

THE NORTH AMERICAN SPECIES OF ASTERELLA.

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INTRODUCTION.

The genus *Asterella* was published by Palisot de Beauvois, probably in 1805,¹ and was based on the two Dillenian species, "Lichen pileatus parvus carinatus, capitulis fimbriatis" and "Lichen pileatus parvus, foliis crenatis."² In the first edition of his *Species Plantarum* (1753) Linnaeus had recognized both of these species and had included them in his composite genus *Marchantia*, giving them the binomial names *M. tenella* and *M. hemisphaerica*. Palisot de Beauvois accepted these specific names and designated his two species *Asterella tenella* and *A. hemisphaerica*. According to modern ideas the genus as originally defined was a composite, its two species no longer being considered congeneric. In spite of this fact it was adequately published and deserves recognition in a restricted sense, if the current rules of nomenclature are followed. Botanists, however, persistently ignored its claims for over 50 years, and many refuse to admit their validity even at the present time. This is due partly to the confusion caused by Lindberg and Trevisan in their attempts to reestablish the genus and partly to the fact that two other genera, proposed for the reception of the Linnaean *M. tenella* and *M. hemisphaerica*, had come in wide use.

The genera in question are *Reboulia* and *Fimbriaria*. *Reboulia* was published by Raddi in 1818³ and was based on *M. hemisphaerica*; *Fimbriaria* was published by Nees von Esenbeck in 1820⁴ and included *M. tenella* and three other species. If Raddi had known of Palisot de Beauvois's genus and had recognized its composite nature, the establishment of a new genus upon either of its component species

¹ Lam. Dict. Sci. Nat. 3: 257. 1805 (?). This citation has been kindly supplied by Dr. John Hendley Barnhart, of the New York Botanical Garden. Dr. Barnhart states that the date is somewhat doubtful but that the volume cited could not have been published later than 1806.

² Hist. Musc. 521. pl. 75, f. 4; 519. pl. 75, f. 2. 1741.

³ Opusc. Sci. Bologna 2: 357. 1818. The name was originally spelled "*Rebouillia*."

⁴ Hor. Phys. Berol. 44. 1820. The name was originally spelled "*Fimbraria*."

would have been a perfectly justifiable procedure, and the name *Asterella* would naturally have been reserved for the remaining species. Even in the absence of such knowledge the retention of the name for *A. tenella* is logically demanded, according to the Vienna Rules, since *Reboulia* preceded *Fimbriaria* by two years. Nees von Esenbeck's genus would then naturally lapse into synonymy, since the other species included in *Fimbriaria* are all congeneric with *A. tenella*. These conclusions seem inevitable and were clearly stated by Underwood¹ over 20 years ago.

Unfortunately Lindberg,² when he revived the genus *Asterella* in 1868, restricted the name to *A. hemisphaerica* instead of to *A. tenella*, although he gives no reason for so doing. Six years later Trevisan,³ in ignorance of Lindberg's action, revived *Asterella* independently, referring to it five species, all congeneric with *A. tenella*. Soon afterwards, however, upon learning of Lindberg's work, he adopted the genus *Asterella* in the Lindbergian sense and revived Corda's genus *Hypenantron* for *A. tenella* and its allies,⁴ the name *Fimbriaria* in his opinion being untenable. At almost the same time Lindberg⁵ also changed, and used *Asterella* in the sense originally suggested by Trevisan (that is, for *A. tenella* and its allies), the name *Reboulia* thus again becoming available for *A. hemisphaerica*. These facts are set forth with much ridicule by Le Jolis,⁶ who advocates the abandonment of the name *Asterella* altogether on account of the different senses in which it has been used, not only by different writers but by the same writers at different times. His arguments would perhaps have more weight if Palisot de Beauvois himself, rather than his successors, had been responsible for the confusion. Since this is not the case, there seem to be no adequate reasons for giving up the name but many good reasons for retaining it in the sense originally suggested by Trevisan, a course which recent writers in America and Scandinavia have consistently maintained. At the same time most European writers still prefer *Fimbriaria*; and both Stephani and Schiffner, at the Brussels Congress in 1910, definitely recommended that *Fimbriaria* and *Reboulia* be placed among the *nomina conservanda*, to the exclusion of *Asterella*.

Of the four species originally assigned to *Fimbriaria* the first, which may be regarded as the type of the genus, was the African *F. marginata* Nees, the remaining species being *F. fragrans* Nees, *F. saccata* (Wahl.) Nees, and *F. tenella* (L.) Nees. During the next

¹ Bot. Gaz. 20: 59. 1895.

² Not. Sällsk. Faun. Fl. Fenn. Förh. 9: 286. 1868.

³ Rend. Ist. Lombardo II. 7: 785. 1874.

⁴ Mem. Ist. Lombardo III. 4: 440. 1877.

⁵ Hep. Utveckl. 49. 1877.

⁶ Mém. Soc. Sci. Nat. Cherbourg 29: 131. 1895.

quarter century the genus gradually increased in size, partly through the transfer of species from other genera and partly through the addition of new species. When the Synopsis Hepaticarum was published in 1847 the number of species recognized had grown to 24. Five of these were recorded from Europe only, 4 from Africa, 7 from Asia, and 2 each from North America, South America, and Australasia; the two remaining species were reported from both Europe and North America, one of them also from Asia. When Stephani published his monograph of the genus in 1899,¹ the number of species, in spite of certain reductions to synonymy, had more than doubled, 69 being recognized. Three of these are recorded from Europe only, 14 from Africa, 15 from Asia, 16 from North America, 7 from South America, and 11 from Australasia and the Hawaiian Islands; the remaining three species are reported from both Europe and North America, one being reported in addition from Asia, and one from South America. According to the records at hand 28 species, 5 from Africa, 11 from Asia, 3 from North America, 3 from South America, and 6 from the Pacific islands, have been published since 1899, thus raising the total to 97. The majority of these additions were made by Stephani in the sixth volume of his Species Hepaticarum (1917). The writer hopes to show, however, that several of the species recognized by Stephani should be reduced to synonymy, and it is possible that others deserve the same fate.

Trevisan's attempt to replace *Fimbriaria* by *Hypenantron* was based on the existence of an older algal genus *Fimbriaria*, published by Stackhouse in 1809. Since this name was soon repudiated by its author and has been ignored by practically all later algologists, Le Jolis claims that it has no nomenclatorial standing, and that it ought not to stand in the way of maintaining *Fimbriaria* Nees as a valid genus. Fortunately the adoption of *Asterella* makes it unnecessary to decide this point. *Hypenantron* as originally described by Corda² contained a single species, the Swiss *H. ciliatum*. Since no description of this species is given, other than that included in the generic diagnosis, its identity would be in doubt if Nees von Esenbeck³ had not listed it among the synonyms of *Fimbriaria fragrans*. Following the example of Trevisan, certain European writers recognized *Hypenantron* for a while, but it enjoyed a short-lived vogue and has few or no adherents at the present time.

Two other synonyms, *Rhacotheca* Bisch. of 1844⁴ and *Octoskepos* Griffith of 1849,⁵ remain to be considered. *Rhacotheca* was based on

¹ Bull. Herb. Boiss. 7: 84-110, 198-214. 1899.

² Oplz, Beitr. Naturg. 648. 1828.

³ Naturg. Eur. Leberm. 4: 268. 1838.

⁴ Seubert, Fl. Azor. 12. pl. 14. 1844.

⁵ Not. Pl. Asiat. 2: 343; Icon. Pl. Asiat. 2: pl. 69D, f. 1. 1849.

a single species of the Azores, *R. azorica* Bisch., and was admitted into the Synopsis Hepaticarum and several subsequent works. Schiffer reduced the genus to synonymy in 1893,¹ and its single species is now considered identical with *Fimbriaria africana* Mont., or *Asterella africana* (Mont.) Underw., as it should be called, a species known from Madeira, the Canary Islands, and Algeria, as well as from the Azores. *Octoskepos* was likewise a monotypic genus, being based on *O. khasianus* Griffith, of the Himalayas. Mitten, in 1861,² reduced it to synonymy under *Fimbriaria*, to which genus he transferred the single species, and it is retained in this position by Stephani.

Of the North American species recognized by Stephani in his monograph the following eight were originally described by American writers: *A. bolanderi*, *A. palmeri*, and *A. violacea* by Austin; *A. austini*, *A. pringlei*, and *A. wrightii* by Underwood; *A. lateralis* and *A. nudata* by Howe. The remaining species were all described by Europeans. Soon after the appearance of Stephani's monograph Howe³ published an account of the species occurring in California and found it necessary to reduce *A. nudata* to synonymy under *A. palmeri*. His treatment of the genus, which is remarkably full and clear, is accompanied by detailed illustrations of most of the Californian species and has been of great assistance to the writer in the preparation of the present report.

MORPHOLOGICAL NOTES ON THE GENUS.

The species of *Asterella* grow on earth, often among rocks, and sometimes form depressed mats of considerable extent. Although the genus has many tropical representatives, it extends as far south as Chile, Australia, and New Zealand, and as far north as Greenland, Alaska, Siberia, and Scandinavia. The European species, in fact, are characteristically alpine or arctic in their distribution, and most of them are found also in the northern parts of America and Asia. The genus includes both xerophytic and mesophytic species, some of the latter being at times almost hygrophytic in their appearance. Pigmentation with purple or red is a common phenomenon, although certain species usually show no signs of it. The pigmentation is especially well marked in xerophytic species, in which the thallus becomes involute upon drying, but it is often found almost as abundantly under more mesophytic conditions. The ventral surface is the first region to be affected, but pigmented dots or blotches

¹ Engl. & Prantl, Pflanzenfam. 1²: 33. 1893.

² Journ. Proc. Linn. Soc. Bot. 5: 126. 1861.

³ Mem. Torrey Club 7: 46-57. pl. 95-99. 1899.

often appear on the dorsal surface and a broad purple margin is sometimes a distinctive feature. The receptacles, both male and female, may also be subject to pigmentation.

Many of the structural features of *Asterella* were clearly described by Leitgeb¹ in 1881, in connection with his work on the more complex Marchantiales. He assigned the genus to his group Operculatae, partly on account of the method of dehiscence of the capsule, but partly also on account of the morphology of the female receptacle, as he conceived it. Campbell,² in 1895, showed that Leitgeb's interpretation of the receptacle would not apply to the Californian *Asterella californica* (Hampe) Underw., in which the female receptacle is of the type associated with the group Compositae, and it has since been shown that there are other species of *Asterella* and other genera of the Operculatae to which Leitgeb's interpretation will not apply. Although one of the latter author's most important distinctions between the Operculatae and the Compositae has thus been proved inconstant, the groups are still to be regarded as natural assemblages of genera, a fact which Cavers³ has recently emphasized.

Two types of branching are regularly found in *Asterella*, terminal branching by forking and intercalary branching by means of ventral outgrowths arising from the sides of the thickened median portion of the thallus. The terminal branches are broad from the beginning; the intercalary branches broaden out abruptly from a narrow stalk-like base. A supplementary type of branch, also intercalary in nature, is the apical innovation. This arises usually when the growth of a thallus is limited by the formation of an inflorescence, and the power of forming such branches does not appear to be at all general. As pointed out by Leitgeb, an abundant production of one type of branch is associated with a limited production of the other. Dichotomous branching, in fact, is characteristic of certain species, while ventral branching is characteristic of others. It is doubtful, however, if one type ever replaces the other altogether. In certain species the receptacles seem to be confined to ventral branches, which are usually limited in growth and are sometimes greatly abbreviated; in other species the receptacles are much less definite in position.

The thallus shows the usual differentiation into epidermis, green tissue with air spaces, and compact ventral tissue, the lower surface bearing scales and rhizoids of the two characteristic types. The epidermal cells exhibit considerable variety with regard to size and thickness of wall, but seem to be arranged invariably in a single layer. The variation in size is sometimes marked on an individual

¹ Unters. Leberm. 6: 84-87, pl. 4. 1881.

² Mosses and Ferns 57. f. 19. 1895.

³ New Phytol. Repr. 4: 34. 1911.

thallus, so that differences in size are not of much value in distinguishing the species. The thickness of the walls is also rather inconstant: in some cases the walls are distinctly and uniformly thickened; in others they are exceedingly thin. In fact, a great deal of variation in this respect is often found in a single species under different environmental conditions. Trigones, as a rule, are not present, but in certain species they form a more or less conspicuous feature of the epidermal cells. Scattered cells containing oil bodies occur in certain species and are sometimes distinguished from the other epidermal cells by their smaller size, as well as by their contents.

The epidermal pores on the vegetative thallus are of the simple type usual in the Operculatae. The opening is surrounded by a hyaline membrane representing the vestiges of a ring of disorganized cells, and around this are narrow and specialized cells arranged in radiating and concentric series. The pores vary in relative abundance, in size, and in number of specialized cells by which the openings are surrounded, and a great deal of variation is often to be found in a single species. In an average case each pore is surrounded by six radiating series of cells with three in each series, the outer cells being scarcely different from the ordinary epidermal cells. In some species the walls separating the radiating series of cells are more or less thickened, and this condition may be so marked that the pores acquire a stellate appearance, similar to what is found in most members of Leitgeb's *Astroporae*. Pores of this type, however, are very exceptional; it is much more usual for the radial walls to be only slightly thickened or even thin throughout. In most cases the pores project but slightly above the dorsal surface of the thallus.

