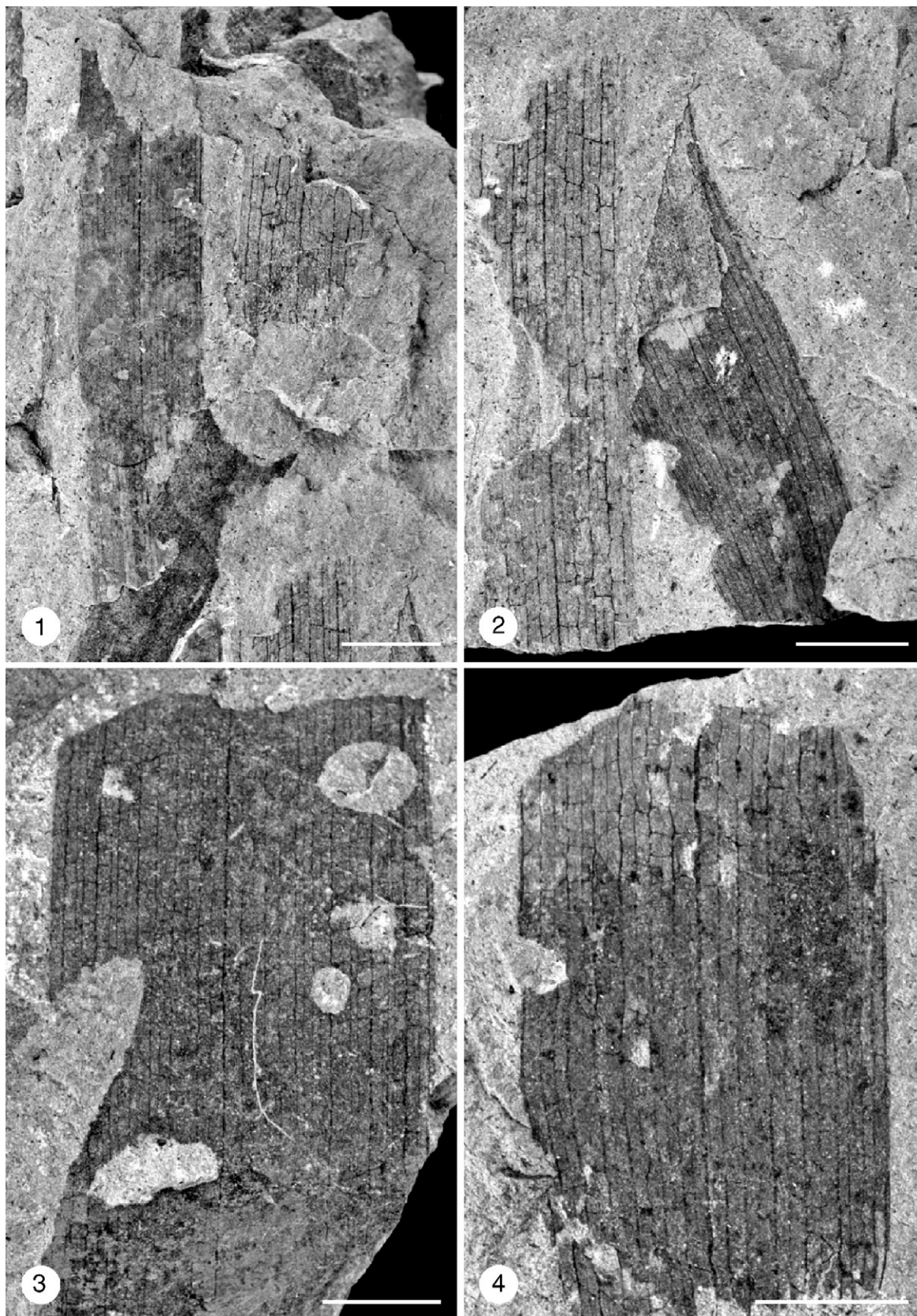


Plate III (caption on page 306).

missing (probably lost with the counterpart), which explains the presence of only one set of fiber strands.

NHMM LI 30606-1 (Plate VII, 5, 6): leaf fragment 7.5 mm wide, similar to NHMM LI 4606, but veins generally thinner (midrib 60–70  $\mu\text{m}$ ), without thinner fiber strands, and with many  $\pm$ isodiametrical dark specks (possibly tannin cells) of 60–120  $\mu\text{m}$  diameter. This leaf fragment contains only the middle mesophyll zone, so that it shows only the veins, and not the more superficial fiber strands.

NHMM LI 451/452 (Fig. 3d, e; Plate I, 3, 4): leaf fragment 12 mm wide, similar to NHMM LI 4606, but between adjacent veins in many places two close fiber strands, one adaxial and one abaxial, can be observed. *Anatomy*: NHMM LI 4174 (Plates V, 1–3; VI; VII, 1–4) contains the silicified remains of amassed leaf fragments, which could be studied in thin-sections. In addition, several surface views were available. Complete cross-sections were rare, but together, the fragments provide sufficient details for reconstruction of the anatomy of the leaf blade.

Surface views (Plate V1, 2) and  $\pm$ tangential sections (Plates V, 3; VI, 2, 3): epidermis without stomata or distinctly larger or smaller cells. Epidermis cells in longitudinal rows, 10–45  $\mu\text{m}$  (av. 24.4  $\mu\text{m}$ ) long, 8–21  $\mu\text{m}$

(av. 14.0  $\mu\text{m}$ ) wide, about rectangular, longitudinally to transversely elongate; length/width 0.52–3.60 (av. 1.19); cell shape is much less diverse within a single row. Anticlinal cell walls straight to sinuous. Hypodermis cells in one layer of longitudinal rows, larger than the epidermis cells, 20–62  $\mu\text{m}$  (av. 34.3  $\mu\text{m}$ ) long, 26–45  $\mu\text{m}$  (av. 36.8  $\mu\text{m}$ ) wide; about rectangular to about hexagonal, longitudinally to transversely elongate; length/width 0.53–1.67 (av. 1.03). Parenchyma cells between both hypodermis layers not in rows, larger than the hypodermis cells,  $\pm$ isodiametrical, 52–95  $\mu\text{m}$  (av. 71.6  $\mu\text{m}$ ) diameter.

Cross sections (Plates VI, 4, 5; VII, 3, 4) and longitudinal sections (Plate VII, 1, 2): leaf c. 250  $\mu\text{m}$  thick (one measurement), probably isobilateral. Epidermis without distinctly larger or smaller cells. Epidermis cells 18–25  $\mu\text{m}$  (av. 21.5  $\mu\text{m}$ ) high; outer wall relatively thick. Hypodermis cells in a single layer, 15–26  $\mu\text{m}$  (av. 21.6  $\mu\text{m}$ ) high. Parenchyma cells between hypodermis layers sometimes with bulging extensions, or with a brown contents (possibly tannin cells). Air channels possibly present (hard to demonstrate, due to the fragmentary condition of the material). Veins 35–140  $\mu\text{m}$  in diameter; fiber sheath 2–3 cell layers thick; vascular tissue consisting of thin-walled

Plate IV (see plate on page 311). Bar=0.5 cm (3–5) or 1 cm (1, 2).

1–3. *Thalassotaenia debeyi*, gen. et sp. nov.

