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*I would like to dedicate this work to Professor Leon Stuchlik to express my gratitude for long years of friendship, research cooperation and support, often in difficult times.*

# The fossils of *Rhodoleia* Champion (Hamamelidaceae) in Europe

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ABSTRACT. Four species of the genus *Rhodoleia* Champion from the European Upper Cretaceous, older and younger Tertiary are described. The formal species *Saxifragaceaecarpum bifolliculare* Menzel is revised also to *Rhodoleia*. All species are essential elements in rainforest-like laurel forests under subtropical humid climatic conditions, and provide a good example of Engler's theory of a "palaeotropical geoflora".

KEY WORDS: *Rhodoleia*, Hamamelidaceae, palaeotropical geoflora, Upper Cretaceous, Tertiary, Europe

## INTRODUCTION

A curious fossil seed cluster from the Upper Cretaceous attracted the author's attention in the 1980[s]. Together with E. Knobloch he was able to assign these structures to the south-east Asian genus *Rhodoleia* Champion from the Hamamelidacae (Rhodoleioideae) (Knobloch & Mai 1986), because of their resemblance to similar seeds from the Upper Eocene (Mai & Walther 1985). Their presence in the Tertiary was puzzling. Light was shed on this mystery by material from Herzogenrath (Lower Rhineland) which Menzel (1913) had described as *Saxifragaceaecarpum bifolliculare*. In one part of a capsule imbricatedly arranged seeds were found which resembled the curious cluster from the Upper Cretaceous.

Investigations of all the fossil fruits and seeds belonging to *Rhodoleia* Champion were subsequently investigated followed, almost immediately, by analysis of characteristic structures of the seed testa under the SEM. This technique had previously been impossible due to lack of proper equipment.

The genus has some significance for the history of vegetation as is also mentioned in this monographic study.

## ***RHODOLEIA***
## CHAMPION EX HOOKER F.

Bot. Magaz. 3(6), pl. 4509 (1850)

### CARPOLOGY

### ***Rhodoleia championii*** Hook.f.

Fig. 1A; Pl. 1 figs 1–3, Pl. 2 figs 1–3, Pl. 3 figs 1–6, Pl. 4 figs 1,2

The Rhodoleideae consisting of the recent monotypic genus *Rhodoleiea* Champion, differ from the related Hamamelidaceae in such characters as shape and venation of the leaves, condensed inflorescences in simple heads and, primarily, in their fruits and seeds. The multiovulate carpels are worthy of note. The ovary is semi-inferior being fused below the middle with the slightly elongated hypanthium. The carpels are compressed, woody, bifid and pointed, two-septate and four-valved (Pl. 1 fig. 1). The capsules are fused, 5 to 10 per head. Dehiscence is both loculicidal and septicidal. The pericarp is woody or leathery.

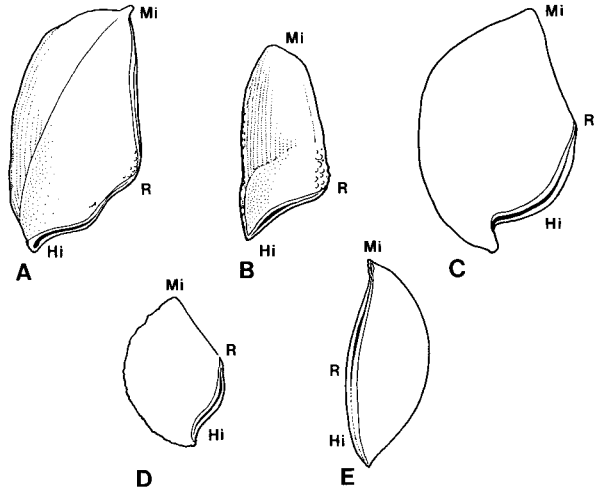


**Fig. 1.** Schematic view of seeds of *Rhodoleia* (Hi = hilum, Mi = micropyle, R = raphe). **A** – *Rhodoleia championii* Hook.f.; **B** – *R. bifollicularis* (Menzel) comb. nov.; **C** – *R. bellmannii* Mai in Mai & Walther; **D** – *R. cretacea* Knobloch & Mai; **E** – *R. hercynica* Mai (after Mai 1968, 1987; Mai & Walther 1985; Knobloch & Mai 1986, emended)

The exocarp is single and very often separated, the endocarp horny or cartilaginous. The two styles of the carpel are relatively long and narrow and slightly divergent at the apex, indicating the former presence of the stigma which had fallen off during the ripening of the fruit.

Each locule of the capsule has many (10–20) seeds which are compressed, angular in shape and imbricate. Most are sterile and wingless with only a few fertile, triangular in cross-section, compressed and narrowly winged. The ventral margin of the seed is mostly arched and the dorsal one angled. From the dorsal margin the hilum is visible as a crevice or distinct rim. The raphe extends from the hilum to the chalaza, relatively being sharp-edged at first but ultimately becoming filiform. The micropyle is apical, sometimes forming a small point, more often appearing as a small hole. It is always directed outwards and upwards (epitropous) (Pl. 2 fig. 2).

The testa of the seed is hard, with an indistinct polygonal sculpture on the outer surface (Pl. 3 figs 1, 2) which is often matt. At the dorsal margin papillate sculptured elements are very often developed (Pl. 3 fig. 1). They consist of round cells with thickened walls. The ventral margin or wing shows longitudinal structure of isodiametric cells with strongly undulate walls (Pl. 3 fig. 4). The dimensions of recent diaspores are approximately 10–25 mm diameter for fruiting heads, capsule length 6–10 mm and seeds 3.5–5.5 mm × 2.5–3.5 mm; larger size has been reported for fertile seeds (Vink 1957, Melchior 1964, Mai & Walther 1985).

