

COMPTONIA-LIKE LEAVES FROM THE GERMAN MIDDLE EOCENE

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ABSTRACT: Leaves and leaf fragments similar to those of the monotypic extant genus *Comptonia* (Myricaceae) are described for the first time from the Middle Eocene maar filling of Eckfeld near Manderscheid (Eifel, Germany). Two previously described leaf fragments of the same kind from the slightly older deposits of Messel have been re-investigated for comparison. The fossil material is not only compared to extant *Comptonia*, but also to similar leaves in the proteaceous genera *Banksia* and *Dryandra* and leaflets of *Lyonothamnus* (Rosaceae). It is assigned to the broadly defined species “*Comptonia*” *difformis* (Sternberg 1825) Berry 1906 for which an emended diagnosis is presented. Compared to the widely distributed and sometimes almost identical fossil material, the only present species of *Comptonia* is quite restricted in geographical and ecological distribution.

KEY WORDS: Fossil leaves, Middle Eocene, Palaeogene, Germany, Messel, Eckfeld, *Comptonia*, Myricaceae, palaeoecology

INTRODUCTION

Comptonia today is a monotypic genus of the Myricaceae which is restricted in distribution to eastern and central North America ranging from Manitoba and Nova Scotia in the North to Georgia and South Carolina in the South. The deciduous shrubs are occupying dry and poor acidic habitats with sandy to rocky soils (e.g. Berry 1906, Radford *et al.* 1964, Krüssmann 1960, Morin 1997). Their quite characteristic leaves are deeply asymmetrically lobed with rounded to slightly pointed lobes.

Fossil leaves similar to the leaves of extant *Comptonia* have been described for the first time by Sternberg 1821 from the Lower Miocene of Bohemia (type specimen re-figured in Kvaček & Straková 1997: pl. 17, fig. 3). Brongniart (1828) recognized them for the first time as belonging to the modern genus. Later they have sometimes been referred to the proteaceous genus *Dryandra* (e.g. Ettingshausen 1851) which led Ettingshausen (1851, 1853) even to suggest floristic relationships of the European Tertiary floras to the extant flora of Australia. Further papers of Ettingshausen and Unger on the subject which we have not been able to get access to are cited in Kirchheimer (1937) and an extensive discussion of putative proteaceous fossils may be found in Schimper & Schenk (1890). In spite of the existing form genera which are discussed below, the *Comptonia*-like leaves have quite commonly been assigned to the modern genus over the last decades (e.g. Huzioka 1961, Christensen 1975, Rüffle 1976, Wilde 1989, Walther 1999).

FOSSIL HISTORY OF *COMPTONIA*-LIKE LEAVES

Comptonia-like fossil leaves are known from Europe (extensive overview in Rüffle 1976), North America (e.g. Berry 1906), and East Asia (including Japan) (e.g. Nathorst 1888, Endo & Morita 1932, Huzioka 1961, Matsuo 1965) with the oldest probably being of Upper Cretaceous age. They are a common element of many of the European Tertiary floras, but in most cases not occurring in noteworthy quantities. Accordingly, *Comptonia*-seeds have also been recorded (e.g. Dorofeev in Budantsev 1994, Mai & Walther 1978, 1991). The youngest unequivocal record in Europe is a leaf fragment from the Upper Pliocene of Willershausen (Lower Saxony, Germany) (Knobloch 1998). A Pliocene record is also existing for Japan (Huzioka 1961). Morphologically, all of the European material is quite similar. But more recently, cuticular data provided potential evidence for some diversity (Wilde 1989, Walther 1999).

The first *Comptonia*-like leaves of the German Middle Eocene have been described from the Geiseltal-area (Hofmann 1930, Beyn 1940, Rüffle 1976). Later, two fragments were described from Messel (Wilde 1989) and have been revisited for the present paper. The slightly younger maar filling of Eckfeld near Manderscheid (Eifel, Germany) is the source of numerous plant fossils (Wilde & Frankenhäuser 1998), including some *Comptonia*-like leaves which are described for the first time in the present paper.

MATERIAL AND METHODS

Most of the specimens described in the present paper were recovered from the filling of an upper Middle Eocene maar lake in the vicinity of Eckfeld near Manderscheid (Eifel, Germany) (Wilde & Frankenhäuser 1998). Two additional specimens from the lower Middle Eocene of Messel near Darmstadt (Hesse, Germany) (Wilde 1989) have been reinvestigated. The material from Eckfeld is housed in the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, the material from Messel in the Palaeobotanical Section of the Forschungsinstitut Senckenberg, Frankfurt am Main.

The material from both localities is preserved as compressions in organic-rich sediments ("oilshale"). They have been studied by applying epifluorescence (Friedrich & Schaarschmidt 1977, Wilde 1989) with minor success. For preparation of cuticles, tiny fragments of the organic material were removed from the compressions and subsequently oxidised by hydrogen peroxide (H₂O₂). Remaining organic material was afterwards dissolved in a diluted solution of potassium hydroxide (KOH). The isolated fragments of cuticles were finally picked up, rinsed in water and stained.

Leaves of the extant species *Comptonia peregrina* (Lam.) Coulter were taken for comparison from specimens growing in the Botanical Garden of the University of Mainz. These plants were originally received from the Garden of the Blue Ridge, Linville, N-Carolina, U.S.A. Abscised leaves of *Lyonothamnus floribundus* A. Gray subsp. *asplenifolius* were collected from a parking lot under a tree growing in front of the Santa Barbara Botanic Garden, California, U.S.A.

SYSTEMATIC DESCRIPTION

Comptonia L'Hér. ex Aiton

Remarks: Because we are exclusively dealing with leaves and leaf fragments it would appear most consequent to apply a form genus to the fossil material described in the present paper. The genus *Comptoniophyllum* Nathorst 1888 which was apparently never properly diagnosed and of which *Comptomyrca* Boyd 1998 is obviously a later synonym could be a nice suggestion. But recently Kvaček & Straková (1997) recalled the fact that the genus *Aspleniopteris* Sternberg 1825 is based on the type material of "*Asplenium difforme* Sternberg 1821". This would require to prioritize a systematically misleading name. For practical reasons we therefore decided to follow a combination with the extant genus, but to express our reservations by quotation marks.

