Seagrass stems with attached roots from the type area of the Maastrichtian Stage (NE Belgium, SE Netherlands): Morphology, anatomy, and ecological aspects

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A R T I C L E I N F O

A B S T R A C T

Seagrasses are the only seed plants to have invaded marine environments successfully. Seagrass fossils are both rare and have received scant attention so far. However, among the limited number of plant fossils from marine strata in the Maastrichtian type area, remains of seagrasses are relatively common. The present paper provides a detailed description of the morphology and anatomy of the stems and attached roots of *Thalassocharis bosquetii* Debey ex Miquel, 1853, mainly on the basis of silicified material. This has enabled an interpretation of features of the abundant imprints (external moulds) among the specimens studied, inclusive of the type material. Contrary to the outcome of earlier studies, the internodes have been found to constitute leaf scars. *T. bosquetii* is considered to have been a seagrass, but has a complex stem anatomy, including a substantial central stele with numerous sheathed vascular bundles, an inner cortex with many small intercellular cavities, a middle cortex with distinct fibre strands, and an outer cortex with conspicuously thickened vascular bundles, each of which constricts into a thin vascular strand just below a furrow/pit on the leaf scar. The last-named feature underlies the characteristic stem surface pattern seen in *Thalassocharis*. The stem anatomy of *T. bosquetii* is clearly more complex than that of extant seagrasses, which, due to prolonged adaptation to their aquatic habitat, show a more or less reduced anatomy. As far as the complexity of the stele is concerned, *T. bosquetii* reminds more of some non-marine Alismatales, such as the pondweed family Potamogetonaceae and the monotypical peat bog family Scheuchzeriaceae.

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1. Introduction

Seagrass communities are important ecosystems in relatively warm, shallow seas (Green and Short, 2003). They are renowned for their high biodiversity and over the last decades there has been considerable research into numerous aspects of seagrass biology and ecology (e.g., Brasier, 1975; Larkum et al., 1989, 2006; Reich et al., 2015). Seagrasses are the only seed plants to have invaded marine environments successfully. At present, they constitute an ecological, polyphyletic group of species in five families (Cymodoceaceae, Hydrocharitaceae p.p., Posidoniaceae, Ruppiaceae and Zosteraceae) in at least three clades within the monocot order Alismatales (Les et al., 1997; Kato et al.,

2003; Liu and Li, 2010; Stevens, 2001 onwards). Considerable monocot diversification took place during the Early Cretaceous, and seagrasses probably evolved from freshwater monocots towards the Late Cretaceous (Janssen and Bremer, 2004).

In general, seagrass fossils are rare (e.g., Stockey, 2006; Benzecry and Brack-Hanes, 2008; Reich et al., 2015), but among the comparatively rare plant fossils in the fully marine strata of the Maastrichtian type area (NE Belgium, SE Netherlands), remains of seagrasses are common. Worldwide, the oldest records refer to stem material from the lower Campanian of SE Netherlands (*Thalassocharis muelleri*; Debey, 1848, 1851; Pomel, 1849) and the Harz Mountains in Germany (*T. bosquetii*; Debey, 1865). Voigt and Domke (1955) published an extensive paper on the morphology and anatomy of *T. bosquetii* from the upper Maastrichtian of Kunrade (SE Netherlands), in which they analyzed silicified stems and attached roots, considering these to have been most closely similar to those of

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the extant genus *Cymodocea* (Cymodoceaceae). Leaves that may represent the foliage of *T. bosquetii* were described as *Thalassotaenia debeyi* (Van der Ham et al., 2007). These leaves are always found detached and incomplete, and are commonly poorly preserved, showing only a faint imprint with indistinct venation. However, fragments preserved in flint have permitted a detailed anatomical description, as well as statements on the affinity of the seagrass foliage from the Maastrichtian type area. There is no unequivocal match with the leaves of any of the extant genera or families of seagrasses. However, *Amphibolis* and *Thalassodendron* (Cymodoceaceae) and *Posidonia* (Posidoniaceae) display the greatest resemblance.

Since Voigt and Domke (1955) published their study of anatomically preserved material of *T. bosquetii* from Kunrade, in the eastern part of the Maastrichtian type area, a lot of new stem material has been recovered, in particular from the western part of the area (Fig. 1: localities 1–6). Among this material are many specimens embedded in flint and numerous beautifully silicified fragments with roots, which enable a better understanding of the anatomy and morphology of stems of *T. bosquetii*. These lots have proved very helpful in interpreting the features of the abundant imprints (external moulds) among the specimens studied, including the type material.

2. Material, localities and stratigraphy

Our material of *Thalassocharis bosquetii* (*c*. 275 specimens; see 4.2: Additional material, Table 1) originates from the Maastrichtian type area (Fig. 1), from the upper Maastrichtian *Belemnitella junior* and *Belemnella kazimiroviensis* cephalopod zones (Fig. 2). The material from the western part of the area is from the fully marine facies of the Gulpen and Maastricht formations (Lanaye to Meerssen members), while specimens from the northeastern part (Kunrade area) originate

from the Kunrade Formation, which is the more littoral facies of the uppermost Gulpen Formation and the lower/middle Maastricht Formation. Anatomically preserved specimens stem mostly from the Gronsveld Member (Maastricht) and from residual flint deposits ('flint eluvium', 'clay with flint') that originated by dissolution of the chalky matrix from the top of the Lanaye Member and the base of the overlying Maastricht Formation (Hallembaye, Loën, Vijlenerbos; Fig. 1: localities 1, 2 and 11), from the Schiepersberg Member or Emael Member (Elst; Fig. 1: locality 3) and from the Nekum Member (Sluizen, Eben Emael; Fig. 1: localities 3 and 4).

To date, no material of *T. bosquetii* is available from Campanian, lower-middle Maastrichtian (Vijlen and Lixhe 1–3 members) and lower-middle Danian deposits in the Maastrichtian type area. However, a stem has been recorded from the lower Campanian of the area (*Thalassocharis muelleri*; Debey, 1848, 1851; Pomel, 1849), unidentified stem fragments were collected from the upper Campanian Zeven Wegen Member (*Thalassocharis* sp.), and seagrass foliage (*Thalassotaenia debeyi*) is on record from the upper Campanian, lower-middle Maastrichtian and lower Danian (Fig. 2; Plate X, 3, 4; Van der Ham et al., 2007). See further 6.2. Comparison with fossil seagrasses.

3. Methods

The material consists of imprints (external moulds; e.g., Plate II, 1) and of silicified stem fragments (e.g., Plate III, 1) in surface views, which did not require any further preparation (see 5.1. Morphology). Anatomical features of broken silicified fragments (e.g., Plate IV, 8) were studied immersed in water with a Wild stereo dissecting microscope. Thin sections were prepared of the following specimens: NHMM JJ 13026a, b, NHMM MD 3253.4 and NHMM RH 967 (see further 5.2. Anatomy), and studied with a Leitz Dialux 20 microscope.
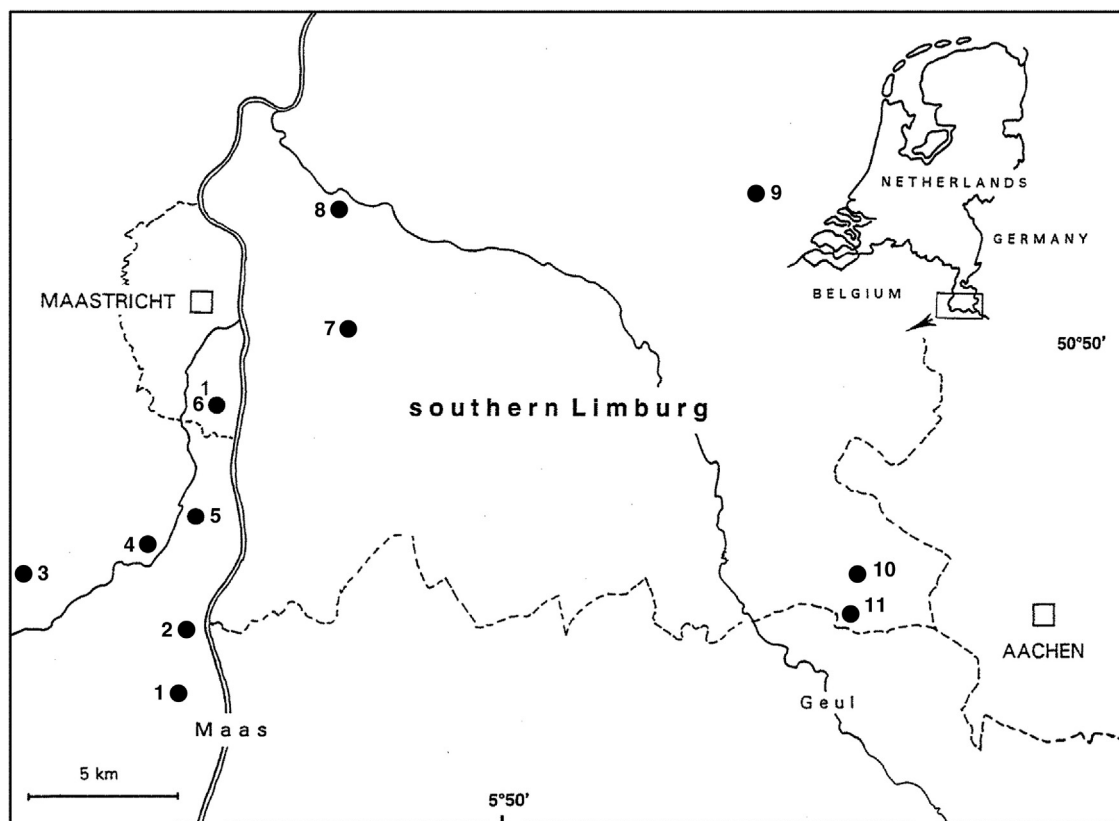

Fig. 1. Map of the Maastrichtian type area, showing the localities mentioned in the present study. Localities 1–9, 11: *Thalassocharis bosquetii*, locality 10: *T. muelleri*. 1. Hallembaye (former CPL quarry, now Kreco), 2. Loën (CBR-Lixhe quarry), 3. Elst, Sluizen. 4. Eben Emael (CBR-Romontbos quarry), 5. Eben Emael (Marnebel quarry), 6. Maastricht (ENCI-HeidelbergCement Group quarry), 7. Cadier en Keer ('t Rooth quarry, formerly Nekami), 8. Geulhem (former Curfs quarry), 9. Kunrade area (De Dael, Kunrade, Kunderberg, Putberg and Schunck quarries, Welten), 10. Vaals (Holset), 11. Vijlenerbos.

Table 1

Material of *Thalassocharis bosquetii*: 154 out of the *c.* 275 available specimens, i.e. the type material, most of the silicified material and a stratigraphically representative selection of the imprints. Headings and column 1: formations and members, more or less in stratigraphical order (see Fig. 2). Columns 2 and 3: localities and quarries; the numbers in column 3 refer to the map (Fig. 1). Column 4: specimens, in alphabetical order per locality and quarry. Column 5: remarks, mostly additional stratigraphical information (see Fig. 2).