The green tissue is built up on the *Reboulia* type¹ and incloses several layers of air chambers separated by partitions one cell thick. In some species the tissue is very loose, the air chambers being large; in other species the tissue is more or less compact. When the tissue is loose the dorsal chambers may not be subdivided at all, and each chamber under these conditions has its epidermal pore. This is the case, for example, in *A. tenella*, *A. ludwigii*, and *A. palmeri*. Even when the tissue is loose, however, the dorsal chambers may be somewhat subdivided by supplementary partitions, as in *A. lindenbergiana* and *A. californica*, and some of the chambers seem on this account to be destitute of pores. When the tissue is compact the subdivision of the dorsal chambers is carried much further, so that narrow and canal-like secondary chambers are formed, only a few of which show pores. *A. elegans* and *A. bolanderi* are good examples of this type. When a thallus is studied in cross section, the secondary partitions look as if they were free filaments and they have some-

¹ See Evans, Bull. Torrey Club 45: 235. 1918.

times been described and figured as such. It is doubtful, however, if actual filaments ever occur, even in the vicinity of the pores, although marginal cells of partitions may project as teeth. Cells containing oil bodies are scattered among the green cells, even when they do not occur in the epidermis.

The compact tissue forms a distinct keel in the median portion of the thallus and thins out more or less gradually on the sides, disappearing altogether at some distance from the margin. The keel formed is usually broad and rounded, but is narrow and sharp in *A. lindenbergianu*, where it constitutes one of the distinctive features of the species. The compact tissue is composed of uniform parenchyma, except for scattered cells with oil bodies. The walls are sometimes thin throughout, but are usually thickened to a greater or less extent and then show crowded and minute pits of the simple type. In certain species mycorrhiza is usually present, and it sometimes occupies a broad median strand, elliptical in section. The walls of the cells containing the mycorrhiza often, but not always, show a distinct purple pigmentation; otherwise the compact tissue is colorless or nearly so. In *A. californica* scattered slime cells may usually be observed, not only in the compact tissue but also in the partitions between air spaces. These cells vary greatly in abundance, and are sometimes absent altogether.

The ventral scales, as in most of the Marchantiales, are arranged in two longitudinal rows. As a rule the scales of one row alternate with those of the other, but this relationship is not always apparent. In specialized regions, such as the basal portion of a ventral branch or the terminal portion of a branch bearing a female receptacle, the arrangement tends to be irregular, and it is sometimes difficult to distinguish the two rows clearly. The scales often yield valuable characters in distinguishing species, but in considering them a certain amount of variability must be assumed and it is unwise to draw conclusions from too limited a number of examples. The scales are often exceedingly fragile, especially on plants developed in the shade or under moist conditions, and it is necessary to dissect them one by one from a mature thallus in order to secure an adequate idea of their form and structure. The division of the scales into basal portion and appendage or appendages is usually well marked, although the transition is sometimes very gradual. The basal portion is ovate to lunulate and is composed of cells distinctly smaller than those of the appendages. In most cases the marginal cells are considerably smaller and more irregular than those of the median portion. The margin itself is either entire or more or less denticulate, the teeth often representing the short and irregular stalks of slime papillae. Scattered about among the other cells are occasional cells containing

oil bodies, but rhizoid-initials are apparently not present. The appendages vary in number from one to four, when the genus as a whole is considered, and a good deal of variation is to be expected in most of the species. In certain cases, to be sure, a single appendage is the rule, but even here prolonged search will usually bring to light scales with two appendages. Sometimes, under these circumstances, one appendage is smaller than the other or appears in the form of a basal lobe. The appendages vary greatly also in size, in form, in the character of the margin, and in the apex, many of the variations being associated with environmental differences. In certain cases specific differences have been based upon these inconstant features. Stephani, for example, described the appendages of *A. wrightii* as being sometimes armed with a single large spine, and on the basis of this character placed the species in a group with dentate or lacerate appendages, instead of in the same group as *A. elegans*, of which it is actually a synonym. In this case the marginal teeth represent a somewhat unusual feature, possibly associated with a more xerophytic environment. He likewise assigns acuminate appendages to *A. tenella*, in which, as a matter of fact, rounded appendages are not infrequent.

The inflorescence in *Asterella* may be paroicous, autoicous, or dioicous. As a rule, each species shows a definite type of inflorescence, but certain autoicous species sometimes exhibit a tendency toward a dioicous condition. When the inflorescence is paroicous, as in *A. tenella*, the antheridia form a vaguely defined cluster close to the base of the stalk of the female receptacle. Such an androecium is very slightly elevated, the ostioles are low, and there is no surrounding fringe of narrow scales. In the autoicous species the androecium is more clearly defined. In some cases, as in *A. pringlei*, it forms an elongated and slightly elevated median patch which may be forked; the ostioles are more pronounced than in the paroicous species, and a scanty fringe of paleae may be present. Such an androecium apparently never limits the growth of the branch and makes its appearance at some distance behind the apex. In other cases, as in *A. elegans*, the androecium forms an oval or circular disk, distinctly elevated, and usually with a well-developed fringe of paleae. Such an androecium limits the growth of the branch and thus appears terminal in position. In *A. californica*, the only definitely dioicous species at present known in America, the androecium is of the elongated type, which does not limit the growth of the branch. So far as observed, the epidermal pores of the androecia are simple.

The female receptacle is borne on an elongated peduncle composed of compact parenchyma throughout and showing on its morphologically ventral side a single furrow with tuberculate rhizoids.

The peduncle is sometimes white or pale green but usually shows more or less purple pigmentation. In most species it bears scattered filamentous scales, these tending to be more numerous in the apical portion, but in certain species the scales are scanty or even absent altogether. The peduncle arises from the apex of a branch, the growth of which is almost invariably brought to an end. This branch is sometimes elongated and sometimes very short; in the latter case it is usually ventral in position, although in some instances one or both branches of a dichotomy may give rise to female receptacles almost immediately. Leitgeb mentions a single specimen of *A. ludwigii* (*Fimbriaria pilosa*) in which an abortive female receptacle failed to limit the growth of a branch, and makes the deduction that such limitation must therefore be a secondary, rather than a primary, result of the development of the receptacle and that the latter is dorsal in origin. No examples of this kind have come to the attention of the writer, but the remarkable conditions sometimes found in *A. californica* may be noted in this connection. In this species, as figures by Howe¹ clearly show, the receptacle may grow out from the bottom of a dichotomy, an ordinary branch appearing on each side. This would seem to indicate a dorsal origin, the apical region of the branch continuing its growth but undergoing a dichotomy at once. The subject, however, deserves further study.

The disk of the female receptacle, as already noted, has been the subject of considerable discussion. In the earliest developmental stages described by Leitgeb the archegonia, three or four in number, had already become displaced to the ventral surface through the active intercalary growth of the dorsal portion. They appear singly in low grooves, evenly distributed near the periphery, which at first shows no indication of lobing. Alternating with the archegonia are short furrows with rhizoids, continuous with the furrow of the peduncle. Since the archegonia occurred singly, Leitgeb concluded that the receptacle did not represent a branch system. Campbell found, however, that the archegonia of *A. californica* did not occur singly but in short radiating groups, those of each group arising in acropetal succession, and he concluded that in this species the receptacle must represent a branch system. According to the ideas of Goebel² such distinctions, which Leitgeb considered characteristic of the groups Operculatae and Compositae, are less important than has been supposed. In both cases the receptacle represents a branch; if the receptacles are similar in other respects, it is not of much significance whether this branch becomes subdivided or not.

¹ Mem. Torrey Club 7: pl. 95, f. 1-5. 1899.

² For a discussion of these ideas see Evans, Bull. Torrey Club 42: 271-274. 1915.

As development proceeds, the dorsal portion of the disk increases further in size and develops active photosynthetic tissue with air spaces in several layers. Those of the uppermost layer are bounded on the outside by an epidermis with pores of the compound or dolioform type. Sometimes the surface is fairly smooth, but in certain species the ceiling of each chamber projects in a vaultlike way, the surface thus becoming coarsely tuberculate. In *A. echinella* the projections reach an extreme development, attaining a height of a millimeter, and the surface acquires an almost spiny appearance. Sometimes the margin of the disk remains undivided, but more or less distinct lobes are usually developed, each lobe corresponding to an archegonium or group of archegonia. On the ventral surface two protective structures, in addition to the calyptra, make their appearance, although they remain abortive in the absence of fertilization. These structures are the involucre and the pseudoperianth.

The involucre, as Leitgeb noted, is not uniform throughout the genus. In the more usual cases it represents an outgrowth of the sides of the groove in which an archegonium (or group of archegonia) is situated and is then continuous with the edges of the lobes, forming a thin membranous expansion. This expansion, which never incloses the sporophyte on the outer side, is only one cell thick along the margin and is composed of colorless cells, among which scattered cells with oil bodies stand out conspicuously. When the margins of the lobes are strongly involute, the involucre is relatively narrow, as in *A. palmeri*, but this condition is exceptional, the involucre often attaining a width of 1 to 1.5 mm. Between the sporophyte and the peduncle the halves of the involucre become continuous, although there is sometimes a deep indentation in this region. When it is unusually deep, as in *A. californica*, the involucre appears to be divided into two parts. The involucre in such species as *A. africana* deviates somewhat from this account, as Leitgeb clearly shows. It represents a short membranous flap between the sporophyte and the peduncle, gradually narrowing out on the sides and reaching only part way to the margin. In all cases the margin of the involucre is either entire or vaguely and irregularly crenulate or denticulate.

The pseudoperianth is the most distinctive structure found in the genus and at once separates *Asterella* from all the other genera of the Operculatae. It consists of a tubular membranous sheath, narrowed at the apex to a small pore but more or less strongly inflated throughout the rest of its extent. When the sheath is young it is perfectly continuous, and this condition seems to be long maintained in the Persian *Fimbriaria silachorensis* Schiffn.,¹ a species allied to *A. ludwigii*. In most cases, however, the pseudoperianth becomes

¹ Oesterr. Bot. Zeitschr. 58: 229. pl. 7, f. 1. 1908.

longitudinally split at a comparatively early age, the splits beginning close to the apical pore and extending for a variable distance toward the base. In most cases the segments thus formed remain united at the apex, the wind sifting in between them and thus scattering the spores; but in a few species the segments become completely free with age. The number of segments varies usually from 8 to 16 but, more rarely, between wider limits. A good deal of variation, in fact, is sometimes encountered in a single species. With regard to color, also, the pseudoperianth varies. In certain species it is, apparently, always colorless; in others, such as *A. lindenbergiana*, it shows a deep purple pigmentation; in still others it may be colorless, or pigmented in varying degree. Although so distinctive for the genus as a whole, the characters derived from the pseudoperianth often have to be employed with considerable caution in distinguishing species.

If Goebel's ideas are to be accepted, the distinct discoid androecium found in certain autoicous species represents the most primitive type, because it approaches most closely the stalked androecia of *Marchantia* and *Preissia*. The median elongated androecia, with or without paleae, would then represent a more advanced type which has arisen through reduction, and the poorly defined androecia of the paroicous species would represent the most advanced condition found in the genus. A gradual loss of the power of limiting growth would be associated with this reduction. Of course here, as in other genera, the female receptacle is more conservative than the male, retaining its stalk even when the androecium has almost lost its individuality. It retains also its compound pores, which have come down to it from its more complex ancestors, while the androecia seem to have lost them altogether.

Similar deductions might be drawn from the related genus *Grimaldia*, although the conditions shown are less diverse. In *G. fragrans* (Balb.) Corda, for example, the androecium is much the same as in *A. elegans*, while in *G. dichotoma* Raddi it bears a strong resemblance to that of *A. pringlei*. Here again the epidermal pores are of the simple type. So far as the androecia are concerned, *Reboulia* occupies a somewhat intermediate position between the more complex genera and *Asterella*. The androecia are clearly defined, as in *A. elegans*, and often limit the growth of the branches bearing them, but they still show epidermal pores of the compound type; these pores, however, are composed of fewer tiers of cells than those of the female receptacle.¹

The sporophyte is of the type characteristic of the Operculatae. It consists of a bulbous foot, an exceedingly short stalk, and a rela-

¹ See Cavers, *Naturalist* 1904: 248. *f. 4.* 1904.

tively large capsule of a general globose form. The wall of the capsule is composed of a single layer of cells and is usually deep brown in color. The cell walls are more or less thickened and often show trigones; annular and spiral thickenings, however, are absent altogether. The upper part of the wall forms a more or less distinct circular lid, which falls off intact or in fragments, leaving behind a cup-shaped portion with an entire or irregularly dentate or lacerate margin.