1. Wide leaf fragment with veins, alternating fiber strands and  $\pm$  perpendicular cross-veins (Renkens 21505, Meerssen Member, ENCI).
2. Leaf fragment with veins and alternating fiber strands (NHMM RH 807, Danian part of Meerssen Member, Geulhem).
3. Leaf fragment with vague veins and cross-veins (NHMM RH 811, Lixhe I Member, Loën).
- 4, 5. *Zosterites* sp. (spp.?) (Vaals Formation, Hallembaye).
4. Leaf fragment with vague equal veins (JMS 52117).
5. Leaf fragment with distinct equal veins (JMS 52116).

Plate V (see plate on page 312). Bar=10  $\mu\text{m}$  (1–3) or 100  $\mu\text{m}$  (4).

1–3. *Thalassotaenia debeyi*, gen. et sp. nov. (NHMM LI 4174, Nekum Member, residual chert deposit, Sluizen).

- 1, continued in 2. Scanning electron micrographs of epidermis, showing rows of transversally to longitudinally elongate epidermis cells with straight to sinuous anticlinal cell walls (compare with Plate V, 3, 4).
3. Thin-section showing rows of longitudinally epidermis cells with straight to sinuous anticlinal cell walls.
4. *Amphibolis antarctica* (Labill.) Sonder et Aschers., light micrographs of epidermis, showing rows of transversally to longitudinally elongate epidermis cells with straight to sinuous anticlinal cell walls (Thorne and Carolin 27057, Tasmania; compare with Plate V, 1, 2).

Plate VI *Thalassotaenia debeyi*, gen. et sp. nov. (NHMM LI 4174, Nekum Member, residual chert deposit, Sluizen). (see plate on page 313). Bar=50  $\mu\text{m}$  (3, 5), 100  $\mu\text{m}$  (2, 4) or 0.5 cm (1).

1. Unprepared crack surface of specimen used for thin-sectioning, showing the silicified remains of amassed leaf fragments; the arrows indicate the thick marginal veins of a single leaf (note also the thick midrib).
2. Near-tangential section showing rows of hypodermis cells (h) and large parenchyma cells (p; not in rows).
3. Detail of Plate VI, 2, showing rows of hypodermis cells (h) and several vague overlying epidermis cells (e).
4. Almost complete cross-section of a leaf fragment, showing both epidermis layers, both hypodermis layers and large parenchyma cells in between.
5. Detail of Plate VI, 4, showing epidermis cells (e), hypodermis cells (h) and large parenchyma cells (p).

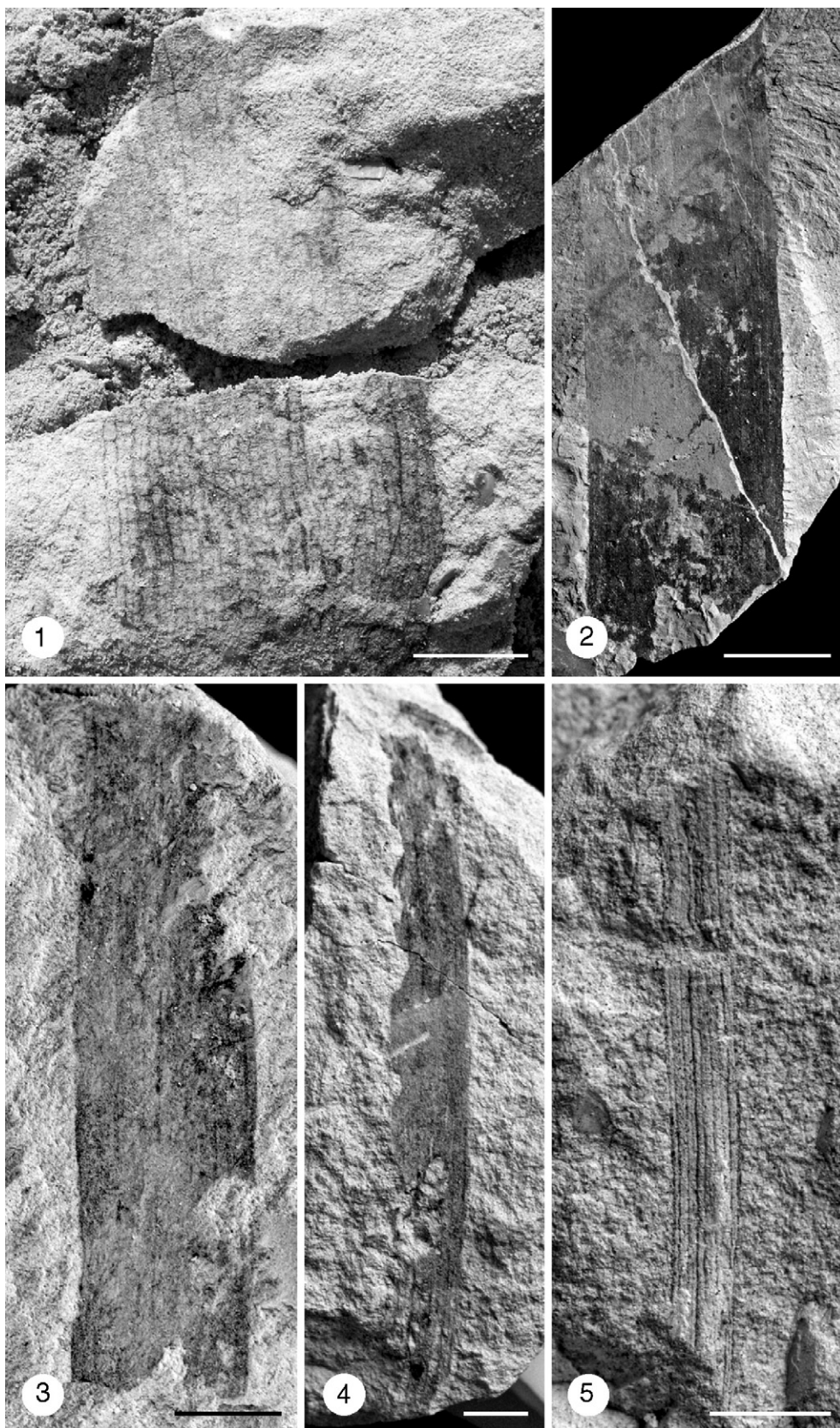


Plate IV (caption on page 310).