## FOSSIL FINDINGS

The fruits and seeds of *Rhodoleia* Champion were first described in the fossil state by Mai and Walther (1985). The present author succeeded in determining 6 seeds in widely varying states of preservation, taken from the Upper Eocene at Weißelster Basin (Saxony), as *Rhodoleia bellmannii* Mai in Mai & Walther.

Better preserved and more abundant fossil material was obtained from the grey clays of the Upper Maastrichtian (Upper Cretaceous) from Walbeck in the Allertalgraben, south of Oebisfelde (Saxony – Anhalt). In addition to several round and wedge-like single seeds, gatherings were also made of being coalified seeds which were identified as seed clusters in the locule of a capsule. This material was described by Knobloch and Mai (1986) as *Rhodoleia cretacea*.

One year later Mai (1987) described two further seeds with the suggestion of a wing from the Upper Palaeocene clays of a drilling at Gonna near Sangerhausen (Saxony – Anhalt) as *Rhodoleia hercynica*.

From the time of Menzel (1913) a related type of seed was frequently mentioned in publications, but, from the taxonomic point of view, it was incorrectly assigned to *Saxifragaceaecarpum bifolliculare* Menzel (Raniecka-Bobrowska 1962, Mai 1968). In the present paper locule casts of seed clusters from the Middle Miocene of Herzogenrath near Düren (Lower Rhineland ) and the Lower Miocene quartzites of Osieczów (Lower Silesia) are recognised as fossil fruits and seeds of *Rhodoleia bifollicularis* (Menzel) comb. nov. and prove the continued presence of this genus in the Miocene of Europe.

The characteristic fruits and seeds of several species of *Rhodoleia* Champ. are, therefore, known in Europe from the Upper Cretaceous to the younger Tertiary. However, no fossil leaves, wood or pollen have so far been found.

## KEY TO SPECIES

1. Seeds large, 2.0–4.0 mm in diameter ..... 2
– Seeds small, only 1.2–2.0 mm in diameter ..... 3

2. Seeds winged on one margin, wing distinctly developed, opposite margin bearing the hilum and raphe; relatively thin-walled. Seeds in two longitudinal rows, imbricately arranged in a fusiform locule ..... *Rhodoleia bifollicularis* (Menzel) comb.nov.

– Seeds wingless with only a slight wedge-like extension opposite the margin bearing the angled hilum and raphe; relatively thick-walled ..... *Rhodoleia bellmannii* Mai in Mai & Walther

3. Seeds round and wedge-shaped, with the angled hilum and raphe; relatively thin-walled. Seeds in two longitudinal rows, imbricately arranged in a boat-shaped locule-filling ..... *Rhodoleia cretacea* Knobloch & Mai

– Seeds long, in shape of an orange segment, margin bearing the hilum and raphe slightly curved, but not angled; thick-walled ..... *Rhodoleia hercynica* Mai

## DESCRIPTION OF SPECIES

### ***Rhodoleia bifollicularis*** (Menzel) **comb. nov.**

Fig. 1B, Pl. 1 figs 4–9, Pl. 2 figs 11–15, Pl. 3 figs 7, 8, Pl. 4 figs 6, 7

Basionym. *Saxifragaceaecarpum bifollicu-lare* Menzel 1913, p. 32, Pl. 4 figs 7–9.

Holotype. Menzel 1913, Pl. 4 fig. 7; MfN Berlin, Orig. No. 407.

Syntype. Pl. 2 fig. 11 in this paper; MfN Berlin, Orig. No. 408.

Diagnosis. Inflorescence in heads; carpels united in an ovary which is semi-inferior on account of the presence of a zygomorphic cupule-like hypanthium extending to 1/3 of the length of the fruit. It has sepicidal, and suggestion of incipient loculicidal, dehiscence. The placenta is axile with two rows of imbricately arranged seeds in each locule. Seeds numerous, winged on one margin. The side containing the hilum and raphe is angled. The apical or subapical micropyle is situated on the edge of the wing. The testa is thin-walled, with nodular thickened cells in the upper part of the seed body and longitudinal cells with undulate walls above of the wing margin.

Occurrence. Herzogenrath, Rhineland – Menzel 1913, p. 32, Pl. 4 figs 7–9 (Coll. Natural History Museum, Humboldt University in Berlin, Nos 407–409) – Middle Miocene – Mai 1968, p. 185–189, Pl. 38 figs 1–8. Osieczów (West Poland) – Raniecka-Bobrowska 1962, p. 149, Pl. 18 figs 4–6 (Coll. State Geological Institute, Warsaw Nos 103–105) – Lower Miocene (Floral zone VI).

Remarks. In Mai's revision of Menzel's (1913) original materials the author (Mai 1968) gave a detailed description of this taxon. The ovary consists of two carpels, fused from base to apex, leathery to slightly woody, compressed, 16–21 mm long, 8–11 mm wide and 4–5 mm thick. The ovary is semi-inferior, fused with the hypanthium below the middle. Carpels of unequal length, the larger set obliquely, extending beyond the tip of the pedicel, slightly curved, elongate-oval, with a short and beak-like style. The involute margins and adjacent faces of the carpels are fused below to form a thick partial septum towards the base of the loculus. The calyx (receptacle) extends 4–8 mm beyond the base of the pedicel strongly involuting the syncarpium (Pl. 1 figs 4–9), which is semi-inferior. Calyx slightly asymmetric, extending beyond the larger carpel and, in one case, bearing one, long-triangular, membranous lobe. The calyx is covered in longitudinal wrinkles, which indicate the vascular bundles or points of attachment of the petals. Fruits sessile, 2–3 in each fructification. Dehiscence septicidal, from apex to base along the suture of the carpels, loculicidal at the apex, so that the valve at the tip is widely open (Pl. 1 fig. 4). Placenta straight bearing several imbricately arranged ovules.