The great importance of the spores in *Asterella* for taxonomic purposes has been emphasized by Howe.¹ It must be kept in mind, however, that the spores vary greatly in size, in color, and in surface markings, the differences often being due to varying conditions during critical stages of development. Spores, for example, which would be large, deeply pigmented, and coarsely reticulated under the best conditions, might be much smaller, paler, and almost smooth if the conditions had been bad. Taking the genus as a whole, the spores are of a fair size and show a distinct tetrahedral form, the base being represented by a spherical triangle; upon this base the surface markings usually attain their most typical development. The other three faces of the spore are plane triangles. On the six edges of the spore distinct membranous wings are present; these often vary considerably in width, even in a single species, and the wings bounding the spherical face are usually broader than the three wings formed at the junction lines of the plane faces. The outer wall layer, which of course yields the distinctive markings, is always more or less pigmented with yellow, brown, or purple, and sometimes becomes so nearly opaque that the markings are difficult to demonstrate. These markings are of two types: fine, irregular points or lines, representing local and often pigmented regions of thickening in the membrane; and coarser ridges, representing folds of the membrane. Sometimes the fine markings are the only ones present, and sometimes they anastomose to form a delicate and irregular reticulum. The coarser ridges in many cases unite to form a more regular reticulum, but they are often crowded together irregularly or unite vaguely and indiscriminately. The distinctive features of the spores will be considered in greater detail in connection with the individual species.

The pigmentation which is so characteristic of the spores usually affects the elaters also, although in a lesser degree. In most cases it is restricted to the spiral bands, but sometimes the rest of the wall is more or less colored, in rare cases to such an extent that the spirals are detected with difficulty. The number of spirals varies from one to three and is not always the same throughout the entire length of an elater. In *A. elegans*, for example, the middle portion usually

¹ Bull. Torrey Club 25: 191. 1898.

shows two spirals, while the ends show only one. Considerable variation in both length and diameter is to be expected.

SYSTEMATIC TREATMENT.

The subdivisions of the genus which have been proposed have not been very widely accepted. In the Synopsis Hepaticarum two subgenera of *Fimbriaria* are recognized. In the first, to which no special name is assigned, are placed the "species genuinae," characterized by a pseudoperianth which definitely surpasses the involucre; in the second, called *Brachyblepharis*, the pseudoperianth is said to be but little longer than the involucre, and the latter is described as being remote from the margin of the receptacle. The first subgenus is further divided into two sections, the first with pendent pseudoperianths, the second with horizontally spreading pseudoperianths.

Many years later Stephani¹ proposed a division into two groups (or sections), based on the structure of the thallus. In the first group, *Spongiosae*, the thallus is said to be comparable to that of *Ricciella*; in the second group, *Marchantioides*, it is said to have chlorophyllose filaments.

Schiffner² combined both classifications under the generic name *Hypenantron*. To his first group, the equivalent of the first subgenus of the Synopsis, he gave the name *Euhypenantron* and retained the name *Brachyblepharis* for the second. He regarded the groups as sectional in value, however, rather than as subgeneric. Under the first section he included Stephani's two groups.

In Stephani's monograph of 1899 these attempts at classification are ignored and a new classification, based primarily on the form of the female receptacle, is proposed. Four subdivisions are recognized. In the first the receptacles are described as disciform; in the second, as hemispherical in the center; in the third, as distinctly conical; in the fourth, as highly umbonate. Under each of these subdivisions (except the last) subordinate groups are recognized, based on differences in the appendages of the ventral scales.

Although many of the distinctions thus noted are often helpful in separating species, some of them at least are based on vague and inconstant characters, and the writer feels that they are hardly sufficient to characterize subgenera or even sections. This view seems to have been held by Howe, who made no attempt to divide the genus into subordinate groups, and Müller also, in his treatment of the European species, leaves the genus intact.

In the preparation of this paper the writer has had the privilege of examining the specimens in several herbaria and would express

¹ Hedwigia 31: 122. 1892.

² Engl. & Prantl. Pflanzenfam. 1³: 34. 1893.

his thanks to the various curators who have made this possible. In citing specimens under the individual species the following abbreviations are used: N. Y., for the herbarium of the New York Botanical Garden; H., for the herbarium of Harvard University; U. S., for the United States National Herbarium; C., for the herbarium of the Canadian Geological Survey; C. C. H., for the herbarium of Miss Caroline C. Haynes; and Y., for the herbarium of Yale University.

Duplicate types of the new species proposed have been deposited in the United States National Herbarium.

KEY TO THE SPECIES.

- a.* Dichotomous branching the usual type, ventral branching rare or lacking... *b.*
a. Dichotomous branching rare or lacking, ventral branching the usual type; dorsal air chambers subdivided by numerous supplementary partitions, the epidermal pores apparently fewer than the chambers..... *j.*
b. Dorsal air chambers not subdivided by supplementary partitions; epidermal pores clearly as numerous as the dorsal chambers..... *c.*
b. Dorsal air chambers more or less subdivided by supplementary partitions; epidermal pores apparently fewer than the chambers..... *f.*
c. Cells with oil bodies present in the epidermis; cells immediately surrounding the epidermal pores with thin radial walls; inflorescence parolcous; segments of pseudoperianth becoming free with age; spores yellow, coarsely reticulate (at least on the spherical face)..... *d.*
c. Cells with oil bodies lacking in the epidermis; cells immediately surrounding the epidermal pores with thickened radial walls; segments of pseudoperianth not becoming free with age; spores dark brown to nearly black, not coarsely reticulate..... *e.*
d. Female receptacle distinctly lobed, smooth or nearly so; spores mostly 80 to 90 μ in diameter, the surface with fine lines in addition to the coarse reticulum..... 1. *A. tenella* (p. 261).
d. Female receptacle scarcely lobed, covered with low and coarse tubercles; spores mostly 60 to 65 μ in diameter, the surface punctulate.
2. *A. ludwigii* (p. 266).
e. Inflorescence autoicous; female receptacle hemispherical, with low and coarse tubercles and short but distinct lobes; pseudoperianths extending obliquely outward..... 3. *A. pringlei* (p. 271).
e. Inflorescence parolcous; female receptacle bluntly conical, smooth or nearly so, scarcely lobed; pseudoperianths extending almost vertically downward..... 4. *A. palmeri* (p. 273).
f. Xerophytic in habit, the margins of the thallus strongly incurved when dry..... *g.*
f. Not xerophytic in habit, the margins of the thallus scarcely or not at all incurved when dry..... *h.*
g. Appendages of the ventral scales 1 or 2, forming a conspicuous white cluster at the tip of the thallus; inflorescence monoicous; spores with wings and a fine surface reticulum, but without coarse ridges on the faces.
5. *A. saccata* (p. 276).
g. Appendages of the ventral scales (mostly) 2 to 4, not forming a conspicuous white cluster at the tip of the thallus; inflorescence dioicous; spores with coarse ridges on the faces, in addition to the wings and the fine surface reticulum..... 6. *A. californica* (p. 280).

- h. Pseudoperianth with purple segments..... 7. *A. lindenbergiana* (p. 283).
 h. Pseudoperianth white or pale throughout..... i.
 i. Thallus 1.5 to 4 mm. broad, the margins not closely undulate-crispate. 8. *A. venosa* (p. 286).
 i. Thallus 8 to 10 mm. broad, the margins closely undulate-crispate. 9. *A. rugosa* (p. 289).
 j. Not xerophytic, the margins scarcely or not at all incurved when dry---- k.
 j. More or less xerophytic, the margins incurved when dry; sexual branches short; spores with coarse reticula on the faces, the meshes mostly 15 to 20 μ in diameter..... n.
 k. Male branches variable in length; spores with coarse reticula on the faces, the meshes 8 to 20 μ in diameter..... l.
 k. Male branches short; spores with fine and irregular reticula on the faces, the meshes mostly 2 to 8 μ in diameter..... 15. *A. versicolor* (p. 307).
 l. Meshes on spore surface mostly 15 to 20 μ in diameter..... m.
 l. Meshes on spore surface mostly 8 to 12 μ in diameter. 13. *A. reticulata* (p. 302).
 m. Tubercles of female receptacle less than 0.5 mm. long. 10. *A. elegans* (p. 290).
 m. Tubercles of female receptacle 0.5 to 1 mm. long. 11. *A. echinella* (p. 298).
 n. Pseudoperianth mostly 8 to 10-cleft; reticula on spore surfaces rarely involving the marginal wings; elaters mostly 12 to 14 μ wide. 12. *A. lateralis* (p. 299).
 n. Pseudoperianth mostly 10 to 16-cleft; reticula on spore surfaces usually involving the marginal wings; elaters mostly 8 to 12 μ wide. 14. *A. bolanderi* (p. 303).

1. *Asterella tenella* (L.) Beauv.

Marchantia tenella L. Sp. Pl. 1137. 1753.

Asterella tenella Beauv.; Lam. Dict. Sci. Nat. 3: 257. 1805 (?).

Fimbriaria tenella Nees, Hor. Phys Berol. 45. 1820.

Fimbriaria nigripes Bisch.; Lehm. Nov. Stirp. Pugill. 6: 19. 1834.

Fimbriaria tenella β *porphyrocephala* Bisch. Nov. Act. Acad. Caes. Leop. Carol. 17: 1023. pl. 69, f. II. 1835.

Fimbriaria tenella γ *brachypus* Gottsch., Lind. & Nees, Syn. Hep. 563. 1847.

Fimbriaria brachypus Mont. loc. cit., as synonym.

Fimbriaria mollis Tayl. Lond. Journ. Bot. 5: 411. 1846.

Hypnantron tenellum Trevis. Mem. Ist. Lombardo III. 4: 440. 1877.

Hypnantron molle Trevis. op. cit. 441. 1877.

Thallus bright green, often more or less pigmented with purple, especially on the ventral surface and along the margin, mostly 0.5 to 1.5 cm. long and 1.5 to 3 mm. wide, plane or somewhat concave, with undulate margins, branching regularly by forking, very rarely by ventral outgrowths, keel broad and rounded; epidermis composed of cells with slightly thickened walls, sometimes showing trigones, averaging about $40 \times 25 \mu$; pores slightly or not at all elevated, averaging (with their surrounding cells) about $40 \times 30 \mu$; surrounded by (4 to) 6 series of cells with 2 (or 3) cells in each series; cells containing oil bodies few and scattered, occurring in the epidermis, the green tissue, and the compact ventral tissue; green tissue loose, the air chambers in 4 or 5 layers (in the median portion), those of the dorsal layer larger than the others, not subdivided, each with an epidermal pore; compact tissue occupying about half the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about halfway to the margin, composed of cells with more

or less thickened, pitted walls; mycorrhiza sometimes present in the ventral tissue; ventral scales ovate to lunulate, more or less pigmented, cells containing oil bodies mostly 10 or fewer, scattered, appendages 1 or 2, narrowly to broadly ovate, mostly 0.25 to 0.45 mm. long and 0.15 to 0.3 mm. wide, entire or more or less dentate on the margin, the teeth very irregular, the apex acute to rounded, the cells in median portion mostly 40 to 80×30 to 50μ , the marginal somewhat smaller; inflorescence paucicous, the antheridia forming a small indefinite group close to the peduncle of the female receptacle; ostioles low and inconspicuous; peduncle naked, often more or less pigmented with purple, 2 cm. long when well developed; disk of receptacle mostly 2 to 4 mm. across, the center hemispherical, smooth or nearly so but becoming rugose when dry, the lobes mostly four, short but distinct, extending obliquely downward, the margins and the deeply bifid involucre entire or irregularly sinuate or crenate; pseudoperianth mostly 8 to 12-cleft, hyaline or more or less pigmented with yellow or purple, the divisions finally free, ovate to lanceolate; capsule opening by a circular line of dehiscence above the middle, the operculum coming off in one piece; spores yellow, 70 to 110μ in diameter (mostly 80 to 90μ), with wavy wings 8 to 15μ wide along the edges, the entire surface covered with a system of numerous fine and irregular lines, sometimes anastomosing, the spherical face showing in addition a coarse and regular reticulum, the meshes mostly 16 to 18μ wide, inclosed by the marginal wing and a series of similar anastomosing ridges, each plane face usually with an irregular transverse ridge distinct from the wings; elaters yellow, straight or somewhat curved, mostly 140 to 200μ long (rarely 300μ) and 10 to 12μ wide, slightly tapering toward the blunt ends, the median portion with 2 (very rarely 3) spirals, one or both of the ends often with a single spiral for a variable distance.

The present species is widely distributed in eastern North America, its known range extending from Maine and Ontario to Georgia and Alabama, with a westward extension to Illinois, Missouri, and Texas. So far as the writer has been able to learn, all reports from localities outside this area have been based on incorrect determinations. The plants are largely, if not entirely, confined to the lowlands. They prefer relatively damp soil and may often be found in old fields, along roadside banks, or among rocks bordering streams. On account of their delicacy they are not well fitted for a xerophytic environment. In most cases the plants grow scattered or in small clusters but they sometimes form extensive mats, the numerous receptacles on their slender stalks giving them a distinctive and beautiful appearance under favorable conditions. There is little danger of confusing *A. tenella* with other members of the genus, since none of our species, with the possible exception of *A. echinella*, are known to encroach upon its range. When sterile, however, it has often been confused with *Reboulia hemisphaerica* and *Grimaldia fragrans*, to both of which it bears a certain resemblance. The following specimens have been examined:

ONTARIO: Windsor, 1892, *J. Macoun* 404 (N. Y.).