"*Comptonia*" *diformis* (Sternberg 1825)

Berry 1906, emend.

Fig. 1, Pls 1, 2, 4, 5 figs a-f

Basionym: *Aspleniopteris difforme* Sternberg 1825

Holotype: National Museum Prague, No. G 2113 (compare Kvaček & Straková 1997: 63, pl. 17, fig. 3)

Type area: Bohemia (the exact locality is unclear; Kvaček & Straková 1997: 63)

Stratum typicum: Lower Miocene (obviously not known in more detail; Kvaček & Straková 1997: 63)

Material: PB 1996/94 LS, PB 1995/159 LS, PB 1993/84 LS, PB 1996/95 LS, PB 1995/363 LS, PB 1995/164 LS, PB 1995/167 LS, PB 1993/83 LS, PB 1995/162 LS, PB 1995/163 LS, PB 1995/161 LS, PB 1995/160 LS, SM.B ME 3048, SM.B ME 3661 (PB-numbers for specimens from Eckfeld in the collections of the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Mainz; SM.B ME-numbers for specimens from Messel in the collections of the Palaeobotanical Section of the Forschungsinstitut Senckenberg, Frankfurt am Main).

Emended diagnosis: More or less asymmetrically lobed leaves, elliptical to lanceolate in shape; dissection between individual lobes not consistently complete. Shape of the lobes triangular to rounded or elongate, frequently asymmetric with a more or less straight apical side and a decurrent basal side; distal margin rounded to pointed, toothed or almost serrate. Lobes progressively fusing and decreasing in size towards tip and base of the leaves. Few (in most cases two) more or less well defined secondaries per lobe, leaving the midvein at an angle approximately between 60° and 90°. Secondaries curving upwards until reaching the margin or running into teeth, sometimes branched.

Nomenclatural remarks: Some nomenclatural confusion was caused by the fact that the specific epithet originally used by Sternberg (1821) is illegitimate because it is a later homonym of *Asplenium difforme* R. Br. (Vassiljev & Zhilin 1968). But as pointed out recently by Kvaček & Straková (1997), "*diformis*" as used by Sternberg (1825) has priority and is available. The combination of Sternberg's (1825) epithet with *Comptonia* was obviously for the first time used by Berry (1906; see Kotlaba 1961).

Description of the material: Leaves narrow, all specimens incompletely preserved (Fig. 1, Pl. 1), maximum length of individual fragments 55 mm, width 3–10 mm; midvein strong, rhachis-like; individual leaves deeply lobed, but dissection rarely reaching the midvein. Individual lobes pinnule-like, sometimes of comparable length on both sides of the midvein, sometimes of quite irregular length, length along the midvein 5–10 mm, extension from the midvein 1.5–5 mm, in most cases asymmetrically arranged and only rarely opposite to each other. Proximal margin of the lobes curving upward from the dissections, sometimes directly towards a distal tip (Pl. 1, figs b, c, l) sometimes grading into a distinct lateral margin which may be ornamented by one to several irregular teeth (Pl. 1, figs d, h, k, m), sometimes even approaching an irregular serrate condition (Pl. 1, figs e, f, i). Tips of the lobes and teeth straight to acuminate, sometimes distinctly pointed. Distal margin of the lobes

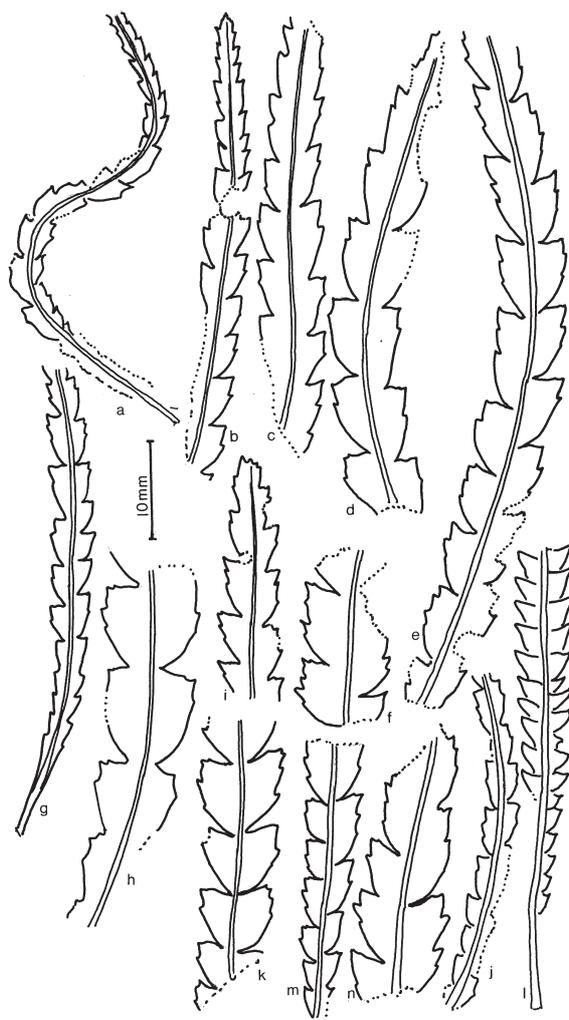


Fig. 1. Outline drawings showing morphologic variability in all of the “*Comptonia*” *difformis* leaves and leaf fragments hitherto recovered from the Middle Eocene of Eckfeld (PB) and Messel (SM.B ME) (for respective photographs see Pl. 1, figs a, g, h, k and l have been composed from part and counterpart of the specimens). Scale 10 mm. a: PB 1996/94 LS; b: PB 1995/159 LS; c: PB 1993/84 LS; d: PB 1996/95 LS; e: PB 1995/363 LS; f: PB 1995/164 LS; g: PB 1995/167 LS; h: PB 1993/83 LS; i: PB 1995/162 LS; j: PB 1995/163 LS; k: PB 1995/161 LS; l: PB 1995/160 LS; m: SM.B ME 3048; n: SM.B ME 3661

straight to slightly oblique or slightly curved in an upward direction, rarely slightly curved downwards, sometimes showing a minor tooth near the tip of the lobe (Pl. 2, figs e-h). Lobes progressively fusing and decreasing in size towards tip and base of the leaves (Pl. 1, figs b, c, l, m).