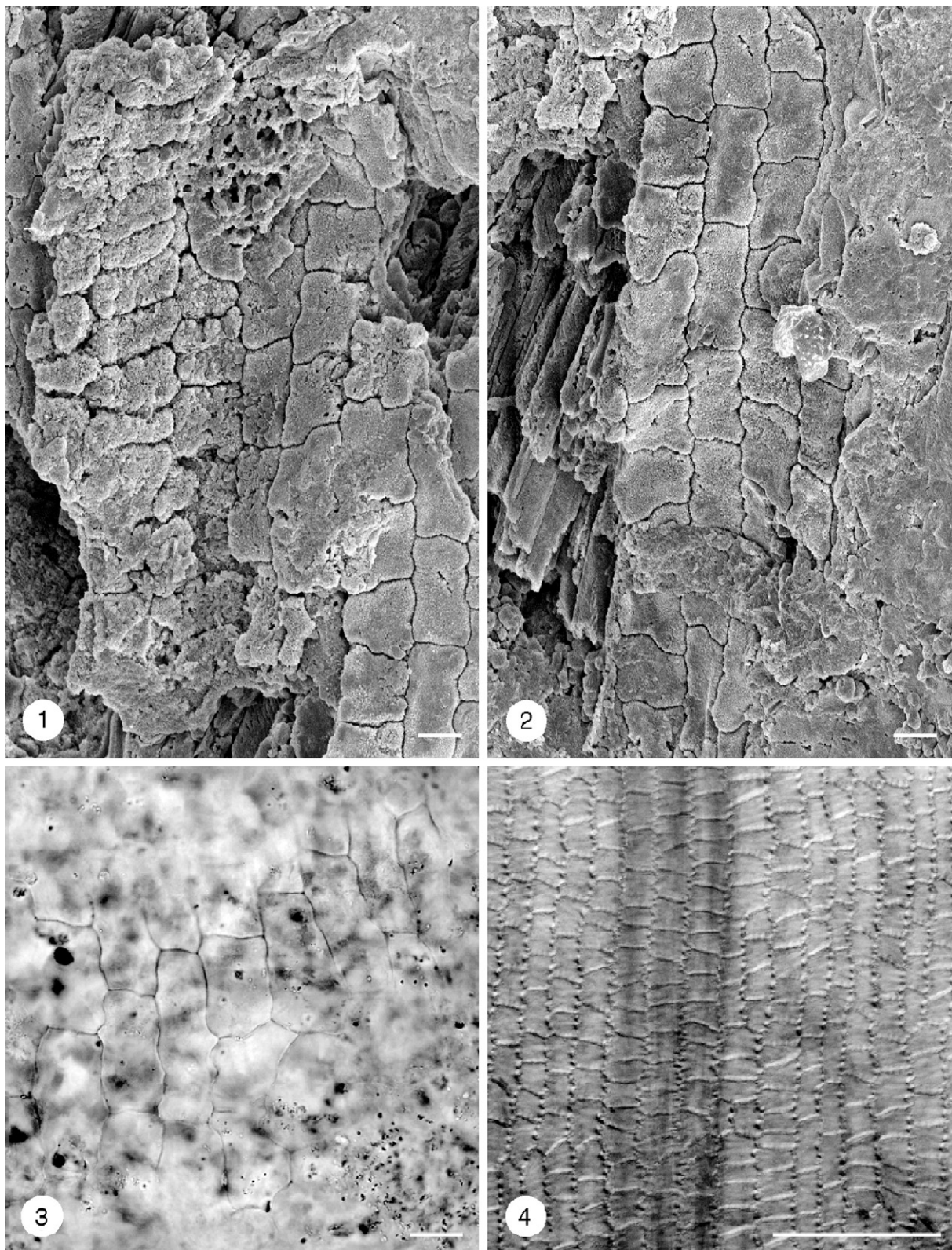


Plate V (caption on page 310).

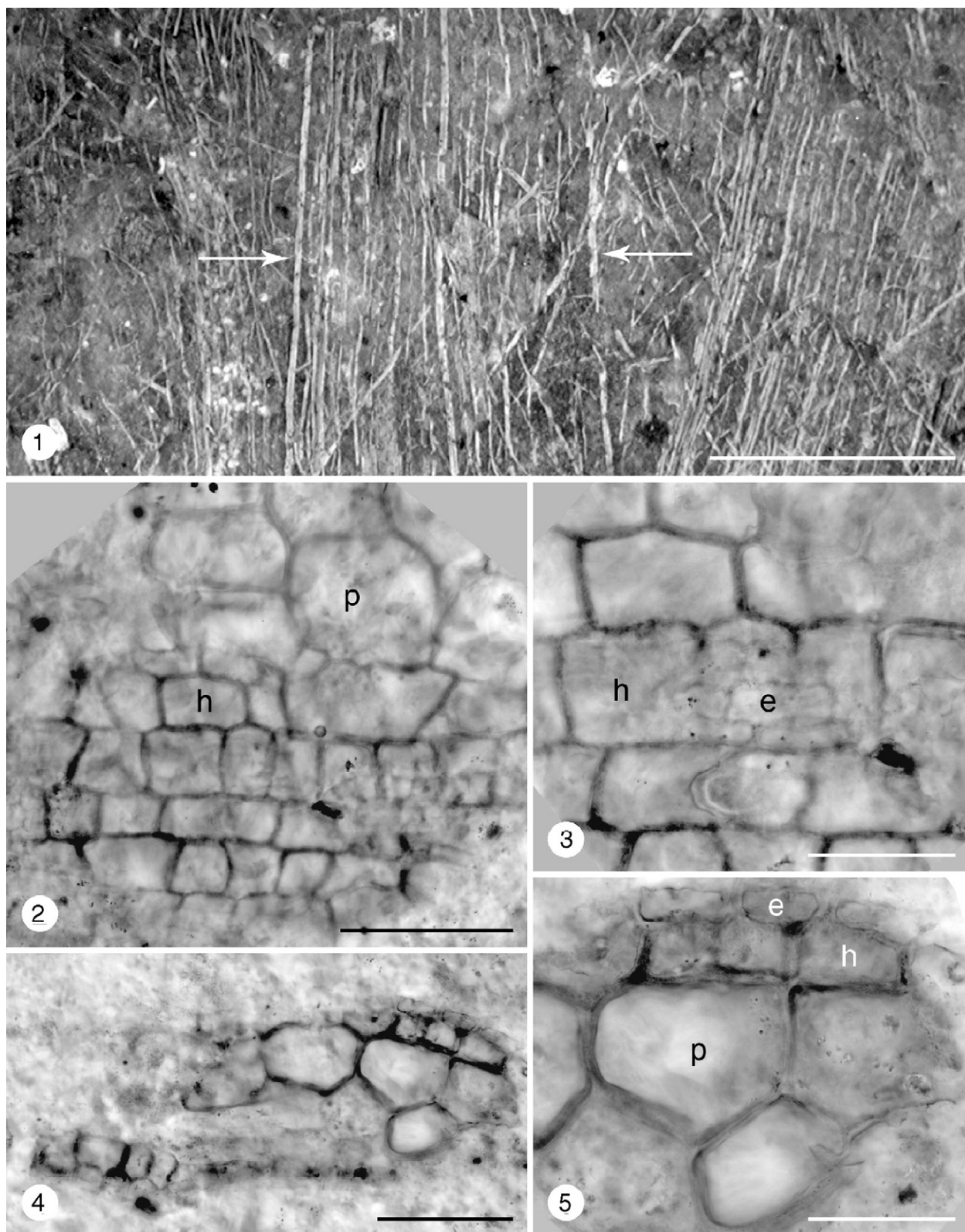


Plate VI (caption on page 310).