MAINE: Buckfield, 1877, *J. A. Allen* (Y.); Monmouth, *Merrill* 3 (N. Y., Y.); Kittery Point, *Thaxter* (H., Y.). First reported from Maine by the writer (*Rhodora* 5: 170. 1903), no localities being given.

NEW HAMPSHIRE: Cornish, 1904, *Haynes* 723b (Y.; listed by the writer in *Rhodora* 7: 58. 1905).

VERMONT: Jerico, *Evans* (Y.); Newfane, *Grout* (Y.); East Pownal, *Lorenz* 167 (N. Y.); Woodstock, *Kittridge* (N. Y.). Recorded by C. D. Howe (*Contr. Bot. Vermont* 3: 9. 1899); an earlier record of Frost seems to have been based on an incorrect determination.

MASSACHUSETTS: Amherst, 1871, *Jesup* (C.); Amesbury, *Huntington* (C. C. H., Y.); Wellesley, *Hallowell* (H.), *Cummings* (N. Y.); Bridgewater, *Crocker*

(N. Y.) ; Middlesex Falls, *Underwood* 2825 (N. Y.). First reported from Massachusetts by Tuckerman & Frost (Cat. Pl. Amherst Coll. 52. 1875), no localities being given.

RHODE ISLAND: Providence, *J. F. Collins* 1850 (C. C. H., Y.). First reported from Rhode Island by Bennett (Pl. Rhode Island 66. 1888), no localities being given.

CONNECTICUT: Hamden, 1868, *D. C. Eaton* (Y.) ; Redding, *Underwood* (N. Y.) ; Woodbridge, *F. W. Hall* (Y.) ; Orange, *Evans* (N. Y., Y.) ; Middletown, New Milford, Cheshire, Salisbury, and North Haven, *Evans* (Y.) ; East Haven, *J. A. Allen* (Y.) ; Andover, *Weatherby* (Y.) ; Bolton and Bethany, *Nichols* (Y.) ; Canterbury, *Hadley* ; Oxford, *Harger* (Y.) ; Weathersfield, *C. Wright* (H.). First reported from Connecticut by Eaton (Cat. Berzelius Soc. 68. 1878).

NEW YORK: Stiles, 1889, *Underwood* (N. Y.), *Fischer* (C., N. Y., U. S., Y.) ; distributed in *Underwood & Cook*, Hep. Amer., no. 44, as *Fimbriaria tenella* ; Crotona Park, New York City, *Santal* (N. Y.) ; northern Washington County, *Mrs. R. C. Burnham* (Y.).

NEW JERSEY: Closter, 1861, *Austin* (C.) ; Hoboken, 1818, *J. Torrey* (?) (N. Y.) ; Bergen, *Austin* (N. Y.) ; Little Falls, *Underwood* (N. Y.) ; Bound Brook, *Stout* (N. Y.). First recorded from New Jersey by Torrey (Cat. Pl. N. Y. 84. 1819), the locality given being Bergen. Distributed, presumably from New Jersey material, by Austin, in Hep. Bor. Amer., no. 136, as *Fimbriaria tenella*.

PENNSYLVANIA: Reading, 1828, *T. G. Bischoff* (Lindenberg Herbarium, type of *Fimbriaria nigripes* Bisch. and *F. tenella* β *porphyrocephala* Bisch.) ; Philadelphia, *Lyon* (N. Y.; listed by Taylor, as *Fimbriaria mollis*, in Lond. Journ. Bot. 5: 411. 1844), *T. P. James* (N. Y.).

DELAWARE: Faulkland, 1886, *Commons* (N. Y., U. S.).

MARYLAND: Near Lanham, 1905, *Wheeler* (U. S.).

DISTRICT OF COLUMBIA: Washington and Rock Creek, 1889, *Coville* (U. S., Y.) ; beneath Chain Bridge near the Virginia side, *Rosen* (U. S.).

VIRGINIA: Alexandria, specimen from the James Herbarium (N. Y.) ; near Brandywine, *Ravenel* (Y.) ; Great Falls, *Mary F. Miller* 124 (C. C. H., U. S.). The type material of *Marchantia tenella* L. was collected in Virginia by J. Clayton.

NORTH CAROLINA: Hillsboro, *Curtis* (N. Y.) ; near Crowders Mountain, *H. A. Green* (U. S.). First reported from North Carolina by Curtis (Geol. & Nat. Hist. Surv. N. C. 3: 75. 1867), no localities being mentioned.

SOUTH CAROLINA: Chester, 1884, *H. A. Green* (C. C. H., U. S.) ; Summerville, *DuBois* (N. Y.).

GEORGIA: Toccoa Falls, 1891. *Underwood* 2559 (N. Y., U. S.) ; Rocky Face Mountain, Whitfield County, and between Lafayette and Pigeon Mountain, Walker County, *Harper* (N. Y., U. S.).

ALABAMA: Auburn, Lee County, 1897, *Earle & Baker* 20, 35, 47 (N. Y., U. S.).

MISSISSIPPI: Enterprise, 1897, *Tracy* 3084 (N. Y.).

OHIO: Waverly, 1889, *Herrick* (N. Y.). First reported from Ohio by Beardslee (Bot. Gaz. 1: 22. 1876), no localities being mentioned.

INDIANA: Owen County, 1893, *Underwood* (N. Y.).

ILLINOIS: Canton, 1880, *Wolf* (U. S.) ; Cobden, *Seymour* (N. Y.) ; near Williamsfield, *V. H. Chase* (Y.). First reported from Illinois by Wolf & Hall (Bull. Ill. State Lab. Nat. Hist. 1: 18. 1878).

TENNESSEE: Jackson, 1893, *Bain* 10 (N. Y.).

MISSOURI: Mine La Motte, *O. D. Allen* (Y.) ; Perryville, *Demetrio* 12 (N. Y., U. S.) ; Campbell, *Bush* 7 (N. Y.) ; Elmout, *Emig* 1007 (Y.).

ARKANSAS: Little Rock, *G. Engelmann* (N. Y.).

LOUISIANA: Sicily Island, specimen from the Hooker Herbarium (N. Y.; type of *Fimbriaria mollis*); Chateaugues, *Langlois* (C. C. H., U. S.); Mandeville, *Frère Celestin* (C. C. H., U. S.); without definite locality, *Short* (N. Y.).

TEXAS: Hunt County, *Saunders* (N. Y., Y.); College Station, 1914, *Blodgett* (N. Y., Y.); Austin, *McAllister* (N. Y., Y.).

First reports from Ontario, New York, Delaware, South Carolina, Georgia, Indiana, Tennessee, and Missouri were made apparently by Underwood (*Bot. Gaz.* 20: 60. 1895), no localities being mentioned in any case.

Asterella tenella was one of the first distinctively American liverworts to be described. Accompanying the description of Dillenius an older synonym of Clayton is quoted, as follows: "Lichen terrestris pileatus Clayt. n. 377. apud Gronov. *Fl. Virg.* p. 127." This quotation, however, deserves a word of explanation. In the first part of the first edition of the *Flora Virginica*, published in 1739, the work to which Dillenius refers, Gronovius does not list Clayton's plant as a distinct species but merely as a synonym of "*Hepatica vulgaris major, vel officinarum, Italiae. Mich. Pl. Gen.* p. 3." Now Mitchell's plant is clearly *Conocephalum conicum* (L.) Dum., and Dillenius recognized the fact that Clayton's plant was amply distinct, because he added to his citation the phrase, "Ubi recidendum synonymon *Mich.*" It is of interest to note that Gronovius, in the second part of his *Flora Virginica*, published in 1743, follows the example of Dillenius and accepts Clayton's species, although he uses the Dillenian name. He adds the curious observation that the plant, mixed with black pepper, is recommended for use in case of mad dog bites. In a later edition of the *Flora Virginica*, published in 1762, Gronovius again lists the species, quoting the description from the *Species Plantarum* as authoritative, without adopting the binomial name which Linnaeus had proposed.

In the original description Dillenius gives as the English equivalent of his Latin polynomial, "The small channelled Liverwort, with fringed Caps." He calls attention to the forked branching of the thallus, to the abundance of the receptacles, and to the fringes at the margin of the disk, the color being described as whitish in the lower part and purple above. His figures show most of these features clearly and bring out in addition the long and slender stalks of the female receptacles. He cites the species from Virginia only, basing it entirely upon Clayton's specimens, and Linnaeus likewise restricts it to the same locality. The American origin of the species is thus adequately established. Before long, however, certain European writers confused *A. tenella* with various Old World species and assigned to it a very extensive geographical distribution. The confusion which thus arose will be considered more fully in connection with the following species. It came to an end in 1836, when Taylor¹ definitely restricted the name *Fimbriaria tenella* to plants from the United States, and since this date the species has rarely been reported from other localities.

The two synonyms, *Fimbriaria nigripes* and *F. mollis*, may now be considered. *F. nigripes* was based on specimens collected near Reading, Pennsylvania, in 1828, by T. G. Bischoff, an uncle of the author of the species. In the original description, which was written presumably by Lindenberg, the plant was compared with *F. tenella* and was said to differ in its terete, dark purple peduncles, in its larger umbonate receptacles, and in the inflexed purple segments of its pseudoperianth, the apices alone being white and hyaline. In *F. tenella* the peduncles were said to be striated and brown, the receptacle to be much smaller and not umbonate, and the segments of the pseudoperianth to be plane and white throughout. The year after the publication of *F. nigripes*, Bischoff himself reduced it to a variety *porphyrocephala* of *F. tenella*, and illustrated his

¹ *Trans. Linn. Soc.* 17: 386. 1836.

account with a series of excellent figures. He still accepted the species in a broad sense, including under it various Old World material, and called attention to the great variability in color which the plants sometimes exhibited. He was also the first, apparently, to note that the elaters varied with respect to the number of spirals, one of the elaters figured being unispiral throughout, and another bispiral in the middle and at one end and unispiral at the other. Some of Bischoff's material in the Lindenberg Herbarium at Vienna has been examined by the writer and is clearly attributable to *A. tenella*.

Taylor's species, *F. mollis*, was based on two specimens. The first of these, which may be considered the type of the species, was collected at "Sicily Island, near New York," and came from the Hooker Herbarium; the second was collected near Philadelphia and came from G. I. Lyon's herbarium. The Sicily Island material is well represented in the Mitten Herbarium, but there is no island of that name in the vicinity of New York. There is, however, a place called Sicily Island in northeastern Louisiana, and it is probable that the specimens were collected there. This idea is supported by a second specimen in the Mitten Herbarium, collected in Louisiana, presumably by C. W. Short, and dated 1837. In all essential respects the two specimens are identical. According to Taylor's description, *F. mollis* is characterized by a pale green thallus; by purple scales with a single lanceolate tooth on each side; by a short twisted peduncle, brown below and yellowish green above; by a succulent hemispherical receptacle, soft and compressible; and by whitish or pale yellow, concave, obtuse segments on the pseudoperianth, with incurved margins. These features might easily come within the limits to be expected in a variable species, and some of them are due to immaturity, as the specimens in the Mitten Herbarium clearly show. The species, in fact, enjoyed but a short period of recognition. Although it was listed in the Synopsis in 1847, it was reduced to a synonym of *F. tenella* by Sullivant in 1856¹ and has since found no advocates.

A few other items dealing with the history of the species may be of interest. In 1803 Michaux² listed it from Canada, but this record must be considered doubtful on account of the rarity of the species within the Canadian boundaries. In 1819, Torrey³ recorded it from "Bergen;" fortunately this record is fully supported by a correctly named specimen, collected in 1818 on "hills at Hoboken" and preserved in the Torrey Herbarium, Hoboken being situated in Bergen County, New Jersey. In 1821 Schweinitz⁴ reported it from Pennsylvania and New York, but these records according to Nees von Esenbeck⁵ were based on specimens of *Grimaldia fragrans*. In the Synopsis Hepaticarum a variety γ *brachypus* is recognized, in addition to the typical form of the species and Bischoff's variety *porphyrocephala*. It was based on a manuscript species, *F. brachypus* Mont., collected in "Carolina." This variety, as the Synopsis admits, is distinguished by vague and unimportant characters, and there seems to be no good reason for recognizing it.

Stephani's account of *Asterella tenella* is full and accurate on the whole, although the ventral scales are far more variable than he implies. According to his description they are large and purple, with a large and hyaline, obliquely triangular, "acuminato, acuto" appendage, and on the basis of these features he places the species in a group with lanceolate appendages, thus separating it widely from some of its closest allies. As a matter of fact, the appendages

¹ In A. Gray, Man. ed. 2. 688. 1856.