Two or few weak secondaries per lobe leaving the midvein at an angle approximately between 60° and 90°. Course of the secondaries more or less irregular, curving upwards towards the tip of the lobe or one of its major teeth (Pl. 2, figs f, i). If the margin is irregularly serrate, secondaries may be branched or forked irregularly with individual branches running into subordinate teeth (Pl. 2, fig. i). Sometimes subordinate intersecondaries may be

distinguished. Tertiary veins forming a coarse irregular network between the secondaries, including a dense network of higher order venation (Pl. 2, fig. h).

Cuticles on both sides of the leaves weak, fragile, surface appearing granular (Pl. 4, figs a, d; Pl. 5, fig. f). Cuticles of the upper leaf surface showing slightly undulate cell walls (Pl. 4, figs a, d), becoming stronger and more rounded in a deeper focus (Pl. 4, figs b, c). Trichome bases frequent (ca. 15 µm in diameter), typically slightly raised and divided by four transverse walls (Pl. 4, figs d, e) (rarely only by one), sometimes surrounded by about 5 slightly modified but radially arranged cells (Pl. 5, fig. c), sometimes by a ring of about 10 minor cells (Pl. 4, fig. c). Trichomes (observed only by applying epifluorescence; Pl. 4, fig. f) inflated, balloon-like, ?multicellular. Cuticles of the lower leaf surface showing slightly to markedly undulate cell walls (Pl. 4, fig. g, Pl. 5, figs b, e, f). Size of the regular cells on both sides of the leaves ca. 20 × 25 µm. Trichome bases rare. Stomatal complexes comparatively large, broadly oval to circular (length ca. 30µm, width ca. 25 µm), anomocytic (Pl. 4, figs g, h; Pl. 5, figs c, d, e, f).

DISCUSSION

Such kind of lobed leaves today are restricted to the monotypic genus *Comptonia* (Myricaceae) and some genera of the Proteaceae like *Banksia* (figured by e.g. Matsuo 1965, George 1984), *Dryandra* (figured by e.g. Ettingshausen 1851, 1861, Matsuo 1965). Compound leaves with similarly lobed leaflets are found in *Lyonothamnus*, a monotypic genus of the Rosaceae which is today endemic to the Channel Islands of California (Odion 1992). Within the only species of the genus they are even restricted to one of the two subspecies (*L. floribundus* A. Gray subsp. *asplenifolius*).

Two of the leaf remains from Eckfeld (Fig. g, l; Pl. 1 fig. g) are showing proximal (“basal”) petiole-like segments. This is clearly indicating that we are dealing with fragments of leaves and not of leaflets (compare leaflets of *Lyonothamnus* on Pl. 3, fig. f). Furthermore, our lobed leaves and leaf fragments are obviously related to the extant species of *Comptonia* because of only few more or less weakly developed secondary veins per lobe and an irregular higher order venation (Pl. 2, figs f-i; compare to extant material figured by Berry 1906, Christensen 1975, and on Pl. 3, figs a-e). The secondaries curve upward until they reach the margin (Pl. 2, figs. h, i; compare to extant material figured on Pl. 3, figs. b-e). *Dryandra* (compare e.g. leaves figured by Ettingshausen 1861) and *Lyonothamnus* (Pl. 3, fig. g) in contrast have a number of straight secondaries per lobe which are running more or less perpendicular to the midvein and loose their identity

before reaching the margin. As mentioned by Boyd (1998), the dissection between the lobes is consistently complete in *Lyonothamnus* (Pl. 3, figs. f, g) which is in contrast to extant *Comptonia* and our fossil material where the dissection is not consistently complete. An almost complete dissection between the lobes of the leaves is obviously also existing in the respective extant species of *Banksia* and *Dryandra* (Proteaceae; compare figured leaves in Ettingshausen 1851, 1861, Matsuo 1965, George 1984).

Convincing additional evidence for an assignment of our material to the myricaceous *Comptonia*-alliance is presented by cuticular structures. Both, our extant material of *Comptonia peregrina* (Lam.) Coulter and our fossil leaves share a characteristic type of trichome bases consisting of four cells on the upper and lower surface of the leaves (Pl. 5, fig. h, and Pl. 4, figs g, h; Pl. 5, figs a-f, respectively). In both, the trichomes themselves are inflated balloon-like (Pl. 5, fig. h and Pl. 4, fig. f, respectively). Another shared character of the extant material and the fossil leaves are undulating cell walls of the epidermis mirrored in both, adaxial and abaxial cuticles. Furthermore, broadly oval to circular anomocytic stomata have been observed in the abaxial cuticles of the extant and the fossil material (Pl. 5, fig. g and Pl. 4, figs. g, h; Pl. 5, figs. a-f, respectively; Wilde 1989).

For extant and fossil *Comptonia*, Ruffle (1976) mentioned papillae overarching the stomata from the neighbouring cells, but such structures have neither been observed by us or figured in any paper known to us.

The only extant species of *Comptonia* is characterized by rounded to slightly pointed lobes which are only rarely dissected at the margin (Pl. 3, figs a-e). The shape of the individual lobes in our fossils is varying between rounded (Pl. 1, figs d, h, k) and more triangular (Pl. 1, figs b, c, l). In most of them the margin of the lobes is ornamented by distinct teeth (Pl. 2, figs c-f) or even almost serrate (Pl. 2, figs g, i) whereas rounded to only slightly pointed lobes are the exception (Pl. 1, figs g, k). In the Geiseltal-material, there is a slight tendency for elongated lobes (Ruffle 1976: Pl. 54, figs 1–12) which have hitherto not been observed in Eckfeld or Messel. But, a comparable suite of leaves including narrow ones and such with elongated lobes was described e.g. from the upper Palaeogene of Kazakhstan (Akhmetiev 1991, Zhilin 1991). Considerable variation in the fossil material from Japan was discussed by Matsuo (1965).

