LIVING AND FOSSIL SPECIES OF COMPTONIA

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INTRODUCTION

WHEN we find a genus which is monotypic in the existing flora, or one which contains but two or three geographically remote species, we may rest assured that the genus in question had an interesting geological history, and that its living representatives are relicts of a day when the genus was widespread and dominant. Notable examples, such as Liriodendron, Sequoia, and Nelumbo, may be cited. Comptonia is no exception to this rule. The single living species is confined to eastern North America, ranging as a low shrub from Nova Scotia to Manitoba and southward to North Carolina, Indiana, and Tennessee, while the number of ancient forms that have been described, is upwards of three score and amply proves the cosmopolitan character of the genus during the Tertiary period.

Recent paleobotanists refer them as a subgenus to Myrica, as is done in case of the living species by Engler (*Natürlichen Pflanzenfamilien*, vol. 2, pt. 1, p. 28, 1889). Modern usage in this country, however, gives Comptonia generic rank, quite rightly so it seems to me.

The space of a generation has passed since Schimper's classic *Traité de Paléontologie Végétale* sought to unify paleobotany, and the chaos of described species is even greater to-day than it was previous to 1870. Paleobotany is surely far enough advanced, it seems to me, for a more philosophical treatment, and while this little essay makes no pretension at embodying such a treatment, it is hoped that it will furnish the material that will be useful for that purpose when the proper time arrives.

It is obvious enough to most botanists that existing species vary in their leaf characters through very wide limits. I have had considerable to say about the leaf variation, atavistic and otherwise,

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of Liriodendron and Sassafras, and the same variability is true of that most interesting relic of bygone days, the Ginkgo; while numerous instances of similar variations in other genera could be cited. For a number of years I have been engaged in collecting leaf specimens to illustrate this variability in a number of genera, and I find this task to be a never-ending source of interest in addition to the invaluable data which it furnishes for the understanding of earlier floras.

If it be objected that the consideration of geographically widely removed forms as identical leads only to confusion, the answer is — a consideration of the variability in the living Comptonia, the unmistakable proof in its present and past distribution of its wide range, coupled with the tendency to call a certain form by a certain name because it is like a form perhaps wrongly named by Brongniart or Heer or Lesquereux, without a very serious consideration of the generic affinities, in fact it can scarcely be said that we have any generic limits in a host of Mesozoic and Neozoic genera; all these tend to discredit specific distinction based on geographical remoteness.

These considerations lead me to think that the present is not an inopportune time for an attempt to work out the relations of such forms as may be referred to Comptonia, and to see if even a little light cannot be shed on their history. And at the same time to reduce the number of species (so called), often based as they are upon irrecognizable fragments. Surely several score of species, some entirely inadequate, leave room for more confusion than slight errors in the opposite direction. The forms here considered as identical all show such slight variations as would not be considered for a moment were we dealing with leaves in the existing flora.

The Succession of Forms

Comptonia branched from the Myrica stock, most probably during the lower Cretaceous. Its original home was in all probability in the greatly extended lands of the semitropical or warm temperate Arctic region, although the earliest known speciNo. 475]

men from that region is from the Cenomanian of Greenland (Atane beds). One of the first floral migrations southward during the Mesozoic was along the Atlantic coastal plain, which at that time was possibly continuous along the northeastern coast of America from Greenland south. Traces of this ancient coastal plain are said to have been found off the present New England coast, and the difficulties of accounting for the remarkable similarities in the Cretaceous flora of Greenland and that of the Atlantic coastal plain seem insurmountable unless we predicate some sort of a direct land connection, so that floral distribution tends to furnish support to Suess's theory as to the origin of the Atlantic ocean.

The Myricas were a prominent element in this Mesozoic migration, a single species being recorded from the lowermost Cretaceous of Virginia. In strata of approximately Albian age (Raritan, etc.) there are ten species of Myrica, and at this time occurs the earliest known Comptonia, in the Raritan of New Jersey.

The resemblance of this and other primitive Comptonia leaves to those juvenile and atavistic leaves of the modern species is discussed in a later portion of this paper.

That Comptonia is derived from Myrica, aside from the morphological and other evidence furnished by a study of existing species, seems probable (1) from the fact that it originated among an abundant display of Myrica species some of which preceded it in time, (2) from its progressive increase in the number of species and in their ever widening distribution up to the close of the Miocene, paralleling a like history for the genus Myrica, (3) the numerous leaf remains that have been found intermediate in character between Myrica and Comptonia, (4) the resemblance to Myrica of the oldest Comptonias and of the leaves of modern seedlings.

As an example of the variation in Myrica leaves and their tendency to approach the Comptonia form, I may cite $Myrica \ lignitum$ Unger, an undoubted Myrica, abundant in the Oligocene and Miocene of Europe. Ettingshausen and Standfest¹ in their study of the abundant remains of these leaves from the late Tertiary of

¹Ettingshausen und Standfest. "Ueber Myrica lignitum Ung., und ihre Beziehungen zu den lebenden Myrica Arten." Denkschr. math.-natur. Akad. Wiss. Wien, vol. 54, pp. 1–8, pls. 1, 2, 1888. Styria, recognize thirty varieties of which several are very close to Comptonia, in fact were it not for the closely related intermediate forms as well as the characteristic Myrica fruit, we would be justified in considering them as referable to Comptonia.

Contemporaneous with the southward advance of Comptonia in eastern North America, we find a like advance through northern Europe via the then extended Scandinavian peninsula, recorded by a primitive species of Comptonia (antiqua Nilss.) from the greensand of Köpinge, Sweden, followed by the appearance of the same species in Transylvania (Cenomanian). This species is very close to its American and Arctic congeners, so similar that one cannot but see in these leaves the strongest sort of an argument for a common ancestry, a theory which receives additional strength, not only from the form of the juvenile leaves of the existing species, but also from the fact that there is nothing in our present knowledge of floral distribution in past time or of the disposition of the land masses of the northern hemisphere during the Mesozoic that does other than add support to such a theory.

Some authors (e. g., Hosius and von der Marck) would include Dryandra cretacea of Velenovsky from the Cenomanian of Bohemia in this genus. While it is true that the form and venation of the leaves is the same as that characterizing the leaves of certain Miocene species of Comptonia, and that with the aid of mutation (as used by deVries, not Osborn) there would be no difficulty in deriving this species from the contemporaneous Myrica stock, especially when we note that we have no evidence that in habit and structure it differed from the contemporaneous Myricas, the only difference about which we know anything is the difference in leaf-form, and the evolution of leaf-form is a comparatively simple affair. Still I think that the inordinate length of these specialized leaves, combined with the character of the marginal serrations, together with their geological position, renders it probable that Dryandra. is a more reasonable index of their real botanical relations. I certainly do not feel that the evidence is sufficient for making the change in generic affinity suggested.

The upper Cretaceous history of Comptonia is a blank in so far as America is concerned. In Europe, however, we find a characteristic Comptonia (*tenera* Hos. & v. d. Marck) in the Senonian of Westphalia. This species shows a considerable progression from the earlier Cretaceous form, and clearly foreshadows the later type of leaf, so abundant in the Tertiary floras, and which is not very different from the typical modern leaf.

With the ushering in of the Eocene, we find this type of leaf continued in considerable abundance and showing more or less variability in the direction of other species. The European records of this age are far superior to those of America; while the Arctic region unfortunately has thus far furnished no evidence (except for the single leaf which I have referred to *Comptonia microphylla* and whose age is doubtful).

The Atlantic coastal plain, where we would expect to have found a most interesting group of species, had the records only been preserved, fails us entirely, as no leaf beds have been found in their marine formations. Western America it is true furnishes us with Eocene Comptonias, but these are relics of an independent line of migration from the Arctic region during which three species occurred in Alaska. These either represent the genus *en route* for Asia, or are stragglers which were left behind during the Asiatic advance. The Green River beds, besides some fragmentary remains, furnish us with a beautiful species, which we picture as a prominent element in the flora that clothed the site of the present Rocky Mountain region.

Asia has thus far failed to show Comptonias in strata earlier than the Miocene, due no doubt to our lack of knowledge of earlier Tertiary formations and floras in that region. As previously mentioned it is in Europe that we find the most satisfactory evidence of Comptonia development.

Beginning with the same type of leaf as that of the Senonian *tenera*, which is common during the Eocene as *Comptonia schrankii*, and which becomes widespread, we find various lines of variation leading to the closely related and equally abundant *Comptonia diforme*, and to the less common forms which I have shown in the genealogical diagram.

We find at this time the modern type of leaf and the same variations from this type, i. e., small leaves, large leaves, leaves with acute lobes, and leaves with obtuse or rounded lobes; in all, some twelve forms which appear to be valid species. The next period, the Oligocene, shows a considerable broadening out in their development and distribution. From the vindobonensis type we get, by a series of slight gradations, Comptonia aningensis, and by equally slight steps this type gives rise to that most beautiful species, Comptonia laciniata with its large leaves and serrated lobes. This form is strongly suggested in the leaves of the modern species. The small-leaved types of schrankii and diforme continue through this period, and near them we have the large and handsome form, Comptonia dryandroides, so like the modern leaf, besides two or three other species of more doubtful value — in all twelve species.

It is in the next period, however, the Miocene, that the genus reaches its acme of development. Numerous leaf remains, often beautifully preserved, are present at nearly every locality where plant beds of this age have been opened, from Greece and Bohemia to France and the Baltic. We find a continuation and further development of all of the Oligocene types, the small *schrankii* with both rounded and acute lobes, the somewhat larger and rather acute-lobed *diforme*, the obtuse-lobed *aningensis* and *vindobonensis*, and the related large-leaved *laciniata* and *dryandroides*, besides numerous other forms, including the gigantic grandifolia.