² Fl. Bor. Amer. 2: 276. 1803.

³ Cat. Pl. N. Y. 84. 1819.

⁴ Spec. Fl. Amer. Crypt. 23. 1821.

⁵ Naturg. Eur. Leberm. 4: 225. 1838.

show a wide range of variation, especially with respect to the margin and apex. The margin, for example, may be quite entire or it may be more or less dentate, the teeth varying from vague crenations to distinct lobelike structures, 3 or 4 cells long and 2 or 3 cells wide at the base. With regard to the apex, the acute condition seems to be the most usual, but obtuse or even rounded apices may often be demonstrated. In spite of their fairly large size the ventral scales are very delicate; along their margins scattered and short-lived slime papillae may often be detected, even on the appendages, and the pigmentation sometimes extends from base to apex. The appendages, moreover, sometimes occur in pairs. Stephani's description of the spores as "grosse lobato-cristatae" hardly implies their reticulate surface markings, and his account of the pseudoperianth as "hyalina" seems to ignore the purple pigmentation which it often shows. These, however, are points of minor importance.

Since there are no other species of *Asterella* in eastern North America, it is usually easy to recognize *A. tenella* in the field, even when sterile. The plants in most cases are distinctly aromatic and this will help to separate the species from the more robust *Reboulia hemisphaerica*, while the delicate and inconspicuous scale appendages are very different from the large and prominent appendages of *Grimaldia fragrans*, which usually form a conspicuous cluster at the apex of the thallus. The outlines of the dorsal air chambers can usually be seen with the aid of a lens in the *Asterella* but not in the other two species; and the flat thallus, showing little tendency to become involute upon drying, is also distinctive.

2. *Asterella ludwigii* (Schwaegr.) Underw.

- Marchantia tenella* Retz. Fl. Scand. Prodr. ed. 2. 270. 1795, not L. 1753.
Marchantia polycephala Schleich. Cat. Pl. Helv. ed. 2. 31. 1807, nomen nudum.
Marchantia pilosa Wahl. Fl. Lapp. 399. 1812, not Hornem.
Marchantia ludwigii Schwaegr. Hist. Musc. Hep. Prodr. 33. 1814.
Marchantia gracilis F. Web. Hist. Musc. Hep. Prodr. 105. 1815.
Marchantia nana Schleich. Cat. Pl. Helv. ed. 4. 1821, nomen nudum.
Fimbriaria nana Lindenb. Nov. Act. Acad. Caes. Leop. Carol. 14: Suppl. 109. 1829.
Fimbriaria pilosa Tayl. Trans. Linn. Soc. 17: 386. pl. 13, f. 3. 1837.
Fimbriaria schleicheriana Corda; Nees, Naturg. Eur. Leberm. 4: 273. 1838, as synonym.
Dictyochiton pilulare Corda, op. cit. 280. 1838, as synonym.
Fimbriaria gracilis Lindb. Not. Sällsk. Faun. Fl. Fenn. Förh. 10: 282. 1868.
Asterella pilosa Trevis. Rend. Ist. Lombardo II. 7: 785. 1874.
Fimbriaria ludwigii Limpr.; Cohn, Krypt. Fl. Schles. 1: 340. 1876.
Hypenantron gracile Trevis. Mem. Ist. Lombardo III. 4: 440. 1877.
Hypenantron nanum Trevis. loc. cit.
Hypenantron pilosum Kuntze, Rev. Gen. Pl. 1: 89. 1891.
Asterella gracilis Underw. Bot. Gaz. 20: 61. 1895.
Asterella ludwigii Underw. loc. cit.
Fimbriaria macounii Stephani, Bull. Herb. Boiss. 7: 99. 1899.

Thallus green, often more or less pigmented with purple, especially on the ventral surface and along the margin, mostly 0.5 to 1.5 cm. long and 1 to 2 mm. wide, but often 3 to 5 mm. wide on broadened-out fertile plants, plane or somewhat concave, with thin undulate margins, sometimes more or less incurved when dry, branching regularly by forking, the keel broad and rounded; epidermis composed of cells with thin or slightly thickened walls, usually with more or less distinct trigones, averaging about $25 \times 20 \mu$; pores slightly elevated, averaging (with their surrounding cells) about $80 \times 65 \mu$, surrounded by

6 (rarely by 5, 7, or 8) series of cells with 2 (or rarely 3) cells in a series; cells containing oil bodies as in *A. tenella*; green tissue loose, the air chambers in 4 or 5 layers (in the median portion), those of the dorsal layer larger than the others, apparently never subdivided, each with an epidermal pore; compact tissue occupying from one-third to one-half the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about halfway to the margin, composed of cells with slightly thickened, pitted walls; mycorrhiza not observed; ventral scales ovate to lunulate, deeply pigmented, sometimes vaguely crenulate or denticulate; cells containing oil bodies mostly 15 or fewer, scattered (rarely 2 side by side); appendages 1 or (rarely) 2, slightly or not at all constricted at base, lanceolate to ovate, rarely broadly ovate, mostly 0.2 to 0.6 mm. long and 0.15 to 0.3 mm. wide, entire or vaguely crenulate, the apex mostly acute to acuminate, rarely rounded, the cells in median portion mostly 50 to 80×25 to 40μ , the marginal ones somewhat smaller; inflorescence parvicous, the antheridia forming a small irregular group close to the peduncle of the female receptacle, the ostioles low and inconspicuous; peduncle naked or with a very few scattered paleae, more or less pigmented with purple, 3 cm. long when well developed; disk of receptacle about 2 mm. across, hemispherical, covered with low tubercles, the lobes mostly 3, scarcely evident, extending obliquely downward, the margins and the narrow involucre entire or nearly so; pseudoperianth mostly 8-cleft, hyaline, the divisions soon becoming free and irregularly spreading, narrowly lanceolate; capsule opening by a circular line of dehiscence above the middle, the operculum coming off in one piece; spores yellow, mostly 60 to 65 μ in diameter, with a wavy wing 6 to 10 μ wide along the edges, the entire surface minutely and sometimes indistinctly punctulate, the spherical face covered over with a coarse reticulum (sometimes irregularly or incompletely developed), the meshes mostly 9 to 12 μ wide, inclosed by the marginal wing and a system of anastomosing ridges of a similar character, each plane face sometimes with a similar reticulum and sometimes with a single transverse ridge connected with the wings; elaters yellow, variously curved and contorted, mostly 150 to 200 μ long and 8 to 10 (rarely up to 14) μ wide, distinctly tapering, the median portion with 2 or 3 spirals, the ends with 2 spirals.

The geographical distribution of this arctic and alpine species is extensive. In North America it is known from Greenland, the Rocky Mountains, and the Pacific Coast region; in Europe, from Finland and Scandinavia, from Iceland, from the mountains of eastern Germany, and from the Alps; in Asia, from Japan. The plants grow on earth among rocks and rarely occur abundantly. The following specimens from Europe and North America have been examined:

ALBERTA: Southeast end of Pabocton Pass, 1908, *Brown* 1086 (N. Y., Y.).

BRITISH COLUMBIA: Yale, 1875, *J. Macoun* (C., N. Y.); Eagle Pass, west of Revelstoke, *J. Macoun* (C., N. Y.); Mount Erskine, Salt Spring Island, Gulf of Georgia, *J. Macoun* (C., N. Y., U. S., Y.; listed, as *F. tenella*, by Pearson in List Canad. Hepat., 27. 1890; distributed under the same name by Macoun, Can. Hep., no. 73; listed, as *A. gracilis*, by Underwood in Bot. Gaz. 20: 62. 1895; type of *F. macounii* Steph.); Victoria and vicinity, *J. Macoun* (C. C. H., N. Y.; distributed, as *A. gracilis*, by Macoun, Can. Liv., no. 4); Agassiz, *J. Macoun* (C., N. Y.); Sproat, *J. Macoun* (N. Y.); Comax, Vancouver Island, *J. Macoun* (N. Y., U. S., Y.; distributed, as *F. pilosa*, in Can. Hep., no. 72); Hector, *J. Macoun* (same distribution); Goldstream, *J. Macoun* (C.); Kicking Horse Lake, *J. Macoun* (C., N. Y.); Chilliwack, *J. M. Macoun* (C., N. Y.). Many of these specimens are listed by Macoun in Cat. Can. Pl. 7: 4. 1902.

MONTANA: Long Baldy, Little Belt Mountains, 1896, *Flodman* 5 (N. Y., U. S.); Sperry Glacier, *Jones* 10690 (Y.).

COLORADO: Foothills 5 miles west of Fort Collins, 1896, *Baker* (U. S.); Boulder, *Bethel* 4 (Y.); near Tolland, *Young* (Y.). The second and third specimens have been listed by the writer, as *A. gracilis*, in *Bryologist* 18: 45. 1915.

UTAH: Headwaters of Little Cottonwood Creek, above Alta, 1905, *Rydberg* 6869a (N. Y.); Big Cottonwood Canyon, above Silver Lake Post Office, *Garrett* (N. Y., Y.).

WASHINGTON: Yakima region, 1882, *T. S. Brandegee* (N. Y.; listed by Underwood, as *A. gracilis*, in *Bot. Gaz.* 20: 62. 1895); Tacoma, *Flett* (Y.); Mount Rainier, *Piper* 93 (N. Y.), *Flett* (Y.); Queets River Valley, Olympic Mountains, *Frye* 53 (Y.); bluffs near Cathlamet, *Foster* 513 (C. C. H., Y.; listed, as *A. gracilis*, by Miss Haynes in *Bryologist* 12: 65. 1909); Gate, Pierce County, *Foster* (C. C. H., N. Y., U. S., Y.; distributed by Miss Haynes in *Amer. Hep.*, no. 106, as *A. gracilis*).

OREGON: Snow line, Mount Adams, 1894, *Lloyd* (N. Y.).

CALIFORNIA: Near Mineral Spring, Tulare County, *Coville & Funston* 1420, 1510 (N. Y., U. S.; listed by Coville, as *F. bolanderi*, in *Contr. U. S. Nat. Herb.* 4: 230. 1893; also by Underwood, as *A. gracilis*, in *Bot. Gaz.* 20: 62. 1895).

FINLAND: Lojo, Skraddarla, 1878, *Lindberg* (C.).

SWEDEN: Gottsund, Upsala, *Myrin* (N. Y.); Jönköping, Småland, *Arnell* (C. C. H., Y.; distributed by Husnot, as *A. pilosa*, in *Hep. Gall.*, no. 170).

NORWAY: Dovres Kongswold, 1854, *Zetterstødt* (N. Y.); Tjöme, *Bryhn* (Y.); Opdal, Vangohen, *Hagen* (C. C. H.).

GERMANY: Near Charlottenbrunn, Weissertztal, Silesia, 1860, *Milde* (N. Y., Y.; distributed by Gottsche & Rabenhorst, as *F. pilosa*, in *Hep. Eur.*, no. 161).

SWITZERLAND: Locality not stated, 1806, *Schleicher* (N. Y.; labeled *Marchantia polycephala*).

ITALY: Mont-Cenis, date and collector's name wanting (N. Y.); Valsesia, *Carestia* (N. Y.; distributed in *Erb. Critt. Ital.*, II., no. 956, as *F. pilosa*).

Among the species which certain writers have confused with *A. tenella* a prominent place is held by *A. ludwigii*. Apparently the first to fall into this error was the Danish botanist Zoëga,¹ who recorded *Marchantia tenella* somewhat doubtfully from Iceland. His example was soon followed by the Swedish botanist Retzius, who listed the species from Scandinavia, at first doubtfully² and then positively, as indicated in the synonymy. *M. tenella* was afterwards included in a number of floristic works by other early writers, especially in Sweden and Germany, but all these records, so far as known, were based on *A. ludwigii*.

Early in the nineteenth century Schleicher discovered the species in Switzerland and distributed specimens under the name *Marchantia polycephala*. Unfortunately he failed to establish this name by adequate publication. A few years later Wahlenberg found the plant in the parish of Folden in northern Norway. He recognized the fact that it was the same as the *M. tenella* of Zoëga and Retzius but he made the error of confusing it with *Marchantia pilosa* Hornem.,³ now known as *Neesiella pilosa* (Hornem.) Schiffn. Of course this makes the name *M. pilosa* Wahl. a mere homonym of *M. pilosa* Hornem. and therefore without nomenclatorial standing; but certain later writers have attempted to maintain the validity of both names, citing the present species as *Asterella pilosa* (Wahl.) Trevis. or *Fimbriaria pilosa* (Wahl.) Tayl.

¹ In Olafsen & Povelens, *Reise igiennem Island*, Tilhang 14. 1772.

² *Fl. Scand. Prodr.* 222. 1779.

³ *Fl. Dan. pl.* 1426. 1810.

