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The identification of Potamogetonaceae fruits found in The Netherlands

R. T. J. CAPPERS*

University of Groningen, Department of Plant Biology and Biologisch-Archaeologisch Instituut, Poststraat 6, 9712 ER Groningen, The Netherlands

SUMMARY

From recent litter, deposited by both the River Rhine and the North Sea, and from a Weichselian Pleniglacial deposit, many pondweed endocarps were isolated and identified. Seventeen species could be identified, among which were two subfossil species that were also regularly found in recently deposited litter. To improve future identification, all species are presented by SEM photographs and their characteristic features are described.

Key-words: Groenlandia densa†, fruit morphology, palaeobotany, *Potamogeton* spp., seed identification.

INTRODUCTION

In the Netherlands, 18 of the 80–90 pondweed species (*Potamogeton* spp.) occur, making it one of the most species-rich genera of the Dutch flora (Weeda & Van der Meijden 1989). In archaeobotanical studies, where the identification of herbs is mostly restricted to seeds and fruits, pondweed fruits are frequently found as a result of good conditions for preservation. However, only a relatively small part has been identified with certainty to the species level. The main reason for this is the incompleteness of reference collections for this genus, due to the rareness and low seed production of some of the species and the difficulty in collecting the fruits. Furthermore, the identification of pondweeds is problematic, because of their diagnostic features, intraspecific variability and hybridization. However, hybridization is probably a less frequent phenomenon than is generally assumed (Wiegleb 1988). *P.* × *zizii* is the only hybrid in The Netherlands that regularly produces mature fruits, although its viability is still unproven (Van der Ploeg 1990; Stace 1991).

Both vegetative and generative characters have a diagnostic value, of which fruit characters are considered to be of special importance. The fruit wall consists of a one-layered exocarp of cubic cells, an outer parenchymatous mesocarp, an inner mesocarp of 1–18 layers of sclereids and a one-layered endocarp of long and narrow cells with massive thickened cell walls (Takaso & Bouwman 1984). The outer mesocarp is mostly rather fleshy and in the long run will disappear together with the exocarp. The remaining hard 'fruit stone' is normally referred to as endocarp s.l. (as in this study). In

*Present address: Cito, PO Box 1034, 6801 MG Arnhem, The Netherlands.
†Nomenclature follows Van der Meijden (1990).

contrast to *Potamogeton* spp., fruits of opposite-leaved pondweed (*Groenlandia densa*=*Potamogeton densus*) lack the sclerified thickening of the mesocarp, as a result of which the fruit wall is soft. When the outer layer has disappeared, the one-layered endocarp shows clearly the elongated cells, orientated with their long axis parallel to the embryo. This cell pattern is the same for the inner layer of the endocarps of *Potamogeton* spp. Because of the taxonomic relationship between *Groenlandia* and *Potamegeton*, both genera are dealt with in this study.

For species that may be found in The Netherlands, few studies present characters of complete fruits (e.g. Clason 1964; Beijerinck 1976). However, the diagnostic features of the exocarp are restricted and more details are obtained by removing the fleshy part of the fruits. Important studies which deal with the identification of the pondweed endocarps are those of Jessen (1955), Martin & Barkley (1961), Katz *et al.* (1965) and Aalto (1970). A thorough description, supplemented by numerous illustrations, is presented by the last author. *P. nodosus*, which has a southern distribution, is the only Dutch species missing in this study dealing with Fennoscandian species. Aalto's key emphasizes the shape, size and cell pattern of the endocarp surface. The main shortcoming of Aalto's work is the lack of clear photos, which makes it difficult to distinguish between species.

The aim of this study is to improve the identification of pondweed endocarps by presenting SEM photographs of 17 *Potamogeton* spp. and of *Groenlandia densa*, accompanied by identification remarks. Only those characters are mentioned that proved to be of significant diagnostic value. Special attention is paid to the presence of fruits from species for which the present distribution does not include The Netherlands.

MATERIALS AND METHODS

Fruits of pondweeds were isolated from litter collected along the Dutch coast (sites 1–16, Fig. 1) and the River Rhine (sites 17–18) and from sediment samples derived from an archaeological excavation site near Orvelte (site 19). The litter was collected in 1991 and 1992 and concerns recently deposited sediments. The samples varied from 200 ml to 3 l, depending on the amount of botanical remains. The samples from Orvelte were collected from a deposit of Weichselian Pleniglacial time and comprised about 30 l. Samples were washed through a stack of sieves of mesh sizes 2·0 mm, 1·0 mm and 0·5 mm. The fruits were isolated from the sieve residues under a dissecting microscope. For a full species list and discussion of the botanical macroremains from the sites, see Cappers (1993) and Cappers *et al.* (1993).

Identification of the pondweed fruits was mainly carried out with the help of Aalto's (1970) key. Additionally, a private reference collection was used and specimens from the Rijksherbarium of Leiden were consulted. For comparison, the exocarp and outer mesocarp were removed by boiling the fruits for some minutes in KOH (5%). Fruit shape and size were examined under a dissecting microscope; under a high-powered microscope the cell patterns were observed with incident light. Representative specimens were selected for SEM photographs. From all species, photographs were taken of both the entire fruit and the central part of the side adjacent to the ventral lid. To facilitate comparison, photographs are presented in the same orientation, with the exception of *Groenlandia densa*.