We find laciniata getting over into Asia Minor from southeastern Europe. Eastern Asia (Japan) furnishes two good species which are identical with European forms. Northwestern America furnishes two additional forms also identical with European forms, one of them being the same as one of the forms from Japan. Whether we have in these occurrences the evidence of an interchange of species between the continental regions or independent lines of southward migration from the Arctic region is not positively determinable. I incline to the latter assumption, however, which is supported by the evidence of dryandroides (cuspidata of Daws.) from western Canada which is identical with naumanni Nath. from Japan, both in turn identical with the leaves which occur in southeastern Europe from this and earlier horizons. It would seem that the Japanese and Canadian leaves had both traveled southward along the foothills bordering the valleys, which in their general trend run north and south, rather than that they came overland from Europe to Asia then across Behring Straits

and down the western American coast or *vice versa*. In all, we have during the Miocene, forms which may be divided up into nine "good species."

With the refrigeration of Pliocene and Pleistocene climates in temperate latitudes, and the resulting wholesale extinction and redistribution of species, we see Comptonia exterminated from all except American soil. The story is apparently the same for numerous other genera which are exclusively American in the existing flora; the Mediterranean Sea in Europe and the high altitudes of southern Asia apparently cutting off their retreat before the advancing ice sheet.

Comptonia is a hardy shrub at the present time and thrives in almost any habitat, possibly as the result of its struggles with severe conditions during the Glacial period.

VENATION

In spite of the considerable variation in leaf-form shown by the leaves of Comptonia peregrina (Linn.) Coulter, the venation is monotonously uniform. In a general way it may be characterized as follows: there are two or three secondaries in each lobe, generally two in the smaller lobed forms and three in the larger, although those with two seem to be the commoner irrespective of size. They all branch from the midrib at a wide angle, often 90 degrees, and describe a slight upward curve, which is greater in the lobes toward the tip of the leaf. The uppermost secondary in each lobe usually runs directly to the tip of the lobe when the latter is pointed, or directly to the margin in those leaves with rounded lobes, its position on the margin being indicated by a slight mucronate point. The one or two secondaries below the upper are inserted at equal distances apart and become somewhat more curved as they proceed outward, curving upward to join a short downwardly directed lateral branch from the secondary next above. The tertiary venation in the border region is festooned along the margin of the leaf, being particularly noticeable along the lower margins of the lobes. Where the lobes have a somewhat serrated margin or are divided somewhat similarly to those of

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the fossil species Comptonia laciniata, this arching of the veins along the border is more or less interfered with, and a branch from the nearest secondary proceeds to the tip of the tooth. Where the lobes are not separated to the midrib there is usually a vein of the same caliber as the secondaries which proceeds directly to the sinus between the lobes, where it forks and its two branches arch along the borders of the adjacent lobes on each side (above and below). The finer areolation shows three-, four-, or five-sided reticulations. On the whole the venation cannot be said to show any especially characteristic and distinctive features. The usual style of leaf is finely figured by Schimper in his *Traité de Paléontologie Végétale*, Plate 84, Fig. 4 (1874), which is copied from a figure of Ettingshausen, in his *Blattskelette der A petale*.

Reverted Form of Seedling Leaves

In discussing *Comptonia microphylla* I have mentioned the curiously shaped leaves of the seedlings of the existing species, the first six or seven of which are indistinguishable from those of the earliest Comptonias from the Mid-Cretaceous, and which are evidently true reversions. Some of these are well shown on Plate 3. I have collected numerous examples of these leaves and believe this form to be a constant feature of the seedling leaves, furnishing admirable proof of the correct identification of their Cretaceous ancestors.

As might be expected, the various fossil species of Comptonia probably had leaves on their seedlings which were similar to this form. Seedling plants, as can be readily understood, are rare as fossils. I am convinced, however, that the leaves which Heer¹ refers to *Myrica latiloba* from the Miocene of Locle and Oeningen are to be so understood. Their form and venation are exactly that of the modern seedling leaves and they have the same thin texture and thickened midrib. Lesquereux's Fig. 12 of *Myrica alkalina* from the Green River group of Wyoming is also a young leaf, probably of *Comptonia insignis* (Lx.) Berry.

¹ Heer. Fl. Tert. Helv., vol. 3, p. 176, pl. 150, fig. 12-15, 1859.

STIPULES

The stipules on the modern plant are large, ordinarily of an odd, three-lobed form, the upper lobe being produced into a horn which runs close to the petiole. These stipules are pronounced in seedlings and spring shoots, no doubt serving as a protection from the cold. They become, however, much reduced in size and abbreviated in form on the later shoots. They are also very variable, some of the extreme forms being shown on Pl. 1, Figs. 8–12, Figs. 11 and 12 being the more typical. As in Liriodendron, they are probably descended from the basal lobes of the leaves of their ancestors, for we find basal lobes in the modern plant which approximate the stipular form and which are entirely separated from the lobes next above. Pl. 1, Figs. 4–7, illustrates some of these basal lobes and serves admirably to show how strikingly they approximate the stipules in appearance.

Compound Leaves

The leaves of the modern species show occasional examples of a tendency toward the formation of compound leaves. Usually it is toward the tip that the midrib forks, forming two lobes. Sometimes, however, a basal lobe will assume the size and proportions of a division of a compound leaf. On Pl. 1, Figs. 1–3, are shown three examples of this tendency. In Figs. 1 and 3 the midrib forks about halfway to the tip, thus forming two divisions of equal rank. In Fig. 2 the tendency seems to be toward a tripalmate division, the central division being bilobed and separated by an interval of petiole (midrib) from the rest of the leaf.

I know of no fossil remains which approach these modern leaf variations.

It has been suggested to me that the leaf variations in the existing species may indicate that this apparently monotypic form may be segregated into a number of closely related species, like so many aggregations of the Asa Gray period. This may be so; it were rash nowadays to doubt the possibilities of any species in this direction after seeing what has happened and is happening to Crategus and other genera. However, no evidence in this direction is furnished by the variations in leaf form, for with the exception of the atavistic character of the seedling leaves which appears to be a constant feature, and the usual reduction shown by the senescent leaves, the leaf variation is entirely fortuitous, if one may use that term in this sense for the result of unknown, or at least not well understood morphological and physiological causes.

The Fossil Species

That the number of fossil species of Comptonia has been multiplied beyond what the facts warrant, seems probable without any very serious consideration. That we should have, for instance, in the area of Europe, ten or a dozen Eocene, Oligocene, and Miocene species seems improbable, and this off-hand conclusion is borne out by an examination of the species. We find that the limits of variation within a single species as conceived by the various writers who have studied members of this genus, judging by the diverse forms referred to the same species, are so wide as to include in almost any of the described species (so called), greater differences of size, form, or venation than exist between what are usually regarded as really valid species by the individual authors. In addition we find species founded upon obscure fragments of doubtful value, or upon what are very probably immature or abnormal leaves. More especially does this seem to be the case when we examine the leaves of the sole existing species for comparison. The latter show wide variations (see Pl. 2). The typically mature leaves are usually divided nearly to the midrib, although the sides of the lobes often overlap, giving them the appearance in some cases of being only slightly incised. This would be particularly true of similarly lobed leaves preserved as fossils. The leaves are progressively simpler toward the flowers and in the seedlings, becoming merely servate or even entire and lanceolate (Pl. 3). Thus the juvenile and senescent leaves are both more or less atavistic. The lobes vary greatly in outline duplicating many of the fossil leaves in appearance; their margins are usually entire but may be incised as in several of the fossil leaves.

On the whole I feel justified in suggesting the changes which

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follow, the discussion falling naturally under the respective species. While the synonymy does not pretend to be complete, I have endeavored to include all references to figured specimens and have been at much pains to verify them in so far as the facilities of the United States National Museum and the New York Botanical Garden would permit.

Work of this sort is as laborious as it is unappreciated, indeed the author who has the temerity to break away from the traditional names in paleobotany is more than likely to be criticised for having "done nothing but burden an already overburdened synonymy." I have been working on Comptonia for several years and have long hesitated about publishing my results for just this reason until perfectly convinced that it was entirely impossible to get any idea of the past history of the genus without correlating the various remains, either positively or at least provisionally. To leave them as they were would be about as sensible as it would be to have species of Comptonia in the existing flora based upon the political divisions in which the plants are found and further dependent on the slight variations in leaf-form exhibited by the individual plants. A number of doubtful forms such as Comptonia contzeniana Debey, Comptonia chironis Massal, Comptonia heerii Ettings., etc., and such obvious errors as Comptonia mirabilis Brongn. cited in Prestwich's Geology are entirely omitted.

Comptonia diforme (Sternb.) Berry

Asplenium diforme Sternb., Fl. d. Vorwelt, vol. 2, pp. 29, 33, pl. 24, fig. 1, 1822.

Aspleniopteris difformis Sternb., Ibid., vol. 4, p. 21, 1825.

Zamites difformis Presl. in Sternb., Ibid., vol. 2, p. 198, 1822.

Buettner, Rudera Diluvii Testes, pl. 22, fig. 8, 1710.

Pterophyllum difformis Göpp., Ubersicht. d. Arb., p. 137, 1844.

Comptonia acutiloba Brongn., Prod., pp. 141, 143, 209, 1828; Tabl., p. 121, 1849.

Unger, Synopsis, pp. 213, 305, 1845; Gen. et Sp., p. 393, 1850; Foss. Fl. v. Sotzka, p. 32 (162), pl. 8 (29), figs. 6–8, 1850.

Saporta, Périd. Végét., p. 307, fig. 92; Mon. d. Pl., 1879; Orig. Pal. Arbes. Cult., p. 141, 1888.

Gardner, Mem. Geol. Surv. Eng. & Wales, p. 108, 1889.

Boulay, "Fl. foss. Gergovie," Ann. Sci. Brux., vol. 23, p. 73, 1899.