The fruit wall is two-layered; the outer (epicarp) of woody parenchyma contained vessels. It separates very easily from the thick, inner part (endocarp) composed of sclerenchyma. The locule wall consists of a layer of clearly visible lustrous sclereid belts and is spirally striated.

Seeds numerous. In each carpel there are two rows of imbricate, obliquely arranged seeds (Pl. 2 figs 13–15). Seeds slightly compressed, winged on one margin, 3–4 mm long, 1.5–2.5 mm wide. The outline is almost rectangular to semicircular with a raised wing on the lateral margin. The side bearing the hilum and raphe is angled and thickened (Pl. 4 fig. 6) and furnished with tubercles near the raphe. The hilum appears as an oblong scar on this margin. The micropyle, opposite the hilum, is situated at the other end of the seed. The testa is spongy-parenchymatous. The outer surface of the ventral margin bears rows of large elongate cells. These rows begin at the tip of

micropyle, diverge to the ventral edge and curve in the direction of the wing.

The structure of the outer surface was established on the basis of new observations under the SEM. On the margin adjacent to the septum, nodular and circular cells are fully developed (Pl. 4 fig. 7). The wing and ventral margin bear oblong cells which, on account of outer wall abrasion, show distinct and characteristic undulate lateral walls (Pl. 3 fig. 8).

In fossil occurrences the species is associated with well-developed laurophyllous floras. In the Lower Miocene, floristic zone VI ( Mai 1967) marks the period of optimal development of the younger Mastixioideen-Flora. Humid and subtropical climatic conditions explain the occurrence of evergreen, laurel vegetation. Particularly striking evidence of the presence of this vegetation appears the leaf flora from Osieczów (Raniecka-Bobrowska 1962). Similar climatic and ecological conditions established, probably in the Middle Miocene (Kilpper 1969), the Mastixioideen-Flora from Herzogenrath in the Lower Rhineland Brown Coal Basin, which contains the same high percentage of subtropical and extinct species. Its younger age in comparison with the Mastixioideen-Flora of Upper Lusatia is clear from the floristic composition, which reveals species differences in some important genera.

The conclusion by Menzel (1913), endorsed by Mai (1968), that these very well-preserved megafossils were related to the Saxifragaceae or Loganiaceae was incorrect. The capsules with hypanthium, simultaneous loculicidal and septicidal dehiscence, with at least 10 compressed seeds per locule, imbricately arranged on a central placenta, point unequivocally to a relationship with the Hamamelidaceae-Rhodoleioideae. The seeds of this species differ from those of the other species by their size (3–4 mm) and margin bearing a distinct wing.

### ***Rhodoleia bellmannii*** Mai in Mai & Walther

Fig. 1C, Pl. 2 figs 4–10, Pl. 4 figs 3–5

Holotype. Mai & Walther 1985, Pl. 12 fig. 5, MMG Dresden, Coll. Mai No.7974.

Diagnosis. Seeds angular and compressed, of irregular shape, without a wing, rounded or wedge-like, diameter 2.0–3.5 mm, and thickness 0.6–1.1 mm. Hilum ventral, as a small papillate area, the raphe above the angled often appearing somewhat extended hilum-raphe margin (Pl. 4 fig. 3), as a groove. Micropyle subterminal, forming a small papilla or elongate point. Embryo cavity strongly compressed. Testa papillate, especially at the raphe margin (Pl. 4 fig. 5), with additional minute and very delicate polygonal or punctate sculpturing, the ventral margin thicker than the dorsal one, composed of circular to longitudinally elongated sclereids (Pl. 4 fig. 4).

Occurrence. Espenhain near Leipzig, Saxony, interseam layer between coal-seams III and IV, Mai & Walther 1985, pp. 52, 53, Pl. 12 figs 5–10, Fig. 10–11, MMG Dresden, Coll. Mai, No.7974 – Upper Eocene.

Remarks. These seeds of very irregular shape can only be compared with those of *Rhodoleia championii* Hook.f. from Hongkong and Kepong Field, Malaya. The fossils are smaller, thicker-walled and possess a less distinct polygonal sculpture than those of the recent species. They differs distinctly in size from seeds of the Cretaceous and Palaeocene. The Miocene species, *R. bifollicularis*, has clearly winged seeds.

### ***Rhodoleia cretacea*** Knobloch & Mai

Fig. 1D, Pl. 2 figs 16–26, Pl. 3 figs 10–12, Pl. 4 figs 8–11

Holotype. Knobloch & Mai 1986, Pl.7, figs 7,8, MfN Berlin, Coll. Mai No.1993/9255.

Diagnosis. Seeds imbricately arranged in the locule, compressed, clustered in the boat-shaped locule-filling, the ventral margin of this filling rounded, the dorsal one almost flat (Pl. 2 figs 20–23), sharply angled at the raphe-hilum junction. Micropyle epitropous, directed upwards and outwards. Hilum appearing as a long slit which reveals the edge of the seed nearer the placenta (Pl. 4 figs 10, 11), at the angled hilum-raphe-side go the seeds into a sharp raphe ridge. Seeds, in general, round or wedge-like to axe-shaped, small, 1.2–2.0 mm in diameter. Testa thin-walled, composed of sclereids which create a distinct pitted, papillate pattern of polygonal cells (Pl. 3 fig. 10), the ventral and dorsal margins being again formed differently (Pl. 2 figs 25–26).