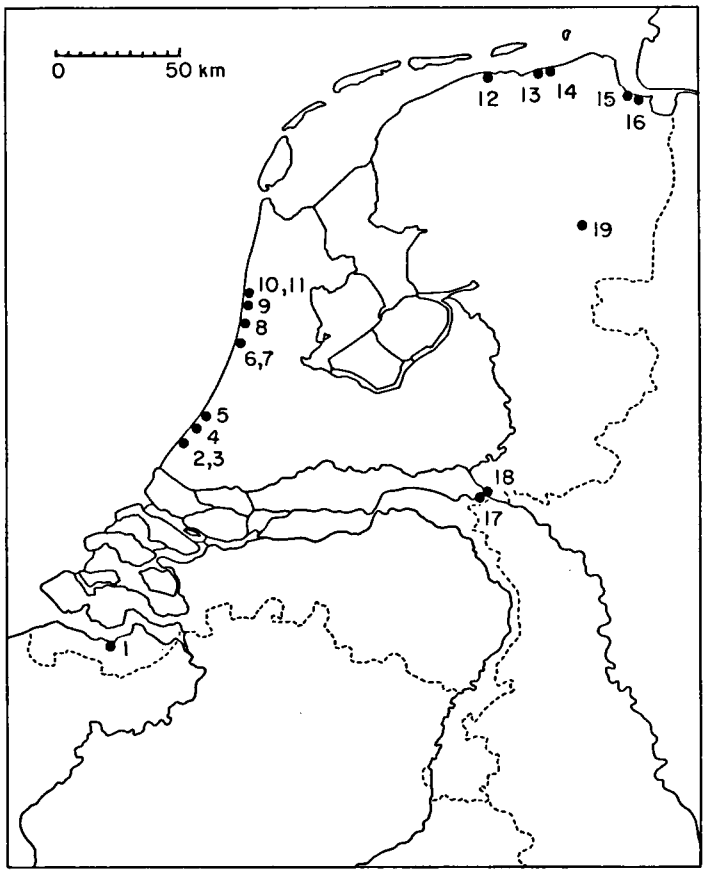

Fig. 1. Location of the sites where samples were collected. The numbers correspond with the site numbers in Table 1.

RESULTS

Altogether, 1157 endocarps of pondweeds were found scattered over 15 sites (Table 1). Some sites yielded no pondweed fruits, partly due to the limited sample size that was examined. Generally, the preservation of the endocarps was good, so that identification to species level was possible. In particular, fragmented endocarps remained unidentified. Parts of the endocarp that are of special interest are indicated in Fig. 4c.

P. natans (Fig. 2a)

Endocarps of this species have a characteristic shape. The beak is mostly in a ventral position and in that position it makes no contact with the top of the lid. Both sides mostly show a central depression, sometimes resembling the natural cavities of *P. polygonifolius* and *P. coloratus*. *P. natans*, however, has clearly bigger endocarps and lacks the typically elongated cells of both these species. If endocarps are seriously eroded, the surface may show a pattern of spongy cells.

Table 1. Number of fruits of *Potamogeton* spp. and *Groenlandia densa* found in litter (sites 1–18) and soil samples (site 19). When identification to the level of species is uncertain, the number is underlined. In the last column the site frequency (SF) is mentioned

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	SF
P. natans	1	.	11	.	.	2	.	1	.	.	.	.	.	.	2	3	1	.	60	8
P. perfoliatus	1	.	12	.	.	2	.	1	1	.	.	1	.	.	.	.	.	.	.	6
P. praelongus	.	.	1	.	.	3	.	1	.	.	.	.	.	.	.	.	.	.	9	4
P. lucens	.	.	4	.	.	4	.	.	.	.	.	.	.	.	1	1	.	.	.	4
P. gramineus	.	.	7	.	1	4	.	.	1	.	.	2	.	.	2	6	.	.	7	8
P. polygonifolius	11	.	7	.	.	11	1	1	.	.	.	2	.	.	4	7	.	.	.	8
P. alpinus	.	.	2	.	.	.	.	2	.	.	.	.	.	.	2	.	.	1	234	5
P. crispus	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
P. pusillus	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2
P. mucronatus	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	8	.	.	374	4
P. acutifolius	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
P. trichoides	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
P. obtusifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19	1
P. vaginatus	.	.	.	.	.	5	.	.	1	.	.	.	.	.	.	.	.	.	8	3
P. filiformis	1	.	5	1	.	27	.	5	1	.	.	3	.	.	2	10	.	.	25	9
P. pectinatus	2	.	28	.	.	19	.	4	.	.	.	.	.	.	.	6	.	1	.	6
Unident. *Potamogeton*	.	.	29	3	1	30	.	.	.	.	.	1	1	.	2	10	2	.	74	10
Groenlandia densa	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Total number	17	—	113	4	2	109	1	15	4	—	—	9	1	—	15	51	3	2	811	