- Dryandra acutiloba (Brongn.) Ettings., Proteac. d. Vorw., p. 27 (735),
 pl. 4 (33), figs. 2, 3, 1851; Foss. Fl. v. Bilin, vol. 2, p. 17, pl. 35, figs.
 18–26, 1868; Proc. Roy. Soc. Lond., vol. 30, p. 232, 1880.
- Myrica (Comptonia) acutiloba Brongn.
 - Schimp., Pal. Végét., vol. 2, p. 560, 1872.
 - Engelhardt, Nova Act. Leop. Carol., vol. 39, p. 375, pl. 23, figs. 7–12, 1877; *Ibid.* vol. 57, p. 153, pl. 6, figs. 4–7, 1891; *Sitzb. naturwiss. Gesell. Isis*, 1880, p. 78, pl. 1, figs. 6, 7, 1881; *Lotos*, neue folge, Bd. 16, p. 5, 1896.

Heer, Fl. Foss. Arct., vol. 7, p. 77, 1883.

- Dryandra comptonia folia Ettings., Beitr. z. kr. foss. Fl. Neuseelands, p. 27, pl. 4, figs. 14–18a; pl. 5, figs. 9–12, 1887.
- Comptonia columbiana Daws., Trans. Roy. Soc. Can., vol. 8, sec. 4, p. 81, fig. 10 (text), 1890.
- Comptonia Vinayi Saporta, Pl. foss. Ark. de Brives, p. 35, pl. 3, figs. 9–13, 1878.
- Dryandra saxonica Friedrich, Abh. geol. Specialk. Preuss u. Thüring., vol. 4, pp. 327, 382, pl. 20, figs. 10a-16; pl. 28, figs. 3-5; pl. 29, fig. 16, 1883.

This was one of the first known species of Comptonia, having been described and figured by Sternberg in 1822 under the name *Asplenium diforme*. What is probably the same thing is mentioned elsewhere in his *Flora der Vorwelt* as *Aspleniopteris difformis* Sternb. and *Zamites difformis* Presl. A similar leaf was figured by Buettner as long ago as 1710 and considered as having Cycadean relationships.

We have in this species, or group of species of the *acutiloba* type, a widespread and persistent type of leaf which is fairly well marked. Some of the smaller specimens, it is true, resemble *Comptonia schrankii*, particularly Ettingshausen's forms from Monte Promina, but the bulk of the leaves referred to the latter species are smaller and have very narrow, two-veined, acute lobes. Heer includes under *Comptonia acutiloba* the *Comptonia incisa* of Ludwig found at several localities in Hesse, and he also identifies a similar leaf from Greenland as *Comptonia incisa*. The Greenland leaf is identical with Ludwig's leaves, but both are obviously distinct from *C. acutiloba*.

Dawson's form from British Columbia belongs here. He says that it is closely allied to *Comptonia matheroniana* Sap., but I fail to see any resemblance to that species. Species which do resemble Dawson's more or less, are *Comptoniphyllum japonicum* Nath., and especial'y *Comptonia partita* Lesq., the latter based upon a poorly drawn fragment from the Green River beds.

The existing Comptonia sometimes furnishes leaves very similar to *diforme*, and I have collected many such, although usually they differ in being somewhat broader, e. g., Pl. 2, Fig. 4.

The many excellent figures published by Ettingshausen furnish adequate and typical examples of the leaves of the species under discussion. This form of leaf makes its appearance during the Eocene at the widely separated localities of the Isle of Wight in England, Brives in France (represented by *C. vinayi* Sap.), and Murderer's Creek in New Zealand. It is possible that the New Zealand leaf, which is identical in form, may have been borne on an entirely different plant, as it is difficult to account for so wide a distribution. It may well be that the New Zealand leaf should be referred to Dryandra as Ettingshausen has done, since several species of the latter genus have been recorded from that region by the same author, all having leaves of the *acutiloba* type. In discussions of the distribution of Comptonia we should constantly bear in mind, however, the meagerness of the record of the upper Cretaceous period.

Comptonia diforme continued through the Oligocene and Miocene, becoming common during the latter age and occurring in beds in this country which have been considered Miocene (Comptonia columbiana Daws.).

Friedrich considers the Saxon leaves which he describes under the name of *Dryandra saxonica* to belong to that genus because of their acute lobes, subcoriaceous texture, and style of venation, in which characters he says they differ from the modern Comptonia leaf. If he had seen a large enough series of the latter he would have found no difficulty in recognizing their similarity and the fact of their identity with both fossil forms whose similarity he does note, *i. e., schrankii* and *acutiloba*, all of which I have included under *Comptonia diforme*.

Comptonia gaudinii Heer

Myrica (Comptonia) gaudinii Heer, Fl. Tert. Helv., vol. 2, p. 34, pl. 70, fig. 9, 1856; Ibid., vol. 3, pl. 152, fig. 19, 1859.
 Schimp., Pal. Végét., vol. 2, p. 559, 1872.

- Comptonia incisa Ludwig, Palæont., vol. 8, p. 96, pl. 30, fig. 7–15, 1860.
 Heer, Fl. Foss. Arct., vol. 2, p. 474, pl. 39, fig. 7, 1871 (referred to Dryandra acutiloba (Brongn.) Ettings).
 Schimp., loc. cit., p. 561.
- Comptonia triangulata Watelet, Pl. Foss. Bass. Paris, p. 124, pl. 33, fig. 4, 1866.
- Myrica credneri Engelh., Nova Act. Leop. Carol., vol. 39, p. 376, pl. 23. fig. 13, 1877.
- Myrica (Comptonia) tschernowitziana Engelh., Ibid., p. 375, pl. 23, fig. 14.

Comptoniphyllum japonicum Nath., Pal. Abh. D. & K., vol. 4, pp. 207, 212, pl. 20, figs. 2, 3; pl. 22, fig. 3, 1888.

This species embraces leaves approaching the acutiloba type, averaging, however, considerably larger in size. They are similar to Comptonia dryandroides Ung. except that the lobes in the latter species are fewer in number and more falcate in outline. As will be seen from the foregoing synonymy I have included a variety of names under this species, most of them having been based upon fragmentary material. Some of these may be entitled to varietal rank, but surely their slight differences do not entitle them to rank as valid species. For instance, Engelhardt's tschernowitziana is based upon a single specimen showing but three lobes on one side and one lobe on the other side. It differs from the typical *qaudinii* in the more rounded upper margins of the lobes, but might easily be a larger leaf of the same author's credneri, both of which I include under Comptonia gaudinii. Individual lobes of Ludwig's incisa which correspond with *tschernowitziana* could be selected without much difficulty. Heer's qaudinii was founded upon fragments as was also the Arctic form which he refers to Dryandra acutiloba, but which seems to belong here. His comparison of gaudinii to dryandroides Ung. is certainly significant. Watelet's triangulata is another fragment showing only three complete lobes on each side. Schimper includes it under Watelet's concisa from which it manifestly differs, however. Nathorst's japonicum shows only the central portions of several large and small leaves. As might be expected when dealing with fragments, the various authors compare their specimens with a variety of other species, for instance Engelhardt compares credneri with macroloba of Wessel & Weber. to which I fail to detect any resemblance.

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Comptonia gaudinii as here constituted, shows considerable range, being represented as early as the Eocene by the leaf described by Watelet which grew on the shores of the Suessonien Gulf, and continued as late as the Miocene of Switzerland and Japan.

Comptonia insignis (Lesq.) Berry

 Myrica insignis Lesq., Ann. Rep. U. S. Geol. & Geog. Surv. Terr., for 1874, p., 312, 1876; Tertiary Fl., p. 135, pl. 65, figs. 7, 8, 1878.
 Myrica alkalina Lesq., Cret. & Tert. Fl., p. 149, pl. 45A, figs. 10–15, 1883.

I regard these two species of Lesquereux as most probably identical, for example his Figs. 13 and 15 of alkalina are particularly close to insignis, especially Fig. 15. It would require but a slight increase in the lobation of the latter to produce the typical *insignis*. Other than this the remains of the two forms are exactly alike in texture and venation, except that in *insignis* the midrib is more slender. As Lesquereux remarks, the leaves which he refers to alkalina are of two types—obtuse, and acute-lobed,—the collected specimens, however, showing every gradation between these extremes, some leaves being acutely lobed on one side and obtusely on the other. As the remains are all from strata of the same age, although Alkali Station, Wyo., is some 300 miles distant from Florissant, Col., I am still inclined to think that the leaves which Lesquereux called *alkalina* are simply the young leaves of which insignis is the mature leaf, for they are (1) much more variable in lobation, (2) smaller in size and definiteness, and in the extent of their lobes, combined with a narrower lamina, and (3) they have a much thicker midrib. This is especially true of Fig. 15 cited above.

All of these are characters which serve to mark the leaves of the immature plants of the existing species. Together these two types of leaf show that a most beautiful species of rather broad-leaved Comptonia dwelt on the site of the present Rocky Mountains during the early Tertiary.

The venation which is well preserved, shows a type which is quite characteristic of the modern Comptonia leaf.

Lesquereux compares alkalina with Myrica vindobonensis Ettings. and with Myrica ungeri Herr (laciniata Ung.) to both of which there is a passing resemblance that is by no means close, however.

Comptonia macroloba (Web. & Wess.) Berry

Dryandra macroloba Web. & Wess., Palaont., vol. 4, p. 147, pl. 25, fig. 11, 1856.

Myrica macroloba (Web. & Wess.) Schimp., Pal. Végét., vol. 2, p. 557, 1872.

Comptonia concisa Watelet, Pl. Foss. Bass. Paris, p. 123, pl. 33, fig. l, 1866.

Myrica concisa (Wat.) Schimp., Pal. Végét., vol. 2, p. 554, 1872.

These leaves resemble those which have been described and figured by the respective authors as *incisa* Ludw. (gaudinii Heer), dryandroides Ung., and acutiloba (diforme (Sternb.) Brongn.), with this difference that the blade in macroloba is incised only half the distance to the midrib, surely not a very important character in view of the variation in this direction often shown by the existing Comptonia.