Gulpen formation				
Lanaye Member	Eben Emael	5	NHMM RH 890	
	Eben Emael	5	Renkens 503	
	Maastricht	6	NHMM JS 168	Between flint levels 10 and 13
	Maastricht	6	NHMM RH 975, 1006	
Gulpen formation (top of Lanaye Member) or Maastricht formation (base)				
Calcaire à silex gris	Maastricht	*c.* 1	U 1122, 1126	Type material; Sint-Pietersberg
Flint eluvium	Hallembaye	1	NHMM LI 420, 455	
	Hallembaye	1	NHMM RH 949, 950, 952–954, 959, 960, 962, 963, 965–968, 979, 995	
	Loën	2	Goffings 151	
	Loën	2	Laffineur 501, 502, 524, 529, 530, 532, 534, 557, 560, 565, 566, 574, 576, 577, 581	
	Loën	2	NHMM JS 874	
	Loën	2	NHMM RH 942–944, 970, 971, 1001, 1004, 1005	
	Loën	2	Strijbos VL50/51, 96	
	Vijlenerbos	11	NHMM RH 126f	
Kunrade formation				
Upper part	Kunrade area	9	JMS 52001, 52002, 52346, 52350, 52356, 52357, 54316b, c	
	Kunrade area	9	NHMM 3634	
	Kunrade area	9	NHMM DE 6/5/13, 27/5/13	
	Kunrade area	9	NHMM RD 34	
	Kunrade area	9	NHMM RH 332, 940	
	Kunrade area	9	RGM 20351, 21372, 21377, 21388, 21391, 21395–21397, 21399, 21402, 21406, 21407, 78239	
	Kunrade area	9	U 392b, 462, 1125, 1129	
	Kunrade area	9	Ubaghs 307, 379–381 (IRScNB)	
Maastricht formation				
Valkenburg Member	Maastricht	6	Goffings 89	
	Maastricht	6	NHMM MD 5004	
	Maastricht	6	NHMM MD 5533	Lichtenberg Horizon
	Maastricht	6	NHMM RH 881, 883, 884, 886	Lichtenberg Horizon
Gronsveld Member	Eben Emael	5	Renkens 14/12/10	
	Maastricht	6	NHMM 2014.026	
	Maastricht	6	NHMM EN 20k, 25v, 73n	
	Maastricht	6	NHMM JJ 7751, 7825, 8575, 8576, 9978a, 10810, 11324, 12789, 13026	
	Maastricht	6	NHMM MA 343	
	Maastricht	6	NHMM MD 3253, 3254, 3894, 3944, 4423, 4672–4674, 4688	
	Maastricht	6	NHMM RH 728, 874–878, 892–894, 897	
	Cadier en Keer	7	NHMM RH 871	
Schiepersberg Mb.	Maastricht	6	MAB 4593	
Schiep./Emael Mb.	Elst	3	NHMM RH 955–957	Flint eluvium
Emael Member	Eben Emael	4	NHMM GC 6328	
	Eben Emael	4	NHMM RD 41	
	Eben Emael	5	Renkens 23/4/16a	Below Lava Horizon
	Eben Emael	5	Renkens 23/4/16b	Below Laumont Horizon
	Maastricht	6	Lemmens without number	
	Maastricht	6	NHMM 2014.032	Below Laumont Horizon
	Maastricht	6	NHMM EN 83j	
	Maastricht	6	NHMM MD 3603	Romontbos Horizon
	Maastricht	6	NHMM RH 888	
	Maastricht	6	NHMM RH 980	Lava Horizon
Nekum Member	Sluizen	3	Laffineur 531	
	Eben Emael	4	NHMM RH 947, 969	Flint eluvium
	Maastricht	6	Laffineur 500	Laumont Horizon
	Maastricht	6	NHMM 1998.030	
Meerssen Member	Maastricht	6	NHMM JJ 13963	
	Geulhem	8	NHMM JJ 7177	
	Geulhem	8	Renkens 501, 514	Berg en Terblijt Horizon

The following abbreviations are used to denote the repositories of specimens: IRScNB: Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; JMS: Jongmans Collection, Naturalis Biodiversity Center, Leiden, the Netherlands; MAB: Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; NHMM: Natuurhistorisch Museum Maastricht, the Netherlands (DE: Dirk Eysermans Collection, EN: Eric Nieuwenhuis Collection, GC: Ger Cremers Collection, JJ: John Jagt Collection, JS: Jules Snellings Collection, LI: Ludo Indeherberge Collection, MA: Frans Maatman Collection, MD: Mart Deckers Collection, RD: Rudi Dortangs Collection, RH: Raymond van der Ham Collection); RGM: Naturalis Biodiversity Center, Leiden, the Netherlands; U: Laboratory of Palaeobotany and Palynology, Utrecht, the Netherlands. The designations 'Goffings', 'Laffineur', 'Renkens', 'Strijbos' and 'Stuwe' refer to the private collections of Luc Goffings (Mol, Belgium), Johan Laffineur (Maasmechelen, Belgium), Sjir Renkens (Bruchem, the Netherlands), Victor Strijbos (Neerpelt, Belgium) and Thomas Stuwe (Ennigerloh, Germany), respectively.

4. Systematics

4.1. Thalassocharis Debey ex Miquel, 1853

1848   *Thalassocharis* (*Mülleri* DB.) — Debey, p. 119 (nomen nudum) (see Remark)
1851   *Thalassocharis* DB.— Debey, p. 568 (nomen nudum)
1853   *Thalassocharis* Debey mss. — Miquel, p. 50, 51, pl. 6, figs. 1–3

1880   *Thalassocharis* Debey — Hosius and Von der Marck, p. 147

Original generic description/diagnosis (Miquel, 1853, p. 50): … dwarse, afwisselend schuins geplaatste geledingen of tusschenschotten dezer platgedrukte stengels, en de op hunne internodiën voorkomende zeer regelmatige overlangsche verhevenheden… (English translation: … transverse, alternately oblique nodes or septa of these compressed stems, and the very regular longitudinal ridges on their internodes…).
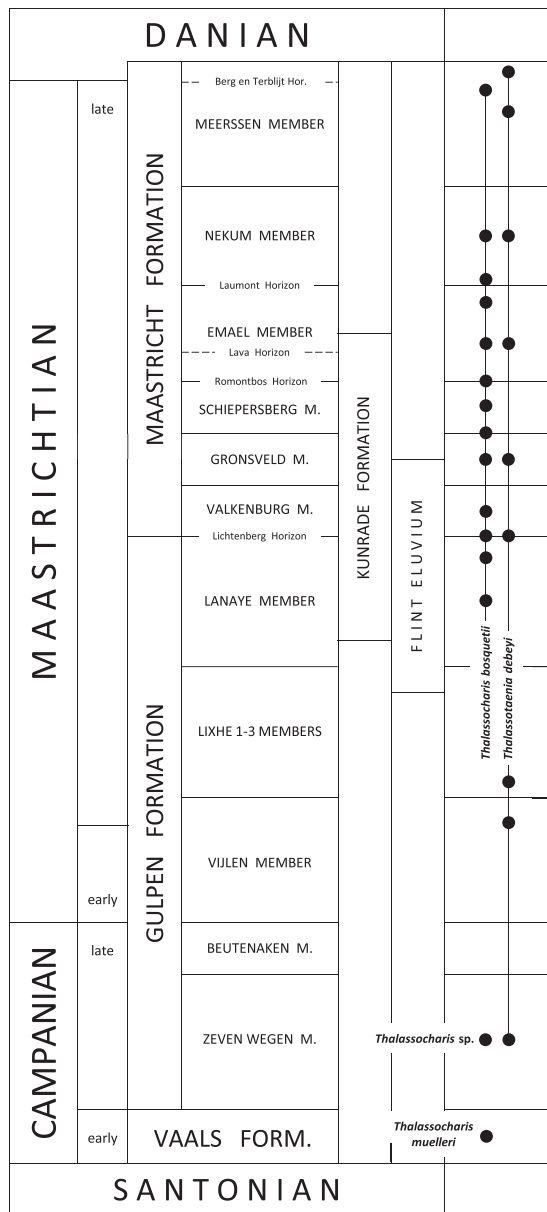
Fig. 2. Chrono- and lithostratigraphy of Cretaceous strata in the Maastrichtian type area, showing the provenance of *Thalassocharis bosquetii*, *Thalassotaenia debeyi* (Gulpen and Maastricht formations), *Thalassocharis muelleri* (Vaals Formation) and *Thalassocharis* sp. (Zeven Wegen Member). See Jagt (1999) and Jagt and Jagt-Yazykova (2012) for further stratigraphical details.

Emended generic diagnosis: (fragments of) stems with distichously arranged, amplexicaul leaf scars separated by narrow, alternately oblique sutures; leaf scars with longitudinal furrows and/or elongated pits.

Type: *Thalassocharis bosquetii* Debey ex Miquel.

Other species: *Thalassocharis muelleri* Debey, *T. westfalica* Hosius et Von der Marck. See 6.2. Comparison with fossil seagrasses.

Geographical and stratigraphical distribution: lower Campanian of SE Netherlands (*T. muelleri*) and NW Germany (*T. bosquetii*?), upper Campanian of NW Germany (*T. westfalica*) and NE Belgium (*Thalassocharis* sp.), upper Maastrichtian of NE Belgium and SE Netherlands (*T. bosquetii*). See 6.2. Comparison with fossil seagrasses. Fig. 3 shows the geographical distribution of *Thalassocharis*: coastal areas along the northwestern margin of the Rhenish Massif (Ziegler, 1990).

Affinity: Monocotyledonae, Alismatales(?).

Remark. The name *Thalassocharis* derives from Greek *thalassa* (sea) and *charis* (beauty), referring to the environment in which the plants were supposed to have grown and the decorative appearance of the stems.

4.2. Thalassocharis bosquetii Debey ex Miquel, 1853 (Figs. 1–4; Plates I–VIII)

1851   *Th. Bosqueti* DB. — Debey, p. 568 (nomen nudum) (see Remark 1)
1853   *Thalassocharis Bosqueti* Debey mss. — Miquel, p. 50, 51, pl. 6, fig. 1, 1a
1853   *Thalassocharis Bosqueti* forma *breviarticulata* — Miquel, p. 51, pl. 6, fig. 2 (see 6.1.2. Miquel's formae *breviarticulata* and *lata*)
1853   *Thalassocharis Bosqueti* forma *lata* — Miquel, p. 51, pl. 6, fig. 3, 3a (see 6.1.2. Miquel's formae *breviarticulata* and *lata*)
1853   *Thalassocharis*? — Miquel, p. 51 (refers to U 1129; see Table 1)
1853   ? *Culmites cretaceus* — Miquel, p. 53 (see Remark 2)
1853   ? *Chondrites Bosqueti* — Miquel, p. 54 (see Remark 3)
1859   *Thalassocharis Bosqueti* Debey — Binkhorst van den Binkhorst, p. 61
1860   *Thalassocharis Bosqueti* Debey et Miquel — Bosquet, p. 417
1865   *Thalassocharis Bosqueti* m. — Debey, p. 57 (excl. material from Wernigerode)
1865   *Th. Binkhorsti* m. — Debey, p. 57 (nomen nudum; see Remark 4)
1880   *Thalassocharis Bosqueti* Deb. mns. — Hosius and Von der Marck, p. 146
1885   *Thalassocharis Bosqueti* De Bey — Ubaghs, p. 28
1955   *Thalassocharis bosqueti* Debey ex Miquel — Voigt and Domke, p. 87–102, pl. 4, figs. 1–7, pl. 5, figs. 1–3, pl. 6–9
1981   *Thalassocharis bosqueti* Debey ex Miquel — Voigt, p. 282, fig. 2C
1998   *Thalassocharis bosqueti* Debey ex Miquel, 1853 — Dortangs, p. 100, pl. 3, figs. 4, 6
2007   *Thalassocharis bosquetii* Debey ex Miquel — Van der Ham et al., p. 301
2013   *Thalassocharis bosquetii* — Van der Ham and Renkens, p. 39, 40

Original specific description/diagnosis: caulibus (compressis) cylindricis? densis, 2–5 millim. crassis, per 2–4 millim. intervalla transverse dissepimentosis, septis (vel cicatricibus?) nunc prominulis plerumque alternatim obliquis, articulis haud contractis longitrorse plicatis, plicis 8^{nis} vel 10^{nis} utplurimum quidquam convergentibus, prominulis, utrique obtusis, in dissepimenta transversa haud continuis, — ? foliis (intermixtis) paucis linearibus 2 millim. circiter latis, laevibus enervibus.

Emended specific diagnosis: (fragments of) monopodially branched, monomorphic stems of 1.5–8 mm (not compressed) or up to 12 mm (compressed) diameter, with distichously arranged, amplexicaul leaf scars 1.5–9 mm long (along median). Sparsely branched roots emerge radially in dense bundles of up to c. 50 from opposite sides of relatively few leaf scars and curve obliquely 'backwards'. Thin sections show an outer cortex with conspicuously thickened vascular bundles, each of which constricts into a thin vascular strand just below a furrow/pit on the leaf scar, a middle cortex with distinct fibre strands, an inner cortex with many small intercellular cavities, and a central stele with many sheathed vascular bundles within and fusing with a thick common fibre sheath.

Type locality: SE Netherlands, Maastricht, Sint-Pietersberg (Fig. 1: south of Maastricht).

Type stratum: calcaire grossier à silex gris (Miquel, 1853), which corresponds to the upper part of the Gulpen Formation and the lower part of the Maastricht Formation (see also Bosquet, 1860), in current terminology; both are of late Maastrichtian, *Belemnitella junior* Zone age (Fig. 2).