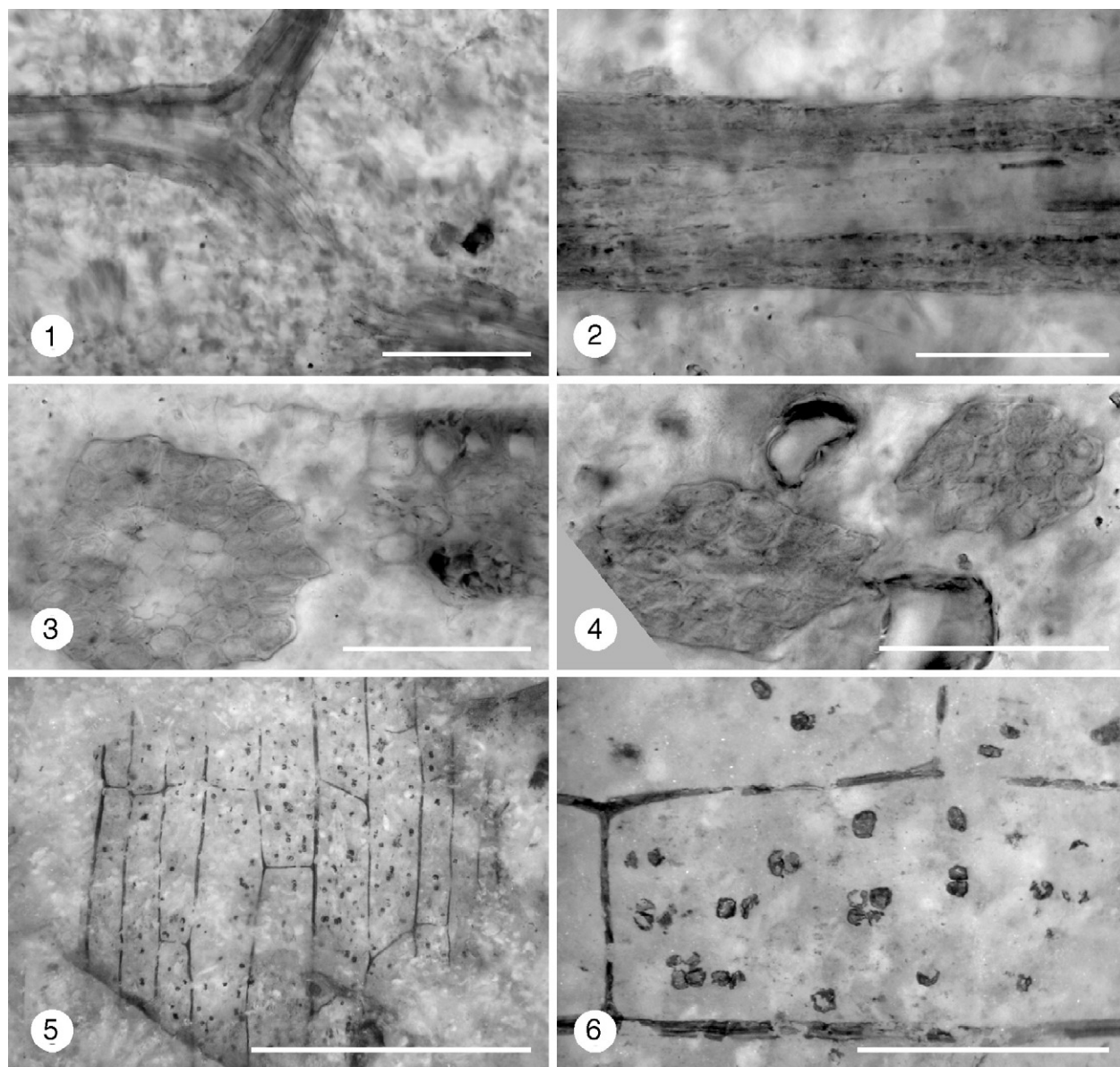


Plate VII. Bar=50  $\mu$ m (2–4), 100  $\mu$ m (1), 1 mm (6) or 0.5 cm (5).

- 1–4. *Thalassotaenia debeyi*, gen. et sp. nov. (NHMM LI 4174, Nekum Member, residual chert deposit, Sluizen).
- 1, 2. Longitudinal sections of veins, showing darker fiber sheath tissue enveloping the lighter conductive tissue.
3. Cross-section of vein (at the left), showing darker fiber sheath tissue with thick-walled fiber cells enveloping the lighter thin-walled conductive tissue.
4. Cross-section of vein (at the left), showing darker fiber sheath tissue with thick-walled fiber cells enveloping the lighter thin-walled conductive tissue, and of fiber strand (at the right), showing only thick-walled fiber cells.
5. Unprepared crack surface, showing 11 veins (midrib and marginal veins thicker; no fiber strand preserved), cross-veins and dark specks that might represent tannin cells (NHMM LI 30606-1, Nekum Member, residual chert deposit, Romontbos).
6. Detail of Plate VII, 5.

cells and sparse cells with spiral thickenings. Fiber strands present just below both hypodermis layers, 15–30  $\mu$ m diameter. Fiber cells 180–300  $\mu$ m long. All fiber cells are thick-walled.

The other anatomically preserved specimens (NHMM LI 451/452, 4606, 30606-1, 2) include isolated leaf fragments in surface views, which were not sectioned. Observation of the anatomical details (epidermis,

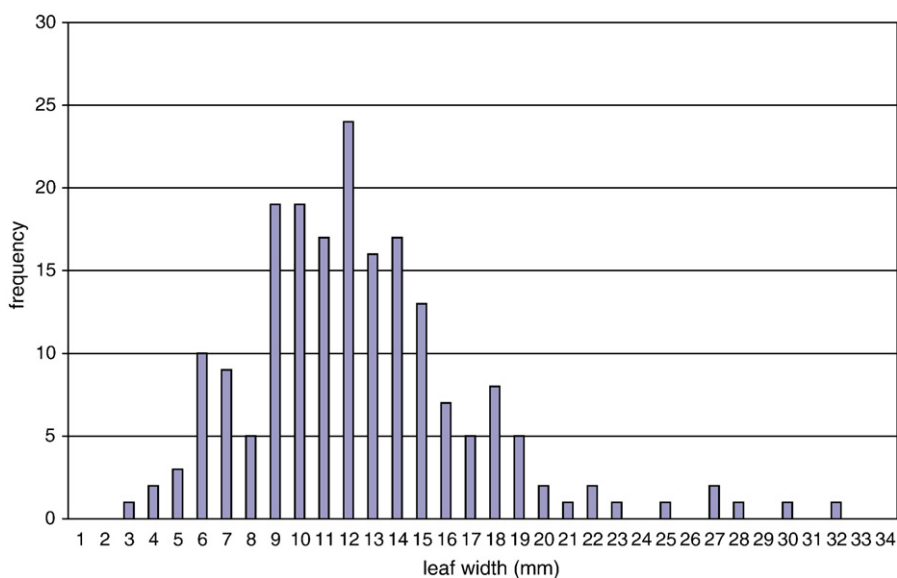


Fig. 4. Leaf width frequency diagram of specimens of *Thalassotaenia debeyi* (3=3–4 mm wide, 4=4–5 mm wide, etc.).

hypodermis and/or inner parenchyma cell patterns and sizes) shows that these are similar to those in NHMM LI 4174.

#### *Zosterites* Brongniart, 1823, emend. Brongniart, 1828.

**Generic diagnosis** (Brongniart, 1828): Feuilles oblongues ou linéaires, marquées d'un petit nombre de nervures toutes égales, assez espacées, sans nervures secondaires (leaves oblong or linear, with few, equal, rather widely spaced veins without secondary veins).

**Type:** *Zosterites orbigniana* Brongniart, 1823, from the Eocene of France.

#### *Zosterites* sp. (spp.?) (Plate IV, 4, 5)

**Material:** Early Campanian (*Inoceramus lingua*/*Gonioteuthis quadrata* Zone), Vaals Formation, Hallem-baye: JMS 52116, 52117.

**Remarks:** The material from the Vaals Formation at Hallem-baye consists of two poorly preserved leaf fragments: one 54 × 6 mm, with 6 or 7 equal veins (Plate IV, 4), and another 61 × 3 mm, with 9 equal(?) veins (Plate IV, 5), both without cross-veins. They might belong to different species, which are probably monocots but not necessarily seagrasses.