Cuticular structures of leaves which were assigned to *Comptonia* have been described only from few localities. The material previously described from the Geiseltal-area is obviously showing rounded but not undulating cell walls on both sides of the leaves (Hofmann 1930, Beyn 1940, Ruffle 1976). Later, a single fragment of a *Comptonia*-like leaf was collected 1991 by one of us (V.

W.) in one of the last active pits in the Geiseltal-area near Krumpa. When studied by epifluorescence it is clearly showing the typical anomocytic stomata but undulating cell walls on the abaxial cuticle. In the leaves described from the Miocene of Denmark (Christensen 1975) an undulating pattern of the cell walls is restricted to the abaxial cuticle. The diversity of cuticular structures led Wilde (1989) to argue in favor of distinct species which are not reflected in the morphology of the leaves (Walther 1999: 116).

Following previous descriptions, personal observations and figured extant material, there is considerable variability within the leaves of the extant species *Comptonia peregrina*. The variability in shape and gross venation as documented most completely by Berry (1906) is even including almost all of the variability that has hitherto been observed in the fossil material across the Northern Hemisphere starting from the Cretaceous! But for more sophisticated comparisons and ecological considerations of the extensive fossil material there is still some need for a more detailed study of the variability of morphological characters across the present distribution of the extant species. Epidermal patterns should also be studied extensively within the extant species before proper delimitation of species will be possible for the fossil material described and discussed in the present paper. For example, four-celled trichome bases and a ring of minor cells surrounding trichome bases have hitherto not been recorded from the extant species (e.g. Chourey 1974, Christensen 1975). Our material is therefore tentatively assigned to the broadly defined fossil species "*Comptonia*" *difformis*.

PALAEOECOLOGY

The single extant species of *Comptonia* is geographically and ecologically quite restricted in distribution. Forming even a dominant component of the so-called *Comptonia*-dwarf shrub heath, it is exclusively growing on poor acidic soils in eastern and central North America (Knapp 1965, Morin 1997). In contrast, *Comptonia*-like fossil leaves are known from the Northern Hemisphere starting in the Cretaceous (e.g. Berry 1906, Ruffle 1976, Knobloch 1998) and throughout the Tertiary (e.g. Berry 1906, Ruffle 1976) including Pliocene records in Germany and Japan (Matsuo 1965, Knobloch 1998). Provided that most of the respective fossil material is indeed related to extant *Comptonia*, the genus was widely distributed across the Northern Hemisphere even until the Pliocene (Mai 1995). There is some contradictory debate about the climatic and ecologic requirements of the fossil plants related to extant *Comptonia*. Some of the authors prefer an actualistic interpretation as indicating poor and/or dry habitats (e.g. Ruffle 1976, Hably & Fernandez-Marron 1998). But we are following the opin-

ion summarized by Mai & Walther (1978) that the present distribution of the single “surviving” species is relic-tual and should therefore not be used in palaeoecological and palaeoclimatic interpretations of the respective floras (Walther 1999). In spite of the fact that the extant species is a deciduous plant of more temperate areas, closely related plants were common even in paratropical floras of the Central European Middle Eocene like Messel, Eckfeld and the Geiseltal-area. The Oligo-/Miocene record in Europe for example is stretching from Iceland in the North (Friedrich 1968) to the Mediterranean area in the South (e.g. Palamarev & Petkova 1987, Hably & Fernandez-Marron 1998). The pre-Quaternary *Comptonia*-alliance was by no means restricted to or more common in floras possibly indicating more dry conditions but is even well known from peat(=coal)-forming environments like e.g. the Middle Eocene of the Geiseltal-area (Rüffle 1976) and the Miocene of FASTERHOLT (Denmark; Christensen 1975). As a consequence fossils related to extant *Comptonia* may serve as a good example where any actualistic interpretation could be misleading!

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PLATES

Plate 1

Complete set of "*Comptonia*" *difformis* leaves and leaf fragments hitherto recovered from the Middle Eocene of Eckfeld (PB) and Messel (SMB.ME). Scale 10 mm

a: PB 1996/94 LS (part and counterpart); b: PB 1995/159 LS; c: PB 1993/84 LS; d: PB 1996/95 LS; e: PB 1995/363 LS; f: PB 1995/164 LS; g: PB 1995/167 LS (figure composed of part and counterpart); h: PB 1993/83 LS (part and counterpart); i: PB 1995/162 LS; j: PB 1995/163 LS; k: PB 1995/161 LS (part and counterpart); l: PB 1995/160 LS (part and counterpart); m: SM.B ME 3048; n: SM.B ME 3661