Occurrence. Walbeck, Saxony-Anhalt, gray clays – Knobloch & Mai 1986, p. 57–58, Pl. 7

figs 7–16, Pl. 48 fig. 2; Fig. 8 (MfN Berlin, Coll. Mai No.1993/9255) – Maastrichtian (Upper Cretaceous).

Remarks. At Walbeck, particularly worthy of notice is the manner in which the loculi of the capsules are filled with seed clusters. This is derived from the bilocular fructification and imbricately arranged seeds (Pl. 4 figs 10,11). These features justify their assignment to the Hamamelidaceae-Rhodoleioideae. Fossil seeds from the Cretaceous are only 1/4–1/3 of the size of the Eocene *Rhodoleia bellmannii*, but they are closely related morphoplogically. The outer surface of the testa shows structures typical of *Rhodoleia*. Near the hilum and raphe the cells are circular with clearly thickened walls (Pl. 3 fig. 10), showing a nodular pattern near the margin (Pl. 3 fig. 11). The ventral winged margin shows elongate and undulate cells on the outer surface, which have not only sinusoidal thickened walls but also distinct, obliquely oriented striae (Pl. 3 fig. 12).

### ***Rhodoleia hercynica*** Mai

Fig. 1E, Pl. 2 figs 27, 28, Pl. 3 fig. 9, Pl. 4 fig.12

Holotype. Mai 1987, Pl. 13 fig.14, MfN Berlin (not MMG Dresden-Mai 1987, p. 206), Coll. Mai No.1993/5986.

Diagnosis. Seeds compressed, crescent-shaped, trapezoidal in cross-section with a slightly bent, curved hilum-raphe and curved opposite margin. Margins acute to slightly winged. Mikropyle apical, indistinct, papillate (Pl. 2 fig. 27). Hilum forming a relatively broad band in the upper part of the slightly curved margin, gradually merging into the raphe. Raphe-hilar margin not angled, but only curved (Pl. 2, fig. 27). Dehiscence by two equal valves. Upper surface finely pitted. Length 2 mm, breadth 0.9–1.1 mm. Testa composed of round, sclerenchymatic cells with thick walls (Pl. 3 fig. 9), and winged margin with elongate straightened cells (Pl. 4 fig. 12).

Occurrence. Only at Gonna near Sangerhausen, Sachsen-Anhalt; Division IV, grey clays in Kernbohrung at 1964 – Mai 1987: 206–207, Pl. 13 figs 14,15; Fig. 4 (MfN Berlin, Coll. Mai No.1993/5986) – Upper Palaeocene (PG.-Zone 9).

Remarks. The seeds show characters of the Hamamelidaceae-Rhodoleioideae, differing from other fossil (Mai & Walther 1985, Knobloch & Mai 1986) and recent ones only in being curved, not angled on the dorsal margin (Pl. 2 fig. 27). The elongate seeds suggest relationships with *Symingtonia* and *Steinhauera* (comp. Mai 1968, 1987).

## DISTRIBUTION AND ECOLOGY

*Rhodoleia*, ("rose without thorns"), rose (Greek "rhodon") with smooth (Greek "leios") stalks alludes to its rose-like flowers on thornless shoots. It is an evergreen tree or shrub, reaching a height of 7-10 m, distributed in the area of upper Myanmar, through eastern Tibet, southern China up to Malaysia and Sumatra (Fig. 2). With its evergreen, leathery, entire-margined and medium-sized leaves it is typical for rain-laurel forests in eastern and southern Asia where, however, it does not play a specific role. Plants of the genus occur in primary rainforest and are scarce in those under pressure from man. They are found at altitudes 330–2000 m (Vink 1957) and extend from the humid tropical zone to the temperate rainforest zone. They are cultivated particu-

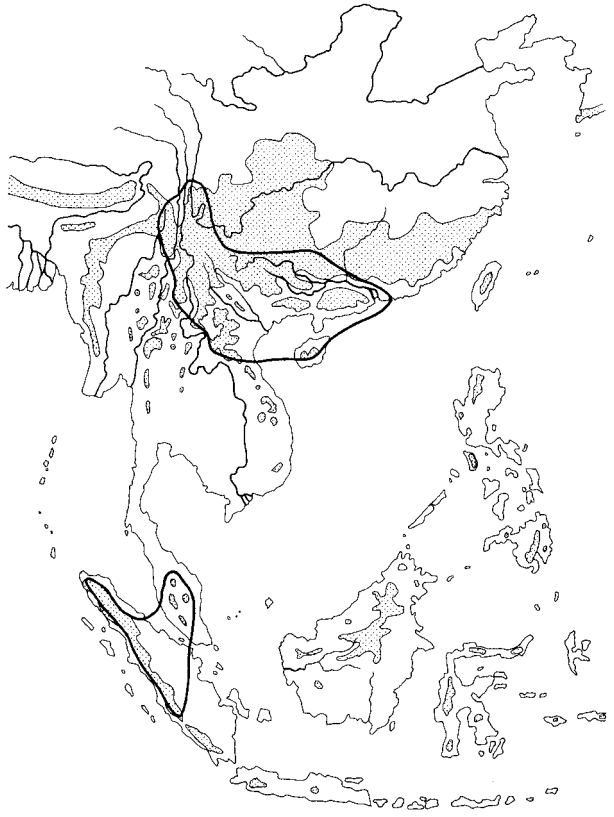

**Fig. 2.** Distribution map of *Rhodoleia* Champion in East and South-East Asia (solid line) projected on the map of laurel- and mountain rainforests (stripple) (from literature data)

larly in parks and beside mountain roads in Java, rarely in Europe in the mild regions of England (Cornwall, in forest on humus rich soils, Krüssmann 1978). All this suggests adaptation to humid subtropical or warm-temperate climatic conditions, without winter frost.