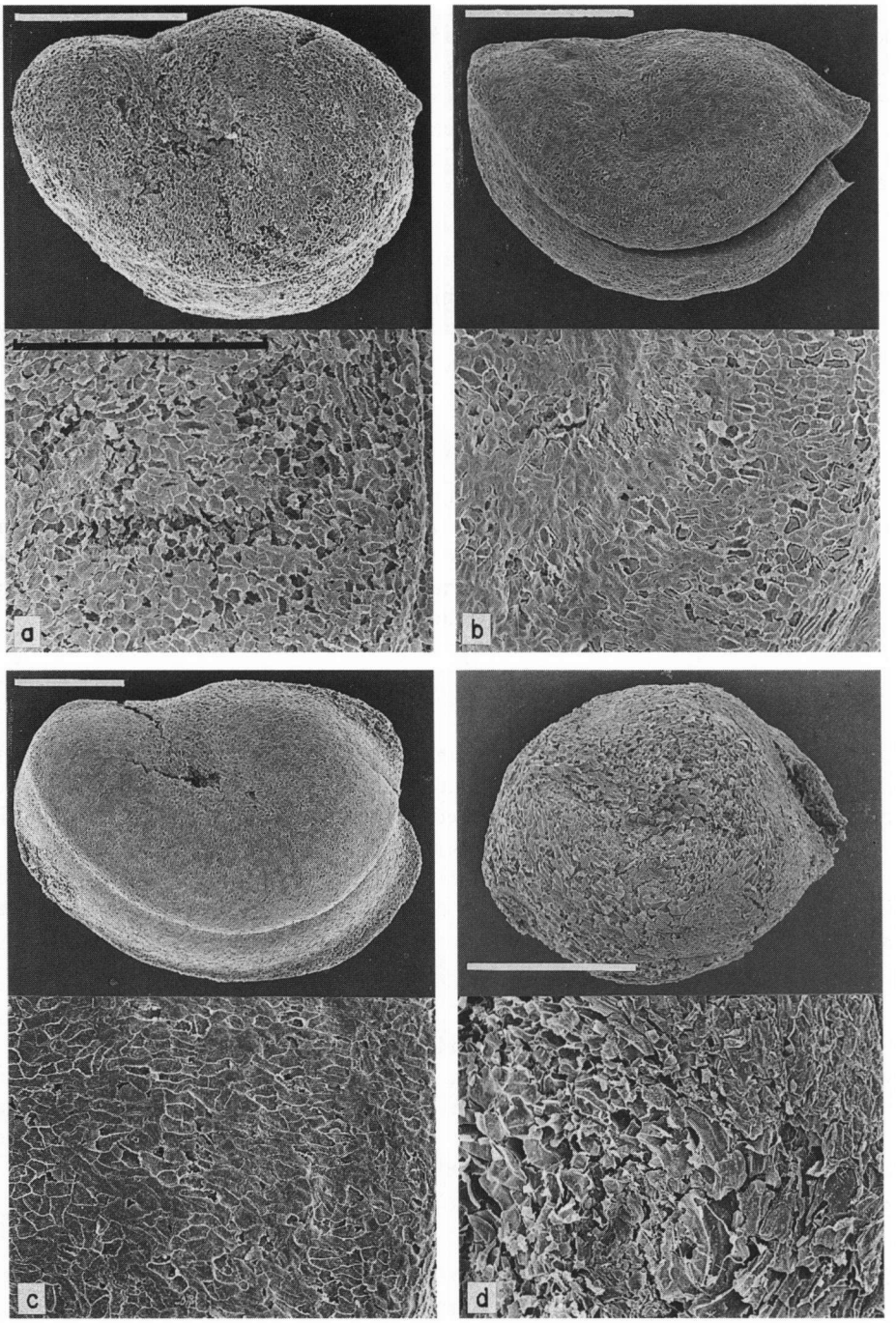

Fig. 2. Recent and subfossil endocarps of *Potamogeton* spp. and *Groenlandia densa*. On the top: side view of the complete endocarp, orientated with the lid to the bottom with the exception of *Groenlandia densa*, for which the lid is on the right side (bar = 1 mm). On the bottom: detail of the cell pattern from the dorsal margin of side. All sections are rotated 90° anti-clockwise (bar = 0·5 mm, only shown for the first species as all sections are presented with the same magnification). (a) *P. natans*; (b) *P. perfoliatus*; (c) *P. praelongus*; (d) *P. crispus*.

P. perfoliatus (Fig. 2b)

The endocarps of this species are quite variable in shape and cell structure, which means it is not always possible to distinguish them from *P. natans*. Diagnostic features are the position of the beak, which is in a more central position and may be decurrent to the dorsal side, and the lid reaching the beak, sometimes even extending along it. The surface may clearly show cells in a radiate pattern and elongated cells bordering the dorsal side.