Type material: U 1122 (imprints of stems with roots; Plate I, 1; compare Miquel, 1853, pl. 6, fig. 1, 1a), U 1126 (type of forma *breviarticulata*, imprint of stem, Plate I, 2; Miquel, p. 51, pl. 6, fig. 2).
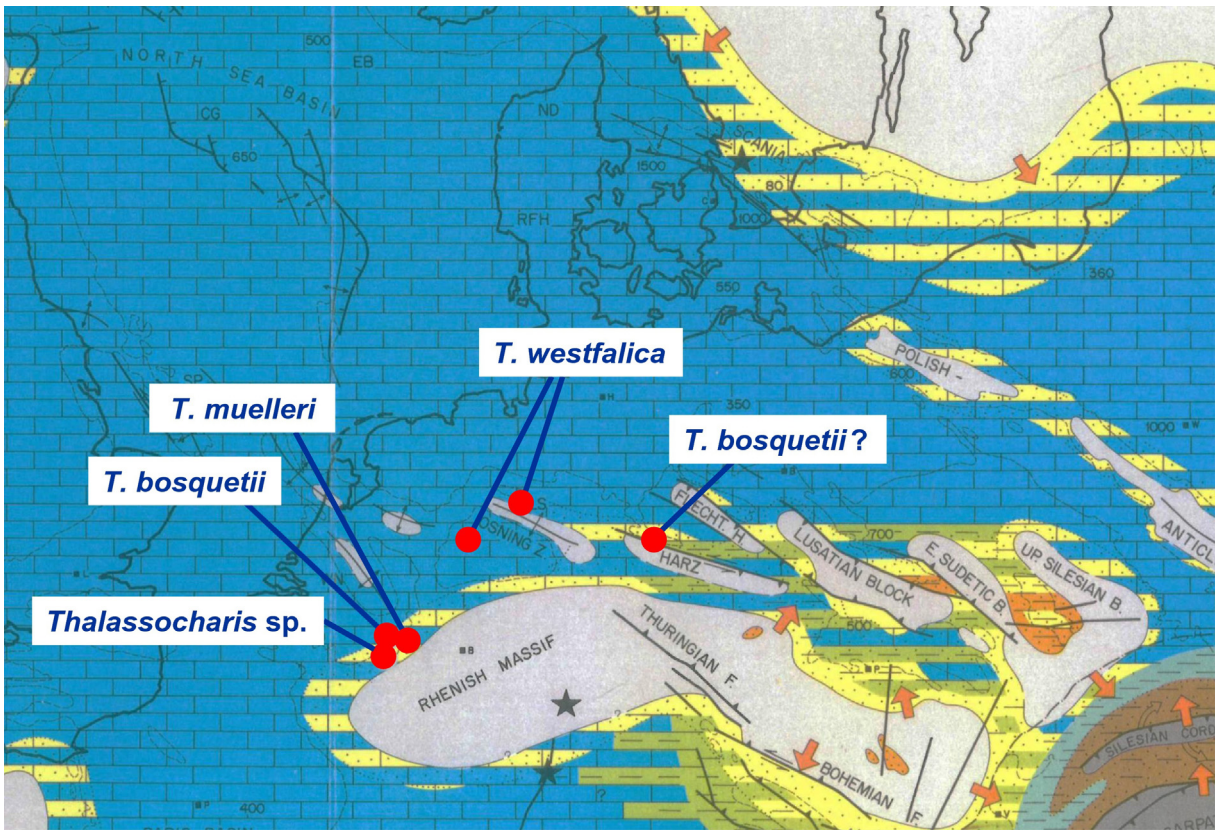
Fig. 3. Geographical distribution of *Thalassocharis* (red dots), plotted on the latest Cretaceous to Danian palaeographical map by Ziegler (1990). *Thalassocharis bosquetii*, *T. muelleri* and *Thalassocharis* sp.: Maastrichtian type area; *T. westfalica*: Coesfeld and Osnabrück; *T. bosquetii*?: Wernigerode. Blue: depositional environment, carbonates, mainly shallow-marine; yellow: depositional environment, deltaic, coastal and shallow-marine clastics; green: depositional environment, shallow-marine, mainly shales; grey: area of non-deposition, cratonic, mainly low relief.

The type of forma *lata* (Miquel, p. 51, pl. 6, fig. 3, 3a) could not be traced. According to Debey and Von Ettingshausen (1859) the interpretation of the imprint by Miquel (fig. 3) was wrong. Consequently they described a new genus and species of red algae, namely *Gelidinium trajectomosanum* (Debey and Von Ettingshausen, 1859, pl. 3, fig. 6, h). However, they did not explain Miquel's fig. 3a, which depicts the imprint of a distinct fragment of a *Thalassocharis bosquetii* stem.
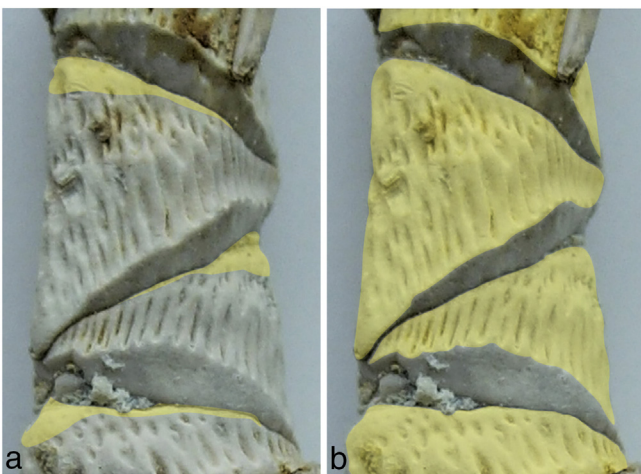
Fig. 4. Stem fragment (NHMM JJ 8575), contrasting the view of the leaf scar surface of Voigt and Domke (1955) with the present interpretation. a. Probable leaf scar according to Voigt and Domke (1955). b. Leaf scar as understood in the present paper; the uncoloured structure at the upper right on the uppermost scar is a descending root. See also Plate III, 2, 3.

Additional material (152 out of the *c.* 275 available specimens, i.e. most of the silicified material and a stratigraphically representative selection of the imprints): see Table 1.

Geographical distribution: NE Belgium and SE Netherlands (Maastrichtian type area; Fig.1), and possibly NW Germany? (see 6.2. Comparison with fossil seagrasses).

Stratigraphical distribution: possibly lower Campanian (NW Germany); upper Maastrichtian (Maastrichtian type area): *Belemnitella junior* Zone (Lanaye Member to lower part of Meerssen Member) and *Belemnella kazimiroviensis* Zone (upper part of Meerssen Member) (Jagt, 1999; Jagt and Jagt-Yazykova, 2012). Oldest specimen: NHMM JS 168, Maastricht (ENCI-HeidelbergCement Group quarry), middle part of Lanaye Member, between flint levels 11 and 13; youngest specimens: former Curfs quarry, upper part of Meerssen Member (IVf-6), Renkens 501, 514 (Fig. 2).

Remarks. 1. The species *Thalassocharis bosquetii* was named after Joseph Augustinus Hubertus de Bosquet (1814–1880), chemist and palaeontologist at Maastricht (Leloux, 2002; Jagt et al., 2012), who collected the type material.

2. The type material of *Culmites cretaceus* Miquel (U 1125; Kunrade Formation, Kunrade area; Plate I, 3; Miquel, 1853, p. 53, not illustrated) is the imprint of a stem of 84 × 8 mm, with distichously arranged, amplexicaul smooth 'internodes' (leaf scars?) that are separated by narrow, alternately oblique sutures. In view of the fact that stems of *Thalassocharis bosquetii* are occasionally ± smooth (longitudinal furrows and/or elongated pits not recognizable), *Culmites cretaceus* might be such a stem of *T. bosquetii*. A thin stem of *T. bosquetii* with roots and *Thalassotaenia debeyi* leaves (not attached) occur in the same specimen.

3. The specimen designated as type material of *Chondrites bosquetii* Miquel (U 1128; Sint-Pietersberg; Plate I, 4) is not the
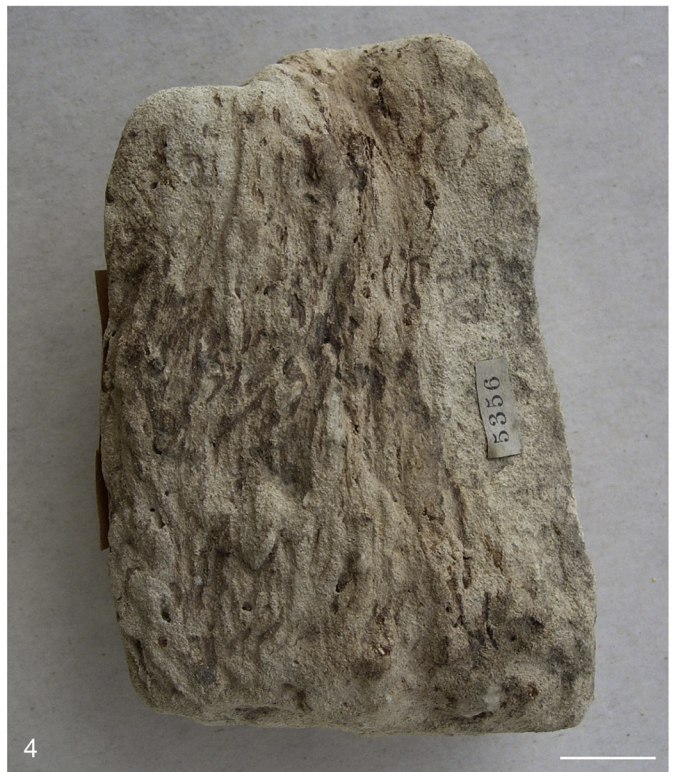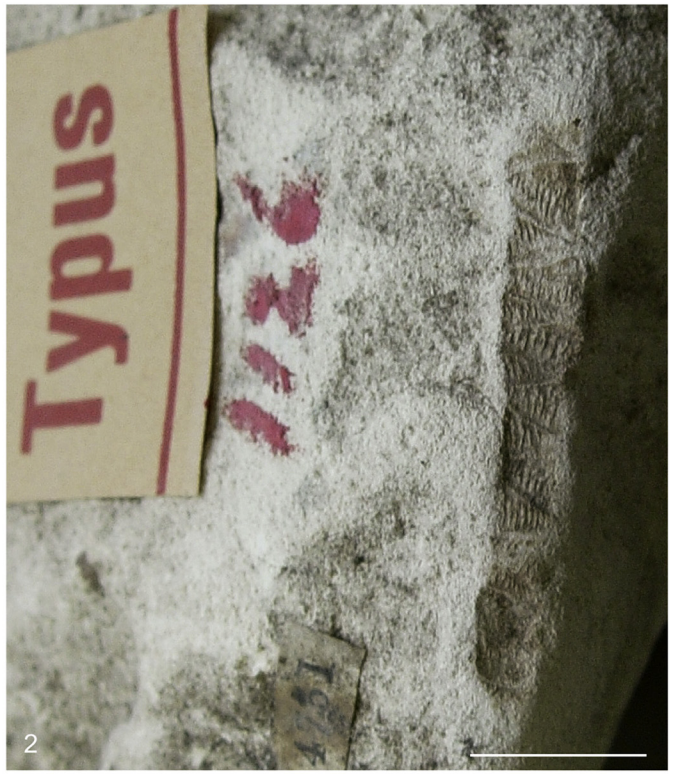
Plate I. Type specimens. Bar = 10 mm. 1. *Thalassocharis bosquetii* Miquel, imprints of stems with roots (arrowhead). Specimen: U 1122. 2. *Thalassocharis bosquetii* forma *breviarticulata* Miquel, imprint of stem. Specimen: U 1126. 3. *Culmites cretaceus* Miquel, imprint of stem. Specimen: U 1125. 4. *Chondrites bosquetii* Miquel, imprints of roots. Specimen: U 1128.

Plate II. *Thalassocharis bosquetii* Miquel, imprints. Bar = 10 mm.1. Stems with roots (arrowhead); note external and internal moulds of associated bivalve shells. Specimen: NHMM RH 940.2. Stems and roots. Specimen: RGM 20351.3. Branched stem with roots (arrowhead). Specimen: NHMM JS 874b.4. Imprint of stem on the attachment area of an exogyrine bivalve, *Amphidonte* (*Ceratostreon*) sp. Specimen: NHMM EN 83j.5. Stem with roots (arrowhead). Specimen: Ubaghs 380 (IRScNB).