### 5. Comparisons

Cretaceous seagrass leaves are known only from the Maastrichtian type area, from Westfalen (Germany) and

from Tennessee (United States), and anatomically preserved Cretaceous material only from the Maastrichtian type area. The leaves of *Nechalea* (nomen nudum) and *Zosterites* from the Santonian of the Maastrichtian type area mentioned by Debey and Von Ettingshausen (1859) might be seagrass leaves, but they were not adequately described and cannot be compared with *Thalassotaenia*. Nine species of *Nechalea* and *Zosterites* were listed by Debey (1848, 1849) and Bosquet (1860, 1868), but all remained nomina nuda.

Miquel (1853) mentioned three '*phyllitae monocotylei*' (monocot leaves) for the Maastrichtian type area, of which the third includes "Onduidelijke afdrukken ..., misschien van een blad afkomstig" (indistinct imprints, possibly of a leaf) from Kunrade (no material cited). He suggested that these leaf-like fossils might be identical to those considered by Debey (1851) as *Thalassocharis* or *Zosterites*. The first of Miquel's *phyllitae monocotylei* might also be a seagrass leaf, but we have been unable to trace the original material. The second of Miquel's *phyllitae monocotylei* was illustrated as *Phyllites monocotyleus* N°. 2 (Miquel, 1853, pl. 1, fig. 3), which name has usually been applied to seagrass foliage from the Maastrichtian type area. The original specimen (U 1123) was labeled as the type of *Phyllites monocotyleus* Miquel. Inspection of this specimen, a flat, more or less rectangular, densely and finely longitudinally, irregularly striate imprint of c. 8 × 4 cm (Plate I, 1), revealed that it is rather different from our material. It is probably not seagrass foliage, but rather the imprint of a piece of wood.

Table 1

	<i>Thalassotaenia debyei</i>	<i>Amphibolis</i> (Cymodoceaceae)	<i>Cymodocea</i> (Cymodoceaceae)	<i>Halodule</i> (Cymodoceaceae)	<i>Syringodium</i> (Cymodoceaceae)	<i>Thalassodendron</i> (Cymodoceaceae)
<i>Leaves</i>						
Sheath	Shed/persistent?	Shed with leaf	Persistent on stem	Persistent on stem	Persistent on stem	Shed with leaf
Ligule	Present/absent?	Present	Present	Present	Present	Present
Blade	Strap-shaped	Strap-shaped	Strap-shaped	Strap-shaped	Terete	Strap-shaped
Length	Up to 16.6 (–100) cm	Up to 10 cm	Up to 30 cm	Up to 15 cm	Up to 30 cm	Up to 15 (–20) cm
Width	3.5–32 mm	2.5–10 mm	3–9 mm	0.25–3.5 mm	0.8–2 mm	6–13 mm
Margins	Entire(?)	Entire	Entire	Entire	–	±Denticulate
Near apex	?	Entire	±Denticulate	±Denticulate	–	Denticulate
Apex	?	2 marginal teeth	Rounded or slightly emarginate	Rounded or with 1–3 teeth	Toothed wing	Rounded, denticulate
<i>Veins</i>						
Middle vein	9–15 Relatively thick	8–21 (23) Relatively thick	7–11 (–17) Relatively thick or not	3 Relatively thick	1+2 or 1+7–12 Relatively thick or not	13–19 (–27) Relatively thick
Marginal veins	Mostly relatively thick	Relatively thick	Not relatively thick	–	–	Relatively thick or not
Cross-veins	Perpendicular to oblique	Oblique	Perpendicular	Absent	Absent?	Oblique
<i>Anatomy</i>						
<i>Epidermis</i>						
Cells	Transv. to longitud. elongate	Transv. to longitud. elongate	±Isodiametric	Elongate	±Isodiametric	Isodiam. to slightly elongate
Anticlinal walls	Straight to sinuous	Distinctly sinuous	Mostly straight	Straight to sinuous	±Straight	±Sinuous
Tannine cells	Absent or not deviating	Not deviating	Larger, elongate	Larger, elongate	Diverging into mesophyll	Not deviating
Hypodermis	Distinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct
Fiber strands	Alternating with veins	Absent	Along veins	Absent	Absent	Absent
<i>Parenchym</i>						
Air lacunae	Possibly present	Small	Small to large	Large	Large	Small
Tannine cells	Possibly present	Present	Absent	Present	Present	Common
<i>Veins</i>						
Fiber sheath	2–3 layers	2–3 layers	1 layer	1 layer	1 layer	1–2 layers
Fiber cells	Thick-walled	Thick-walled	Thick-walled	Thin-walled	Thin-walled	Thick-walled

Table 1 (continued)

	<i>Enhalus</i> (Hydrocharitaceae)	<i>Halophila</i> (Hydrocharitaceae)	<i>Thalassia</i> (Hydrocharitaceae)	<i>Posidonia</i> (Posidoniaceae)	<i>Ruppia</i> (Ruppiaceae)	<i>Zostera et al.</i> (Zosteraceae)
<i>Leaves</i>						
Sheath	Persistent on stem	Absent	Persistent on stem	Persistent on stem	Persistent/shed?	Persistent, sometimes shed
Ligule	Absent	Absent	Absent	Present	Absent	Present
Blade	Strap-shaped	Elliptic to oblong	Strap-shaped	Strap-shaped to terete	Flattened	Strap-shaped to biconvex
Length	30–150 cm	Usually <7 cm	10–70 cm	10–135 cm	Up to 15 cm	2–200 cm
Width	12–18 mm	1–8 mm	4–15 mm	1–20 mm	1–2 mm	(0.5–) 2–15 mm
Margins	Entire to slightly dentate	Entire or dentate	Entire	Entire	±Entire	Entire or slightly dentate
Near apex	Entire	Entire or finely dentate	Finely dentate	Entire	Finely denticulate	Entire
Apex	Rounded, somet. slightly dentate	Rounded, mostly dentate	Rounded, slightly dentate	Rounded	Acute	Rounded to emarginate
<i>Veins</i>						
Middle vein	Up to 27 (30)	3	9–11 (–17)	5–15 (–21)	1 or 3	3–7 (–11)
	Relatively thick, abaxial	Relatively thick	Relatively thick	Relatively thick	Relatively thick	Relatively thick
Marginal veins	Relatively thick	–	Not relatively thick	Not relatively thick	–	Not relatively thick
Cross-veins	Perpendicular to oblique	Perpendicular to oblique	Perpendicular	Perpendicular to oblique	Absent?	Perpendicular to oblique
<i>Anatomy</i>						
<i>Epidermis</i>						
Cells	Isodiam. to slightly elongate	±Isodiametric	±Isodiametric	Isodiametric to elongate	Isodiametric to slightly elongate	Isodiametric to slightly elongate
Anticlinal walls	Straight	Mostly straight	Straight	Straight to sinuous	Straight	Straight
Tannine cells	Not deviating	Larger	Larger	Not deviating	Larger	Absent
Hypodermis	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct	Indistinct
Fiber strands	Along veins	Absent	Along veins	Throughout blade	Absent	Throughout blade
<i>Parenchym</i>						
Air lacunae	Large	Small to large	Large	Absent or small	Large	Large
Tannine cells	Absent	Absent	Present	Present	Absent	Absent
<i>Veins</i>						
Fiber sheath	Fragmentary	Indistinct	Indistinct	1–2 layers	Indistinct	Fragmentary
Fiber cells	Thick-walled	–	–	Thin-walled	–	Thick-walled

*Posidonia cretacea* from the Late Campanian of Westfalen (see Riegraf, 1995 for stratigraphical details) is based on stems with attached fibrous leaf base (sheath) remains (Hosius and Von der Marck, 1880). The leaf base remains cannot be compared with *Thalassotaenia* leaf fragments, because these lack basal parts.