Watelet's leaf is not different, except in the foregoing particular from the fragment which he named *Comptonia triangulata* and which I have referred to *Comptonia gaudinii* Heer.

Both of the forms which I have united to form the species under consideration are fragments of the basal portions of single specimens and possibly their similarity may be due to this fact. Neither has any individual characters of much specific weight and perhaps it would be wiser to discard them altogether or to refer them to some of the above mentioned and better characterized species. The French specimen is from the lower Eocene while the Prussian is from the later Tertiary (Aquitanian), which may be considered an objection to considering them identical. However, they are of no great importance in any event, and do not throw any additional light upon the evolution of the genus in Tertiary times.

Comptonia antiqua Nilsson

Phyllites (Comptonia ? antiqua) Nilss., Vetens. Akad. Handl., for 1831, p. 346, pl. 1, fig. 8, 1832.

Sap., Arch. Sci. Phys. & Nat., vol. 28, p. 110, 1867.

Comptonites ? antiquus Nilss., Pfl. Kreidegebirges, p. 121.

Hisinger, Lethaa Suec., p. 111, pl. 34, fig. 7, 1837.

Unger, Synopsis, p. 213, 1845; Gen. et Sp., p. 395, 1850; Sitzb. Akad.

Wiss. Wien, vol. 51, p. 379, 1865.

Brongn., Tabl., p. 111, 1849.

Dryandra antiqua Ettings., Proteac. d. Vorwelt, p. 31 (739), 1851.

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During the time that *Comptonia microphylla* Heer was spreading southward along the Atlantic coastal plain in America, a very similarly leaved plant had reached Europe by way of the Scandinavian peninsula. This species is represented by the leaf which Nilsson described in 1832 from the Greensand of Köpinge, Sweden. That this species became more widespread in Europe than the fossils which have been discovered show, is indicated by its occurrence at almost the opposite end of Europe in the Cenomanian at Déva, Transylvania.

It was a small leaf with a few rounded lobes and was very similar in appearance to its Arctic and American congeners. In size and outline it is identical with Heer's type figures of *Comptonia parvula* and *microphylla*, particularly the latter, while his Fig. 3 of the former is indistinguishable from the European leaf. Newberry's leaf from New Jersey is larger and has somewhat more pointed lobes, and Heer's *parviflora* is also somewhat larger.

The occurrence of this same type of leaf on the seedlings of the modern plant, and as the earliest known Comptonia leaves in the Cretaceous of such geographically remote localities in Europe, Greenland, and New Jersey, amounts to a demonstration, it seems to me, that we are dealing with an ancestral form of Comptonia leaf, and as a corollary, that the juvenile leaf-forms in the modern plant are truly atavistic.

Comptonia tenera Hos. & v. d. Marck

Comptonia tenera Hos. & v. d. Marck, Palæont., vol. 31, p. 227 (3), pl. 19 (1), figs. 3, 4, 1885.

The next occurrence of Comptonia in Europe after that of Comptonia antiqua Nilss, of the mid-Cretaceous, is this species, which Hosius and von der Marck found in the upper Senonian of Westphalia at Höpingen, three and one half miles west of Münster. They compare it to Myrica dryandræfolia Brong. (Comptonia schrankii) and consider the resemblance to be very close. They also make comparisons with Dryandra cretacea Velen., which they think is identical with Dryandra brongniarti Ettings. from Häring, both of which species they would refer to the genus Comptonia. The venation of Comptonia tenera is not shown in the speci-

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mens figured but there can be no doubt of its being a Comptonia. A large number of the smaller leaves of the existing species are counterparts of these Senonian forms, the most similar figured specimen being the leaf shown on Pl. 2, Fig. 1.

This species differs decidedly from *Dryandra cretacea* Velen., which I would retain in the Proteaceæ, otherwise the authors comparisons are most fortunate and it is very probable that we have in *Comptonia tenera* the Cretaceous ancestor of *Comptonia schrankii* which is so common from the Eocene through the Miocene.

Comptonia dryandroides Unger

Comptonia dryandroides Unger, Foss. Fl. v. Sotzka, p. 31 (161), pl. 6(27), fig. 1, 1850.

Andrä, Jahrb. k. k. geol. Anst., vol. 5, p. 562, 1854.

Dryandra ungeri Ettings., Proteac. d. Vorwelt, p. 30 (738), pl. 4, fig. 1, 1851.

Unger, Foss. Fl. v. Kumi, vol. 35 (59), pl. 9, fig. 16-18, 1867.

- Myrica (Comptonia) dryandroides Pilar, Acta Acad. Sci. Slav. Merid., vol. 1, p. 31, pl. 13, fig. 18, 1883.
- Comptoniphyllum naumanni Nath., Pal. Abhandl. D. & K., vol. 4, p. 8, pl. 2, fig. 2, 1888.

Myrica (Comptonia) cuspidata (Lesq.) Dawson, Trans. Roy. Soc. Can., vol. 8, sec. 4, p. 80, fig. 9, 1890.

A large-leaved and beautiful species of which Unger has figured a perfect leaf from Sotzka, which is identical with, but somewhat larger than Nathorst's *Comptoniphyllum naumanni* from Japan. These leaves are practically the counterparts of numerous leaves of the existing species (cf. Pl. 2, Figs. 3, 4). Those which are described by Unger from Kumi have a prolonged base, which the other included leaves lack. This is, however, a variable feature, often present, though in a somewhat less degree, in the existing species. Ettingshausen refers these leaves to Dryandra making comparisons with *Dryandra armata* R. Br. of the existing flora. His comparison is not, however, particularly fortunate as the latter species has leaves which incline to a runcinate form, while the basal portion of the leaf is much more narrowly lobed, some of the lobes being several times longer than they are wide and separated by an

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interval of midrib. I altogether fail to see any but the most general resemblances.

With regard to the relations of *Comptonia dryandroides* to the other fossil species of Comptonia the following points may be mentioned.

The lobes are of the form of *schrankii* but much larger and the leaves as a whole are comparatively less elongated. There is somewhat of a resemblance to the typical acutiloba leaves but the size is greater and the lobes are longer and incurved. The leaves of *aningensis* have similar lobes when they are deeply lobed, but the leaf as a whole is smaller and the incisions never seem to reach the midrib as they do in dryandroides. Heer's aventica (vindobonensis) is intermediate in form between this species and *anin*gensis. Ludwig's incisa also includes very similar leaves which have, however, narrower, less incurved, and more rectangularly placed lobes. Whether this species spread from Greece to Japan or from Japan to Greece via southern Asia is problematical, but it was probably more plentiful throughout parts of southern Asia and on the hills of the incipient Himalayas than the fossils indicate. The leaf from British Columbia which Dawson referred to Comptonia cuspidata Lesq. differs from that species in size and in the shape of the lobes. It is somewhat smaller than Unger's type material of *dryandroides* but is identical with the Japanese leaf referred here. Dawson says (p. 81): "Allied with *aningensis* Heer, obtusiloba Brongn., and dryandroides Ung. all of which may be varieties of one species." To *aningensis* I fail to see any resemblance except in the tip which is a variable character of little weight. What Dawson means by obtusiloba Brongn. I have not been able to make out.

Comptonia cuspidata Lesq.

Comptonia cuspidata Lesq., Proc. U. S. Nat. Mus., vol. 5, p. 445, pl. 6, fig. 10–12, 1883.

Myrica (Comptonia) cuspidata (Lesq.) Knowlton, Proc. U. S. Nat.
 Mus., vol. 17, p. 221, 1894; Ann. Rep. U. S. Geol. Surv., vol. 17, pt.
 1, p. 885, 1896 (non Dawson).

This must have been a particularly beautiful plant with its large, almost falcately lobed leaves. That these acute, upwardly directed

lobes are not anomalies is indicated by the three leaves that Lesquereux figures, which are of widely different sizes, his larger figure indicating a leaf about fifteen centimeters in length and showing perfectly the characteristic venation of this genus.

Lesquereux compares this species with *Comptonia acutiloba* Brongn., to which, however, the resemblance is not especially close, not so close as it is, for instance, to Ludwig's larger figure of *Comptonia incisa* (gaudinii Heer). In both of these species, however, the lobes are laterally pointed and not ascending. The European leaf which is the closest to *cuspidata* is Unger's specimen of *dryandroides* from the Oligocene of Styria, in which the resemblance is quite striking although the lobes of the latter are somewhat less ascending.

The occurrence of *Comptonia cuspidata* and *premissa* in Alaska during the early Tertiary would seem to indicate that they represent the invasion of the genus into Asia from the Arctica-North America region which probably shortly preceded or followed this Alaskan occurrence, as they are not so different from the two forms which occur in the Miocene of Japan as to preclude the idea of their standing in ancestral relations to the latter.

Comptonia premissa Lesq.

Comptonia p emissa Lesq., Proc. U. S. Nat. Mus., vol. 5, p. 445, pl. 6, fig. 13, 1883.

Myrica (Comptonia) premissa (Lesq.) Knowlton, Ibid., vol. 17, p. 222, 1894; Ann. Rep. U. S. Geol. Surv., vol. 17, pt. 1, p. 885, 1896.

This lower Tertiary species from Coal Harbor and Chignik Bay, Alaska, had leaves very similar to the younger leaves of the living species of Comptonia and not especially close to any of its known European contemporaries. Were the remains of Heer's *laharpii* more definite it might possibly be compared with the Alaskan form, while Sternberg's type figure (*Fl. d. Vorwelt*, Pl. 24, Fig. 1) of *Comptonia diforme* shows the closest resemblance to it of any of the forms known to me.

Comptonia gracillima (Heer) Berry

Dryandra gracilis Heer, Fl. Tert. Helv., vol. 3, p. 311 (note), 1859. Myrica gracillima (Heer) Schimp., Pal. Végét., vol. 2, p. 559, 1872.