Plate II.
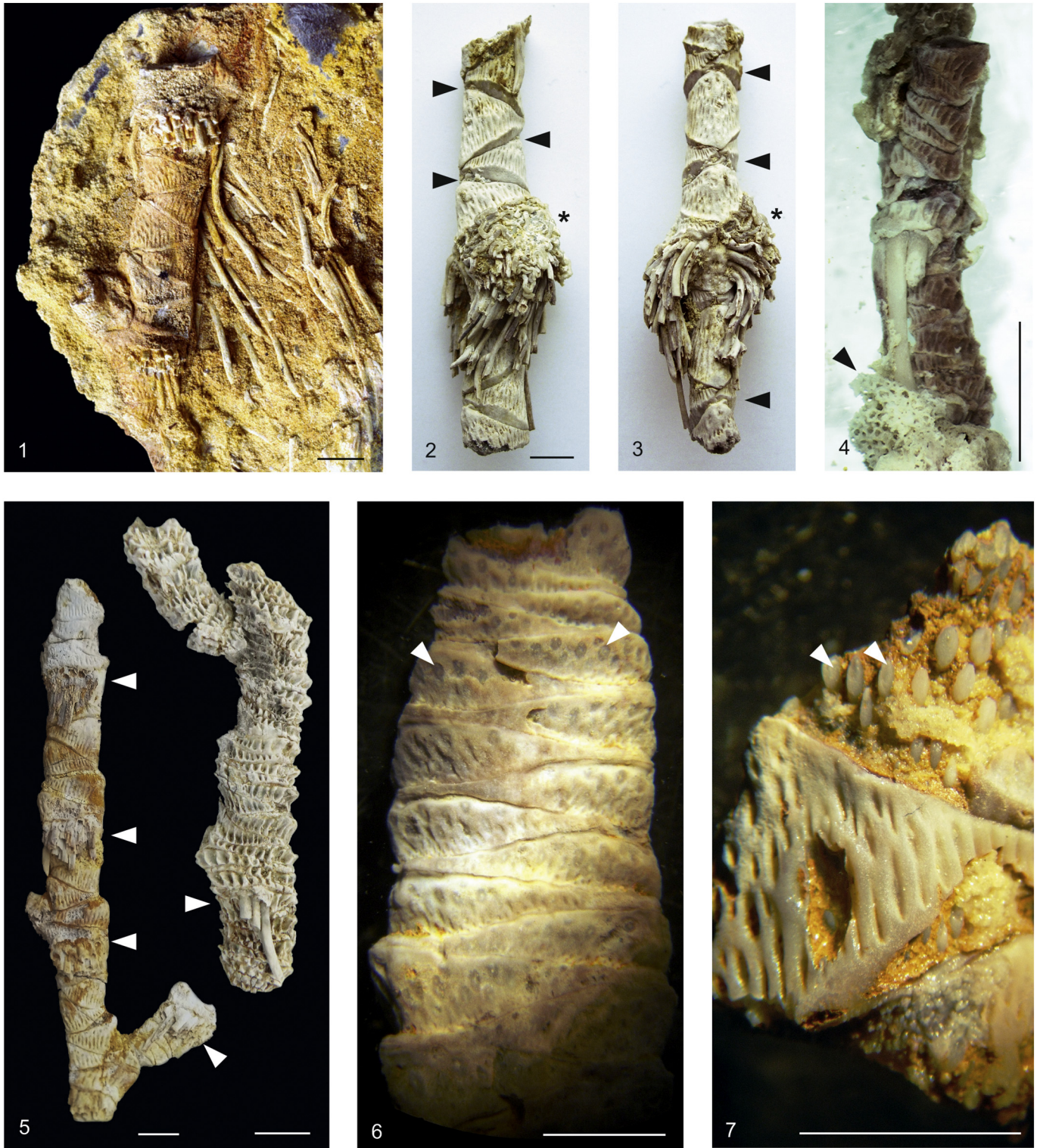
Plate III. *Thalassocharis bosquetii* Miquel, silicified material. Bar = 5 mm. 1. Branched stem with roots. Specimen: NHMM RH 871. 2, 3. Stem with roots and epibiont sabellid worm tubes (*Glomerula lombricus*; asterisk; compare Jäger, 2012); see also Plate VII, 1. Note the axillary buds (arrowheads). Specimen: NHMM JJ 8575. 4. Stem with roots and epibiont calcareous sponge (*Oculospongia* sp.; arrowhead). Specimen: NHMM RH 728. 5. Branched stems with roots (arrowheads). Specimens: NHMM MD 3253 (left), NHMM MD 4423.1 (right). 6. Stem, superficially eroded, showing leaf scars with many sections (grey; arrowheads) through thickened parts of vascular bundles in middle/outer cortex ('pears'). The lighter central spot in each section represents vascular tissue. Specimen: Lemmens (unnumbered) 7. Stem, partly eroded. In the lower and middle leaf scar the outer cortex is still largely present; in the upper leaf scar the ground tissue of the outer cortex has largely disappeared, so that the thickened parts of a number of vascular bundles in the middle/outer cortex ('pears'; arrowheads) are exposed. Specimen: NHMM JJ 8575.

specimen that was illustrated by Miquel (1853), pl. 6, fig. 4) but it does match Miquel's description very well, representing a bundle of roots similar to those often found attached to stems of *Thalassocharis bosquetii*.

4. In addition to *Thalassocharis bosquetii*, also *T. binkhorstii* (nomen nudum; Debey, 1865) was recorded from the upper Maastrichtian of the type area. In view of the origin ('Schichten von Kunraed', i.e. Kunrade formation), *T. binkhorstii* probably refers to material of *T.*

bosquetii from that unit at one of the well-known localities in the Kunrade.

5. Description

The morphological section is based on silicified material and imprints (Plates II; III; IV, 1; VI, 4; VII, 1, 2). The anatomical section is based on thin sections and fractures of silicified material (Plates IV–VI; VII, 3, 4; VIII). It has been tried to address as much as possible the features of extant seagrasses described by Tomlinson (1982). Squamules ('squamulae intravaginales') are small scales (without veins) that occur in the axils of leaves and leaf-like organs of certain aquatic plants (Tomlinson, 1982). The following abbreviations are used: ax. = size in axial direction, rad. = size in radial direction, tang. = size in transverse tangential direction.

5.1. Morphology

Stem fragments ± straight, monomorphic axes with distichous phyllotaxis (leaves absent, leaf scars distinct), up to 20 cm long, in cross section usually ± elliptical (leaf scar medians mostly on edges, rarely on 'flat' sides), occasionally circular; diameter 1.5–8 mm (not compressed), up to 12 mm (compressed), within a fragment usually ± constant, sometimes slightly increasing and/or decreasing.

Branching sparse, monopodial (but see 6.1.1. Branching type), in a single plane; branches inserted just above leaf scar medians, at their base less wide than adjacent part of main axis; axillary buds occasionally seen (Plates III, 2, 3; IV, 1), in same position as branches, up to 0.3 mm ax., 0.2 mm rad. and 2 mm tang. Squamules or traces of squamules not observed (see 6.1.3. Squamules).

Stem surface with ± amplexicaul leaf scars; sutures between leaf scars narrow, straight to slightly sinuous, typically zigzagging on 'flat' sides of stem; leaf scars relatively short to long (ax.; compared to stem width); long side (=median) of scar 1.5–9 mm, short side (opposite median) 0.3–2.5 mm, occasionally with a longitudinal to oblique suture (Plates III, 3, VII, 1); scar surface with ± longitudinal, ± distinct furrows and/or elongated pits, which usually occur throughout the scar, but sometimes leave a proximal smooth zone (Plates III, 2; IV, 1) (occasionally complete 'scar' ± smooth; Plate VI, 3; see 6.4. Ecological aspects); furrows/pits 16–20 per leaf scar in narrow stem fragments, up to 50 in wider fragments, ± perpendicular to proximal suture of leaf scar, slightly zigzagging on 'flat' sides of stem (changing direction at sutures), often showing a ± central vascular bundle scar (small wart, pit or light dot; Plates II, 5; III, 7); scar of median vascular bundle often distinct in pit below distal margin of leaf scar (Plate III, 3); shape and surface details of leaf scars within a stem fragment (including branches) ± constant.

Roots emerge ± radially from opposite 'flat' sides of relatively few leaf scars and curve in proximal direction ('backwards'), up to c. 15 (rarely up to c. 50) in a single dense bundle on each side of scar (Plate III, 2, 3); in a few stem fragments, root bundles occur on leaf scars separated by five to eight void ones (Plate III, 1, 4, 5); root fragments up to 30 mm long, in cross section circular (0.8–1.2 mm) to elliptical (largest diameter up to 2.2 mm; compressed?), not or sparsely branched, but occasionally two or three branches emerging within a few millimetres.

5.2. Anatomy

5.2.1. Stem with leaf scars
Cross section (Plates IV, V)
Material: thin sections of three stem fragments: 1. NHMM JJ 13026a (Plate IV, 1; section 4.6 × 3 mm), 2. NHMM MD 3253.4 (Plate V, 1; section 6.1 × 4.5 mm), 3. NHMM JJ 13026b (Plate VI, 3; section 49 × 3.8 mm); complemented with numerous fractured surfaces (various specimens).
Epidermis absent; outer cell layer (=leaf scar surface) with irregularly arranged cells that are similar to underlying outer cortex cells (Plate IV, 4).

Cortex consisting of three layers (Plates IV, 3, 8; V, 1); **outer cortex** with up to ten irregular layers of radially elliptical, thick-walled cells up to 45 × 25 μm, traversed by vascular bundles, slightly thinner in furrowed/pitted area of leaf scar; **middle cortex** with 30–70 grouped/fusing fibre strands separated by narrow radial areas of thick-walled cells similar to those in outer cortex, traversed by vascular bundles; fibre strands in cross section circular to radially elliptical, up to 0.6 × 0.35 mm, consisting of polygonal thick-walled cells (up to 15 μm diameter) with a small ± circular lumen (Plate IV, 5); **inner cortex** relatively thick between leaf scar medians and stele, with polygonal thin-walled cells and many circular (up to 15 μm) to elliptical (up to 20 × 10 μm) intercellular cavities (Plate IV, 6), traversed by vascular bundles; **endodermis** (Plate IV, 6) consisting of tangentially elongate ± rectangular, thin-walled cells of 7–15 × 5–8 μm (smaller than other cells of inner cortex) with slightly thickened radial walls (Casparian thickenings); **vascular bundles** obliquely ascending from stele to leaf scar, with thin fibre sheath traversing inner cortex and passing between fibre strands through inner layer of middle cortex; fibre sheath much thickening from outer layer of middle cortex through outer cortex, ending bluntly/concavely just below stem surface in furrow/pit in leaf scar (thickened part of vascular bundle in middle/outer cortex pear-shaped, up to 0.35 mm diameter; Plates III, 6, 7; IV, 4, 5, 8; V, 1, 2, 4–6; VI, 2; VIII, 5), while vascular strand proceeds (with some fibres?) and ends at surface of furrow/pit (sometimes in small wart in furrow/pit; see also Plates II, 5; III, 7); median vascular bundles (one per leaf) often distinct between stele and distal margin of leaf scar; the pyriform structures ('pears') vary as to size and number; where the 'pears' are large and numerous, the outer cortex is relatively thick (compare Plates IV, 8 and V, 1 with Plate IV, 3) and the fibre strands in the middle cortex often thin and less conspicuous (compare Plate V, 5, 6 with Plate IV, 3).

Stele 38–46% of stem diameter, 2.1–2.3 × 1.45–1.8 mm in the thin sections, with 0.35–0.7 mm thick fibre sheath with cells similar to those of cortical fibre strands (compare Plate IV, 4); locally, cavities (artifact?) or thin-walled cells occur between fibre sheath and endodermis (Plate IV, 6); fibre sheath locally traversed by vascular bundles from centre of stele to cortex (Plate IV, 3); inside sheath (Plates IV, 3; V, 3) up to 36 vascular bundles occur in an irregular matrix of thick-walled cells (and intercellular cavities?); outer bundles ± fused with sheath of stele; inner bundles isolated by matrix cells; bundles with light strand(s) of thin-walled vascular tissue cells surrounded by relatively thick fibre sheath (Plate IV, 7); most peripheral bundles thin, 0.10–0.15 × 0.12–0.27 mm; one to three central bundles larger, 0.16–0.20 × 0.40–0.47 mm, with vascular tissue and dark thin-walled cells up to 15 μm diameter (the latter also in branches to cortex); phloem and xylem elements not recognizable (but see description of longitudinal section).

Longitudinal section (Plate VI)
Material: thin section of one stem fragment (NHMM JJ 13026b; Plate VI, 3), complemented with several fractured surfaces (various specimens). NHMM JJ 13026b: ± oblique section, 29 × 4.9 mm; sutures between leaf scars recognizable as cross sections through up to 0.4 mm deep, up to 0.1 mm wide furrows; branches present on two successive leaf scars. The description below consists mainly of additions to the description of the cross section.

Epidermis present in and along sutures between leaf scars (Plate VI, 5), at adaxial side of leaf base thinner (c. 10 μm) than at abaxial side (c. 30 μm); cells with thick outer wall, especially abaxially.