It is no general agreement as to how many contemporary species belong to the genus. In Vink's opinion (1957) only one polymorphic population of *Rhodoleia championii* Hook.f. is represented, a view shared by the majority of present authors. Exell (1933) recognised seven species having small, endemic distributions and this treatment was supported by Krüssmann (1978). On the basis of the author's own study in the Herbarium of the Botanical Museum at Berlin-Dahlem it appears that the fruits of the four species in this Museum cannot be separated, so the author shares Vink's opinion (1957). However, the genus was not formerly monotypic according to fossil evidence. In Europe from the Upper Cretaceous to the Miocene, four distinct species grew all associated with rainforest. Engler (1882) named the evergreen, laurophyllous vegetation of the European Tertiary "palaeotropical geoflora". Extinct today, that flora came from a primary developmental centre in the Upper Cretaceous in Europe and died out in the Tertiary. The contemporary existence of some endemic families in SE Asia: Mastixiaceae, Pentaphylaceae, Nepenthaceae and such important genera as *Dichroa, Gironnniera, Manglietia, Mastixia* and *Pentaphylax*, already present in the European Upper Cretaceous and older Tertiary, confirm Mai's opinion (1995). The distribution of the species rich, laurel genus *Rhodoleia* Champion, today confined to SE Asia, once again provides evidence supporting Engler's (1882) theory of a "palaeotropical geoflora".

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# P L A T E S

Plate 1

1–3. *Rhodoleia championii* Hook.f., extant. Capsules of different size, × 5
1. Part of one fructification with two four-valved capsules showing loculicidal and septicidal dehiscence
2. Single fructification with distinct septum
3. Another dehiscent capsule with a cluster of winged seeds on the placenta of the left valve

4–9. *Rhodoleia bifollicularis* (Menzel) comb. nov., capsules of various sizes and different states of preservation. Herzogenrath, Rhineland, × 5
4. Capsule with four valves and distinct receptacle – holotype of Menzel 1913 (MfN Berlin No. 407)
5. Another capsule viewed from both sides, abraded so that only part of the style remains
6. Remains of one carpel with pedicel and receptacle; note the central hole
7. Capsule with preserved receptacle
8. Carpel from one fruit showing broken receptacle
9. Carpel with hole created by an insect, margin view of Pl. 2 fig. 15

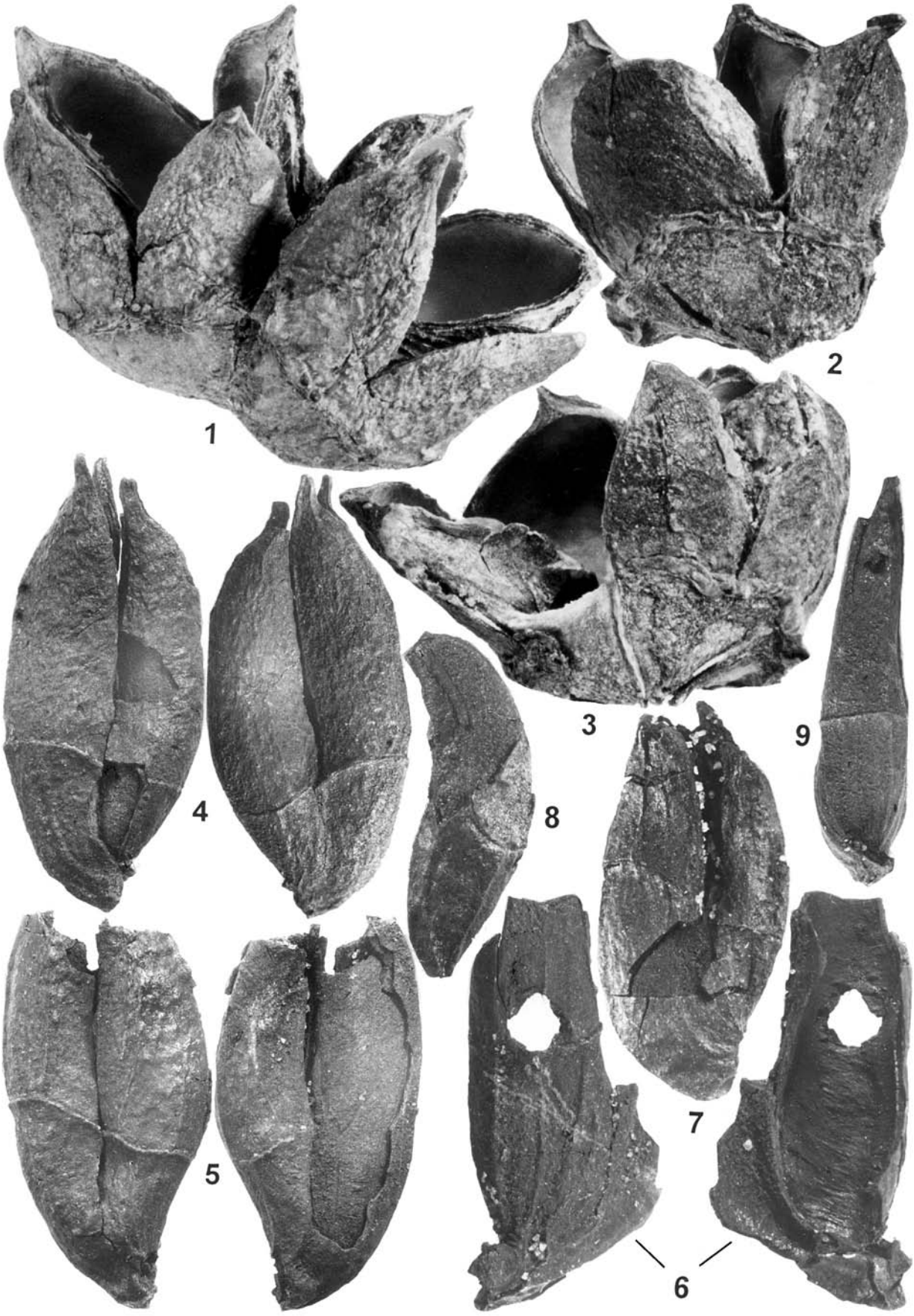
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Plate 2