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?Myrica minima Sap., Etudes, vol. 1, p. 199, 1863.
Schimp., loc. cit., p. 562.
?Myrica pusilla Sap., loc. cit.
Schimp., loc. cit., p. 561.

Heer's species was from the Oligocene of Spechbach in Alsatia while Saporta's were both from the Oligocene of Saint Zacharie in France. These three species, so called, are all from strata of about the same age, and not widely removed geographically, none are figured by their authors, they are all founded on very small obtusely lobed leaves, and while they may represent one or more valid species of small size, it seems more probable that they are founded upon immature leaves such as are so common on terminal shoots in close proximity to the fruit in the modern species, of one of the dominant Oligocene species, *Comptonia schrankii* for instance.

I have united them provisionally under Heer's name, which has priority, since if left as distinct forms they indicate an abundance and variety of species of Comptonia which is apt to be very misleading when based upon such insufficient evidence.

Comptonia grandifolia Unger

Comptonia grandifolia Unger, Chlor. Protog. (inedit.); Synopsis, p. 213, 1845; Gen. et Sp., p. 394, 1850; Foss. Fl. v. Sotzka, p. 31 (161), pl. 8 (29), fig. 1, 1850; Foss. Fl. v. Radoboj, p. 161, 1869.
Brongn., Tabl. p. 118, 1849.

Dryandroides grandifolius Ettings., Proteac. d. Vorwelt, p. 34 (742), pl. 5, fig. 2, 1851.

This species is founded upon rather poor and indefinite remains of a gigantic leaf with obsolete secondary venation from the lower Miocene (Mayencian) of Radoboj in Croatia. The specimen is 5.5 cm. wide across the more perfect lobes, while the largest leaf of the existing Comptonia which I have been able to find is 3.5 cm. wide, or seven elevenths of the size of the Radoboj leaf. Largeleaved fossil Comptonias of undoubted authenticity are *magnifica* of Watelet which is 3.2 cm. wide, and *matheroniana* of Saporta which is 3.8 cm. in width. *Comptonia grandifolia* is almost identical in size and outline with the leaves of the existing *Banksia* grandis Willd. as pointed out by Ettingshausen (*loc. cit.*) so that its reference to Comptonia may be regarded as largely problematical.

Comptonia suessionensis Watelet

Comptonia suessionensis Wat., Pl. Foss. Bass. d. Paris, p. 122, pl. 33, fig. 2, 1866.

Myrica suessionensis (Wat.) Schimp., Pal. Végét., vol. 2, p. 553, 1872.

A rather large leaf, exceptionally broad considering its narrow lobes, somewhat similar to the leaf of the existing species shown on Pl. 2, Fig. 2. Watelet's figure shows us a curious combination of rounded and acute lobes, and it seems quite probable that his specimen is not correctly depicted. Schimper (*loc. cit.*) says that this species greatly resembles *Myrica dryandræfolia* Brongn. (*Comptonia schrankii*) but I fail to detect any very close resemblance.

With considerable doubt regarding the propriety of retaining this as a valid species, I still see no other disposition to make of it at present.

Comptonia laciniata Unger

Comptonia laciniata Unger, Gen. et Sp., p. 394, 1850; Foss. Fl. v. Parschlug, p. 35, 1848; Foss. Fl. v. Sotzka, p. 31, pl. 8, fig. 2, 1850; Iconogr., p. 33, pl. 16, fig. 8, 1852 (aments); Foss. Fl. v. Radoboj, p. 161, 1869; Fl. Tert. Asia Mineur in Tschitacheff, Asia Min., pt. 4, p. 320, 1869.

Brongn., Tabl., p. 121, 1849.

Dryandroides laciniatus Ettings., Proteac. d. Vorw., p. 33, 1851.

Myrica ungeri Heer, Fl. Tert. Helv., vol. 2, p. 35, pl. 70, fig. 7, 8, 1856. Ibid., vol. 3, p. 176, pl. 150, fig. 22 (fruit)?, 1859 (non fig. 21, which is referable to vindobonensis).

Massal., Pianti. Terz. Vicentino, pp. 243, 258, 1851.

Schimp., Pal. Végét., vol. 2, p. 556, 1872; Atlas, pl. 85, fig. 8, 1874.

Lesq., Proc. U. S. Nat. Mus., vol. 11, p. 27, 1888.

Boulay, "Fl. Foss. Gergov.", Ann. Sci. Brux., 1899, pp. 59, 131.

(Non Ludw., Palæont., vol. 8, p. 95, pl. 29, fig. 2, 2a; pl. 30, fig. 2, 3, 1860.)

Myrica græffi Heer, Fl. Tert. Helv., vol. 3, p. 176, pl. 150, fig. 19, 1859 (non fig. 20 which is referable to vindobonensis).

This is a beautiful species with large leaves some fifteen centimeters in length and upwards of three centimeters in width, irregularly lobed; each lobe with one or more serrations of the margin besides the rather larger, somewhat falcate, usually pointed tip. There is considerable variation in the depth of the sinuses, Unger's type figure from Sotzka showing a leaf with deep sharp sinuses, while the handsome specimen figured by Heer (*loc. cit.*, Pl. 70, Fig. 7) has more shallow and slightly rounded sinuses. The sharpness of the serrations and tips of the lobes tends to be much softened in the basal and apical portions of the leaves, in fact one of the leaves figured by Heer has them distinctly rounded.

As remarked under *Comptonia vindobonensis*, some of the leaves of that species are quite close to this one and are also represented by variations of the modern leaf, an example of which is figured on Pl. 2, Fig. 5. The latter, while shorter and not exactly similar to *laciniata*, has precisely the same character of serrated lobes. Unger observed in the collections from Parschlug, Styria, a staminate inflorescence which he says is indistinguishable from that of the existing Comptonia and which he refers to *laciniata*.

This species appears in some numbers in the late Oligocene of the upper Rhone and Jura regions of central Europe and continues into the Upper Miocene (Tortonian) of Styria. It has been recorded by Lesquereux from Spanish Peak, California, but was not figured and I have been unable to locate the material upon which his determination rests, so that this occurrence may be considered very doubtful for the reason that undoubted Myrica species have leaves which are not very different from *laciniata*. This is especially to be seen in the leaves from Florissant, Col., and Wycliffe, Ky., which Lesquereux named *Myrica copeana*, regarding which I found it impossible to reach a decision until after consulting the type material in the U. S. National Museum.

Comptonia matheroniana (Sap.) Berry

Myrica (Comptonia) matheroniana Sap., Etudes, vol. 2, p. 93, pl. 5, fig. 7, 1865.
Schimp., Pal. Végét., vol. 2, p. 555, 1872; vol. 3, p. 691; Atlas, pl. 55, fig. 10, 1874.

Boulay, Fl. Foss. Gergov., p. 73, 1899.

Probst, Jahresb. vaterl. Naturk. Würtemberg, p. 190, 1883.

Comptonia magnifica Watelet, Pl. Foss. Bass. Paris, p. 123, pl. 33, fig. 3, 1866.

Myrica magnifica (Wat.) Schimp., loc. cit., vol. 2, p. 554, 1872.

Leaves of extremely large size with lobes similar to the normal lobes in the leaves of the existing species. Saporta's leaf is only slightly larger, however, than the modern leaf shown in Pl. 2, Fig. 6.

The Eocene and Oligocene forms are very similar, what little differences are apparent being probably due to the careless drawing of the leaves from the Paris basin. Saporta's figure, however, does show a few serrations on some of the lower lobes which are wanting in its Eocene ancestor, if we may draw such a conclusion from the small amount of material available for study. I was at first inclined to keep these two leaves separate, appearing as they do at such different horizons, but there are a number of other identical species from the two horizons, and others with even a greater range in the Cenozoic, so that it has seemed best to unite them as above indicated. It is, of course, within the range of possibility that they do not constitute a valid species but in each case are simply abnormally large leaves of contemporary and smaller-leaved forms; for instance, Watelet's leaf might be merely a giant leaf of the Belleu species which he named triangulata (gaudinii Heer). Schimper notes the resemblance of these leaves to such Proteaceous forms as those of Banksia grandis and repens of Robert Brown, but the resemblance is much closer to the large leaves of the modern Comptonia. Saporta in his revision of the Aix flora records this species from that locality and notes its resemblance to Myrica aculeata.

Comptonia microphylla (Heer) Berry

Myrica (Comptonia) parvula Heer, Fl. Foss. Arct., vol. 7, p. 20, pl. 55, fig. 1–3, 1883.

Newberry, Fl. Amboy Clays, p. 63, pl. 19, fig. 6, 1896. Myrica (Comptonia) parvifolia Heer, loc. cit., p. 77, pl. 71, fig. 12, 1883. Rhus microphylla Heer, loc. cit., vol. 3, pt. 2, p. 117, pl. 32, fig. 18, 1874.

It is difficult to understand upon what ground Heer founds his two species *parvula* and *parvifolia* unless it is because they are from different horizons. He compares both to the European $Myrica \ aningensis$ (Braun) Heer, although their resemblance to that species, as a matter of fact, is not very close.

The two are exactly similar except that the form *parvifolia* is somewhat the larger. The Raritan leaf which Newberry refers to *parvula* is more like *parvifolia*, which fact is noted by the latter author, who, I suppose, hesitated about referring a Cretaceous leaf to a species of the late Miocene as these Arctic deposits were thought to be at that time.

I can see no reason for maintaining them as separate species, even though one is Cretaceous and the other Tertiary, a statement not altogether beyond question in view of the fact that labels are sometimes misplaced, and in the case of *parvifolia* the name was based upon a single imperfect specimen which might readily enough become included with other collections from earlier strata, both having been collected by Professor Steenstrup's expedition. In addition to the above, it may be remarked that the exact age of the Greenland Tertiary deposits has never been definitely and satisfactorily settled, and in all probability the Atanekerdluk deposits are not younger than the Oligocene and more probably are upper Eocene.