Soon after Wahlenberg's account of the plant, under the incorrect name *M. pilosa*, had been published, *M. ludwigii* Schwaegr. and *M. gracilis* F. Web. were proposed as new. *M. ludwigii* was cited from Germany and doubtfully from Switzerland; later publications show that the type specimens were collected by Ludwig in the Sudetic Mountains of Silesia, no more definite locality being given. *M. gracilis* was based on material collected by Wahlenberg in the vicinity of Upsala, Sweden. The latter species has long been recognized as a synonym of *M. pilosa* Wahl., but the status of *M. ludwigii* has been doubted. Nees von Esenbeck,¹ for example, in citing it as a possible synonym, suspected that it might really represent *Grimaldia fragrans*. Gottsche implies that this doubt was unfounded. In the critical remarks which he appends to Rabenhorst's Hep. Eur. no. 161, where material collected in Silesia by J. Milde is distributed, he alludes to Ludwig's specimens and to Nees von Esenbeck's remarks, and speaks of Milde's *rediscovery* of the species. Limpricht is even more definite, citing *M. ludwigii* as a synonym and following the citation with an exclamation point. Since, however, he recognizes the validity of *M. pilosa* Wahl., at least provisionally, he retains the name *Fimbriaria pilosa* for the species and merely proposes *F. ludwigii* as an alternative name, in case *F. pilosa* should ever be given up. As shown above, *Marchantia pilosa* Wahl. is untenable and therefore the names *Fimbriaria pilosa* and *Asterella pilosa* can not be maintained. The combination *Asterella ludwigii*, first tentatively proposed by Underwood, is therefore advocated.

When Nees von Esenbeck proposed the genus *Fimbriaria*, he cited his fourth species, *F. tenella*, from Virginia and Canada only. *Marchantia gracilis*, *M. ludwigii*, and *M. pilosa* he gave as possible members of the genus, but did not definitely include them on account of the fact that the divisions of their perianths become free. A few years later² he included *M. gracilis* and *M. ludwigii* among the synonyms of *F. tenella* and cited the species from Sweden, Germany, Switzerland, and Java, as well as from Virginia. He therefore fell into the old error of Zoëga and Retzius, which Wahlenberg, Schwaegrichen, and Weber had escaped. This error was repeated by Lindenberg,³ by Hübener,⁴ and by Bischoff,⁵ who understood *F. tenella* in the same broad sense. When Taylor definitely restricted the name *F. tenella* to North American plants and gave the name *F. pilosa* to the European plant, Nees von Esenbeck accepted his distinctions. At first, however, he continued to cite the Javan specimens under *F. pilosa*. In the Synopsis Hepaticarum he made these Javan specimens the type of a new species, *F. blumeana* Nees, and included under *F. pilosa* a long series of European specimens and also a specimen from Greenland, collected by Vahl, this being the first record for North America.

Lindenberg's *Fimbriaria nana* was based on Swiss material collected by Schleicher and distributed as *Marchantia nana*. Without having seen specimens, Nees von Esenbeck accepted the species in his Naturgeschichte, but stated that it might perhaps be nothing more than a form of *F. pilosa*. It is retained also in the Synopsis Hepaticarum, where no doubt is thrown on its validity. Later writers on Swiss Hepaticae rarely mention *F. nana*, although it is accepted as a species by both Dumortier⁶ and Sydow.⁷ In 1899 Stephanl included

¹ Naturg. Eur. Leberm. 4: 273. 1838.

² Nov. Act. Acad. Caes. Leop. Carol. 12: 411. 1825.

³ Nov. Act. Acad. Caes. Leop. Carol. 14: Suppl. 100. 1829.

⁴ Hep. Germ. 6. 1834.

⁵ Nov. Act. Acad. Caes. Leop. Carol. 17: 1022. 1835.

⁶ Hep. Eur. 158. 1874.

⁷ Leberm. Deutschl. Oesterr. Schweiz 79. 1882.

it as a doubtful synonym under *F. pilosa*, and Müller¹ has since reduced it definitely to synonymy. The characters which Lindenberg assigned to it might easily come within the range of variability to be expected in a species of *Asterella*.

The known range of *A. ludwigii* in North America has been gradually extended since the time of Nees von Esenbeck. In 1875 Berggren cited several new stations for Greenland, and other stations have since been added by Lange, C. Jensen, and Stephani. In 1884 Underwood recorded the species from British Columbia, in 1891 from Washington, and in 1895 from California. In 1915 the writer listed two stations from Colorado, and stations from Montana, Utah, and Oregon are reported in the present paper. The stations in British Columbia were given in detail by Pearson in 1890 and by Macoun in 1902. One specimen, which was cited by Underwood in 1895 under *Asterella gracilis*, has been the cause of considerable confusion. It was collected by Macoun on Salt Spring Island in the Gulf of Georgia and is listed by Pearson under the name *Fimbriaria tenella*, the station being given as Vancouver Island. By Stephani this specimen was made the type of a new species, *F. macounii*. According to his description the appendages of the ventral scales are oblong or ovate and rounded at the apex, while in *F. pilosa* (as he calls it) the appendages are said to be lanceolate and sharp-pointed. These differences are, unfortunately, inconstant, and the other differential characters brought out in the description are equally subject to variation. The writer therefore has no hesitation in reducing *F. macounii* to synonymy.

Although the ranges of *A. tenella* and *A. ludwigii* do not overlap, and although one is an inhabitant of temperate lowlands while the other prefers arctic regions and mountains, the two species have many features in common, and it is not surprising that they have given rise to much confusion. They are both of about the same size; they branch regularly by forking; they show a loose green tissue, the dorsal air chambers being undivided and each having an epidermal pore; the appendages of their ventral scales are similar in both form and size; their inflorescence is paricous; the peduncles of their female receptacles are nearly or quite destitute of paleae; their disks are hemispherical; their pseudoperianths are normally 8-cleft, the divisions separating sooner or later; and they both have yellow spores, distinctly reticulated on the spherical face. These resemblances show a close relationship between the species. In separating them certain characters derived from the ventral scales, the female receptacles, the divisions of the pseudoperianths, the spores, and the elaters can usually be relied on. In *A. tenella* the appendages of the scales, if enough are examined, show examples with distinct marginal teeth; the female receptacles have a smooth or almost smooth surface and distinct though short lobes; the divisions of the pseudoperianth often show a purple pigmentation and tend to be ovate; the spores are mostly 80 to 90 μ in diameter, the surface is marked with fine lines, and the plane faces show short ridges not extending all the way across; the elaters, finally, often show a single spiral at one or both ends. In *A. ludwigii*, on the contrary, the appendages either are entire or show vague crenulations only; the female receptacles are covered over with low tubercles and their lobes are scarcely apparent; the divisions of the pseudoperianth are uniformly white and lanceolate; the spores are mostly 60 to 65 μ in diameter, the surface is punctulate, and the plane faces are sometimes reticulated and always show ridges extending all the way across; the elaters, finally, show (apparently always) 2 spirals at each end. Perhaps on account of its inclement habitat, the plants of *A. lud-*

¹ Rabenh. Krypt. Fl. 6: 273. 1907.

wighti tend to show a less luxuriant development than those of *A. tenella*, and the thallus often appears simple on account of the death of the older parts.

3. *Asterella pringlei* Underw.

Asterella pringlei Underw. Bot. Gaz. 20: 64. 1895.

Fimbriaria pringlei Stephani, Bull. Herb. Bolss. 7: 96. 1899, not Stephani, Rev. Bryol. 36: 139. 1909.

Thallus sometimes green throughout, becoming brownish or purplish with age, but usually somewhat pigmented with purple even when young, especially on the ventral surface, mostly 1 to 1.5 cm. long and 3 to 5 mm. wide, plane or slightly concave, with thin, undulate, more or less crispate and crenate margins, branching most frequently by forking, more rarely by apical innovations, apparently never by ventral outgrowths, the keel broad and rounded; epidermis composed of thin-walled cells without trigones, averaging about $40 \times 25 \mu$; pores somewhat elevated, mostly isodiametric (at least in the median portion), measuring (with their surrounding cells) 40 to 60 μ in diameter, surrounded by 4 to 6 series of cells, with 2 cells in each series, the cells next the opening with more or less thickened radial walls; cells with oil bodies not observed in the epidermis, otherwise as in *A. tenella*; green tissue compact below, looser above, the air chambers in 4 or 5 layers, those of the dorsal layer larger and higher than the others, not subdivided, each with an epidermal pore; compact tissue occupying about three-fifths the thickness of the thallus in the median portion, thinning out gradually or abruptly on the sides and extending from one-half to two-thirds the distance to the margin, composed of cells with thin unpitted walls; mycorrhiza not observed; ventral scales contiguous, not reaching the margin, usually more or less pigmented with purple, ovate, the cells containing oil bodies mostly 1 to 3; appendages borne singly or rarely in pairs, broadly subulate and not constricted at the base, often hyaline, mostly 0.7 to 1 mm. long and 0.15 to 0.45 mm. wide at the base, the margin entire or irregularly spinose-dentate, the teeth mostly 1 to 5, 1 to 6 cells long and 1 or 2 cells wide at the base, each tooth as well as the acute to short-acuminate apex tipped with a more or less persistent slime papilla, sessile papillae of a similar nature often present also, the cells throughout appendage mostly $40 \times 30 \mu$; inflorescence autoicous; male inflorescence consisting of a long and narrow median cluster of antheridia, not surrounded by paleae, borne on an ordinary branch and not limiting its growth, the ostioles long and slender; peduncle naked, arising from the apex of a more or less elongated branch, yellow to brown, not pigmented with purple, mostly 1 to 1.5 cm. long; disk of receptacle mostly 3 to 4 mm. across, green to purple, hemispherical, covered with low and coarse rounded tubercles, the lobes mostly 4, short but distinct, extending obliquely downward, the margins and the involucre entire or nearly so; pseudoperianth mostly 12 to 16-cleft, white or pale, the divisions lanceolate, coherent at the apex; capsule circumscissile above the middle by a jagged line, the small operculum coming off in one piece; spores dark brown, sometimes almost opaque, mostly 80 to 120 μ in diameter, with a wing 6 to 8 μ wide along the edges, the entire surface covered with a system of fine and irregular darker ridges 1 to 2 μ high, on a paler background, the ridges sometimes anastomosing and forming an irregular network with meshes 2 to 4 μ across and sometimes not, the surface sometimes showing in addition a system of low and broader folds about 4 μ high and more or less anastomosing but never forming a network, the periphery of spores appearing coarsely or finely crenulate; elaters brown, more or less curved, mostly 200 to 220 μ long and 12 to 16 μ in diameter, tapering slightly toward the rounded ends,

sometimes with a single spiral throughout but usually with 2 spirals in the median portion for a variable distance.

Known only from central Mexico; inhabiting damp banks and rocks. The following specimens have been examined:

JALISCO: Near Guadalajara, 1890, *Pringle* (N. Y., type); Barranca de Oblatos, Guadalajara, *Barnes & Land* 121 (Y.).

VERACRUZ: Near Orizaba, *Barnes & Land* 671 (Y.).

This interesting and distinct species is still known from very few localities, so few in fact that its range of variability may be greater than the description implies. The type material in the Underwood Herbarium represents a somewhat more lax and delicate form than the specimens collected by Barnes and Land, but the plants agree closely in their more essential features and there is little doubt regarding their identity. Underwood's original description calls attention to the general aspect of the thallus, to the most important characteristics of the female receptacle and its peduncle, to the white pseudoperianths with their coherent segments, and to the dark spores covered over with narrow reticulations. He assigns to the spores, however, a diameter of 118 to 135 μ , which is a trifle high, and states that the elaters have 2 or 3 spirals, making no allusion to the fact that they are unispiral at each end and sometimes throughout their entire extent. He makes no mention, moreover, of the various tissues composing the thallus or of the male inflorescence, and his account of the ventral scales as "slender whitish [and] lanceolate" omits mention of the curious teeth which their appendages often show.

Stephani's description is somewhat more explicit and supplies some of the deficiencies in the original account. He notes the monoicous inflorescence; the occurrence of the antheridia on leading branches; the small epidermal pores, each surrounded by 6 radiating series of cells with 2 cells in each series; and the large hyaline appendages of the ventral scales, sometimes armed with a spine. At the same time a few of his statements are open to criticism. He describes the branching, for example, as being usually by apical innovations, and adds that the female branches always arise from the side of costa. According to the writer's observation, apical innovations are rare and the female inflorescence is borne on a leading branch produced by forking, agreeing in this respect with the male inflorescence. Stephani's description of the spores as "grosse tuberculatae" is also misleading.

The ventral scales present several features of interest. The basal portion is normally pigmented with purple, but often shows a broad hyaline border. Its cells decrease slightly in size toward the margin, but do not show the marked increase in irregularity which is usual in the genus; and the slime papillae are short-lived and inconspicuous. The small number of cells containing oil bodies is also noteworthy. The appendages are remarkable for their large size and wide range of variability. At their junction with the basal portion they are scarcely constricted, as Stephani notes, and from this rather broad base they taper gradually to the sharp-pointed apex. On their sides they may be quite entire, but it is not unusual for teeth, irregular in number and in size, to be present, and the persistent slime papillae, tipping the teeth or borne directly on the margin, represent an unusual peculiarity and stand in marked contrast to the short-lived papillae of the basal portion.