Outer cortex thinner in furrowed/pitted area of leaf scars; cells ± rectangular, up to 65 μm ax. and 45 μm rad., around sutures curved, relatively long and narrow; **middle cortex** with branching and anastomosing fibre strands; **inner cortex** with axially elongate (up to 200 × 15 μm) intercellular cavities; **endodermis** consisting of axially elongate ± rectangular cells of up to 35 × 5–8 μm with slightly thickened radial walls (Casparian thickenings); course and features of **vascular bundles** in cortex as observed in cross sections.
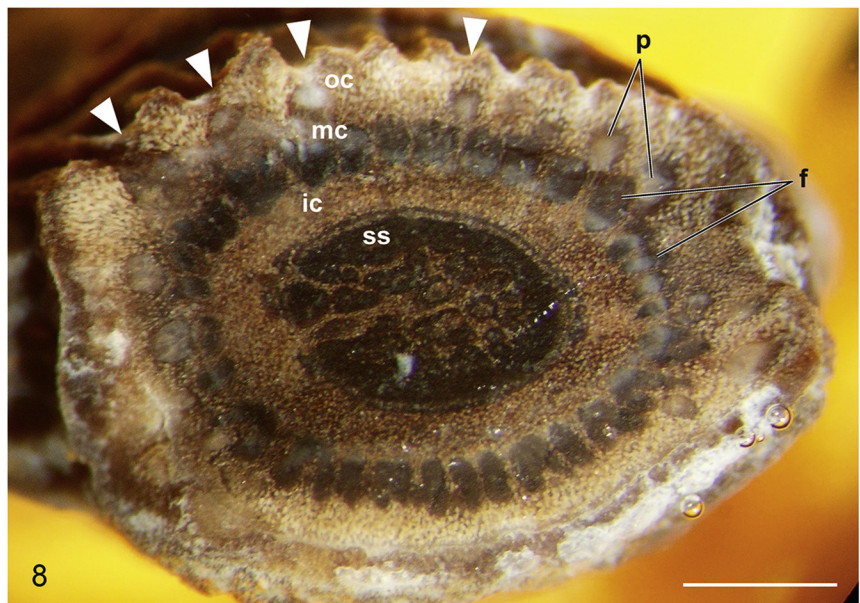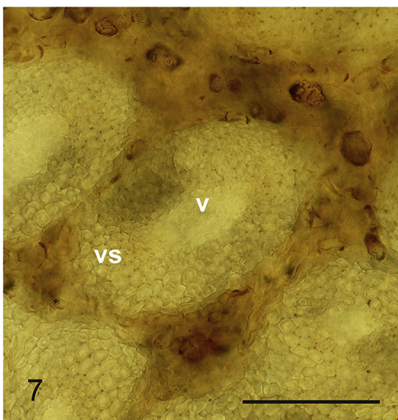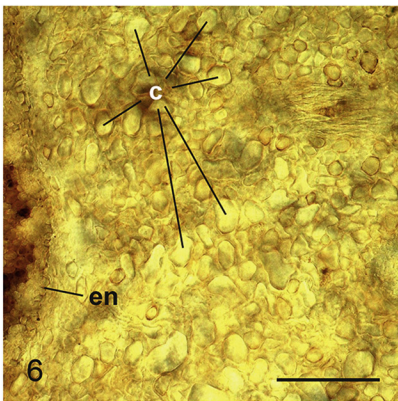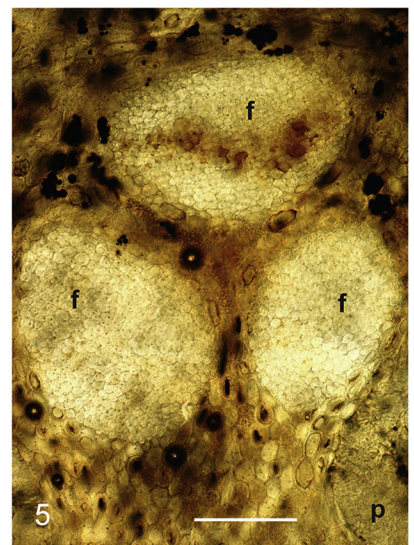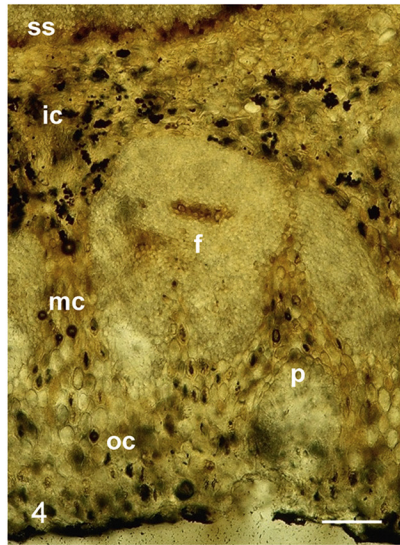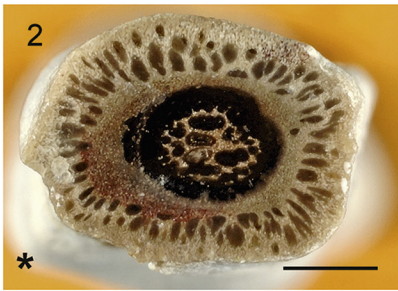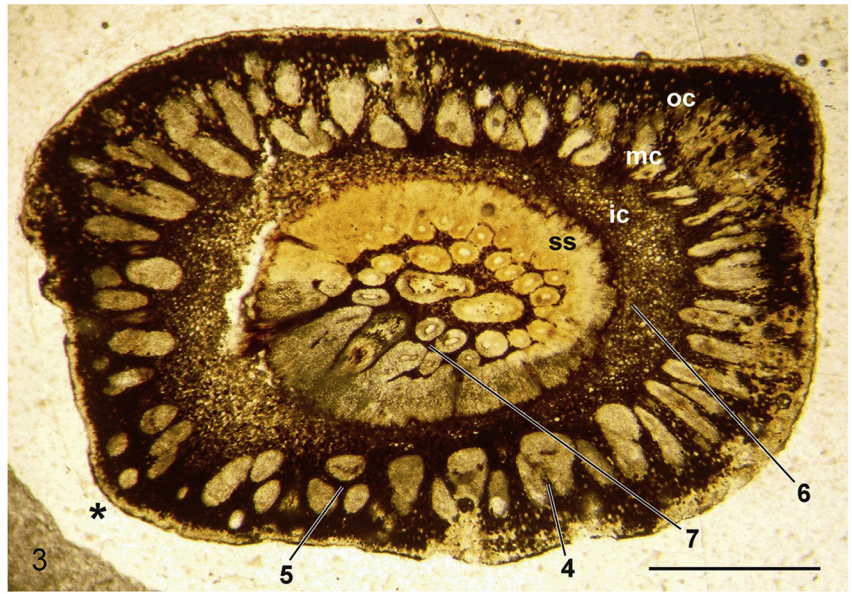
Plate IV.

Stele with vascular bundles branching and anastomosing mutually and from/with sheath of stele, with numerous branches of vascular bundles obliquely ascending into cortex; matrix cells in ± axial rows, isodiametric to axially elongate, up to 50×25 μm; vascular strands in central bundles (including branches to cortex) with axially elongate dark thin-walled cells up to 150×15 μm; xylem elements with spiral cell wall thickenings locally distinguishable.

5.2.2. Stem with leaf bases

Material: a number of cross to longitudinal thin sections of small (subapical?) stem fragments present in a slide (NHMM RH 967) with many roots are described here separately (Plate VIII, 5, 6).

Stem fragments 9–11 × 1.5–1.8 mm; leaf bases present, ± amplexicaul, patent, curving upwards, ending irregularly (as if blades torn off), separated by sutures (narrow furrows) similar to those observed in longitudinal section of NHMM JJ 13026b; sections through thick and thin parts (near and opposite median, respectively) of leaf bases alternate along longitudinal sections of stem fragments, indicating distichous phyllotaxis (Plate VIII, 5). Squamules or hairs not observed (see 6.1.3. Squamules).

Epidermis present on leaf bases (Plate VIII, 4, 5), adaxially thinner (5–10 μm) than abaxially (12–20 μm); **cortex** stratification as described above; fibre strands in middle cortex and 'pears' with vascular tissue in outer cortex distinct (Plate VIII, 5); vascular strand passing from blunt distal end of fibre sheath into leaf base; **endodermis** locally recognizable (cells smaller than other cells of inner cortex); **stele** comprising 6–9 vascular strands in fibre matrix, of which up to four strands in a single level branch off into cortex; xylem elements with spiral cell wall thickenings often distinct in vascular strands; root primordia emerging radially from outer part of stele into cortex.

5.2.3. Root

Material: many thin sections (a range of orientations) in a single slide (NHMM RH 967; Plate VIII, 1–4), complemented with fractured surfaces of roots attached to stem fragments (Lemmens without number; NHMM JJ 13026e, f). The thin section of specimen NHMM RH 967 includes a number of small stem fragments with root primordia radially emerging from outer part of stele.

Epidermis often present in places (Plate VIII, 3); cells up to 45 μm ax., 15–20 μm rad. and 8–10 μm tang., radial walls and inner tangential wall very thin; outer tangential wall relatively thick (though thinner than hypodermis cell walls); root hairs not observed.

Cortex consisting of three layers (Plate VIII, 3); **outer layer** with **hypodermis** of one layer of large thick-walled cells (up to 60 μm ax., 25–30 μm rad. and 12–17 μm tang.) and up to 8 irregular layers of smaller thick-walled cells; **middle layer** consisting of up to 6 layers of fibre-like cells with a small lumen; **inner layer** with up to eight layers of polygonal thin-walled cells and sparse (many?) intercellular cavities; **endodermis** mostly recognizable, consisting of thin-walled cells (smaller than other cells of inner cortex layer).

Stele 20–30% of root diameter, consisting of a circular to elliptical pith of fibres surrounded by peripheral zone of thin-walled cells (up to 18 μm diameter) with 6–12 indistinct strands of slightly darker cells (Plate VIII, 2); fibre sclereids occur locally in peripheral zone; the strands of darker cells occasionally with indistinct xylem elements (spiral cell wall thickenings); phloem elements not recognizable; fibre cells of pith up to 12 μm diameter.

5.2.4. Dark cells

Cells with a variously brown coloured contents occur in all tissues (Plates IV–VI, VIII), although rarely in the epidermis and fibre strands/sheaths (see 6.1.4. Dark cells).

6. Discussion

6.1. Morphological and anatomical aspects

6.1.1. Branching type

According to Den Hartog (1970) and Larkum and Den Hartog (1989), *Thalassocharis bosquetii* is characterized by a sympodial rhizome. However, the branches usually arise from a distinct main stem (Plate III, 1) and do not take over the growth of this main stem. This branching type is monopodial. Occasionally (Plate II, 3), a stem shows a number of more or less equal divisions (bifurcations), which, according to Tomlinson (1982, p. 58), is basically sympodial.

6.1.2. Miquel's formae breviarticulata and lata

The stems of *Thalassocharis bosquetii* vary in width (1.5–12 mm) and in length of the leaf scars (1.5–9 mm). Miquel's forma *breviarticulata* represents a stem fragment with relatively short leaf scars and short longitudinal furrows, while his forma *lata* is a relatively wide stem fragment (Miquel, 1853, p. 51, pl. 6, figs. 2, 3, 3a). These forms fit the gradual variation seen in stems of *T. bosquetii*, and therefore do not deserve separate status.

6.1.3. Squamules

Squamules (see 5. Description) are present in all Alismatales, with the exception of the Scheuchzeriaceae (*Scheuchzeria palustris*), in which they are replaced by hairs. In seagrasses, 2–20 squamules per leaf axil occur in seagrasses. They originate early in the development of stem and leaves (Tomlinson, 1982), and are described to disappear within two years in the seagrass *Cymodocea nodosa*. Neither squamules, traces of squamules nor hairs could be demonstrated in the present material of *Thalassocharis bosquetii*. This might relate to the defoliated condition of the stems, only leaf scars being present. However, squamules could neither be found in the thin sections of the small (subspical?) stem fragments with leaf bases, which suggests that squamules did not develop in *T. bosquetii*. This would be remarkable, because all extant seagrasses possess squamules in their leaf axils. Nothing is known about the presence/absence of squamules in other fossil seagrasses.

6.1.4. Dark cells

The cells with a variously brown coloured contents found in many tissues (rarely in epidermis and fibre strands/sheaths) might (in part) represent tannin cells, which commonly occur in extant seagrasses (Tomlinson, 1982).