The first five or six leaves on young plants of the existing *Comptonia peregrina* (Linn.) Coulter usually closely resemble this fossil species both in size and in shape. This is well shown by a comparison of the figures which I have reproduced; in fact the existing leaves were they to occur as fossils would unhesitatingly be referred to *parvula* Heer, some of them being exact duplicates of this fossil leaf. Heer's Fig. 1 which shows a more primitive leaf than his other figures, finds its counterpart in the first leaf of the modern seedling, which is almost equally close to the types of *Comptonia microphylla* and *antiqua*. I have collected a large number of leaves of this form, and find this type with more or less accentuation to be present in all the seedlings which I have examined.

We might consider these fossil leaves to be merely the abbreviated leaves which are so common in seedling plants and hence without phylogenetic meaning, or we might consider that this form of fossil

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leaf represented the normal leaves of ancient Comptonia plants. The former view seems to me doubtful, not only because of the perishable nature of seedling leaves in general, but because it is unusual for them to become detached and fossilized. That they are sometimes found as fossils is proven by the leaves from the Swiss Tertiary which Heer calls Myrica latiloba (Fl. Tert. Helv., vol. 3, p. 176, pl. 150, figs. 12-15, 1859). Furthermore no other species of Comptonia has been found in the Raritan clays or Patoot schists from which they could have been derived. We are quite justified in concluding that these leaves are the normal leaves of the earliest known Comptonias and that the modern seedling leaves are truly atavistic. From the abundance of the genus Myrica with nine species in the Raritan, we may assume that the Comptonia stock became separated from Myrica some time during the lower Cretaceous, probably toward its close. While the leaf which Heer calls Rhus is probably from a slightly higher horizon than the Raritan leaf, its smaller size and its occurrence near what was probably the original center of radiation of the genus Comptonia, stamp it as the real starting point for any scheme of Comptonia phylogeny and distribution, and also emphasize the close relation, if not actual identity, between these forms of the New World and Comptonia antiqua Nilss. of Europe.

There are four species of Myrica in the Atane flora and two in that of Patoot; one of the latter $(pr \alpha cox)$ Heer considers as referable to Comptonia. While I do not agree in this reference, the species in question might be considered as showing the close relation between Myrica and Comptonia at this time, although I am strongly inclined to think that $Myrica \ pr \alpha cox$ is a Quercus, to which genus all of the early Comptonias show a passing resemblance, particularly the Raritan leaf.

Comptonia œningensis Al. Br.

Comptonia æningensis Al. Br., Neues Jahrb. f. Miner., p. 108, 1845;
Verz. foss. Pfl. v. Œningen, p. 76, 1851.
Unger, Gen. et. Sp., p. 394, 1850; Foss. Fl. v. Sotzka, p. 32 (162),
pl. 8 (29), fig. 3, 1850.
Brongn., Tabl., p. 121, 1849.
Massal., Pianti Terz. Vicent., p. 243, 1851.

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Dryandra æningensis Ettings., Proteac. d. Vorw., p. 28, 1851.

Myrica aningensis (Al. Br.) Heer, Fl. Tert. Helv., vol. 2, p. 33, pl. 70, fig. 1–4, 1856; Ibid., vol. 3, p. 175, pl. 150, fig. 18, 1859.

Schimp., Pal. Végét., vol. 2, p. 557, 1872; Atlas, pl. 85, fig. 9, 1874.

Comptonia meneghinii Unger, Foss. Fl. v. Sotzka, p. 32 (162), pl. 8 (29), fig. 10, 1850.

Massal., loc. cit., pp. 47, 243.

Dryandra meneghinii Ettings., loc. cit., p. 28.

Myrica meneghinii (Unger) Schimp., loc. cit., p. 555.

Schimper was the first to notice the resemblance of Unger's Comptonia meneghinii to Comptonia aningensis, a resemblance so close that I have been constrained to consider the two forms identical, an additional reason for this treatment being the unimportance of the remains of the former. Ettingshausen refers both forms to Dryandra, comparing the former with Dryandra obtusa and plumosa of Robert Brown and the latter with the same author's Dryandra floribunda and cuneata. It may be noted that their texture is much more membranaceous than obtains in the genus Dryandra. The species may be defined as including medium and rather small leaves of the general proportions of the modern leaf, with triangular, ascending, pointed, obtusetipped lobes. Incisions reaching only part way to the midrib. Base cuneate, more produced than in any specimens of the modern leaf that I have seen. The apex is also produced and shows but incipient indications of lobation.

These leaves approach very near to *Comptonia vindobonensis*, particularly to the Swiss leaves of that species, with which they are almost identical.

Comptonia obtusiloba Heer

Myrica (Comptonia) obtusiloba Heer, Uebers. Tertiarfl. d. Schw., p. 52, 1854; Fl. Tert. Helv., vol. 2, p. 35, pl. 70, fig. 10, 1856.
Saporta, Etudes, vol. 2, p. 105, pl. 5, fig. 7, 1865.
Schimp., Pal. Végét., vol. 2, p. 560, 1872.
Ettings., Blattskel. Dikot., p. 3.
Boulay, "Fl. foss. Gergov.," Ann. Sci. Brux., vol. 23, p. 59, 1899.
Myrica laharpii Heer, Fl. Tert. Helv., vol. 2, p. 34, pl. 70, fig. 11, 12 1856.

Schimp., loc. cit., p. 559.

Myrica rotundiloba Sap., loc. cit., vol. 1, p. 200; vol. 2, p. 46, pl. 5, fig. 3, 1865.
Schimp., loc. cit., p. 554.

Includes leaves with poorly developed, rather irregularly rounded lobes, Saporta's specimen from St. Zacharie showing a few remote serrations. Both the form known as *rotundiloba* Sap., and *laharpii* Heer apparently represent anomalous leaves, the former occurring only as a single fragment and the latter consisting of very imperfect material which Heer says is similar to various Proteaceous leaves except for the thin midrib. The type material of *obtusiloba* is considered by Heer to be very similar to the Sotzka leaves of *acutiloba*, but I fail to see such a resemblance. The *laharpii* form is very similar in outline to Watelet's *Comptonia pedunculata* from the French Eocene, and Saporta notes the close similarity between his *rotundiloba* and Heer's *laharpii*.

The various remains which I have included in this species are all somewhat indefinite in form and venation, and without uniformity in lobal characters, so that they shed but little light upon the relations of the plants which bore them, to the other species of Comptonia.

Comptonia partita (Lesq.) Berry

Myrica partita Lesq., Ann. Rep. U. S. Geol. Surv. Terr. jor 1873, p. 412, 1874; Tert. Fl., p. 134, pl. 17, fig. 14, 1878.

This subcoriaceous fragment, consisting of but two lobes on each side, was collected by Professor Cope from the Eocene of Nevada. Lesquereux compares it with *aningensis* of Braun, and, except for the margin, which was denticulate on the lower border of the lobes, with *incisa* of Ludwig. It is entirely indefinite in character and simply serves to show that there was in the American Eocene, a Comptonia species with leaves of the same general type as the species *gaudinii* Heer, *dryandroides* Unger, and *diforme* Sternb., which are so common in the European Tertiary. The Miocene of British Columbia furnished Dawson with a leaf that he called *Comptonia columbiana* which is almost

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identical with *partita* although I prefer to consider it more closely related to *diforme*. The occurrence of the latter in the late Tertiary in connection with the occurrence of *partita* in the early Tertiary renders it almost certain that Comptonia was better represented and with more widely ranging species in the American Tertiary that the fossil remains hitherto found would indicate, and this is just what we would anticipate from the European evidence.

Comptonia pedunculata Watelet

Comptonia pedunculata Watelet, Pl. Foss. Bass. Paris, p. 124, pl. 33, fig. 5, 6, 1866.

Myrica pedunculata Schimp., Pal. Végét., vol. 2, p. 555, 1872.

Comptonia rotundata Watelet, loc. cit., fig. 7.

Friedrich, "Beitr. z. Kennt. Tertfl. Sachsen," Abh. geol. Spk. Preuss. u. Thüring., vol. 4, p. 221, pl. 29, figs. 15, 15a, 1883.

All of Watelet's figures in the work cited above have the appearance, both in the venation and outline depicted, of having had the testimony of the specimens largely supplemented by the imagination of the artist. Especially is this true of the leaves which he calls Comptonia pedunculata and Comptonia rotundata. However, we cannot but consider these two forms when combined, to be entitled to specific rank especially as similar leaves have come to light in the lower Oligocene of Saxony, Watelet's types coming from the Eocene (Sables de Bracheux) of Belleu, France. The species is well named *pedunculata*, as Watelet's Fig. 6 has the longest petiole of any Comptonia leaf that I have ever seen, it being several times the length of the petioles in the existing species. Examples of leaves of the latter that greatly resemble the fossil species in outline, are often found among the larger leaves. While the fossil leaves apparently show rounded lobes with but slight incisions, it is probable that the rather full lobes overlapped as they do in so many leaves of the modern species, and that in reality the lobes were distinct as they were in the latter.

In its rounded margins *pedunculata* approaches *laharpii* Heer (*obtusiloba*) although I think that this is only an apparent similarity. Reasoning from the analogy furnished by the abundant

rounded-lobed leaves of the existing species it would be a reasonable conclusion that *pedunculata* is simply a round-lobed form of some of its normally lobed contemporaries, which one, of course, it is impossible to say, but not necessarily the same species in the Oligocene as in the Eocene.