*Thalassocharis westfalica* stems from the Late Campanian of Westfalen sometimes show attached leaves, which are up to 7 mm wide and possibly single-veined (Hosius and Von der Marck, 1880, p. 147, 148, 151, fig. 29, 30). Further veins seem to be absent, but that might be due to the poor preservation of the material (personal observation). Because of the poor preservation the Westfalian leaf fossils cannot be properly compared with *Thalassotaenia*.

Dilcher (in press) described two ligulate seagrass leaves (without base and apex) of c. 5.5 cm long and 0.7–0.9 mm wide, with 7–10 parallel veins, from the Early Maastrichtian of Tennessee. According to Dilcher the leaves are similar to some described as *Cymodocea floridana* from the Eocene of Florida (Ivany et al., 1990). Because anatomical details are missing, further comparison with *Thalassotaenia* is not possible.

Koriba and Miki (1960) described *Archaeozostera* from the Late Cretaceous (Campanian/Maastrichtian?) of Japan, and suggested some relationship with the Araceae and some Zosteraceae (*Zostera*, *Phyllospadix*). According to Den Hartog (1970) and Larkum and Den Hartog (1989) *Archaeozostera* might be a protozosteroid. The leaves are short, stiff and falcate, very different from *Thalassotaenia* leaves, and details of the venation are unknown. The true nature of *Archaeozostera* remains uncertain, but according to Kuo et al. (1989) it is not a seagrass, and possibly not even a marine angiosperm.

Cenozoic seagrass foliage is known from the Late Paleocene of Belgium: *Posidonia perforata* and *Zostera nodosa* (De Saporta and Marion, 1878), the Eocene of Belgium: *Posidonia parisiensis* (Stockmans, 1936), Austria: *P. parisiensis*-type (Gregor, 2003), Italy: *Posidocea frickhingeri* (Gregor, 1991) and Florida: ‘*Cymodocea*’, *Cymodocea floridana*, ‘*Halodule*’, *Thalassia testudinum*, *Thalassodendron auricula-leporis* and an unknown zosteroid (Lumbert et al., 1984; Ivany et al., 1990), and the Miocene of Sulawesi: *Cymodocea micheloti* (Laurent and Laurent, 1926). These seagrass leaves are only rarely anatomically preserved; (sub)epidermal cell patterns are known only for *Posidonia perforata* from the Paleocene of Belgium are known (Stockmans, 1932), but these do not resemble those found in *Thalassotaenia*, the epidermis cells being isodiametrical instead of longitudinally to transversely elongate and the subepidermal cells very large in comparison to the epidermis cells.

Because of the scarcity and poor preservation of our Campanian *Zosterites* material, no attempt has been made to compare it with other finds or discuss its affinities.

## 6. Affinities

About 60 recent seagrass species belonging to 13 genera and five families are recognised (Kuo and McComb, 1989; Les et al., 1997): Cymodoceaceae (*Amphibolis*, *Cymodocea*, *Halodule*, *Syringodendron*, *Thalassodendron*), Hydrocharitaceae (*Enhalus*, *Halophila*, *Thalassia*), Posidoniaceae (*Posidonia*), Ruppiaceae (*Ruppia*) and Zosteraceae (*Heterozostera*, *Phyllospadix*, *Zostera*). The inclusion of *Lepilaena* (Zannichelliaceae) is still a matter of debate (Den Hartog and Kuo, 2006). Due to adaptations to their aquatic environment, seagrass leaves show simple and convergent anatomies (e.g. Les et al., 1997). Still, if morphological and anatomical features are combined, there is enough evidence to make generic attributions on the basis of complete leaves (Den Hartog, 1970). However, the identification of fossil leaves, in which important characters as the apex, base (sheath, ligula), air lacunae and tannin cells are often missing or hard to demonstrate, is much more difficult. For instance, the presence of tannin cells would exclude the Zosteraceae, and the presence of a ligula at the leaf base would exclude the Hydrocharitaceae and the Ruppiaceae. The well-preserved material recorded by Lumbert et al. (1984; see Section 5. Comparisons) demonstrates that modern seagrass genera (Cymodoceaceae as well as Hydrocharitaceae) were definitely present in the Eocene. The genus *Cymodocea* may even extend back to the Maastrichtian (Dilcher, in press).

Table 1 provides a number of morphological and anatomical features of *Thalassotaenia debeyi* and the corresponding states in extant seagrasses, the latter largely based on the studies by Sauvageau (1891), Den Hartog (1970) and Tomlinson (1982). It shows that there is not an easy match between *Thalassotaenia* and any of the extant families or genera. Some genera with very dissimilar leaves (see Table 1) might be readily excluded from the comparison: *Halodule* and *Syringodendron* (Cymodoceaceae), *Ruppia* (Ruppiaceae) and *Halophila* (Hydrocharitaceae). All others have strap-shaped leaves with nearly always more than three veins. Of these, *Cymodocea* (Cymodoceaceae), *Enhalus* and *Thalassia* (Hydrocharitaceae) and Zosteraceae have quite deviating anatomies.

*Thalassotaenia* shows the greatest resemblance to *Amphibolis*, *Thalassodendron* (Cymodoceaceae) and *Posidonia* (Posidoniaceae). With *Amphibolis* it shares

transversally to longitudinally elongate epidermis cells (compare Plate V, 1 with V, 4) and a thick fiber sheath around the vascular tissue in the veins. In *Thalassodendron* and *Posidonia* the epidermis cells are isodiametrical to longitudinally elongate and the vein sheaths are thinner. Other characters of *Thalassotaenia* do not occur in *Amphibolis*, *Posidonia* and *Thalassodendron*. For instance, the leaves of *Amphibolis* and *Thalassodendron* lack fiber strands, while fiber strands are distinct in *Thalassotaenia*. Fiber strands do occur in *Posidonia*, but in this genus they are spread throughout the hypodermal zone instead of alternating with the veins. Further, long (up to 1 m according to Jongmans and Van Rummelen, 1937), relatively wide (up to 32 mm) leaves do not occur in *Amphibolis* and *Thalassodendron* (up to 10×1 cm and 20×1.3 cm, respectively). Because *Amphibolis*, *Thalassodendron* and *Posidonia*, as a group, show the greatest resemblance, *Thalassotaenia* might be considered as an ancestor of the Cymodoceaceae–Posidoniaceae(–Ruppia-ceae) clade found in several phylogenetic analyses (Les et al., 1997; Bremer, 2000; Janssen and Bremer, 2004). However, *Thalassotaenia* shows some features not found in any of the extant seagrasses: fiber strands that alternate with the veins and a well-delimited hypodermis. A hypodermis is also lacking in *Posidonia perforata* from the Paleocene of Belgium (Stockmans, 1932), besides *Thalassotaenia* the only known anatomically preserved fossil seagrass. The phylogenetic analyses mentioned above have demonstrated the polyphyletic origin of the seagrasses in three separate clades: besides the Cymodoceaceae–Posidoniaceae(–Ruppia-ceae) clade also the Hydrocharitaceae clade and the Zosteraceae clade. Therefore, *Thalassotaenia* could also represent another, extinct clade of seagrasses.