Plate IV. *Thalassocharis bosquetii* Miquel, thin section and cross fractured silicified stems. Bar = 10 mm (1), 1 mm (2, 3, 8), 0.1 mm/100 μm (4–7); c = intercellular cavities, en = endodermis, f = fibre strand, ic = inner cortex, mc = middle cortex, oc = outer cortex, p = thickened vascular bundle end ('pear'), ss = fibre sheath of stele, v = vascular tissue, vs = vascular bundle sheath.1. Stem of which the section in Plate IV, 3 was made (at level of dashed line). Below each leaf scar is a relatively large smooth proximal area. The leaf scars themselves are slightly depressed, but do not show furrows and pits. The asterisk indicates the keel in the lower left corner in Plate IV, 2. Note the axillary buds (arrowheads). Specimen: NHMM JJ 13026a.2. Fracture of stem (proximal end) in Plate IV, 1. The keel in the lower left (asterisk) corner is at the right of the stem in Plate IV, 1 (asterisk). The dark structures in the centre of the fracture represent fibre tissue. Compare with Plate IV, 3.3. Section of stem in Plate IV, 1 (asterisk: keel in Plate IV, 1 and 2). The dark (brown) tissues represent parenchyma in the cortex and the stele. The lighter tissues represent fibre tissue in the cortex (fibre strands) and stele (fibre sheaths of stele and vascular bundles). The epidermis is absent, the light surface layer not being the epidermis, but the 'bleached' crust (outer cortex) of the stem. 4, 5, 6, 7: locations of details in Plate IV, 4–7.4. Detail of section in Plate IV, 3, showing cortex with fibre strands.5. Detail of section in Plate IV, 3, showing middle cortex with fibre strands and part of thickened vascular bundle end ('pear') in middle/outer cortex.6. Detail of section in Plate IV, 3, showing inner cortex with intercellular cavities and endodermis.7. Detail of section in Plate IV, 3, showing vascular bundles in stele.8. Fracture of stem (proximal end), showing the same structure as explained in Plate IV, 3, except for the more numerous and more distinct thickened vascular bundle ends ('pears') in the middle/outer cortex. Each 'pear' is situated below a furrow or pit (arrowheads). Specimen: NHMM JJ 13026 g.
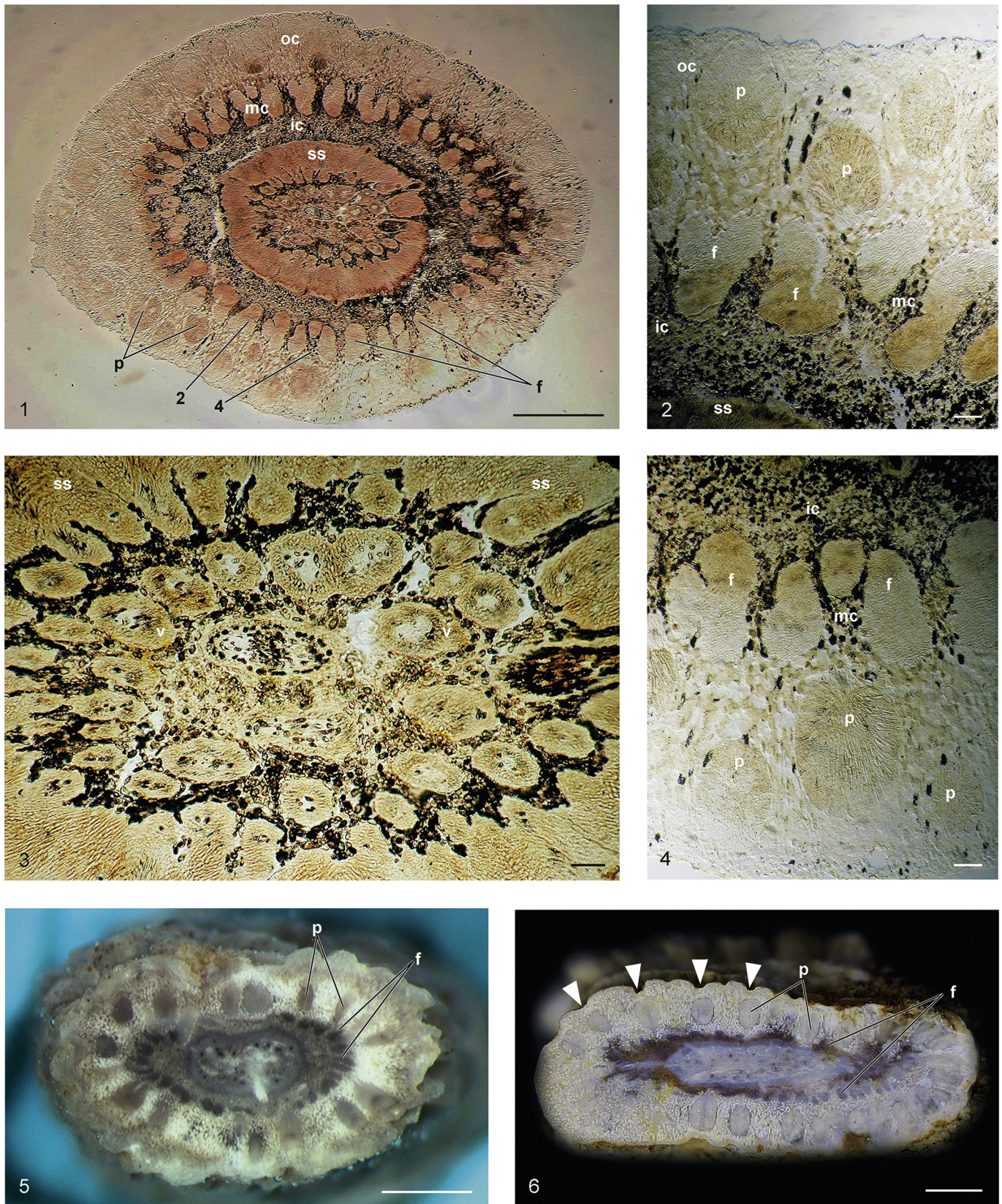
Plate V. *Thalassocharis bosquetii* Miquel, thin section and cross fractured silicified stems. Bar = 1 mm (1, 5, 6), 0.1 mm/100 μm (2–4); f = fibre strand, ic = inner cortex, mc = middle cortex, oc = outer cortex, p = thickened vascular bundle end ('pear'), ss = fibre sheath of stele, v = vascular tissue. 1. Section of stem, showing the same structure as the section in Plate IV, 3, except for the much more numerous and more distinct thickened vascular bundle ends ('pears') in the middle/outer cortex. 2, 4: locations of details in Plate V, 2 and 4. Specimen: NHMM MD 3253.4. 2. Detail of section in Plate V, 1, showing middle cortex with fibre strands, inner cortex with intercellular cavities and stele with fibre sheath surrounding vascular bundles. 3. Detail of section in Plate V, 1, showing stele with fibre sheath and vascular bundles with vascular tissue. 4. Detail of section in Plate V, 1, showing cortex with thickened vascular bundle ends ('pears') and fibre strands. 5. Fracture of stem (distal end), showing the same structure as explained in Plate V, 1, except for the smaller cortical fibre strands. Specimen: NHMM RH 728. 6. Fracture of stem (distal end), showing the same structure as the fracture in Plate V, 5, except for the smaller and less distinct cortical fibre strands. The thickened vascular bundle ends ('pears') in the middle/outer cortex are situated below a furrow/pit (arrowheads). Specimen: NHMM MD 3894.2.

6.1.5. What causes the striated pattern on Thalassocharis stems?

The narrow sutures separating the leaf scars on stems of *Thalassocharis* zigzag transversely, which together with the longitudinal furrows and/or elongated pits between the sutures makes up the characteristic pattern on these stems. Because of this conspicuous striated surface, Debey (1848) regarded *Thalassocharis* as one of the most graceful plant fossils. Several attempts were made to explain the pattern in a morphological and/or anatomical way. Especially the longitudinal furrows appeared to be problematic. While studying *T. westfalica*, Hosius and Von der Marck (1880) considered the possibility that the furrows were impressions of squamules (which were not observed by them), but found this theory acceptable only if the squamules in *T. westfalica* were more rigid and less transitory than those of the extant seagrasses. No squamules were found in the present study.

Voigt and Domke (1955) rejected the 'squamules explanation' and also the possibility that the furrows were impressions of leaf sheath veins. Instead, they favoured an anatomical approach to the question. In their concept, the sutures (their nodes) divide the stem into internodes. A narrow smooth zone just below each suture, *c.* 0.3 mm along the median (with only a single, median vascular bundle scar) and tapering laterally, would probably represent an amplexicaul leaf scar (Fig. 4a). Below this leaf scar are the longitudinal furrows, which extend in proximal direction mostly up to the next suture (Voigt and Domke, 1955, fig. 2a, 3). Our fibre strands in the middle cortex, consisting of polygonal thick-walled cells with a small more or less circular lumen, were interpreted by Voigt and Domke (1955, p. 97) as strands of thin-walled parenchyma cells with central vascular tissue (their 'Rindenparenchymstränge'). Our thick-walled cortex cells between the fibre strands were regarded by them as relatively thick-walled with respect to this 'Rindenparenchymstränge'. According to Voigt and Domke (1955, 1956) the original surface of the internodes was smooth; furrowed internodes would be the result of corrosion of the Rindenparenchymstränge, which they considered to have been less resistant than the surrounding cortex tissue. However, several objections against this explanation can be put forward. First, their Rindenparenchymstränge (i.e., our fibre strands) are probably more resistant than the cortical parenchyma cells. Furthermore, the furrows show a relatively coarse, slightly zigzagging pattern on the 'flat' sides of stem (changing direction at sutures), which we did not observe in the longitudinal, finer and twining arrangement of the fibre strands. In our thin sections the furrows are not subtended by fibre strands and there invariably is outer cortex tissue between the fibre strands and the floor of the furrows (Plates IV, V). In addition, the ridges between the furrows consist of outer cortex tissue (Plates IV, 8; V, 5, 6).

Actually, furrows (and pits) are not associated with fibre strands, but with the endings of vascular bundles ('pears'; Plates III, 6, 7; IV, 8; V, 5, 6). These bundles ascend obliquely from the stele through the cortex (between the fibre strands), the fibre sheath of each vascular bundle ending in a pear-shaped manner just below the floor of a furrow/pit, while the vascular strand proceeds and ends at the floor of the furrow/pit, sometimes in a small wart on the floor of the furrow/pit (Plates II, 5; III, 6, 7). It seems that the whole furrowed/pitted area between two sutures is the abscission surface of a single leaf, and that the morphology of the abscission plane ('*Thalassocharis* pattern') results from the transition of the outer cortex tissues of the stem (including vascular bundle endings) to the leaf base structure (distribution vascular tissue, fibre strands, parenchyma, intercellular cavities). Therefore, the area between two consecutive sutures should not be considered as an internode, but as a leaf scar (Fig. 4b). Apparently, the leaf base and attachment area were much more substantial than in the reconstruction proposed by Voigt and Domke (1955), fig. 2a, 3. Unfortunately, leaf bases are unknown in the seagrass foliage material from the Maastrichtian type area (*Thalassotaenia debeyi*; Van der Ham et al., 2007).

6.1.6. Was Thalassocharis bosquetii a marine plant?

All fibre cells described in the present study were regarded by Voigt and Domke (1955) to be parenchyma cells, probably due to the moderate preservation of their material. This concerns the fibre cells of the cortical fibre strands (see above), those composing the thick fibre sheath of the stele, and the fibre cells of the sheath surrounding each individual vascular bundle inside the stelar fibre sheath. The empty spaces observed by those authors within the sheaths of the stelar bundles were interpreted as the remains of vascular tissue, intercellular cavities or artifacts. They did not find definite intercellular cavities, typical of aquatic plants. Therefore, Voigt and Domke (1955) doubted whether *T. bosquetii* was an aquatic plant, but rather thought of it as a species of temporarily dry, littoral conditions. Den Hartog (1970) mentioned the rigid compact stems and the striking absence of any intercellular cavities as indications of poor adaptation. He did not reject *T. bosquetii* as a seagrass, but later, Den Hartog and Kuo (2006) stated that *T. bosquetii* was not even an aquatic plant. They considered *Posidonia cretacea* Hosius et Von der Marck from Germany to represent the sole fossil to be interpreted beyond doubt as a Cretaceous seagrass, referring to recently collected material from the Cretaceous of Maastricht as a "very fine specimen" of this species. However, this particular specimen (NHMM JJ 8575; Plate III, 2, 3) represents *T. bosquetii*.

On the basis of exquisitely preserved silicified material, we have now been able to observe abundant and distinct intercellular cavities in the inner cortex of both the stems and the roots. Therefore, we do not doubt the aquatic habitat of *T. bosquetii*. The marine conditions of this setting are illustrated by the frequent association of *T. bosquetii* with fully marine fossils, including epibionts on the stems and attached roots (see 6.4. Ecological aspects; see also Voigt and Domke, 1956; Voigt, 1981).

If it could be demonstrated beyond doubt that *Thalassotaenia debeyi* represents the foliage of *T. bosquetii*, then the absence of stomata in these leaves and their similarly close association with marine fossils (Van der Ham et al., 2007) would be strong additional evidence for a marine aquatic habitat of *T. bosquetii*.

6.2. Comparison with fossil seagrasses

In view of the characteristic stem surface pattern, *Thalassocharis* cannot be confused with any other fossil seagrass (stem) genus (see overview in Van der Ham et al., 2007), or any other fossil stem. More or less longitudinally striated stems occur in *Posidonia parisiensis* (Stockmans, 1936, plates 2, 5) from the Eocene of Belgium and *Thalassites parkavonensis* (Benzecry and Brack-Hanes, 2008, fig. 15) from the Eocene of Florida, but otherwise these do not resemble *Thalassocharis* stems: those of *P. parisiensis* are covered with large root scars and/or persistent leaf remains (fibre strands), while those of *T. parkavonensis* are clearly dimorphic.

Above (see 6.1.6. Was *Thalassocharis bosquetii* a marine plant?), the impression is conveyed that *Posidonia cretacea* (upper Campanian, Sendenhorst, Germany) is similar to *Thalassocharis*, but the available specimens (Hosius and Von der Marck, 1880, p. 24, figs. 8, 9; Geologisch-Paläontologisches Institut, Universität Münster, no. 8502 and 8371) do not show the typical stem surface pattern and bear persistent leaf remains (fibre strands).