Comptonia schrankii (Sternb.) Berry

- Aspleniopteris schrankii Sternb., Fl. Vorwelt, vol. 2, p. 29, pl. 21, fig. 2, 1822; vol. 4, p. 22, 1825.
- Comptonia ? dryandræfolia Brongn., Ann. Sci. Nat., ser. 1, vol. 15, p. 49, pl. 3, fig. 7, 1828 (Schimper, Pal. Végét., vol. 2, p. 808, erroneously cites vol. 4); Prodrome, pp. 143, 214, 1828; Tabl., p. 118, 1849.
 - Unger, Synopsis, p. 213, 1845; Gen. et Sp., p. 393, 1850.
 - Squinabol., Cont. Fl. Foss. Terz. Liguria, pt. 4, p. 17, 1892.
- Massal, Sopra Pianti Foss. Terr. Terz. Vicentino, pp. 243, 258, 1851. Myrica (Comptonia) dryandræfolia Saporta, Etudes, vol. 2, p. 104, pl.
- 5, fig. 8, 1865 (reproduced in Schimp., Pal. Végét., pl. 85, fig. 19–21). Dryandra schrankii Ettings., Proteac. d. Vorw., p. 26, pl. 3, fig. 1–8, 1851; Fl. v. Häring, p. 55, pl. 19, fig. 1–26, 1853; Foss. Fl. Monte Promina, p. 34, pl. 14, fig. 5, 6, 1855.

Web. & Wess., Palaent., vol. 4, p. 147 (37), pl. 25 (6), fig. 12, 1856.

- Myrica brongniarti (Ettings.) Lesq., Ann. Rep. U. S. Geol. & Geog. Surv. Terr., for 1873, p. 412, 1874; Tertiary Flora, p. 135, pl. 17, fig. 15, 1878.
- Comptonia breviloba Brongn., in Sedg. & Murch., Trans. Geol. Soc. Lond., ser. 11, vol. 3, p. 373, 1832; Tabl., p. 118, 1849.

Unger, Synopsis, pp. 213, 305, 1845; Gen. et Sp., p. 349, 1850; Foss. Fl. v. Sotzka, p. 32, pl. 8, fig. 9, 1850.

Comptonites dryandræjolius Göpp. in Bronn, Ind. Palæont., vol. 1, p. 322, 1848; vol. 2, p. 45, 1849.

Leaves of this species were described and figured by Sternberg as early as 1822. He thought that he was dealing with a fern and used the generic name Aspleniopteris. With the exception of the somewhat doubtful specimen from the Green River group (Eocene) which Lesquereux refers to Myrica brongniarti, the species is confined to Europe, where it is quite common and extends from the Eocene of the Isle of Wight up through the Miocene, becoming especially common and widespread during the Oligocene and Miocene. I have shown on Pl. 2, Fig. 1, a leaf of the existing species which is very close to this species, particularly

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to that size and form of leaf figured by Brongniart. Both Ettingshausen and Heer, partially followed by Schimper, consider the leaves referred to the various species in the foregoing synonymy, as identical and they compare them with the leaves of the living Dryandra formosa R. Br. They exclude them from Comptonia because of their thick midrib, acute lobes, and coriaceous texture, exactly the characters in numerous instances of the young leaves near the growing tips in the existing Comptonia. I do not think that there can be any doubt regarding the identity of these fossil forms and I fail to see any characters which weigh against their reference to Comptonia unless it be their comparatively greater length. Some of the forms are characteristically those of Comptonia, e. g., some of the leaves from Monte Promina and Häring, which also form a transition series toward Comptonia diforme; and these leaves gradually vary to the slender and acutely lobed forms. If comparisons are made with a large enough series of leaves of the existing species, many resemblances will at once become apparent, especially as remarked, to the slender, coriaceous, thick-veined leaves of the tips of shoots. The latter are not usually acutely lobed but often have that appearance in leaves not completely unfolded, or in herbarium specimens in which the lobes have become somewhat involuted in drying, as they usually do. In this condition they are indistinguishable from the fossil The American leaf of Lesquereux which is included specimens. in this species is less incised than the foreign forms and has rounded lobes. It is connected with the more typical leaves by the form described by Web. & Wess. from Rhenish Prussia. Engelhardt in his "Tertiärflora Jesuitengrabens bei Kundratitz in Nordböhmen"¹ figures what he considers catkins of Myrica. His figures look much more like leaves of this species, however, than they do like catkins.

Comptonia vindobonensis (Ettings.) Berry

Dryandra vindobonensis Ettings., Tert. Fl. v. Wien, p. 18, pl. 3, fig. 6, 1851.

Dryandroides concinna Heer, Fl. Tert. Helv., vol. 3, p. 188, pl. 153, fig. 8–10, 1859.

¹ Nova Acta Leop. Carol., vol. 48, no. 3, pl. 8, fig. 10, 11, 1885.

- Dryandroides bituminosa Sap., Exam. Anal. Fl. Tert. Provence, p. 22, 1861.
- Dryandra aventica Heer, loc. cit., p. 186, pl. 153, fig. 17.

Dryandra Rolleana Heer, Ibid., (footnote), pl. 153, fig. 18.

- Myricophyllum bituminosum Sap., Etudes, vol. 1, p. 221, pl. 8, fig. 1, 1863.
- Myrica (Comptonia) vindobonensis Heer, loc. cit., vol. 2, p. 34, pl. 70, fig. 5, 6, 1856.
- Myrica vindobonensis (Ettings.) Heer, loc. cit., vol. 3, p. 176, pl. 150, fig. 16, 17, 1859; Fl. Foss. Arct., vol. 2, pt. 2, p. 27, pl. 3, fig. 4, 5, 1869; Mioc. Baltic Fl., p. 32, pl. 7, fig. 4–10, 1869.
 - Ludwig, Palaont., vol. 8, p. 94, pl. 28, fig. 6, 7, 1860.
 - Unger, Foss. Fl. v. Kumi, p. 22, pl. 4, fig. 20-30, 1867.
 - Schimp., Pal. Végét., vol. 2, p. 558, 1872; Atlas, pl. 85, fig. 1, 2, 1874.
 Knowlt., Proc. U. S. Nat. Mus., vol. 17, p. 222, 1894; Ann. Rep. U. S. Geol. Surv., vol. 17, pt. 1, p. 885, 1896.
 - Engelh., Tertfl. Jesuitengrab. Kundr. in Nordböhm., p. 19, pl. 1, fig. 40, 1885; Verh. k. k. geol. Reichsanstalt, no. 5, p. 2, 1902.
- Myrica Græffii Heer, loc. cit., pl. 150, fig. 20, (non fig. 19 which is referable to Comptonia laciniata).
- Myrica ungeri Heer, loc. cit., p. 176, pl. 150, fig. 21 (non fig. 22), 1859. Ludwig, loc. cit., p. 95, pl. 29, fig. 2, 2a; pl. 30, fig. 2, 3, 1860.
- Myrica denticulata Ettings., Foss. Fl. v. Koflach, p. 12, pl. 1, fig. 7, 1857.

This species approaches *Comptonia laciniata* quite closely in Unger's leaves from the Grecian Oligocene, which also closely resemble that style of leaf of the modern species shown on Pl. 2, Fig. 5, a type which is not at all rare on certain of the modern plants of Comptonia.

One of the figured leaves which Heer calls *Myrica graffii* is referable to *vindobonensis* and the other to *laciniata*, which shows how closely these two species are related. In the other direction *vindobonensis* approaches quite near to *aningensis*, such leaves for instance as those of Heer from Switzerland and those of Ettingshausen from Koflach coming very near to the last-mentioned species. As is suggested by its extensive synonymy *Comptonia vindobonensis* as here understood, includes somewhat diverse forms, ranging from the small Planera-like leaves from the Baltic region and the Dryandra-like leaves from Switzerland (*concinna*), through the narrow, more elongated, and but slightly lobed leaves of the French Oligocene (Saporta) and Austrian Miocene (Ettingshausen) to the large-lobed leaves from Hesse which Ludwig referred to this species,

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and to those from Switzerland which Heer referred to *rolleana* and *aventica*.

These variations while somewhat wide in their extremes include numerous gradating forms and are not at all inconsistent with their reference to a single species, especially when we consider the duration of this form from the Eocene through the Miocene, during which time it spread all over Europe and possibly to America as well.

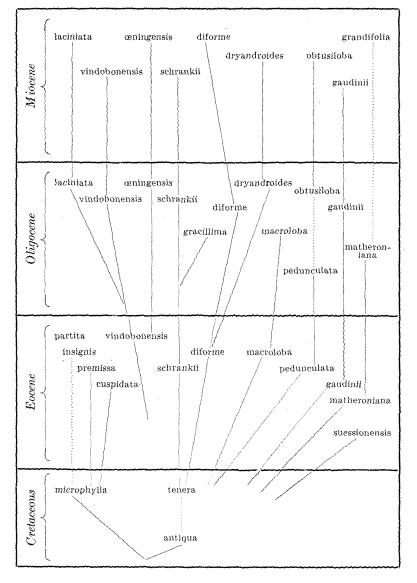


Diagram showing the relationship of the leaves of the fossil species of Comptonia, not necessarily the phylogeny of the plants which bore them.