P. praelongus (Fig. 2c)

Endocarps of this species are easily recognized. They are of considerable size and the cells are not clearly visible with a low magnification (20 ×). The ventral side is curved, as is the relatively broad lid adjacent to it, which mostly bears the remnants of a crest in the apical part.

P. crispus (Fig. 2d)

Fruits of this species are characterized by a substantial beak which is confluent with the ventral side. In an eroded condition, the endocarp appears as a formless body, which may be difficult to orientate in a proper way. Features such as basal warts, stalks or keels are not visible. The cells are quite big and may be of irregular shape. Although strongly eroded endocarps are not representative any more for the pondweed endocarps, the combination of shape and cell structure make them still easy to recognize.

P. lucens (Fig. 3a)

The endocarps of *P. lucens* and *P. gramineus* resemble each other in shape and cell pattern. Both species have flat sides, the beak in a (centro-)ventral position, ridges along the dorsal side and elongated cells arranged in the same direction as the embryo (Fig. 3a, b). Also *P. polygonifolius, P. coloratus* and *Groenlandia densa* are characterized by this cell pattern, but the first two species have much smaller endocarps, while the third one consists of only one cell-layer. The endocarps of *P. lucens* are relatively large and may have a central depression or cavity.

P. gramineus (Fig. 3b)

Endocarps of this species are quite similar to those of *P. lucens*. They can be distinguished by the size of the cells (Fig. 3a, b) and the length of the endocarps: *P. lucens* has large endocarps (2·3–3·5 mm) and *P. gramineus* had small endocarps (1·5–2·3 mm) (Aalto 1970). Furthermore, the lid of *P. gramineus* is relatively broad when compared with the breadth of the sides.

P. polygonifolius (Fig. 3c)

The endocarps of this species may only be confused with those of *P. coloratus*. Both species have small endocarps with a natural cavity and elongated cells all around the cavity. However, *P. coloratus* has smaller endocarps with a drop-shaped cavity. The endocarps of *P. polygonifolius* are also characterized by their top: the lid almost reaches the top while there may be a considerable distance between this top and the eroded beak, comparable with *P. alpinus* (Figs 3c, 4a).