The markings of the spore are likewise subject to great variation. As noted in the description, these markings are of two types, the fine lines and the coarser folds; and the marked development of one type seems to decrease or prevent the development of the other. The type specimens, for example, show the folds with especial clearness; these are more or less elongated and show a somewhat sinuous course, sometimes being free, and sometimes anastomosing

sparingly, but never forming an actual reticulum; the fine markings, on the contrary, are made out with difficulty, although a careful search will usually demonstrate their presence in some part of the wall. In the specimens collected by Barnes and Land (nos. 121 and 671) these conditions are almost reversed; the fine lines here are everywhere distinct and sometimes form an irregular reticulum, but the folds are difficult to see, although the distinct crenulations at the periphery show that such folds must be present. It was thought at first, from a study of these two diverse spore types, that two species might be represented, but the close agreement between the specimens in other respects seems to preclude this idea.

Although *A. pringlei* shares certain characteristics with *A. tenella* and *A. ludwigii*, it would hardly be possible to confuse them. The three species agree in general habit, in their method of branching (which is normally by forking), and in their undivided dorsal air chambers, each opening by an epidermal pore. *A. pringlei*, however, in spite of growing in damp localities, shows a certain tendency toward xerophytism in having these dorsal chambers high and narrow, the more deeply situated chambers being very small. The green tissue thus stands in rather sharp contrast to the much looser tissue of the other two species, where the chambers are larger and approximately isodiametric. The species is further distinguished by the thickened radial walls of the cells encircling the pore, by the lack of cells containing oil bodies in the epidermis, by the thin unpitted walls of the compact tissue, by the autoicous inflorescence, and by the dark and almost opaque spores without a coarse reticulum. In both *A. tenella* and *A. ludwigii* the cells encircling the pore have thin radial walls, cells containing oil bodies are present in the epidermis, the cells of the compact layer usually show pitted walls, the inflorescence is paroicous, and the spores are yellow or pale brown, translucent, and covered over (at least on the spherical face) with a coarse reticulum. The remarkable appendages of the ventral scales bear a certain resemblance to those of *A. tenella*, especially when teeth are present, but these appendages are larger and more uniformly sharp-pointed, and their teeth are usually more spinelike in appearance. The slime papillae on the appendages are also a distinctive feature, no such papillae being present on the mature appendages of *A. tenella*.

4. *Asterella palmeri* (Austin) Underw.

Fimbriaria palmeri Austin, Bull. Torrey Club 6: 47. 1875.

Fimbriaria nudata Howe, Erythea 1: 112. 1893.

Asterella nudata Underw. Bot. Gaz. 20: 61. 1895.

Asterella palmeri Underw. op. cit. 63. 1895.

Thallus green but more or less pigmented with purple on the ventral surface and along the margin, mostly 0.5 to 1 cm. long and 2 to 4 mm. wide, broadened out on fertile plants, more or less concave, especially when dry, the undulate and crispate margins becoming strongly incurved and somewhat scarious, branching by forking, the keel broad and rounded; epidermis composed of thin-walled cells without trigones, averaging about $35 \times 25 \mu$; pores more or less elevated, measuring (with their surrounding cells) 75 to 90 μ in length and 60 to 70 μ in width, surrounded by 6 (sometimes 4, 5, or 7) series of cells with 2 cells in each series, the cells next the opening with more or less thickened radial walls; cells with oil bodies not observed in the epidermis, otherwise as in *A. tenella*; green tissue rather compact, the air chambers in 3 or 4 layers (in the median portion), those of the dorsal layer elongated vertically and much higher than the others, not subdivided, each with an epidermal pore; compact

tissue occupying from one-half to one-third the thickness of the thallus in the median portion, thinning out rather abruptly on the sides and extending about one-third the distance to the margin, composed of cells with thin unpitted walls, mycorrhiza sometimes present; ventral scales imbricated, extending to the margin or beyond, deeply pigmented throughout or with hyaline appendages, the cells containing oil bodies 10 or fewer, scattered, sometimes difficult to demonstrate, the appendages usually borne singly, sometimes in pairs, broadly to narrowly subulate, scarcely or not at all constricted at the base, mostly 0.5 to 0.9 mm. long and 0.1 to 0.25 mm. wide, entire or sparingly dentate on the margin, the teeth usually parallel with the appendage and 2 or 3 cells long, the cells variable in size in different appendages, less so in different parts of the same appendage, mostly 35 to 90 μ long and 25 to 30 μ wide; inflorescence parvicous, the antheridia forming a small irregular group close to the peduncle of the female receptacle, the ostioles low; peduncle naked, arising from the apex of a more or less elongated branch or from the bottom of a dichotomy, somewhat pigmented with brownish in the lower part, mostly 1 to 2 cm. long; disk of receptacle about 4 mm. high and 2.5 to 4 mm. wide, obtusely conical, smooth or nearly so when fresh, rugose when dry, scarcely lobed, the margins and the very narrow involucre entire or nearly so; pseudoperianths mostly 3 or 4 (rarely 2, 5, or 6), extending vertically downward, white, sometimes constricted at the base, 8 to 12-cleft, the segments adherent at the apex; capsule opening by an irregular circular line above the middle, the operculum coming off in one piece; spores dark brown to almost black, often opaque, 60 to 80 μ in diameter, with a low wavy fold or wing about 5 μ wide along the edges and similar folds on the faces of the spore, otherwise smooth or obscurely punctulate, the surface folds variable in length (sometimes reduced to tubercles), crowded and variously interwoven but not forming a distinct reticulum, the spore surface often appearing convolute, the periphery of spore coarsely crenate with about 25 crenations in all; elaters pale to dark brown, variously curved, mostly 140 to 180 μ long and 12 to 14 μ in diameter, scarcely tapering toward the rounded ends, sometimes with a single spiral throughout but usually with 2 (rarely 3) spirals in the median portion for a variable distance and one at each end.

Originally described from specimens collected on Guadalupe Island, off the coast of Lower California; now known also from California and from the mainland of Lower California. The following specimens have been examined:

CALIFORNIA: Mill. Valley, Marin County, *Howe* (N. Y.; type of *Fimbriaria nudata*); Jackson, Amador County, *Hansen* (N. Y.); Middle Fork, Amador County, *Hansen* (U. S.); St. Helena, Napa County, 1893, *Jepson* (N. Y., U. S., Y.); Santa Ana Hills, 1884, and Glover Mountain, near San Bernardino, *Parish* 1704, 2744 in part (N. Y.); Santa Monica, *Hasse* (N. Y.); Pasadena and vicinity, *McClatchie* (N. Y.), *Kingman* 702 (C. C. H.), *C. W. Harris* 1 (C. C. H.); Altadena, *Kingman* 1205 (N. Y., C. C. H.); Witch Creek, *Alderson* 908 (N. Y.); San Luis Obispo, *Mrs. R. W. Summers* (U. S.); San Diego, collector's name wanting (N. Y.). Several of these specimens have been listed by *Howe* (Mem. Torrey Club 7: 56. 1899).

LOWER CALIFORNIA: Carrizo Creek, *T. S. Brandegee* (N. Y., C. C. H.); Guadalupe Island, 1875, *Palmer* 119 (N. Y.; type of *Fimbriaria palmeri*), *Rose* 16012 (N. Y.).

Austin, with his usual keenness, emphasizes several of the most striking characteristics of this well-marked species in his original description. He calls attention, for example, to the strongly thickened median portion of the thallus and to the broad margins; to the papulose-areolate appearance of the upper surface; to the blackish purple scales, extending beyond the margin; to the

oblong-conical or ovate-conical receptacle, borne on a naked peduncle; to the white pseudoperianth, with segments coherent at the apex; and to the brown spores, indistinctly granulose-papillose. In stating that the female receptacle is 5-fruited, however, he makes no allowance for variation, and he fails to make enough allowance when he describes the segments of the pseudoperianth as 8 to 10 in number.

When Howe proposed his *Fimbriaria nudata* as a new species he recognized its close relationship to *F. palmeri* but felt justified in separating it, largely because it usually had a 3 or 4-fruited receptacle and a pseudoperianth with 10 or 11 divisions. Both Underwood and Stephani considered Howe's species valid, but Howe himself, after studying authentic material of *F. palmeri*, decided that Austin's species and his own were synonyms, a decision with which the writer fully agrees. Howe's description and figures of *Asterella palmeri*¹ show most of the important features with great clearness. He mentions, among other details not noted by Austin, the group of antheridia close to the peduncle of the female receptacle, the nearly smooth surface of the receptacle, the circumscissile capsule, and the measurements of the spores and elaters. Stephani supplies a few additional data about the epidermal pores and ventral scales and alludes especially to the high and narrow air chambers of the dorsal layer. In the case of *F. nudata* he compares the structure of the green tissue with that of *Riccia*, associating it with a dry climate which prevents the development of a flat and thin thallus.

On the whole the xerophytism of *A. palmeri* is much more distinct than that of *A. pringlei*. It shows itself not only in the narrow air chambers of the green tissue but also in the strong involution of the thallus when dry and in the relatively larger ventral scales. When teeth are present on the appendages, the scales bear a certain resemblance to those of *A. pringlei*, the teeth in both species representing the stalks of slime papillae. But the papillae are very ephemeral in *A. palmeri* and the teeth tend to be fewer and shorter than in *A. pringlei*, in many cases being absent altogether. The teeth usually diverge but slightly and are sometimes detected with difficulty.

The tendency of the spores to cling together in masses until late in the development of the capsule is alluded to by Howe. Usually under such circumstances the spores are somewhat arrested in their growth and fail to show the markings in a typical manner. When well developed the ridges of the spore surface are very distinctive, being low and rounded, instead of high and sharp as in most species of *Asterella* where equally coarse markings are present. The folds are very irregular and often anastomose, sometimes inclosing small areas, but the surface never shows a distinct reticulum, even when these inclosed areas are numerous; it is much more likely to be convolute in appearance. The wings along the edges of the spore are scarcely different from the folds.

Aside from the differences already mentioned, *A. palmeri* differs from *A. pringlei* in its parolcous inflorescence, agreeing in this respect with both *A. tenella* and *A. ludwigii*. Its more xerophytic structure will at once distinguish it from both these species, where the green tissue is very loose and the thallus shows little tendency to become involute when dry. It is further distinguished by the thickened radial walls in the circle of cells around the epidermal pores, by the conical female receptacle, by the pseudoperianths extending vertically downward, by the coherent segments of the pseudoperianths, and by the much darker spores, the spherical faces of which are not covered over by a coarse reticulum.

¹ Mem. Torrey Club 7: 55. pl. 99, f. 1-15. 1899.

5. *Asterella saccata* (Wahl.) Evans.

Marchantia fragrans Schleich. Pl. Crypt. Exsic. Helvet. 3: 64. 1804, nomen nudum; Lam. & DC. Fl. Franç. ed. 3. 2: 423. 1805, not Balb.

Marchantia saccata Wahl. Ges. Naturf. Freund. Berlin Mag. 5: 296. pl. 7, f. 3. 1811.

Fimbriaria saccata Nees, Hor. Phys. Berol. 45. 1820.

Fimbriaria fragrans Nees, loc. cit.

Hypenatron ciliatum Corda; Opiz, Beitr. Naturg. 648. 1828, nomen nudum.

Marchantia umbonata Wallr. Linnaea 14: 686. 1840.

Fimbriaria umbonata Wallr.; Gottsch., Lind. & Nees, Syn. Hep. 559. 1846.

Asterella fragrans Trevis. Rend. Ist. Lombardo II. 7: 785. 1874.

Hypenatron fragrans Trevis. Mem. Ist. Lombardo III. 4: 440. 1877.

Hypenatron umbonatum Trevis. loc. cit.

Hypenatron saccatum Trevis. loc. cit.