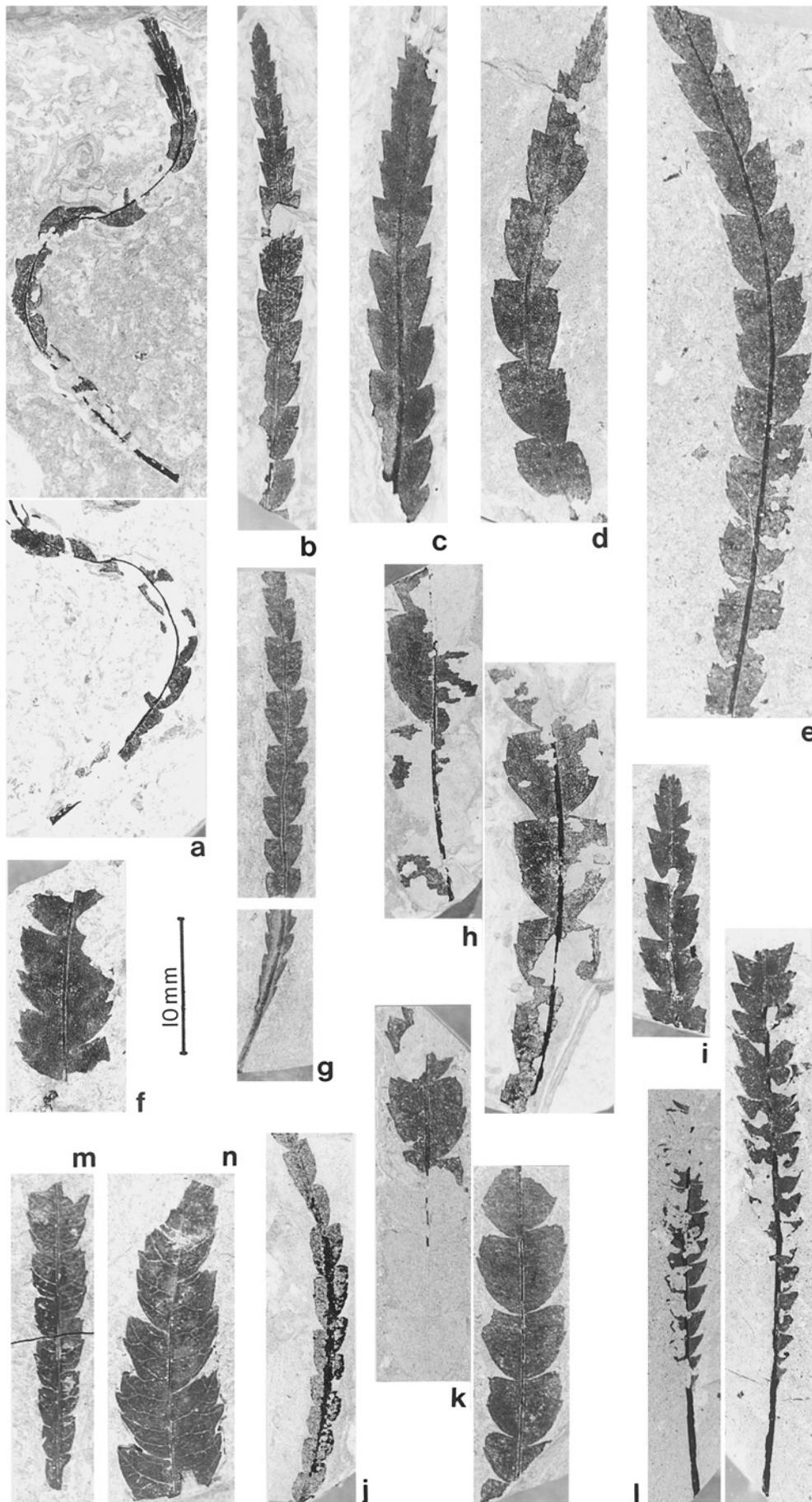


Plate 2

Details of "*Comptonia*" *difformis* leaves and leaf fragments from the Middle Eocene of Eckfeld (PB) and Messel (SM.B ME) as shown on Pl. 1; scale 1 mm

a: leaf tip, PB 1995/159 LS; b-g: range of shape and ornamentation of individual lobes (b: PB 1995/159 LS; c: PB 1993/84 LS; d: PB 1995/363 LS; e: PB 1995/161 LS; f: PB 1993/83 LS; g: PB 1995/164 LS); h and i: details of venation (h: PB 1993/83 LS; i: SM.B ME 3661)

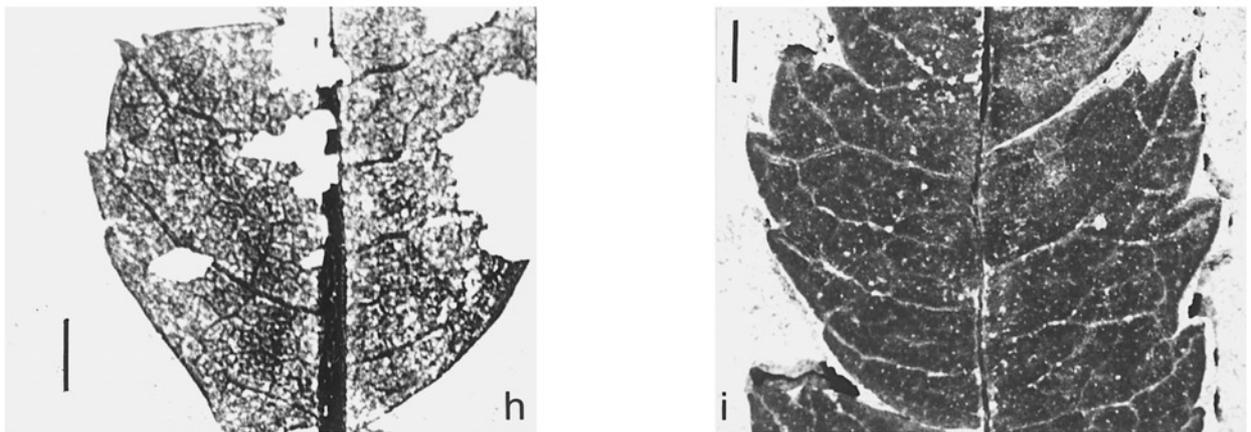
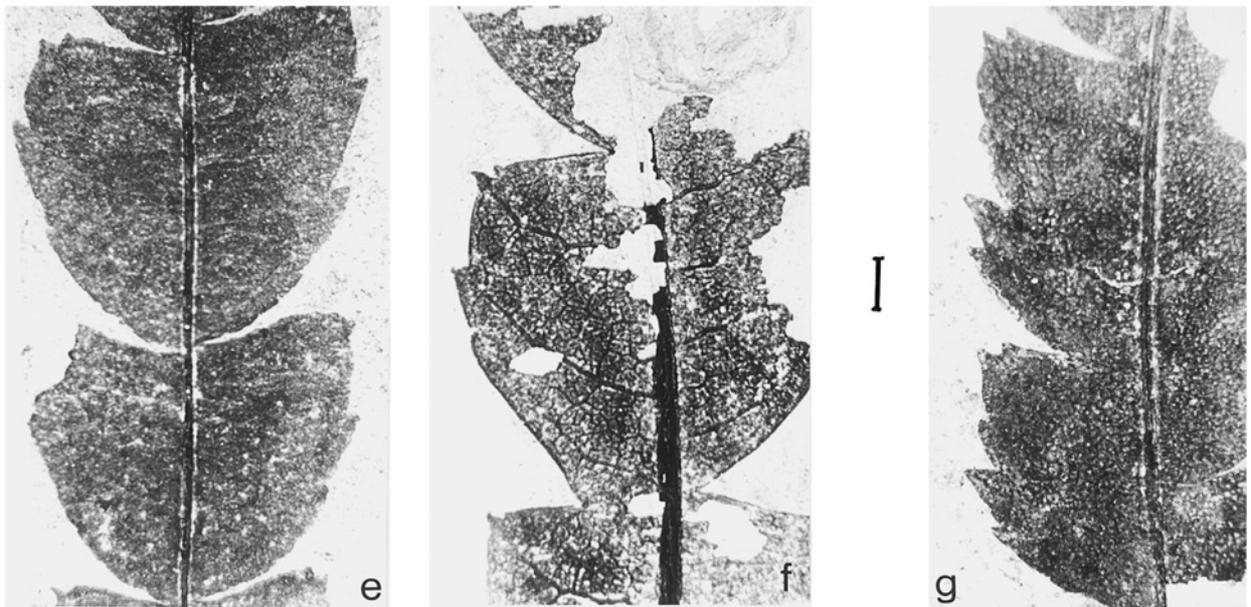
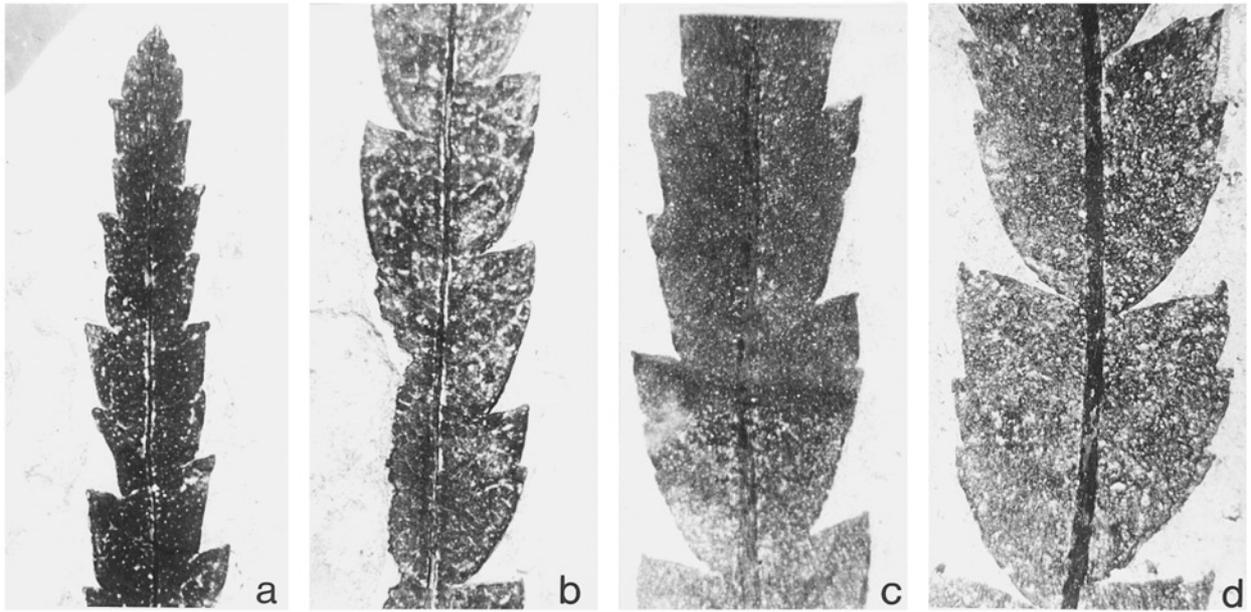