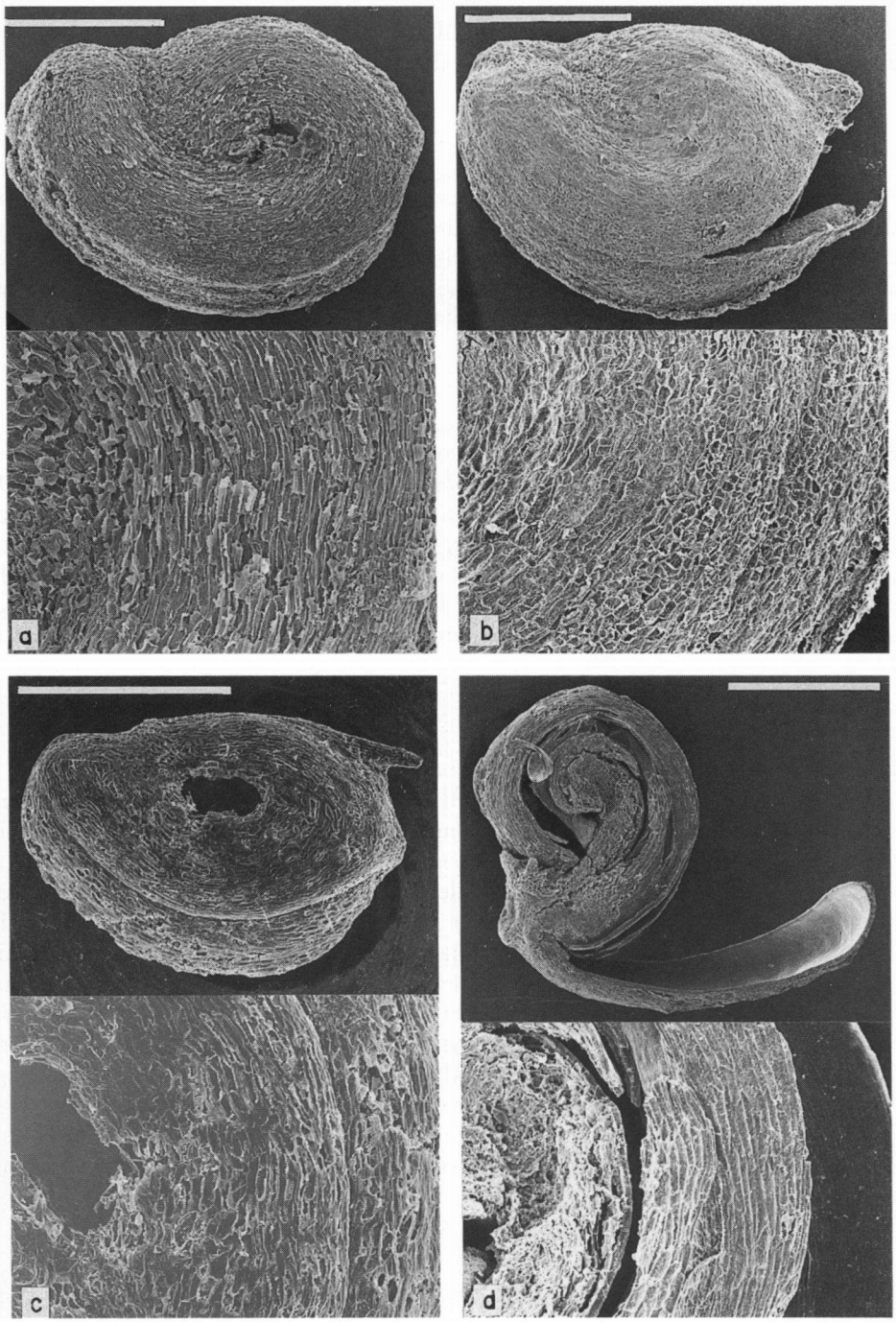

Fig. 3. Recent and subfossil endocarps of *Potamogeton* spp. and *Groenlandia densa*. (a) *P. lucens*; (b) *P. gramineus*; (c) *P. polygonifolius*; (d) *G. densa*. Details as for Fig. 2.

Groenlandia densa (Fig. 3d)

Because the endocarps are only one cell-layer thick, they cannot be confused with the endocarps of any of the *Potamogeton* spp. Due to the thin fruit wall, the endocarp may be easily damaged (Fig. 3d: as a result of the dehydration, the lid is strongly bent backwards). Elongated cells are clearly visible on the flat sides, while remnants of the exocarp may be partly present.

P. alpinus (Fig. 4a)

The medium-sized endocarps of this species may at first sight be difficult to distinguish from those of *P. pusillus, P. berchtoldii* and *P. mucronatus*. An important diagnostic feature of *P. alpinus* is the considerable distance between the ventral-positioned beak and the top of the lid. This flat part of the top may be slightly elevated in the dorsal direction, even stronger than is visible in the specimen illustrated. The sides have a smooth surface.

P. pusillus (Fig. 4b)

The taxonomic status of this species is somewhat problematic, for it is not always possible to distinguish it from *P. berchtoldii* (Wiegleb 1988; Van der Meijden 1990). However, according to Aalto (1970) at least recent endocarps from both species can readily be distinguished from each other. Two small endocarps were keyed to this species. Their shape is obovoid and both beak and stalk are in a medial position. The cells are of irregular shape. Endocarps of *P. berchtoldii*, on the other hand, are ovoid with the greatest width at or below the middle and with more rounded cells (Aalto 1970).

P. mucronatus (Fig. 4c,d)

The endocarps of this species seem to be variable and are sometimes difficult to distinguish from *P. alpinus*. In the samples from Orvelte, the endocarps of *P. mucronatus* could be separated into two groups: oblong specimens (Fig. 4c) and round-oval ones (Fig. 4d). The last group resembles *P. berchtoldii*, but in this species the endocarps are ovoid (greatest width at or above the middle) and the lid is mostly raised along the beak (Aalto 1970). To separate *P. mucronatus* and *P. alpinus* from each other, a combination of features has to be taken into account. The distance between the beak and the lid may also be present in some endocarps of *P. mucronatus*, but its length is restricted and there is no elevation to the ventral side. Whereas *P. alpinus* has a ventral-positioned, erect beak with a small base, *P. mucronatus* has a sloping, broad-based beak in a ventral-cental position. The top of the lid is slightly recurved in *P. alpinus*, while it is straight in *P. mucronatus*. The author experienced great difficulty in detecting the one to two characteristic furrows on sides of the endocarps mentioned by Aalto. The sides of *P. alpinus* lack these furrows and are convex. Endocarps of *P. mucronatus* have basal warts, which are absent in *P. alpinus*.

P. cf. acutifolius (Fig. 5a)

Due to the poor preservation, the two endocarps of this species could not be identified with certainty. The ventral side has a dominant bulge, which is also present in *P. trichoides* and sometimes in *P. compressus*. The endocarps are large and have flat sides.