1–3. *Rhodoleia championii* Hook.f., extant. Seeds of different form and size, × 12
1. Seed with winged edge and distinct hilar scar
2. Winged seed with raphe and micropyle
3. Winged seed, probably sterile, with raphe

4–10. *Rhodoleia bellmannii* Mai in Mai & Walther, seeds of various form and size. Espenhain, Saxony, × 12
4. Seed from both sides, wing broken at the end – holotype of Mai & Walther 1985 (7974)
5. Seed from both sides with distinctly thickened hilum
6. Round seed
7. Another seed with pitted hilum
8. Fragment of a small, probably sterile seed
9. Broken seed with distinct hilum
10. The same seed under SEM, × 20

11–15. *Rhodoleia bifollicularis* (Menzel) comb. nov. Herzogenrath, Rhineland
11. Winged seed from both sides, with hilum and raphe edge – syntype (MfN Berlin No.408), × 12
12. Another winged seed under SEM, × 12
13. Cluster of seeds and remains of carpels, × 5
14. Winged seeds showing their imbricate arrangement on the remains of the placenta, × 5
15. Cluster of seeds in one carpel with the oblique hilar scars distinctly visible, × 5

16–26. *Rhodoleia cretacea* Knobloch & Mai, seeds and seed clusters. Walbeck, Saxony-Anhalt (differing enlargements)
16. Seed with a winged margin – holotype of Knobloch & Mai 1986 (9255), × 15
17. Another seed with signs of damage, × 15
18. Seed with hilum and raphe under SEM, × 12
19. Cluster of seeds showing edge of placenta and oblique hilar scar under SEM, × 12
20. Lateral view of seed cluster, × 15
21. Seed cluster with oblique hilar scars viewed from the placenta, × 15
22. Another cluster, viewed from the placenta, × 15
23. Remains of one cluster of winged seeds with distinct evidence of damage, × 15
24. Margin view of a longitudinally broken seed cluster, × 15

25–26. Various seed surfaces showing different structures under SEM, × 20

27–28. *Rhodoleia hercynica* Mai, seed viewed from both sides. Gonna, Saxony-Anhalt, × 20
27. Seed with hilar scar, raphe and micropyle – holotype of Mai 1987 (5986), × 20
28. Another seed with clearly visible surface, × 20

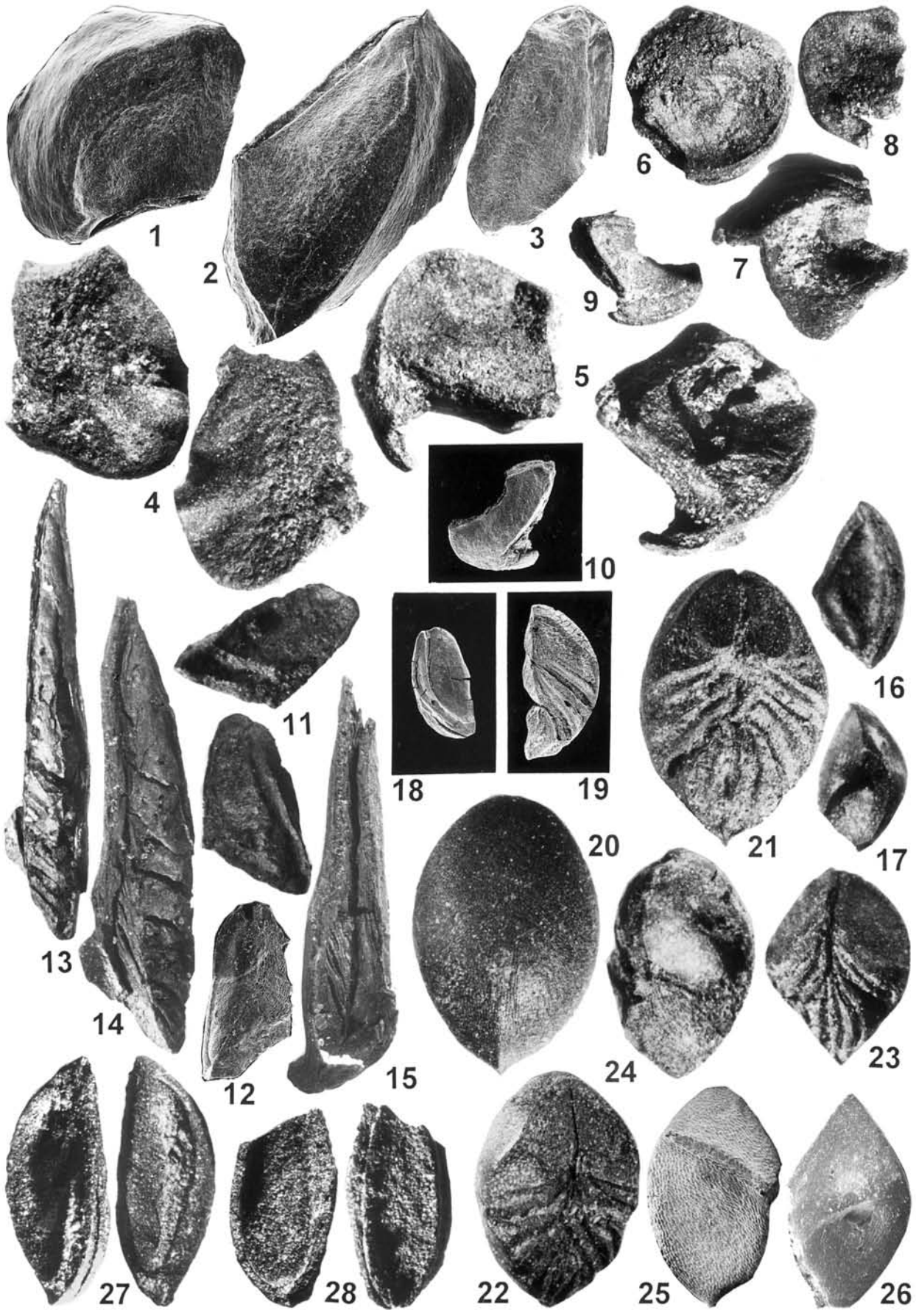
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Plate 3