Plate 3

Extant material for comparison

a: Twigs with leaves and individual leaves of *Comptonia peregrina* (Lam.) Coulter from plants cultivated in the Botanical Garden of the University of Mainz, scale 10 mm

b-e: Details of *C. peregrina* leaves from fig. a (b and c: slightly pointed rounded lobes, $\times 5$ (b: adaxial view showing secondaries and irregular higher order venation; c: abaxial view showing secondaries more clearly); d: lobes with irregular margin, adaxial view, $\times 5$; e: rounded lobes, one of them with a "sublobe", $\times 5$)

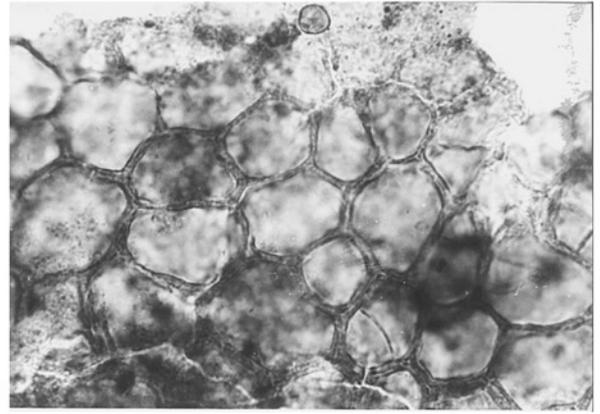
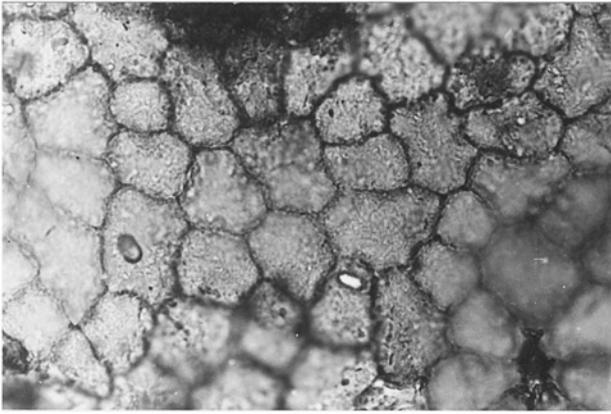
f and g: *Lyonothamnus floribundus* A. Gray subsp. *asplenifolius* (Rosaceae), abscised leaf collected from a parking lot under a tree growing in front of the Santa Barbara Botanical Garden, Santa Barbara, California, U. S. A. (f: almost complete leaf in adaxial view, scale 10 mm; g: detail of a leaflet from f in adaxial view, scale 5 mm)