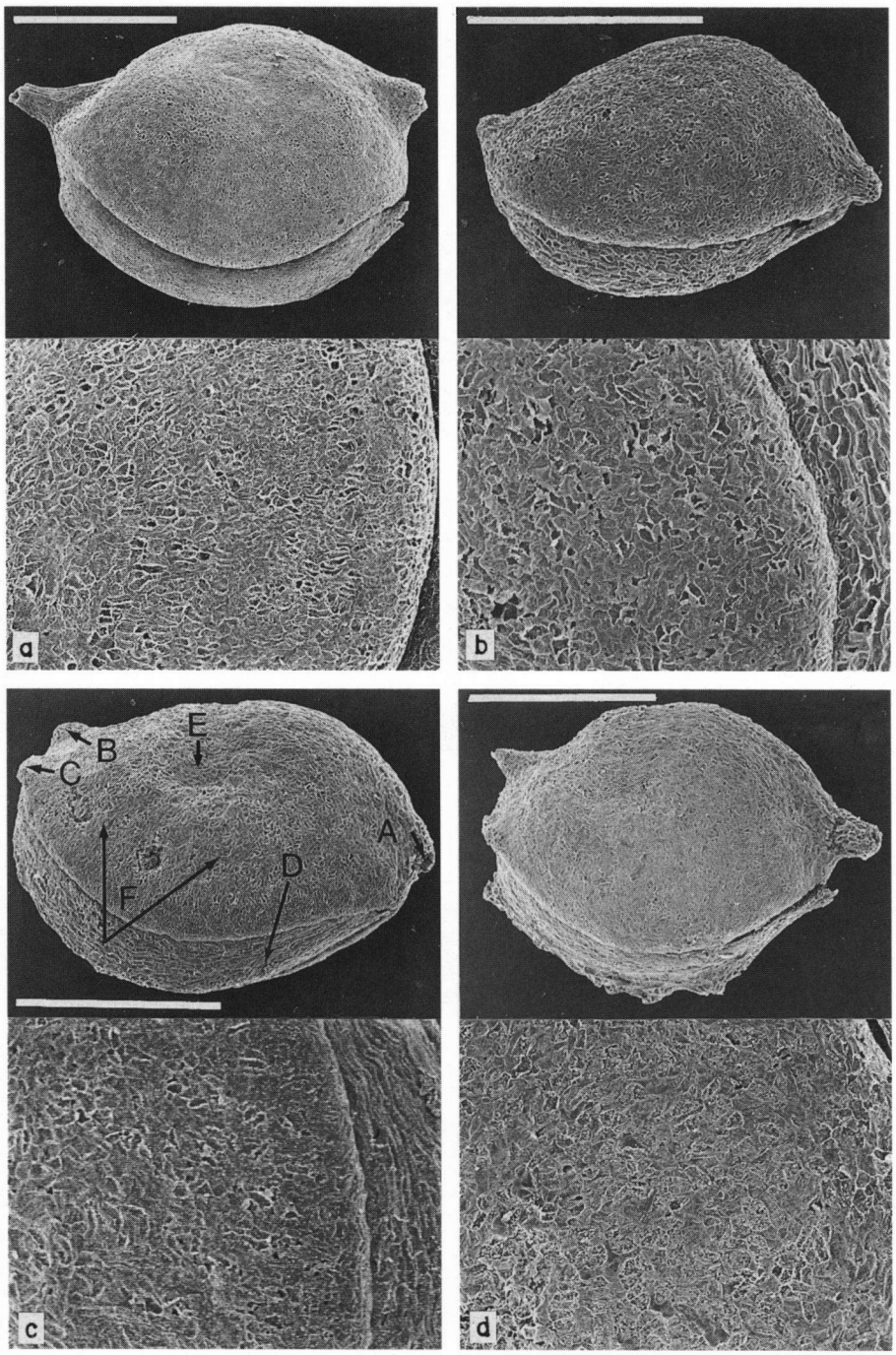

Fig. 4. Recent and subfossil endocarps of: (a) *P. alpinus*; (b) *P. pusillus*; (c) *P. mucronatus* (A, beak; B, stalk; C, basal wart; D, lid; E, central depression; F, furrow); *P. mucronatus*. Details as for Fig. 2.