1–6. *Rhodoleia championii* Hook.f., seeds under SEM (different enlargements)
1. Nodular cell structure viewed laterally, × 300
2. Polygonal cell structure viewed laterally, × 300
3. Transitional cell structure viewed from the ventral margin showing nodular to elongated cells, × 300
4. Elongated, isodiametric cells above the ventral margin, × 300
5. Micropylar opening, × 300
6. Hilum showing beginning of raphe, × 25

7–8. *Rhodoleia bifollicularis* (Menzel) comb. nov., seeds under SEM, × 300
7. Elongated cell structure above the ventral margin
8. Abraded cells with undulate walls above wing

9. *Rhodoleia hercynica* Mai, seed under SEM, rounded cells, abraded, on the lateral surface, × 300

10–12. *Rhodoleia cretacea* Knobloch & Mai, seeds under SEM, × 300
10. Rounded abraded cells at the lateral surface
11. Transitional cell structure at the ventral margin showing nodular to elongated cells
12. Straight cells with oblique cutin striae above the ventral margin

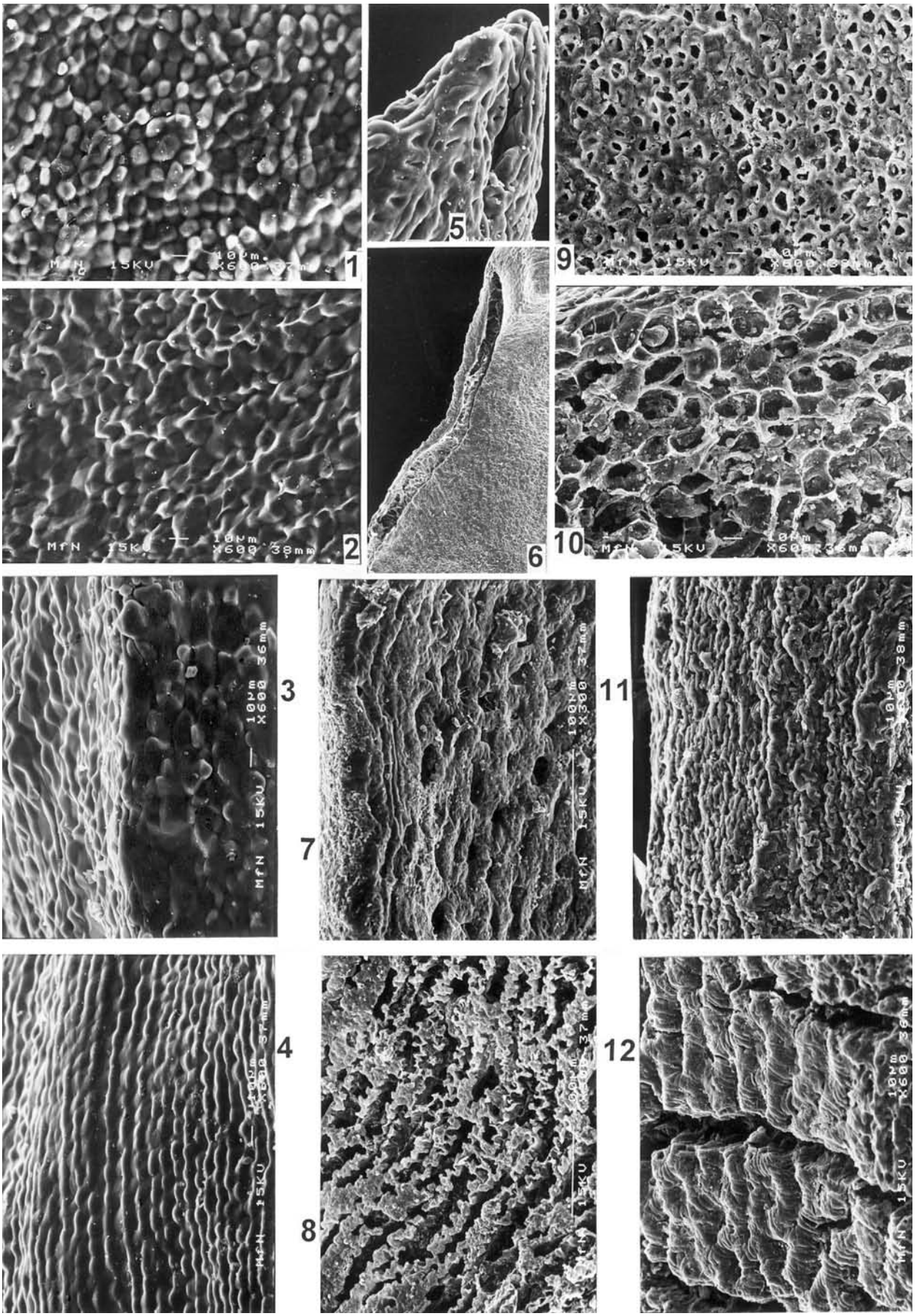
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Plate 4