*Thalassocharis bosquetii* may represent the stem belonging to *Thalassotaenia debeyi*. Voigt and Domke (1955) considered that the stem morphology and anatomy of *T. bosquetii* resembles that of *Cymodocea* most. Den Hartog (1970) found it more similar (e.g. by sympodial growth) to *Amphibolis* and the related genus *Thalassodendron*. According to Den Hartog, these genera may have been derived from *Thalassocharis*-like ancestors (see also Larkum and Den Hartog, 1989). However, on the basis of the absence of air lacunae Den Hartog and Kuo (2006) argue that *Thalassocharis* from the Maastrichtian type area and Westfalen has no seagrass morphology and that it is not an aquatic plant. This is a remarkable conclusion, which seems to deny any relationship between *Thalassocharis* and *Thalassotaenia*, as the latter certainly represents a seagrass. It would also contradict an ancestral position of *Thalassocharis* in any seagrass clade, as the ancestors of seagrasses are supposed to have been freshwater aquatics.

## 7. Ecological aspects

Seagrass communities occur in relatively warm, shallow seas, and are well-known for their high biodiversity (Brasier, 1975; Larkum et al., 1989; Green and Short, 2003; Larkum et al., 2006). As with modern seagrass communities, a diverse assemblage of epibionts, molluscs and echinoderms was found in association with several seagrass species in the Eocene of Florida (Ivany et al., 1990). Voigt (1981a, b) reported on the occurrence of epibionts (an alga, bryozoans, serpulids, bivalves) on seagrass leaves from the Maastrichtian type area (see also Plate II, 4, 5). Moreover, a diverse fauna was found together with the leaves in the present study, for instance ammonites, bivalves, corals and echinoids (Plate I, 3). These observations demonstrate that a rich seagrass community already existed in the Late Maastrichtian. Considering that worldwide the oldest known seagrass is from the Early Campanian (Debey, 1848, 1851: *Thalassocharis mülleri* from the Vaals Formation in the Maastrichtian type area), a Late Maastrichtian age for a well-developed seagrass community is remarkably early.

Further, the stratigraphical distribution of the cheloniid sea turtle *Allopleuron hofmanni* in the Maastrichtian type area (Kuypers, 1998; Mulder, 2003) is very much the same as that of *Thalassotaenia debeyi* (Fig. 2) and they are often found together, which indicates that this sea turtle was an element of the seagrass community and that the seagrass in the area might have formed extensive meadows that could support a sea turtle population (see also Liebau, 1978; Fraaije, 2003). Ivany et al. (1990) mentioned that cheloniid sea turtle remains and the oldest known dugong fossils were found in association with the seagrasses in the Eocene of Florida. As sea turtles, dugongs are renowned grazers of seagrass leaves (Lanyon et al., 1989), but in view of the seagrass–sea turtle connection in the Maastrichtian they were a later addition to this niche.

## Acknowledgements

We wish to thank Paul Hille (Rotterdam), Jacob Leloux (Leiden), Sijr Renkens (Zaltbommel), Jan Smit and Hubert Vonhof (Vrije Universiteit, Amsterdam) and Frank Wesselingh (Nationaal Natuurhistorisch Museum, Leiden) for the material and advise, Johan van der Burgh (Laboratory of Palaeobotany and Palynology, Utrecht), Rudi Dortangs (Amsternrade), John Jagt (Natuurhistorisch Museum Maastricht), Hans Kerp (Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität, Münster) and Isabel van Waveren (Nationaal Natuurhistorisch Museum, Leiden) for the opportunity to examine and/or borrow

material, Wouter Wildenberg (Nationaal Natuurhistorisch Museum, Leiden) for the preparation of thin-sections, Bertie Joan van Heuven and Ben Kieft (both Nationaal Herbarium Nederland) for producing the photographs and plates in this paper, and Else Marie Friis and David Dilcher for their valuable comments on the manuscript.