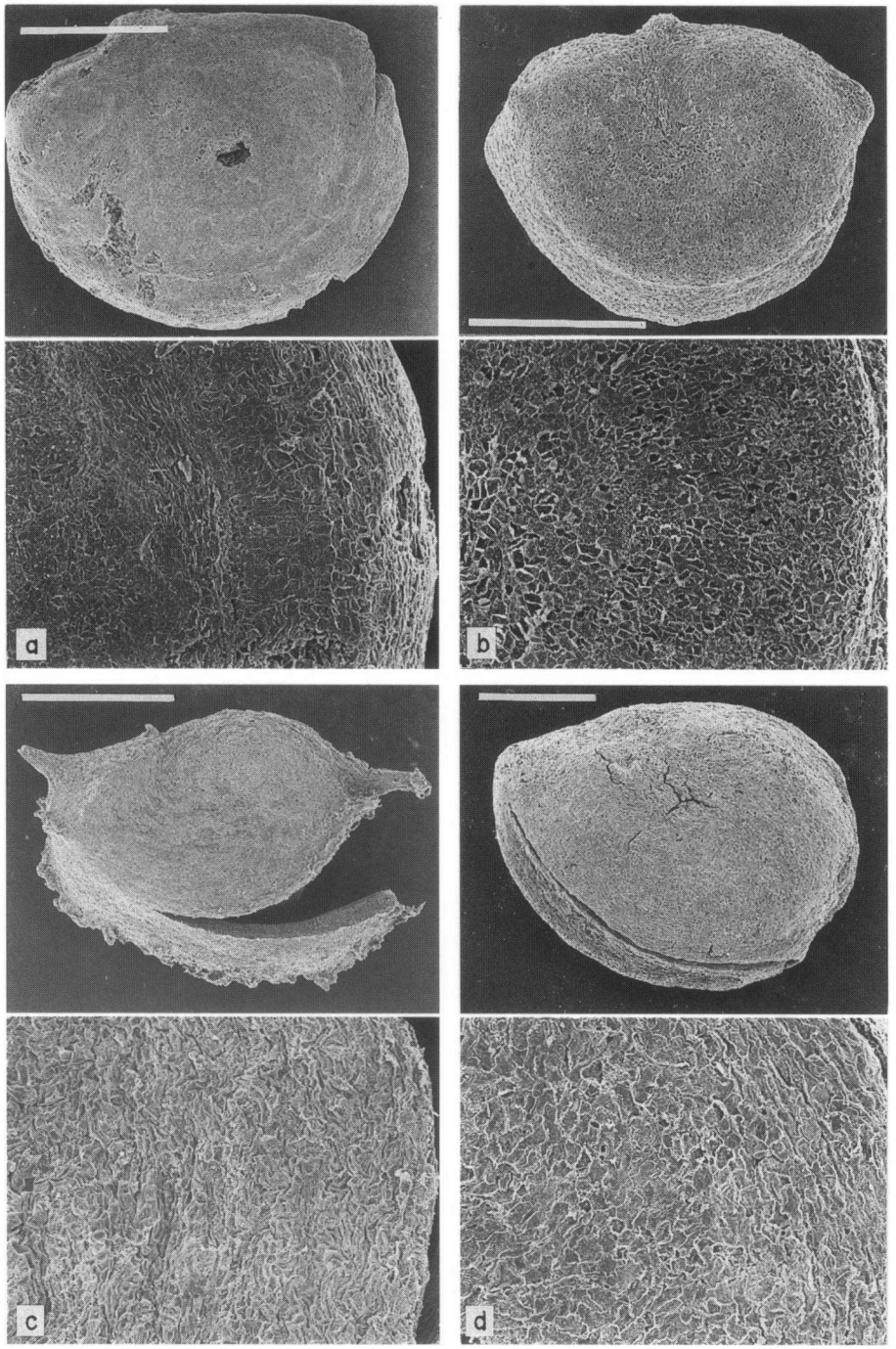

Fig. 5. Recent and subfossil endocarps of: (a) *P. cf. acutifolius*; (b) *P. trichoides*; (c) *P. obtusifolius*; (d) *P. pectinatus*. Details as for Fig. 2.

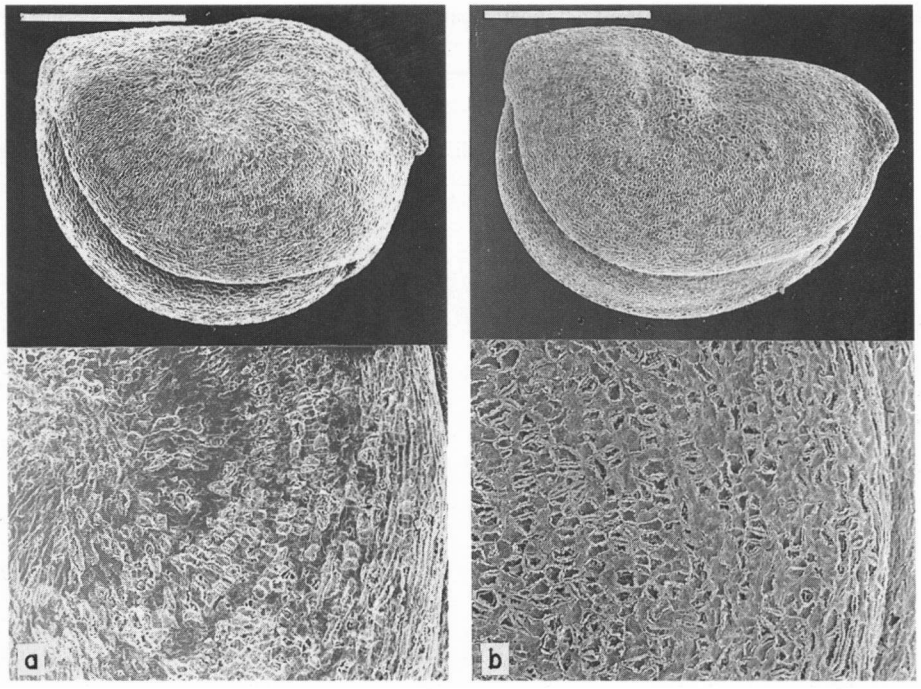

Fig. 6. Recent and subfossil endocarps of: (a) *P. filiformis*; (b) *P. vaginatus*. Details as for Fig. 2.

The lid almost reaches the ventrally placed beak, while the base terminates in a prominent wart.

P. trichoides (Fig. 5b)

The endocarps of this species are smaller than those of *P. acutifolius* and *P. compressus*. The ventral bulge is prominent and always present. Due to the central-placed beak, the shape is more roundish than that of *P. acutifolius*. The dorsal side may be scattered with warts, but these were mostly absent due to corrosion.

P. obtusifolius (Fig. 5c)

The endocarps of this species could easily be recognized by the presence of an oblique wavy ridge of warts bordering a depression nearby the stalk and by the crispate crest of the lid over almost its total length. It is striking that all endocarps of this species still had their crest, although they were of considerable age.