Thalassocharis is known from Upper Cretaceous deposits in the Maastrichtian type area (NE Belgium, SE Netherlands) and northwestern Germany (Fig. 3). The oldest records are from the lower Campanian: *Thalassocharis muelleri* (nomen nudum; Debey, 1848, 1851; Pomel, 1849) from the Vaals Formation (equivalents of *lingua/quadrata* Zone; Jagt, 1999) of Holset near Vaals, SE Netherlands (Fig. 1: locality 10), and *T. bosquetii* (Debey, 1865) from the Trümmerkalk (Ilsenburgmergel, *Becksia soekelandi* Zone; Erdmannsdörffer and Schroeder, 1926; Arnold, 1964) of the Galgenberg near Wernigerode, between Goslar and Quedlinburg, Germany (Fig. 3: *T. bosquetii*?). Unfortunately, the material on which these records were based (a single stem and a few
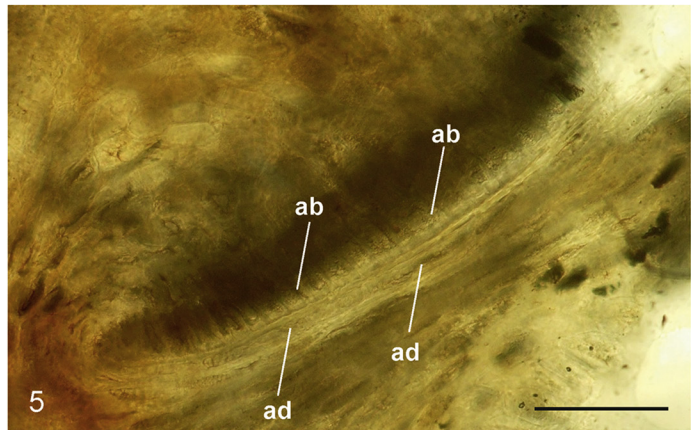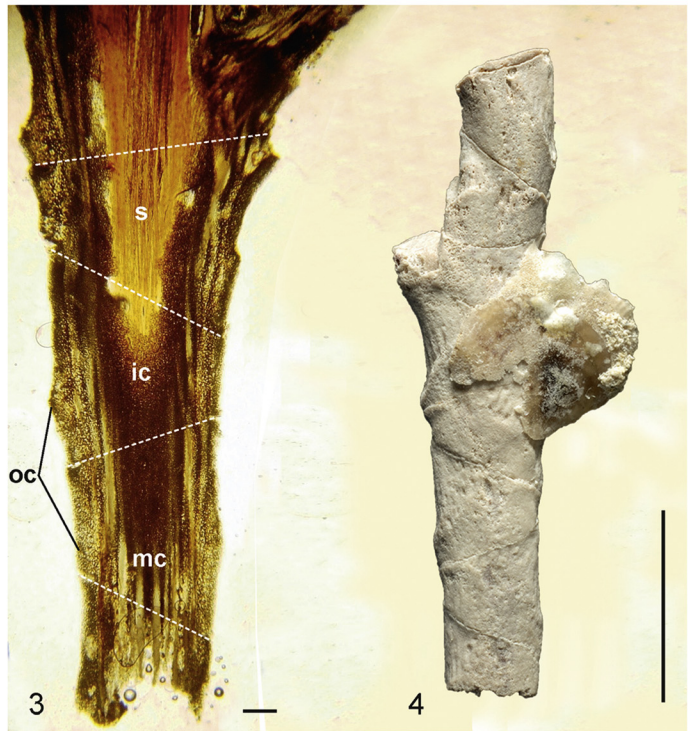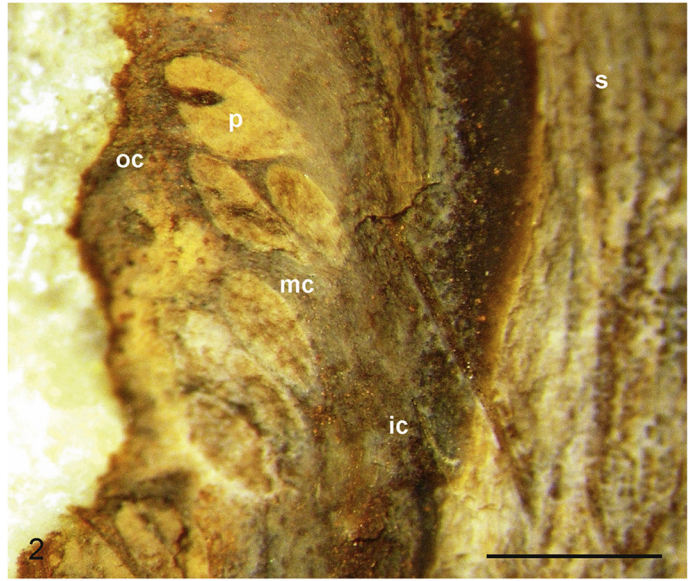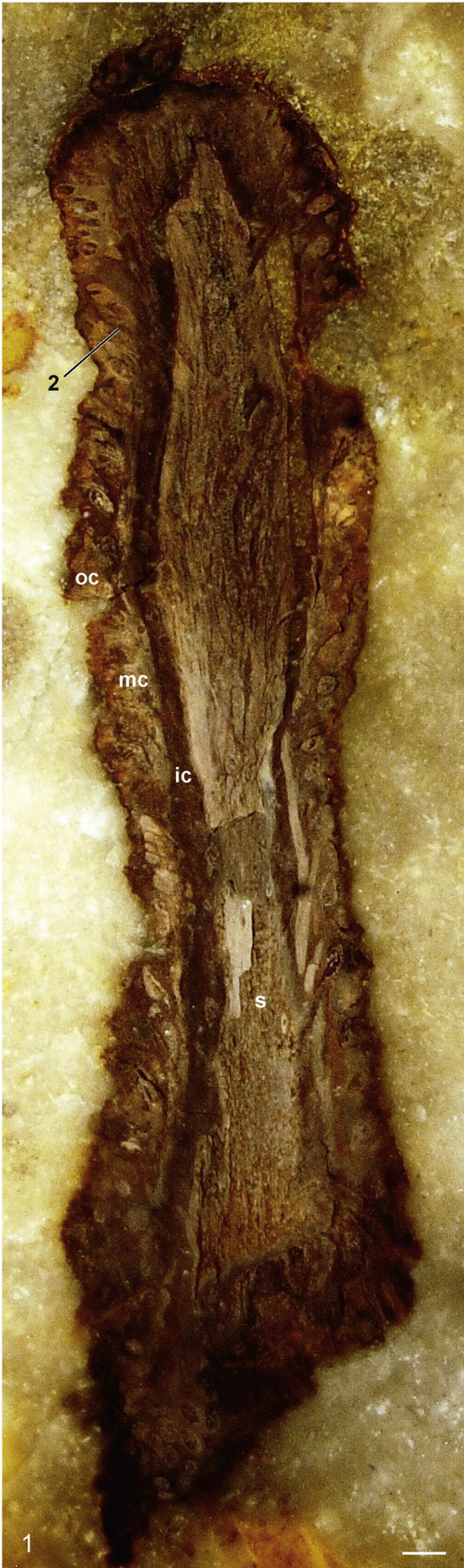
Plate VI.

fragments, respectively) could not be traced, so that a direct comparison with *T. bosquetii* from the Maastrichtian type area is impossible.

Late Campanian records of *Thalassocharis* are known from NW Germany (*Thalassocharis westfalica*) and NE Belgium (*Thalassocharis* sp.). *Thalassocharis westfalica* Hosius and Von der Marck (1880) is known from the Coesfelder Schichten (*Lepidospongia rugosa* Zone; Arnold, 1964; Riegraf, 1995) of the Daruper Berg near Coesfeld, Germany, and from the Baumberger Schichten of the Baumberge near Coesfeld and the Haldemer Schichten of Haldem and Lemförde northeast of Osnabrück, Germany (both *Bostrychoceras polyplocum* Zone; Arnold, 1964; Riegraf, 1995). Hosius and Von der Marck (1880) had no material from the Maastrichtian type area at their disposal, which explains why they could not answer the question whether *Thalassocharis westfalica* (Plate IX, 1–4) coincided with one of Debey's species. Voigt and Domke (1955) considered *T. westfalica* as the undoubtedly closest relative of *T. bosquetii*. Even, one of the specimens from the Daruper Berge (Geologisch-Paläontologisches Institut, Universität Münster, no. 9958; not treated by Hosius and Von der Marck, 1880), in which the stem surface pattern is relatively clear (Plate IX, 1, 2; '*Thalassocharis* pattern'), was referred to as "*Thalassocharis* cf. *bosqueti*" (Voigt and Domke, 1955, plate 5, fig. 4). Stem material of *T. westfalica* present in the collections of the Geologisch-Paläontologisches Institut in Münster consists of imprints (external moulds), probably without silicified structures (RWJMvdH and JHAvK-vC, personal observations, 2005). This hampers a detailed comparison with *T. bosquetii*. Stems of *T. westfalica* are mostly wider than those of *T. bosquetii* (5–20 vs 1.5–12 mm). A qualitative difference seems to be the occurrence of two (possibly intergrading) kinds of roots in *T. westfalica*: dense clusters of thin roots (also present in *T. bosquetii*: Plate III, 1–5) and sparse, thick, stilt-like roots (Plate IX, 1–3; not observed in *T. bosquetii*). Occasionally, the thick roots were interpreted as leaves (e.g., Hosius and Von der Marck, 1880, pl. 27, fig. 39; Voigt and Domke, 1955, pl. 5, fig. 4). However, these 'leaves' do not show any seagrass leaf characters (e.g., multiveined blade; Van der Ham et al., 2007), and they are inserted on stems completely covered with fully developed leaf scars. The specimen illustrated by Voigt and Domke is even upside down, the thick roots having been presented as ascending leaves. One of the specimens of *T. westfalica* from Ostmünsterland present in the Stuwe Collection shows bundles of genuine, multiveined leaves at the ends of the main stem and two branches (Plate IX, 4). This is the only *Thalassocharis* stem with attached leaves known to date, but details of the attachment remain unclear.

Thalassocharis sp. is known from the upper Campanian Zeven Wegen Member (12–14 m below top); *Belemnitella woodi* cephalopod Zone, equivalent to the upper *stobaei/basiplana/spiniger* and *vulgaris* zones [sensu *germanico*]; see Keutgen, 2011) of the CBR-Lixhe quarry near Loën, province of Liège, Belgium (Fig. 1: locality 2). The material consists of imprints of three stem fragments. 1. Unbranched, 10 mm long, 3 mm wide, with attached roots of *c.* 1 mm diameter (Laffineur Collection 535; Plate X, 1). 2. Branched, 10 mm long, main stem 5 mm wide, branches 2–3 mm wide, roots absent (Laffineur Collection 536; Plate X, 2). 3. Unbranched, 40 mm long, 6 mm wide, with attached roots of *c.* 1 mm diameter (Laffineur Collection 582). The first specimen clearly shows the typical striated surface pattern of *Thalassocharis* stems; in the two others this is less distinct. In view of poor preservation, comparison with *Thalassocharis bosquetii* is problematic; with reference to their

stratigraphical provenance (overlapping with Campanian occurrence in NW Germany), the three fragments might even represent *T. westfalica*. Foliage material (Laffineur Collection 505, 528; Plate X, 3, 4) collected at the same level belongs to *Thalassotaenia debeyi* as defined by Van der Ham et al. (2007).

6.3. Comparison with extant seagrasses

About 60 extant species of seagrass belonging to 13 genera and five families have been recognized (Kuo and McComb, 1989; Les et al., 1997; Benzecry and Brack-Hanes, 2008): Cymodoceaceae (*Amphibolis*, *Cymodocea*, *Halodule*, *Syringodendron*, *Thalassodendron*), Hydrocharitaceae p.p. (*Enhalus*, *Halophila*, *Thalassia*), Posidoniaceae (*Posidonia*), Ruppiaceae (*Ruppia*) and Zosteraceae (*Heterozostera*, *Phyllospadix*, *Zostera*). Because all five extant seagrass families belong to the Alismatales (Stevens, 2001 onwards), we assume *Thalassocharis bosquetii* to be a member of this order as well. However, it should be borne in mind that the late Maastrichtian *Mosacaulis spinifer*, although ecologically probably a seagrass, does not belong to the Alismatales (Van der Ham et al., 2011).