LIST OF CHANGES IN COMPTONIA NOMENCLATURE

Aspleniopteris difformis Sternb. < Comptonia diforme (Sternb.) Berry. Aspleniopteris schrankii Sternb. < Comptonia schrankii (Sternb.) Berry. Asplenium diforme Sternb. < Comptonia diforme (Sternb.) Berry. Comptonia acutiloba Brongn. < Comptonia diforme (Sternb.) Berry. Comptonia asplenifolia Gaertn.=Comptonia peregrina (Linn.) Coulter. Comptonia breviloba Brongn. < Comptonia schrankii (Sternb.) Berry. Comptonia columbiana Daws. < Comptonia diforme (Sternb.) Berry. Comptonia concisa Wat. < Comptonia macroloba (Web. & Wess.) Berry. Comptonia dryandræfolius Brongn. < Comptonia schrankii (Sternb.) Berry. Comptonia incisa Ludw. < Comptonia gaudinii Heer. Comptonia magnifica Wat. < Comptonia matheroniana (Sap.) Berry. Comptonia meneghinii Ung. < Comptonia æningensis Al. Br. Comptonia rotundata Wat. < Comptonia pedunculata Wat. Comptonia triangulata Wat. < Comptonia gaudinii Heer. Comptonia ulmifolia Ung. < Planera ungeri Ettings. Comptonia vinayi Sap. < Comptonia diforme (Sternb.) Berry. Comptoniphyllum japonicum Nath. < Comptonia gaudinii Heer. Comptoniphyllum naumanni Nath. < Comptonia dryandroides Ung. Comptonites antiquus Nilss. = Comptonia antiqua Nilss. Comptonites dryandræfolius Göpp. < Comptonia schrankii (Sternb.) Berry. Dryandra acutiloba (Brongn.) Ettings. < Comptonia diforme (Sternb.) Berry. Dryandra antiqua Ettings. = Comptonia antiqua Nilss. Dryandra aventica Heer < Comptonia vindobonensis (Ettings.) Berry. Dryandra brongniarti Ettings. < Comptonia schrankii (Sternb.) Berry. Dryandra comptoniafolia Ettings. < Comptonia diforme (Sternb.) Berry. Dryandra gracilis Heer < Comptonia gracillima (Heer) Berry. Dryandra macroloba Web. & Wess.=Comptonia macroloba (W. & W.) Berry. Dryandra meneghinii Ettings. < Comptonia aningensis Al. Br. Dryandra aningensis Ettings. = Comptonia aningensis Al. Br. Dryandra rolleana Heer < Comptonia vindobonensis (Ettings.) Berry. Dryandra saxonica Friedrich < Comptonia diforme (Sternb.) Berry. Dryandra schrankii Heer < Comptonia schrankii (Sternb.) Berry. Dryandra ungeri Ettings. — Comptonia dryandroides Ung. Dryandra vindobonensis Ettings. < Comptonia vindobonensis (Ettings.) Berry. Dryandroides bituminosa Sap. < Comptonia vindobonensis (Ettings.) Berry. Dryandroides concinna Heer < Comptonia vindobonensis (Ettings.) Berry. Dryandroides grandifolius Ettings. = Comptonia grandifolia Ung. Dryandroides laciniatus Ettings. = Comptonia laciniata Ung. Liquidambar asplenifolia Linn. = Comptonia peregrina (Linn.) Coulter. Liquidambar peregrina Linn. = Comptonia peregrina (Linn.) Coulter. Myrica (C.) acutiloba Brongn. < Comptonia diforme (Sternb.) Berry.

Myrica alkalina Lesq. < Comptonia insignis (Lesq.) Berry.

Myrica concinna (Heer) Schimp. < Comptonia vindobonensis (Ettings.) Berry.

Myrica concisa (Wat.) Schimp. < Comptonia macroloba (W. & W.) Berry. Myrica credneri Engelh. < Comptonia gaudinii Heer.

- Myrica (C.) cuspidata (Lesq.) Daws. (non Lesq. or Knowlton) < Comptonia dryandroides Ung.
- Myrica denticulata Ettings. < Comptonia vindobonensis (Ettings.) Berry. Myrica (C.) dryandræfolia Sap. < Comptonia schrankii (Sternb.) Berry.

Myrica (C.) gaudinii Heer = Comptonia gaudinii Heer.

Myrica gracillima (Heer) Schimp. < Comptonia gracillima (Heer) Berry.

Myrica grandifolia (Ung.) Schimp. — Comptonia grandifolia Ung.

- Myrica græffi Heer in part < Comptonia vindobonensis (Ettings.) Berry. in part < Comptonia laciniata Ung.
- Myrica incisa (Ludw.) Schimp. < Comptonia gaudinii Heer.
- Myrica insignis Lesq. Comptonia insignis (Lesq.) Berry.
- Myrica laharpii Heer < Comptonia obtusiloba Heer.

Myrica latiloba Heer= juvenile Comptonia leaves.

- Myrica macroloba Web. & Wess.=Comptonia macroloba (W. & W.) Berry.
- Myrica magnifica (Wat.) Schimp. < Comptonia matheroniana (Sap.) Berry.

Myrica (C.) matheroniana Sap. — Comptonia matheroniana (Sap.) Berry.

Myrica meneghinii Ung. < Comptonia æningensis Al. Br.

Myrica minima Sap. < Comptonia gracillima (Heer) Berry.

Myrica (C.) obtusiloba Heer = Comptonia obtusiloba Heer.

Myrica aningensis (Al. Br.) Heer < Comptonia aningensis Al. Br.

Myrica partita Lesq. = Comptonia partita (Lesq.) Berry.

Myrica (C.) parvifolia Heer < Comptonia microphylla (Heer) Berry.

Myrica (C.) parvula Heer < Comptonia microphylla (Heer) Berry.

Myrica pedunculata Schimp. — Comptonia pedunculata Wat.

Myrica (C.) premissa (Lesq.) Knowlton = Comptonia premissa Lesq.

Myrica pusilla Sap. < Comptonia gracillima (Heer) Berry.

Myrica rotundiloba Sap. < Comptonia obtusiloba Heer.

Myrica suessionensis (Wat.) Schimp. — Comptonia suessionensis Wat.

Myrica (C.) tschernowitziana Engelh. < Comptonia gaudinii Heer.

Myrica ungeri Heer in part < Comptonia vindobonensis (Ettings.) Berry.

in part < Comptonia laciniata Ung.

- Myrica (C.) vindobonensis Heer < Comptonia vindobonensis (Ettings.) Berry.
- Myricophyllum bituminosum Sap. < Comptonia vindobonensis (Ettings.) Berry.

Phyllites antique Nilss. = Comptonia antiqua Nilss.

Pterophyllum difformis Göpp. < Comptonia schrankii (Sternb.) Berry.

Rhus microphylla Heer < Comptonia microphylla (Heer) Berry.

Zamites difformis Presl. < Comptonia schrankii (Sternb.) Berry.

Myrica asplenifolia Linn.= Comptonia peregrina (Linn.) Coulter.

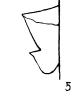
Myrica brongniarti (Ettings.) Lesq. < Comptonia schrankii (Sternb.) Berry.









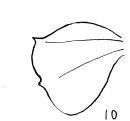


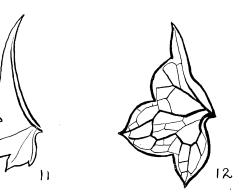






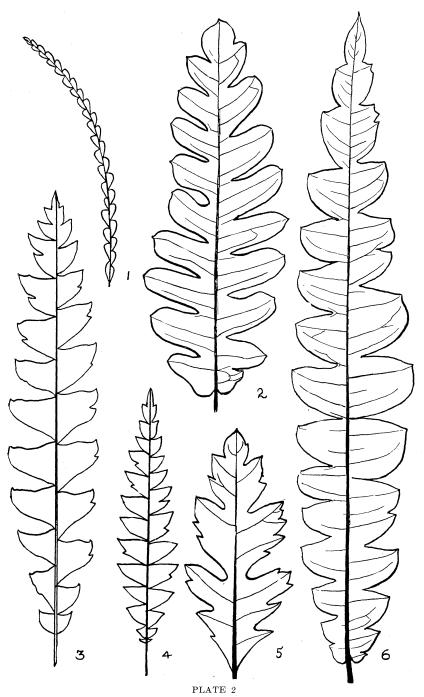




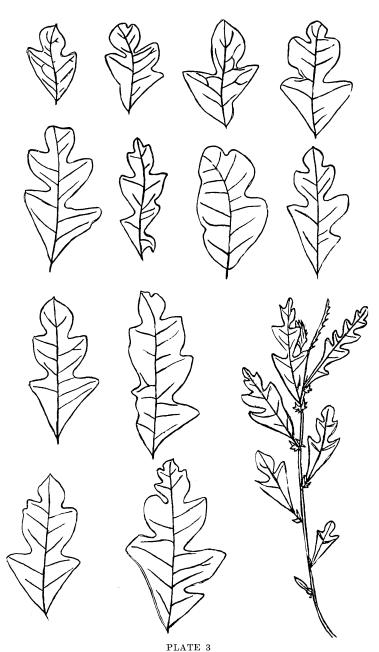




(Figures somewhat enlarged) FIGS. 1-3.— Compound leaves of *Comptonia peregrina* (Linn.) Coulter, FIGS. 4-7.— Basal leaf-lobes of *Comptonia peregrina* (Linn.) Coulter, FIGS. 8-12.— Stipules of *Comptonia peregrina* (Linn.) Coulter,



FIGS. 1-6.— Leaf variations in *Comptonia peregrina* (Linn.) Coulter for comparison with fossil species (all natural size).



Seedling and leaf variations among juvenile leaves of *Comptonia peregrina* (Linn.) Coulter (all natural size).

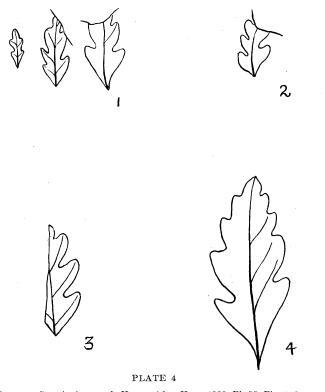


FIG. 1.— Comptonia parvula Heer. After Heer, 1883, Pl. 55, Fig. 1–3.
FIG. 2.— Comptonia antiqua Nilss. After Hisinger, 1837, Pl. 34, Fig. 7.
FIG. 3.— Comptonia parvijolia Heer. After Heer, 1883, Pl. 71, Fig. 1, 2.
FIG. 4.— Comptonia parvula Heer. After Newberry, 1896, Pl. 19, Fig. 6.