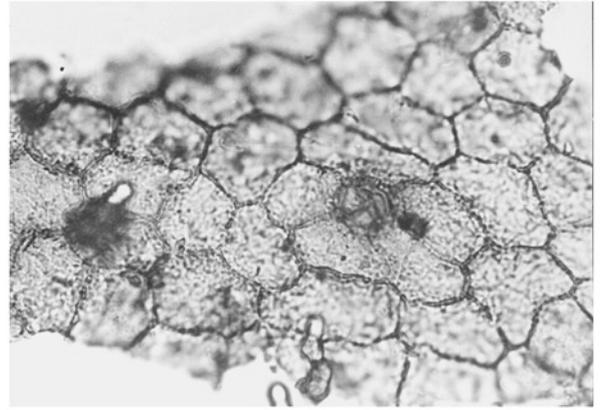
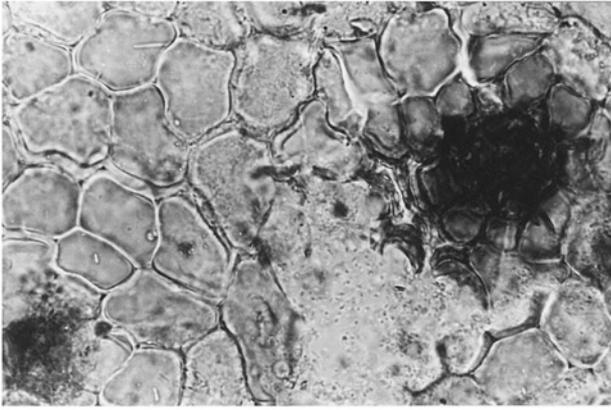
Plate 4

Cuticular structures of "*Comptonia*" *difformis* leaves from the Middle Eocene of Eckfeld (a, c, d, e and h: PB 1995/161 LS; b and g: PB 1996/94 LS; f: PB 1995/163 LS)

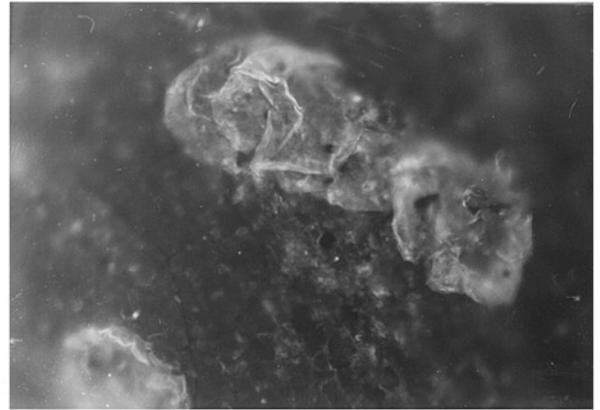
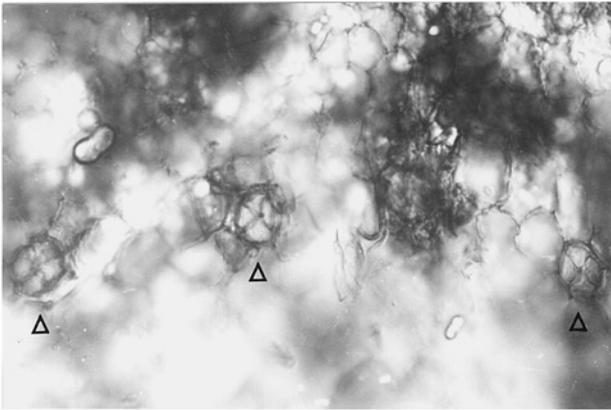
a and b: adaxial cuticle in upper (a) and lower (b) focus, $\times 530$; c-e adaxial cuticle with trichome bases, $\times 530$ (c: lower focus showing dark trichome base surrounded by minor cells; d: upper focus showing four-celled trichome base surrounded by more or less normal cells; e: three four-celled trichome bases in focus, marked by arrows); f: inflated balloon-like trichomes, epi-fluorescence, $\times 350$; g and h: abaxial cuticle showing stomata (arrows), $\times 530$



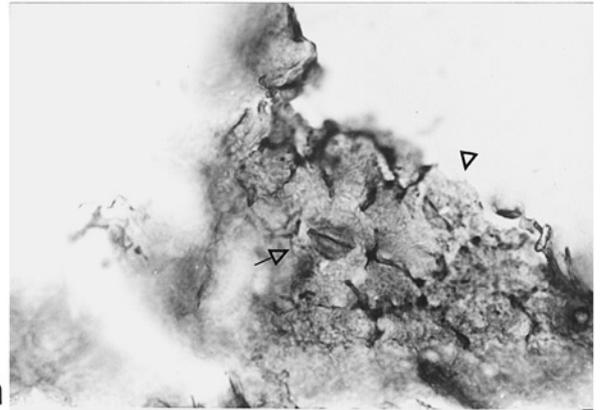
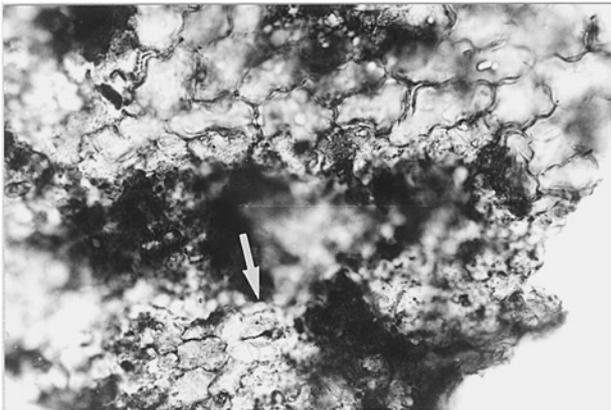
a b