## References

- Binkhorst van den Binkhorst, J.-T., 1859. Esquisse géologique et paléontologique des couches crétacées du Limbourg. Van Osch-America et Cie, Maastricht, 268 pp.
- Bosquet, J., 1860. Versteeningen uit het Limburgsche Krijt. In: Staring, W.C.H. (Ed.), *De bodem van Nederland*, vol. 2. A.C. Kruseman, Haarlem, pp. 361–418.
- Bosquet, J., 1868. Fossiles du massif crétacé du Limbourg. In: Dewalque, G. (Ed.), *Prodrome d'une description géologique de la Belgique*. J.-G. Carmanne, Liège, pp. 355–387.
- Brasier, M.D., 1975. An outline history of seagrass communities. *Palaeontology* 18, 681–702.
- Bremer, K., 2000. Early Cretaceous lineages of monocot flowering plants. *Proc. Natl. Acad. Sci. U. S. A.* 97, 4707–4711.
- Brongniart, A., 1823. Observations sur les Fucoïdes et sur quelques autres plantes marines fossiles. *Mém. Soc. Hist. Nat. Paris* 1, 301–320.
- Brongniart, A., 1828. *Prodrome d'une histoire des végétaux fossiles*. Dict. Sci. Nat., vol. 57, pp. 16–212.
- De Saporta, G., Marion, A.-F., 1878. Révision de la flore Heersienne de Gelinden d'après une collection appartenant au comte G. de Looz. *Mém. Acad. R. Belg., Cour. Sav. Étrang.* 41 (3), 1–112.
- Debey, M.H., 1848. Uebersicht der urweltlichen Pflanzen des Kreidegebirges überhaupt und der Aachener Kreideschichten insbesondere. *Verhandl. Naturhist. Ver. Preuss. Rheinl.* 5, 113–125.
- Debey, M.H., 1849. Entwurf zu einer geognostisch-geogenetischen Darstellung der Gegend von Aachen. Boisserée'schen Buchhandlung, Aachen, 67 pp.
- Debey, M.H., 1851. Beitrag zur fossilen Flora der holländischen Kreide (Vael bei Aachen, Kunraed, Maestricht). *Verhandl. Naturhist. Ver. Preuss. Rheinl.* 8, 568–569.
- Debey, M.H., Von Ettingshausen, C., 1859. Die urweltlichen Thalphyten des Kreidegebirges von Aachen und Maastricht. *Denkschr. math.-naturw. Cl. kais. Akad. Wiss. Wien* 16, 131–214.
- Den Hartog, C., 1970. The sea-grasses of the world. *Verhand. Kon. Ned. Akad. Wetensch., Natuurk.* 2, 59, 1: 1–275.
- Den Hartog, C., Kuo, J., 2006. Taxonomy and biogeography of seagrasses. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, pp. 1–23.
- Dilcher, D., in press. Fossil plants from the Coon Creek Formation. *Tennessee Div. Geol. Bull.* 86.
- Dortangs, R.W., 1998. Planten. In: Jagt, J.W.M., Leloux, J., Dhont, A. V. (Eds.), *Fossielen van de St. Pietersberg*. Grondboor and Hamer, 52, 100–101.
- Fraaije, R.H.B., 2003. Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area. *Contr. Zool.* 72, 119–130.
- Francken, C., 1947. Bijdrage tot de kennis van het Boven-Senoon in Zuid-Limburg. *Meded. Geol. Sticht. C* 6 (5), 3–148.
- Green, E.P., Short, F.T., 2003. *World Atlas of Seagrasses*. University of California Press, Berkeley, 298 pp.
- Gregor, H.-J., 1991. Ein neues fossiles Seegras-*Posidocoea frickhingeri* nov. gen. et spec. im Paläogen Oberitaliens (Verona). *Doc. Nat.* 65, 1–11.
- Gregor, H.-J., 2003. Erstnachweis von Seegrass-Resten (*Posidonia*) im Oberen Eozän der Nördlichen Kalkalpen bei Hallthurm. *Doc. Nat.* 148, 1–19.
- Hosius, A., Von der Marck, W., 1880. Die Flora der Westfälische Kreideformation. *Palaeontographica* 26, 125–236.
- Ivany, L.C., Portell, R.W., Jones, D.S., 1990. Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida. *Palaios* 5, 244–258.
- Jagt, J.W.M., 1999. Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium—Part 1: Introduction and stratigraphy. *Scr. Geol.* 116, 1–57.
- Janssen, T., Bremer, K., 2004. The age of major monocot groups inferred from 800+*rbcL* sequences. *Bot. J. Linn. Soc.* 146, 385–398.
- Jongmans, W.J., Van Rummelen, F.H., 1937. De bodem van Zuid-Limburg. Geologische geschiedenis, mineralen, geologische merkwaaardigheden. De Torentans, Zeist, 79 pp.
- Koriba, K., Miki, S., 1960. *Archeozostera*, a new genus from Upper Cretaceous in Japan. *Palaeobotanist* 7, 107–111.
- Kuo, J., McComb, A.J., 1989. Seagrass taxonomy, structure and development. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of seagrasses*. Elsevier, Amsterdam, pp. 6–73.
- Kuo, J., Seto, K., Nasu, T., Iizumi, H., Aioi, K., 1989. Notes on *Archeozostera* in relation to the Zosteraceae. *Aquat. Bot.* 34, 317–328.
- Kuypers, M.M.M., 1998. Zeeschilpadden. In: Jagt, J.W.M., Leloux, J., Dhont, A.V. (Eds.), *Fossielen van de St. Pietersberg*. Grondboor and Hamer, 52, 146–147.
- Lanyon, J.M., Limpus, C.J., Marsh, H., 1989. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of seagrasses*. Elsevier, Amsterdam, pp. 610–634.
- Larkum, A.W.D., Den Hartog, C., 1989. Evolution and biogeography of seagrasses. In: Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), *Biology of seagrasses*. Elsevier, Amsterdam, pp. 112–156.
- Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (Eds.), 1989. *Biology of Seagrasses*. Elsevier, Amsterdam, 841 pp.
- Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), 2006. *Seagrasses: biology, ecology and conservation*. Springer, Dordrecht, 691 pp.
- Laurent, L., Laurent, J., 1926. Étude sur une plante fossile des dépôts du Tertiaire marin du sud de Célèbes. *Jaarboek Mijnwezen Nederlandsch-Indië*, vol. 54, pp. 169–190.
- Les, D.H., Cleland, M.A., Waycott, M., 1997. Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophyly. *Syst. Bot.* 22, 443–463.
- Liebau, A., 1978. Paläobathymetrische und paläoklimatische Veränderungen im Mikrofaunenbild der Maastrichter Tuffkreide. *N. Jb. Geol. Paläontol.* 157, 233–237.
- Lumbert, S.H., Den Hartog, C., Philips, R.C., Olsen, F.S., 1984. The occurrence of fossil seagrasses in the Avon Park Formation (Late Middle Eocene), Levy County, Florida (U.S.A.). *Aquat. Bot.* 20, 121–129.
- Miquel, F.A.W., 1853. De fossiele planten van het Krijt in het hertogdom Limburg. *Verhand. Comm. Geol. Beschrijv. and Kaart Nederland*, vol. 1, pp. 33–56.
- Mulder, E.W.A., 2003. On latest Cretaceous tetrapods from the Maastrichtian type area. *Publ. Natuurhist. Genoot. Limburg* 44 (1), 1–188.

- Pomel, A., 1849. Matériaux pour servir à la flore fossile des terrains jurassiques de la France. Amt. Ber. 25<sup>ste</sup> Versamm. deutsch. Naturf. Ärzte, Aachen, Sept. 1847: 331–354.
- Riegraf, W., 1995. Radiolarien, Diatomeen, Cephalopoden und Stratigraphie im palagischen Campanium Westfalens (Oberkreide, NW-Deutschland). N. Jb. Geol. Paläontol. Abh. 197, 129–200.
- Sauvageau, C., 1891. Sur les feuilles de quelques monocotylédones aquatiques. Ann. Sci. Nat. 7. Bot. 13, 103–296.
- Smit, J., Brinkhuis, H., 1996. The Geulhemmerberg Cretaceous/Tertiary boundary section (Maastrichtian type area, SE Netherlands); summary of results and a scenario of events. Geol. Mijnb. 75, 283–293.
- Stafleu, F.A., Mennega, E.A., 1998. Taxonomic literature. A selective guide to botanical publications and collections with dates, commentaries and types. Suppl. 5: Da-Di. Koeltz, Königstein. 432 pp.
- Stockmans, F., 1932. *Posidonia perforata* Saporta et Marion des marnes de Gelinden (Paléocène). Bull. Mus. R. Hist. Nat. Belg. 8 (27), 1–9.
- Stockmans, F., 1936. Végétaux éocènes des environs de Bruxelles. Bull. Mus. R. Hist. Nat. Belg. 76, 1–56.
- Taylor, T.N., Taylor, E.L., 1993. The Biology and Evolution of Fossil Plants. Prentice Hall, Englewood Cliffs, 982 pp.
- Tomlinson, P.B., 1982. Anatomy of the Monocotyledons VII. Helobiae (Alismatidae) (including the seagrasses). Clarendon Press, Oxford. 559 pp.
- Ubaghs, C., 1885. Catalogue des collections géologiques, paléontologiques, conchyliologiques and d'archéologie préhistorique du Musée Ubaghs, Maestricht, rue des Blanchisseurs, n° 2384. H. Vaillant-Carmanne, Liège, 32 pp.
- Umbgrove, J.H.F., 1926. Bijdrage tot de kennis der stratigraphie, tektoniek en petrographie van het Senoon in Zuid-Limburg. Leid. Geol. Meded. 1, 255–332.
- Van der Ham, R.W.J.M., Dortangs, R.W., 2005. Structurally preserved ascomycetous fungi from the Maastrichtian type area (NE Belgium). Rev. Palaeobot. Palynol. 136, 48–62.
- Voigt, E., 1981a. Upper Cretaceous bryozoan-seagrass association in the Maastrichtian of the Netherlands. In: Larsen, G.P., Nielsen, C. (Eds.), Recent and fossil bryozoa. Olsen and Olsen, Fredensborg, pp. 281–298.
- Voigt, E., 1981b. Erster fossiler Nachweis des Algen-Genus *Fosliella* Howe, 1920 (Corallinaceae; Rhodophyceae) in der Maastrichter und Kunrader Kreide (Maastrichtium, Oberkreide). Facies 5, 265–282.
- Voigt, E., Domke, W., 1955. *Thalassocharis bosqueti* Debey ex Miquel, ein strukturell erhaltenes Seegrass aus der holländische Kreide. Mitt. Geol. Staatsinst. Hambg. 24, 87–102.