P. pectinatus (Fig. 5d)

Despite the degree of erosion and its variability, almost any endocarp of this species may be identified by the relatively large distance between lid and beak. The lid may be short or long, but will never reach the top of the endocarp. The surface of the sides consists of irregular cells that are not arranged in a striate pattern.

P. filiformis (Fig. 6a)

The length of the interval between lid and beak is intermediate when compared with *P. vaginatus* and *P. pectinatus*. The beak is in a central position and both top and base

Table 2. Summary of the important diagnostic features of the endocarps: m, mostly; s, sometimes; E, endocarp

Species	Beak position	Top of lid reaching top of E	Distance between lid and beak	Orientation of cells	Specific features
P. natans	m. ventral	mostly	variable	irregular	—
P. perfoliatus	central	yes	absent	s. radiate	—
P. praelongus	ventral	yes	absent	irregular	large E
P. lucens	m. central	yes	absent	concentric	flat sides, large E
P. gramineus	central	almost	small	concentric	flat sides, small E
P. polygonifolius	central	almost	small	concentric	natural cavity
P. alpinus	ventral	yes	large	irregular	smooth surface
P. crispus	ventral	no	large	irregular	large cells
P. pusillus	ventr/centr	mostly	variable	irregular	small, spindle-shaped E
P. mucronatus	ventr/centr	yes	variable	irregular	—
P. acutifolius	ventr/centr	yes	a. absent	irregular	ventral bulge
P. trichoides	central	yes	a. absent	irregular	ventral bulge
P. obtusifolius	m. central	yes	a. absent	irregular	depression nearby stalk and crispate crest
P. vaginatus	ventral	almost	medium	radiate	m. dark colour
P. filiformis	central	no	large	radiate	—
P. pectinatus	ventral	no	very large	irregular	shape s. triangular
Groenlandia densa	ventr/centr	yes	absent	concentric	one cell layer thick

of the lid are rounded. Furthermore, endocarps are somewhat smaller, although there is a considerable overlap in range with *P. vaginatus*.

P. vaginatus (Fig. 6b)

Together with *P. filiformis* and *P. pectinatus*, this species is characterized by a considerable interval between the lid and the beak, although from these three species, *P. vaginatus* has the smallest interval. The surface has a pattern of radiated cells, bordered by long, narrow cells along the ventral side, which is also present in *P. filiformis*. The beak is in a ventral position and both the top and base of the lid are V-shaped (Aalto 1970).

A summary of the most important diagnostic features is presented in Table 2.

DISCUSSION

Almost all well-preserved pondweed fruits can be specifically identified, the most important features being the position of the beak and the top of the lid. The cell pattern is of special interest when the cells are arranged in concentric circles or in radiate rows. Even with low magnification (20 ×), the cell pattern is easy to examine.

Besides shape and cell pattern, Aalto (1970) stresses the diagnostic value of the size of the endocarps. Mean, range and standard deviation are presented for both length and breadth of the endocarps. However, the ranges show a considerable overlap, especially for those species that have a close taxonomic relationship to each other. The

t-tests showed significant differences between almost every pair of species for both length and breadth, but these values are no use for the identification of individual specimens. However, the distinction between small, medium and large remains a useful feature.

Fruits of *P* × *zizii* are similar in cell pattern to the parents, *P. lucens* and *P. gramineus*, although intermediate in length. Therefore, the identification of this hybrid will be somewhat arbitrary. In The Netherlands, its dispersal is probably restricted to two localities (Mennema *et al.* 1980).

Conspicuous species are *P. vaginatus* and *P. filiformis*; subfossil endocarps of both were found in several litter samples. It is remarkable that *P. filiformis* is the most frequently occurring species, although it is now absent from The Netherlands (Van der Meijden & Weeda 1983). Records of this species from the Pleistocene however, are known for The Netherlands (Orvelte samples; Ran 1990) and in Britain, endocarps of this species are frequently recorded from the Weichselian (Godwin 1984). The subfossil endocarps of both species dealt with in this study must be interpreted as reworked macrofossils that originated from peat underneath the sea-floor that was locally subject to erosion and regularly deposited on the coast. The occurrence of *P. filiformis* and *P. vaginatus* in recent deposits illustrates very clearly the problems encountered when dealing with the identification of pondweed endocarps. If the possibility of subfossil, rare or exotic species is not considered, the variability of certain species may become vague and the identification will be incorrect or restricted to the genus level.

Pondweed species that were not found in the samples examined are *P. compressus, P. berchtoldii, P. coloratus* and *P. nodosus*. The last two species are very rare in The Netherlands and, to a lesser degree, this is also true for *P. berchtoldii*. Considering the variability of *P. mucronatus* and the close resemblance of this species and *P. berchtoldii*, it is also possible that some of the endocarps of *P. mucronatus* belong to *P. berchtoldii*. Although *P. compressus* is a more common species, it is probably the only one in The Netherlands that has a low seed set after flowering (Van der Meijden 1990).

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