Reproductive structures (e.g., seeds) of *T. bosquetii* are unknown, so that comparisons must rely on vegetative characters only. With respect to growth habit, *Enhalus* (monotypical) and *Posidonia oceanica* belong to the least organized among extant seagrasses (Tomlinson, 1974; see also Waycott et al., 2006, fig. 3): axes monomorphic, branching diffuse (branches produced at irregular intervals), which matches the condition in *T. bosquetii*. In contrast, *T. bosquetii* stems are not dorsoventral, which suggests a more erect habit than shown by the more or less horizontally creeping stems of *Enhalus* and *P. oceanica*. Due to adaptation to their aquatic environment, extant seagrasses show simple (reduced), convergent anatomies (e.g., Tomlinson, 1982; Les et al., 1997; Iles et al., 2015). Although classified by us as a seagrass (see above), *T. bosquetii* has a complex stem anatomy, inclusive of a substantial central stele with many sheathed vascular bundles within and fused with a thick common fibre sheath, an inner cortex with many small intercellular cavities, a middle cortex with distinct fibre strands, and an outer cortex with conspicuously thickened vascular bundles, each of which constricts into a thin vascular strand just below a furrow/pit on the leaf scar. The stem anatomy of *T. bosquetii* is clearly more complex than that of extant seagrasses. Except for the diffuse distribution of the small intercellular cavities in the inner cortex, it is not even near to that of the least reduced extant genera *Enhalus* and *Posidonia* (Albergoni et al., 1978; Tomlinson, 1982). Rather, as far as the complexity of the stele is concerned, *T. bosquetii* recalls some non-marine Alismatales (Stevens, 2001 onwards) such as the pondweed family Potamogetonaceae (occasionally in brackish water) and the peat bog species *Scheuchzeria palustris* of the monotypical family Scheuchzeriaceae (Tomlinson, 1982, figs. 6.4, 9.9–11). However, the stems of representatives of these taxa show more distinct aerenchymatous tissue (much larger intercellular cavities).

Thalassotaenia debeyi may represent the foliage of *Thalassocharis bosquetii* (Van der Ham et al., 2007). Leaves of *Amphibolis*, *Thalassodendron* and *Posidonia* showed the greatest resemblance, but, similar to *T. bosquetii*, *T. debeyi* also reveals some features not found in any of the extant seagrasses: a well-delimited hypodermis and fibre strands that alternate with the veins. A distinct hypodermis occurs also in the Potamogetonaceae and *Scheuchzeria palustris* (Tomlinson, 1982). In addition to being an ancestor of one (or more?)

Plate VI. *Thalassocharis bosquetii* Miquel, longitudinal fracture and longitudinal thin section of silicified stems. Bar = 10 mm (4), 1 mm (1–3), 0.1 mm/100 μm (5); ab = abaxial epidermis, ad = adaxial epidermis, f = fibre strand, ic = inner cortex, mc = middle cortex, oc = outer cortex, p = thickened vascular bundle end ('pear'), s = stele.1. Fracture of stem, showing outer/middle cortex, inner cortex and stele. 2: location of detail in Plate VI, 2. Specimen: NHMM RH 979.2. Detail of fracture in Plate VI, 1, showing outer/middle cortex with thickened vascular bundle ends ('pears'), inner cortex and fibre sheath of stele.3. Oblique longitudinal section of lower part of stem in Plate VI, 4 (up to branch on the right), showing outer/middle cortex, inner cortex and stele. Thickened vascular bundle ends ('pears') scarce and not visible in photograph. The dashed lines connect sections through the sutures on the stem (see Plate VI, 3).4. Stem of which the section in Plate VI, 3 was made (same orientation); a bivalve shell is attached to the branch on the right. Specimen: NHMM JJ 13026b.5. Longitudinal section of upper part of stem in Plate VI, 4 (just above branch at the right), showing epidermis layers above and below suture between two leaf scars.

Plate VII. *Thalassocharis bosquetii* Miquel, silicified roots. Bar = 5 mm. 1. Roots on stem, with epibiont sabellid worm tubes (*Glomerula lombricus*; asterisk; see Jäger, 2012) at upper right; see also Plate III, 2, 3. Specimen: NHMM JJ 8575. 2. Roots in loose biocalcarenite matrix; associated stems not illustrated. Specimen: NHMM GC 6328. 3. Roots with stems (arrowheads) in flint matrix. Specimen: NHMM RH 1006. 4. Branched stem with roots in flint matrix. Specimen: Strijbos VL 96.

of the extant seagrass clades (see 1. Introduction), *Thalassocharis* (and *Thalassotaenia*) may also represent another, extinct clade of seagrasses within the Alismatales, possibly one that is more closely related to the Potamogetonaceae or Scheuchzeriaceae.

6.4. Ecological aspects

Usually, stems of *T. bosquetii* are preserved with attached root fragments. Sometimes, an extensive root ball is present (Plate VII, 1–4),
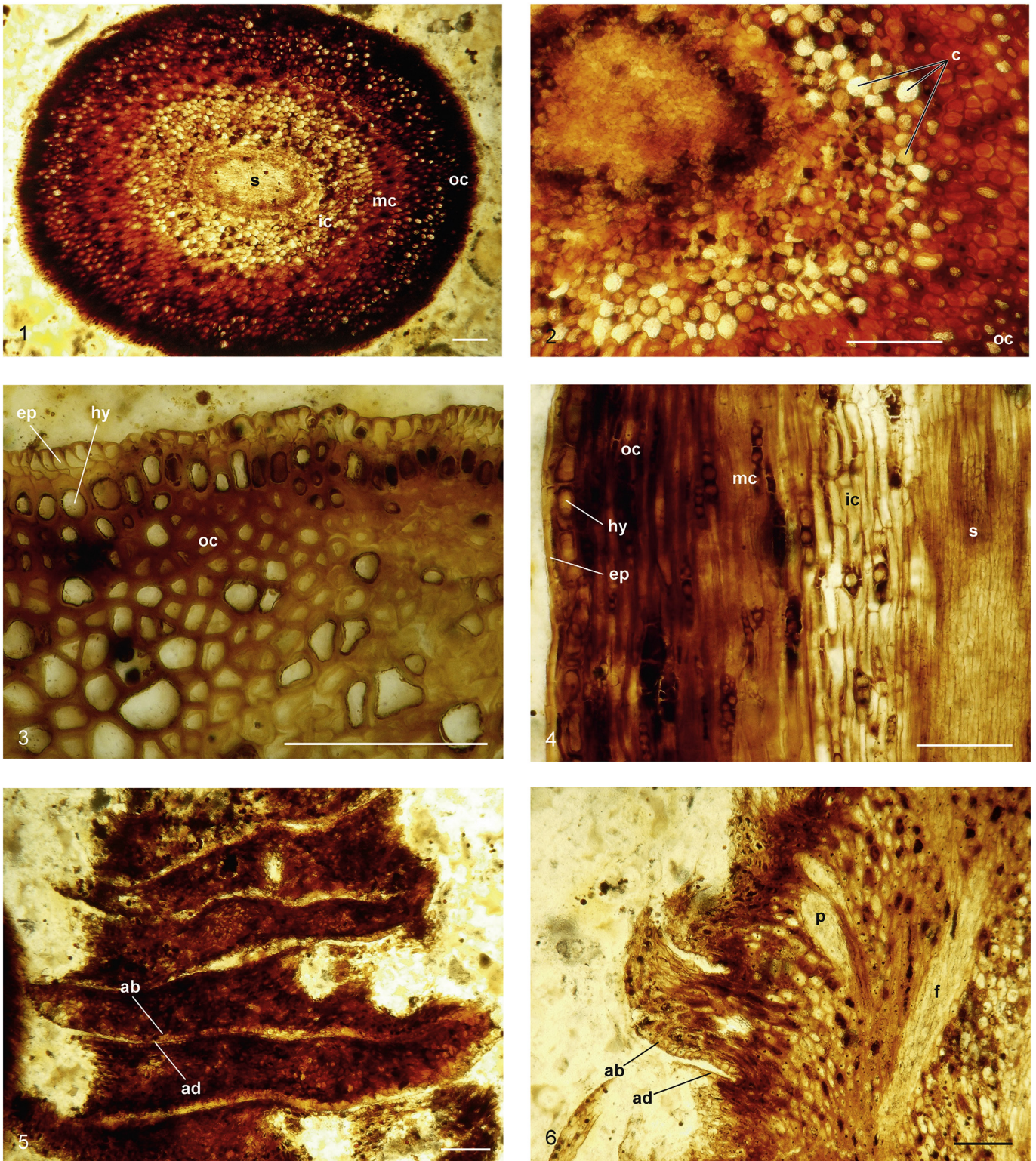
Plate VIII. *Thalassocharis bosquetii* Miquel, thin sections of silicified roots and small (subapical?) stem fragments. Bar = 0.1 mm/100 μm; ab = abaxial epidermis, ad = adaxial epidermis, c = intercellular cavities, en = endodermis, ep = epidermis, f = fibre strand, hy = hypodermis, ic = inner cortex, mc = middle cortex, oc = outer cortex, p = thickened vascular bundle end ('pear'), s = stele. 1. Cross section of root, showing outer and middle cortex, inner cortex with intercellular cavities, and stele. Specimen: NHMM RH 967. 2. Detail of cross section of root, showing outer and middle cortex, inner cortex with intercellular cavities, and stele. Specimen: NHMM RH 967. 3. Detail of cross section of root, showing epidermis, hypodermis and outer cortex. 4. Detail of longitudinal section of root, showing epidermis, hypodermis, outer, middle and inner cortex, and stele. 5. Longitudinal section along small stem fragment, showing leaf bases; thick and thin parts of leaf bases alternate, indicating distichous phyllotaxis. Epidermis of leaf bases adaxially thinner than abaxially. Specimen: NHMM RH 967. 6. Detail of longitudinal section of small stem fragment, showing leaf bases, several thickened vascular bundle ends ('pears') and cortical fibre strand. Epidermis of leaf bases adaxially thinner than abaxially. Specimen: NHMM RH 967.

Plate IX. *Thalassocharis westfalica* Hosius et Von der Marck. Bar = 10 mm. 1. Imprint of stem with roots. Specimen: Geologisch-Paläontologisches Institut, Universität Münster, no. 9958. 2. Detail of specimen in Plate IX, 1: stem with two roots. 3. Imprint of stem with roots. Specimen: Stuwe 71. 4. Imprint of branched stem with leaves. Specimen: Stuwe 70.

Plate X. Seagrass material from the Zeven Wegen Member (Gulpen Formation) of CBR-Lixhe quarry. Bar = 1 mm (1, 2), 10 mm (3, 4).1. *Thalassocharis* sp. Imprint of stem with roots (at left and below). Specimen: Laffineur 535.2. *Thalassocharis* sp. Imprint of branched stem fragment. Specimen: Laffineur 536.3. *Thalassotaenia debeyi*. Imprint of leaf fragment. Specimen: Laffineur 505.4. *Thalassotaenia debeyi*. Imprint of leaf fragment. Specimen: Laffineur 528.

Plate X.

indicative of limited transport (or none at all) of the stem. According to Voigt and Domke (1955) the arrangement of the roots, descending along the stem, demonstrates the erect growth habit of the stem. Further, in contrast to the more or less horizontally creeping stems of *Enhalus* and *Posodonia oceanica*, the stems of *T. bosquetii* are not dorsoventral, bearing roots on both sides, which also suggests an erect (and rigid: fibre strands!) habit. However, the occasional ± smooth stem fragments (leaf scars not recognizable; see 5. Description) may have belonged to creeping stems without leaves. The occurrence of short to long leaf scars (1.5–9 mm along median; see also Hosius and Von der Marck, 1880) might be related to a variable growth rate or even periodicity. Fruits or seeds are lacking to date. Reproduction was probably mainly vegetative. Flowering may have been rare, as for instance in *Posidonia oceanica*.

Often, several stems occur closely together in a more or less parallel arrangement in a single specimen (Plates I, 1; II, 2), which suggests a gregarious habit. The marine conditions of the habitat are illustrated by the common association of stems with fully marine vertebrate and invertebrate taxa (e.g., mosasaurid reptiles, cheloniid turtles, ammonites, coleoids, bivalves, corals, brachiopods, echinoids, sponges, tube worms), including epibionts on the stems and attached roots (Plates III, 3; VII, 1; see also Voigt and Domke, 1956; Voigt, 1981). A few examples of association with a conifer twig, dicot leaf or wood suggest that the coast was not very far removed from the area of deposition.

In view of the coinciding stratigraphical distributions (Kuypers, 1998; Mulder, 2003), Van der Ham et al. (2007) considered the cheloniid sea turtle *Allopleuron hofmanni* to have been a constituent of the seagrass community, assuming feeding on seagrass. However, a direct comparison of *A. hofmanni* bone carbonate $\delta^{13}C$ values with those of several extant marine turtles suggests that *A. hofmanni* had a carnivorous lifestyle (Van Baal et al., 2013). Sirenians (sea cows and dugongs) did not appear until the Eocene (Vélez-Juarbe, 2014), which would mean that the late Maastrichtian seagrass community of the Maastrichtian type area lacked a large herbivore.

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