c d



e f



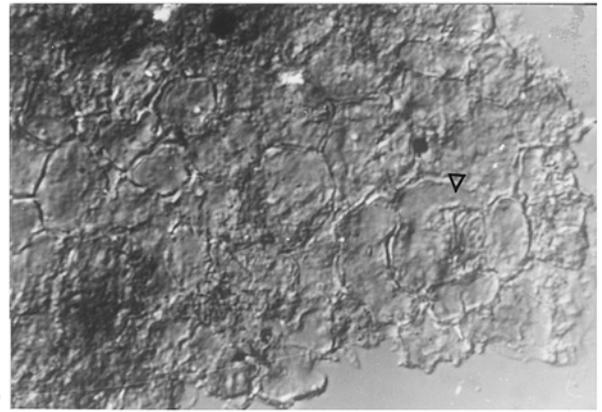
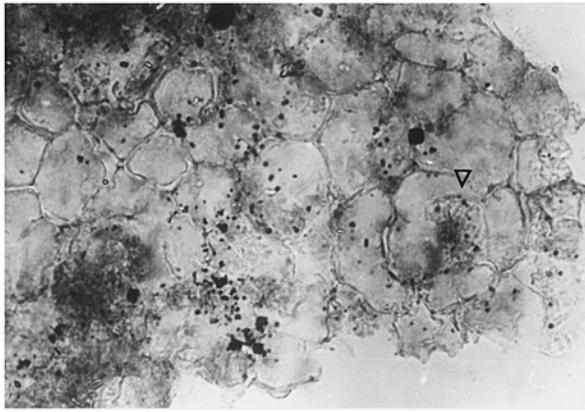
g h

Plate 5

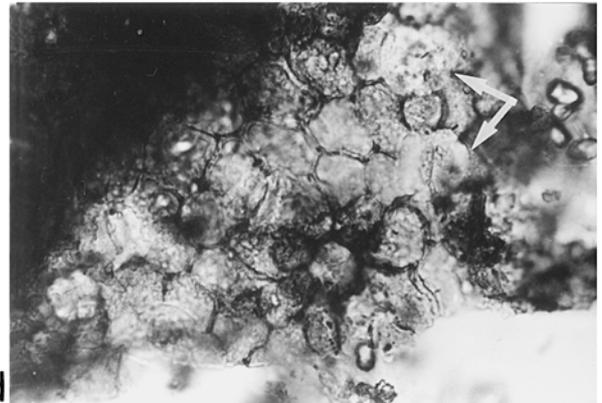
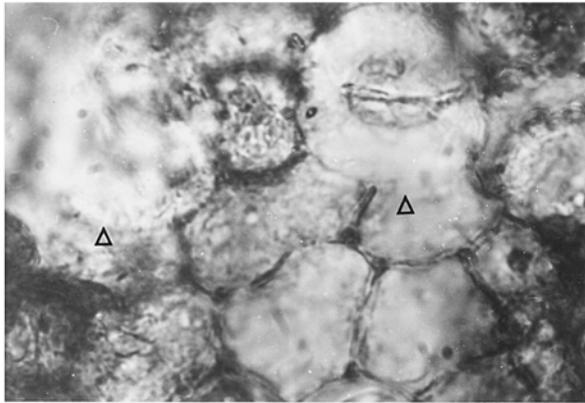
Cuticular structures of “*Comptonia*” *difformis* leaves from the Middle Eocene of Eckfeld (PB) and Messel (SM.B ME) (a-f) and of extant *Comptonia peregrina* (Lam.) Coulter growing in the Botanical Garden of the University of Mainz (g and h)

a and b: abaxial cuticle of PB 1995/161 LS ($\times 530$) with stomatal apparatus (arrow) in ordinary transmitted light (a) and interference contrast (b); c: detail of abaxial cuticle with two stomatal apparatuses, PB 1996/94 LS, $\times 1300$; abaxial cuticle with two stomatal apparatuses, PB 1996/94 LS, $\times 530$; e and f: abaxial cuticle of SM.B ME 3661 with four stomatal apparatuses (arrows) in ordinary transmitted light (e) and interference contrast (f), $\times 530$

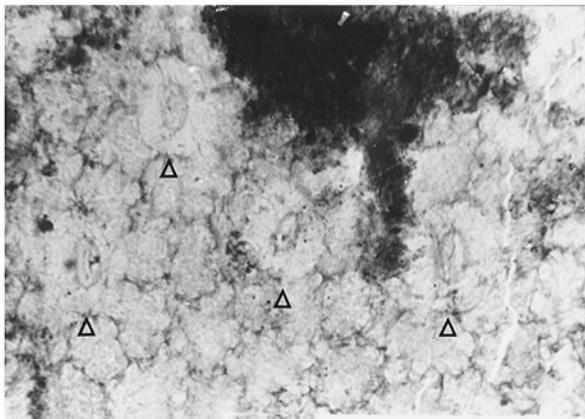
g: abaxial cuticle of extant *Comptonia peregrina* (Lam.) Coulter with several stomatal apparatuses, $\times 530$; h: adaxial cuticle of *C. peregrina* with four-celled trichome base surrounded by minor cells (inlet showing inflated balloon-like trichome), $\times 530$



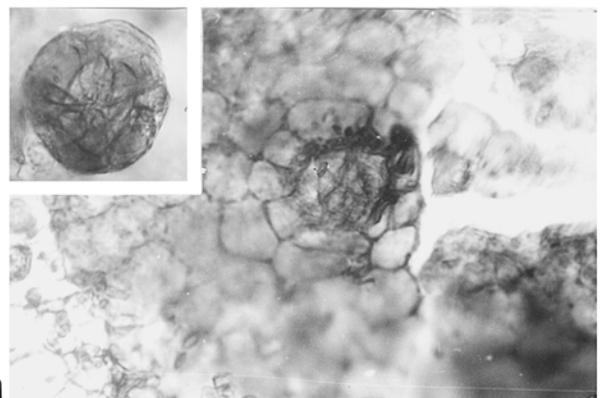
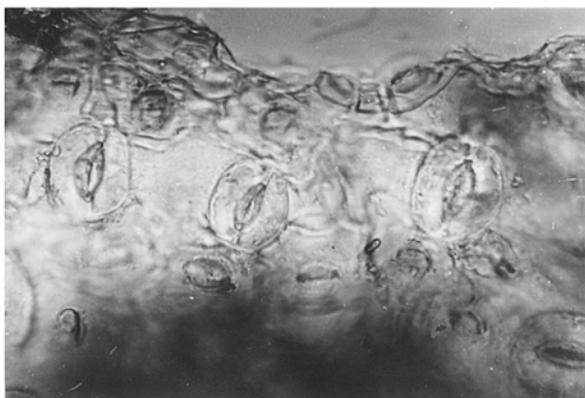
a b



c d



e f



g h