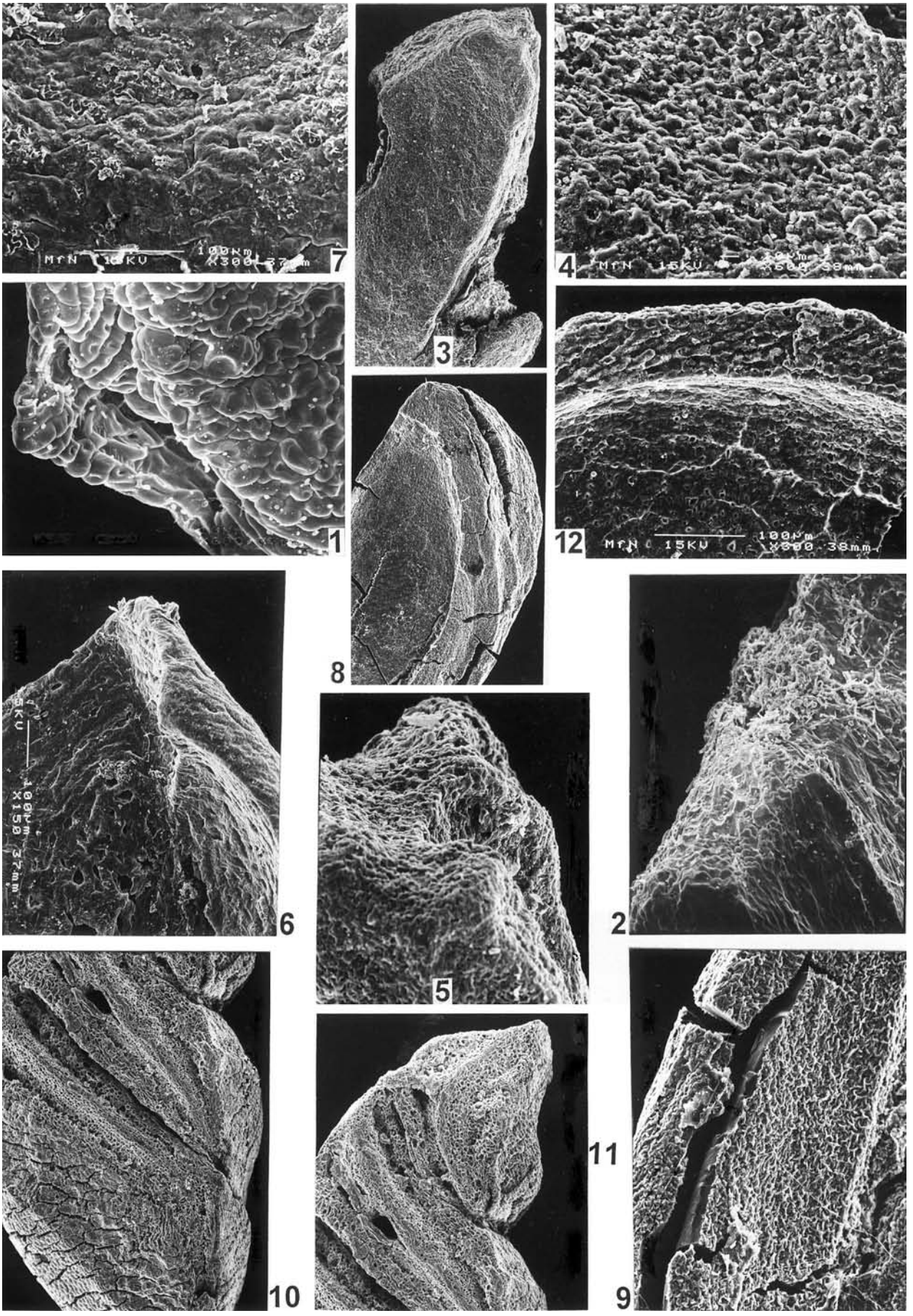
1–2. *Rhodoleia championii* Hook.f., seed under SEM, × 300
1. Cell structure at the hilum
2. Cell structure at the micropyle, strongly abraded, but the open tip is visible, × 300

3–5. *Rhodoleia bellmannii* Mai in Mai & Walther, seed under SEM (differing enlargements)
3. Seed with pitted hilum, raphe and micropyle, × 38
4. Nodular cell structure at the lateral surface, × 300
5. Micropyle with pitted open tip, × 150

6–7. *Rhodoleia bifollicularis* (Menzel) comb. nov., seed under SEM (differing enlargements)
6. Hilum and raphe, × 75
7. Nodular-polygonal cell structure at the lateral surface, × 150

8–11. *Rhodoleia cretacea* Kobloch & Mai, seeds under SEM (differing enlargements)
8. Hilum and raphe at the dorsal margin of a seed, × 38
9. Cell structure at the hilum, × 150
10. Part of seed cluster with oblique hilar scar, × 38
11. Part of the same cluster at the tip, × 38

12. *Rhodoleia hercynica* Mai, seed under SEM, transitional cell structure at the ventral margin, × 150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