Thallus green but more or less pigmented with purple on the ventral surface and along the margin, mostly 0.5 to 1 cm. long and 2 to 3 mm. wide, plane or somewhat concave when moist, the undulate margins strongly incurved when dry, branching by forking, the keel broadly rounded to bluntly carinate; epidermis composed of cells with more or less thickened walls and distinct trigones, averaging about $30 \times 20 \mu$; pores more or less elevated, measuring (with their surrounding cells) mostly 70 to 140 μ in length and 50 to 70 μ in width surrounded by 6 (sometimes 5 or 7) series of cells with 2 or 3 cells in each series, the radial walls thin or with trigones; cells containing oil bodies as in *A. tenella*; green tissue fairly loose, the air chambers in 2 or 3 layers (in the median portion), those of the dorsal layer larger than the others and more or less subdivided by supplementary partitions (sometimes, not quite reaching the epidermis), the chambers thus apparently more numerous than the pores; compact tissue occupying about two-thirds the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about three-fourths the distance to the margin, composed of cells with thin unpitted walls; mycorrhiza not observed; ventral scales imbricated, deeply pigmented with purple except along the minutely and irregularly crenulate or denticulate margin, the cells containing oil bodies mostly 10 to 15, scattered, the appendages borne singly or in pairs, in the latter case sometimes more or less connate, subulate and long-acuminate, scarcely or not at all constricted at the base, mostly 0.7 to 1 mm. long and 0.2 to 0.3 mm. wide, hyaline, forming a conspicuous cluster at the tip of the thallus, the margin varying from entire to sparingly and irregularly dentate or spinose-dentate, the cells averaging about $55 \times 20 \mu$, not varying greatly in different parts, an occasional cell with oil bodies present in the basal portion; inflorescence parvicous or autoicous, the antheridia forming an irregular elongated median group close to the peduncle of the female receptacle or on a separate branch; ostioles low; no palcae present; peduncle arising from the apex of a leading branch, surrounded at the base by a dense cluster of hyaline lanceolate scales, otherwise naked, more or less pigmented, about 2 cm. long when well developed; disk of receptacle bluntly conical, about 3 mm. wide, covered with coarse and low tubercles, shortly 3 or 4-lobed, the lobes extending almost vertically downward, the margins and distinct membranous involucre entire or more or less sinuate; pseudoperianth white, mostly 8-cleft, the lanceolate divisions coherent at the apex; capsule opening by an irregular circular line above the middle, the operculum coming off in one piece; spores brownish yellow, 80 to 90 μ in diameter, with wavy, minutely and irregularly crenulate wings 10 to 12 μ wide along the edges, the whole surface covered over with a very fine and

often regular reticulum, with meshes about $2\ \mu$ wide, formed by delicate lines slightly darker than the rest of the wall and scarcely elevated above the general surface level, the surface otherwise smooth or with occasional low ridges or tubercles, these never forming a reticulum; elaters straight or slightly curved, yellowish brown, mostly 140 to 200 μ long and 10 to 14 μ wide, scarcely tapering toward the rounded ends, the median portion with 1 to 3 spirals, the ends with 1 or 2.

A rare alpine and arctic species, growing on soil among rocks; widely distributed in North America, Europe, and Asia, but still known from comparatively few stations. The following specimens have been examined:

YUKON: Hunker Creek, 1902, *J. Macoun* 61 (N. Y., Y.; cited by the writer, as *A. fragrans*, in *Ottawa Nat.* 17: 14. 1903).

BRITISH COLUMBIA: Telegraph Creek, 1887, *Dawson* 327 (N. Y.; cited by Underwood, as *A. fragrans*, in *Bot. Gaz.* 20: 61. 1895).

IDAHO: Kootenai County, 1891, *Leiberg* 37 (N. Y.; cited by Underwood, loc. cit.).

WASHINGTON: Near Fort Colville, 1861, collector's name wanting (N. Y.).

SWITZERLAND: Branson, near Martigny, *Schleicher* (N. Y.; probable type of *Marchantia fragrans* Schleich.); same locality, 1832, *Blanchet* (N. Y.); between the Riffel and the Gorner Grat, *Mitten* (N. Y.).

ITALY: Mont-Cenis, date and collector's name wanting (N. Y.).

AUSTRIA: Near Krems, *Baumgartner* (C. C. H., N. Y., U. S.; distributed, as *Hypenantron fragrans*, in *Krypt. Exsic. Mus. Vinden.*, no. 282).

The following authentic records for the species may likewise be of interest:

GERMANY: Various localities in the Harz Mountains, *Hampe*, *Wallroth*, *Quelle*, and others (frequently cited in literature).

FRANCE: Col de la Vanoise, 1893, *Sebillé* (listed by Boulay in *Musc. France* 2: 187. 1904).

ITALY: Near Belluno, Cadore, *Pampanini*, and between the Col delle Erbe and the Ricordo Canias, Friuli, *DeGaspari* (both cited by Zodda in *Nuov. Gior. Bot. Ital.* 19: 31. 1912).

AUSTRIA: Groisbach and Dürnstein, *Baumgartner* (cited by Müller, in *Rabenhorst's Krypt. Fl.* 6: 273. 1907).

RUSSIA: Kongur, Perm, *Brenner*, *Arnell* (listed by Lindberg & Arnell, *Svensk. Vet. Akad. Handl.* 23^b: 10. 1889).

SIBERIA: Stolba, Yeniseisk, *Arnell* (cited by Lindberg & Arnell, loc. cit.); Poddale, Amur, *Maximowicz* (cited by Lindberg in *Acta Soc. Sci. Fenn.* 10: 259. 1872); Kamchatka, *Tilesius* (type locality for *Marchantia saccata*).

Several other records for the species may be found in the literature but are more or less open to suspicion. A few of these are noted below.

The synonymy of this rare species is very much involved, owing largely to the fact that the earlier writers confused it with the much more abundant *Grimaldia fragrans* (Balb.) Corda. The latter species was originally described and figured by Balbis,¹ under the name *Marchantia fragrans*, from specimens collected on the southern slopes of the Pennine Alps in northern Italy. A few years later Schleicher discovered *Asterella saccata* at the village of Branson, near Martigny, Switzerland, on the northern slopes of the same range of mountains, and distributed specimens under the name *Marchantia fragrans* Balb., supposing them to be identical with the Italian plant. Schleicher did not publish a description of these Swiss specimens but De Candolle did so, in 1805, the name assigned to them being "*Marchantia fragrans*

¹ *Mém. Acad. Sci. Turin* 12: 76, pl. 2. 1802-03.

Balbi ex Schleich." Similar descriptions were published soon afterwards by Weber and Mohr,¹ by Weber,² and by Wallroth.³

On the basis of these descriptions certain later writers have attempted to maintain a *Marchantia fragrans* Schleich. in addition to a *Marchantia fragrans* Balb., and have cited *A. saccata* under the name *Asterella fragrans* (Schleich.) Trevis. or *Fimbriaria fragrans* (Schleich.) Nees, according to their choice of generic names. This course has little to recommend it. The writers who described Schleicher's specimens supposed that they represented *M. fragrans* Balb., but even if they had considered them distinct the name "*M. fragrans* Schleich." would be nothing more than a homonym of *M. fragrans* Balb. and therefore without nomenclatorial standing.

The case is different with *Fimbriaria fragrans* Nees, the third species of Nees von Esenbeck's genus *Fimbriaria*, as originally described. As a synonym of this species *Marchantia fragrans* Balb. is unfortunately given, but the descriptions quoted are those of Weber and of Wallroth, instead of the original description of Balbis. It is evident, therefore, that Nees von Esenbeck's conception of *F. fragrans* was largely based on Schleicher's specimens, and for this reason it is perhaps justifiable to regard *F. fragrans* as a new and adequately published name. This was clearly the view held by Underwood⁴ when he wrote the name of the species *Asterella fragrans* (Nees) Trevis. But an alternate interpretation is possible: If the true *Marchantia fragrans* Balb. is considered synonymous with *F. fragrans* Nees, then the latter name becomes a mere synonym of *Grimaldia fragrans*.

The revival of Wahlenberg's *Marchantia saccata* removes the necessity of using the name *fragrans* at all in the present connection. *M. saccata* was based on specimens collected by Tilesius in Kamchatka, and Wahlenberg's figures, although not very satisfactory, clearly show the plurifid pseudoperianths of an *Asterella* with the segments connate at the apex. The species was accepted by Schwaegrichen⁵ and by Nees von Esenbeck, the latter author listing it as the second member of his genus *Fimbriaria*, under the name *F. saccata*. Wallroth, however, was apparently the first to recognize its close relationship to the *M. fragrans* of Schleicher's distribution, quoting it, in 1815, among the synonyms of *M. fragrans*. Later on, in 1831,⁶ he no longer included *M. saccata* among the synonyms, showing that he may have changed his mind. In his *Naturgeschichte der europäischen Lebermoose* (1838) Nees von Esenbeck makes no allusion to *F. saccata*, but the authors of the *Synopsis Hepaticarum*⁷ accept it, placing it close to *F. fragrans* and emphasizing its relationship to that species. Apparently no further attention was paid to Wahlenberg's species until Lindberg considered its status many years later. When he first referred to it he included it, with a question mark, among the synonyms of *Düvalia pilosa* (Hornem.) Lindb. (*Necsiella pilosa* Schiffn.),⁸ but he changed his mind afterwards, when he listed "*Fimbriaria fragrans* (Schleich.) N.-Es." from Amur in eastern Siberia,⁹ stating that "*F. saccata* (Wahlenb.) N.-Es." was very

¹ Bot. Taschenb. 391. 1807.

² Hist. Musc. Hep. Prodr. 106. 1815.

³ Ann. Bot. 120. pl. 6, f. 9. 1815.

⁴ Bot. Gaz. 20: 61. 1875.

⁵ Hist. Musc. Hep. Prodr. 33. 1814.

⁶ Fl. Crypt. Germ. 1: 44. 1831.

⁷ Page 559. 1846.

⁸ Not. Sällsk. Faun. Fl. Fenn. Förh. 9: 281. 1868.

⁹ Act. Soc. Sci. Fenn. 10: 259. 1872.

probably referable to *F. fragrans* as a synonym. In 1889 he and Arnell¹ spoke still more positively, saying that *Marchantia saccata* ought without doubt to be referred to *Asterella fragrans* (Schleich.) Trevis. Whether they based their statement on a study of Wahlenberg's type specimen, which is presumably at Upsala, does not appear but is surely to be assumed. In any case they would not have supplanted the name *fragrans* by the name *saccata* because they considered *Marchantia fragrans* Schleich. a valid species, antedating *M. saccata* Wahl. For those who can not accept this view, *M. saccata* represents the oldest valid name for the species.

Although Nees von Esenbeck does not refer to *F. saccata* in his *Naturgeschichte*, he gives a full account of *F. fragrans*² and establishes the generic position of the true *Marchantia fragrans*,³ citing the original publication of Balbis, with which his predecessors had apparently been unacquainted. He deplores the confusion caused by Schleicher's incorrect determination, but admits that he himself as well as others had not been blameless. As a matter of fact, Wallroth, to whom attention has already been called, had been a serious offender. In connection with his description of *M. fragrans* he cites specimens from the vicinity of Halle, Germany, which represent *Grimaldia fragrans*. This error was pointed out by Bischoff,⁴ who showed that Wallroth's figures were drawn partly from the true *F. fragrans* and partly from the *Grimaldia*. Other errors also, based on incorrect determinations, might be noted, including some that have appeared within comparatively recent times. Bernet,⁵ for example, writing in 1888, cites *F. fragrans* from a number of Swiss localities, most of which were afterwards transferred by Boulay⁶ to *Grimaldia fragrans*.

Wallroth's *F. umbonata*, based on specimens collected in the Harz Mountains, Germany, remains to be considered. This species was admitted to the *Synopsis Hepaticarum*,⁷ although attention is there called to the strong resemblance which it bears to *F. fragrans*. It is likewise listed by Hampe.⁸ Stephani,⁹ however, reduced it to synonymy in 1899, citing it under *F. fragrans*, and later writers, such as Loeske, Migula, and Müller, have followed his example.

The earliest record for *A. saccata* in North America was published by Austin¹⁰ in 1873, the specimens upon which it was based having been collected by Fendler at Santa Fe, New Mexico. So far as seen by the writer these specimens are either sterile or else show very immature receptacles. Their ventral scales, however, as well as their epidermal and photosynthetic tissues, differ from the corresponding structures in authentic material of *A. saccata*, and indicate a wrong determination. The North American records cited above, all but one of which have been previously published, seem to be trustworthy.

Although it would be impossible, in the light of our present knowledge, to confuse fruiting specimens of *Asterella saccata* and *Grimaldia fragrans*, the two species resemble each other very closely indeed in a sterile condition. They are both of about the same size; both have a markedly xerophytic habit, the thallus

¹ Svensk. Vet. Akad. Handl. 23⁵: 10. 1889.

² Page 267.

³ Page 225.

⁴ Nov. Act. Acad. Caes. Leop. Carol. 17: 1019. 1835.

⁵ Cat. Hép. Suisse 124.

⁶ Musc. France 2: 190. 1904.

⁷ Page 559.

⁸ Fl. Hercyn. 374. 1873.

⁹ Bull. Herb. Boiss. 7: 211. 1899.

¹⁰ Hep. Bor. Amer., no. 136c (as *Fimbriaria fragrans*).

becoming strongly involute when dry; and both usually show a dense cluster of hyaline scale appendages at the apex. Under ordinary circumstances the *Grimaldia* can be recognized by its characteristic aromatic odor, the *Asterella* being odorless; but since the *Grimaldia* also sometimes lacks the odor, this difference can not always be relied upon. Even in their minute structure the species have much in common, the epidermis, the green tissue, and the scales being a good deal alike. In the *Grimaldia*, however, the epidermis is composed of smaller cells (averaging only $15\ \mu$ in length), the trigones are more conspicuous, and there are no cells containing oil bodies; the green tissue is a little more compact, the dorsal chambers being more subdivided; and the scales show a more abrupt transition between the basal portion and the appendages. The median cells of the basal portion, moreover, are distinctly smaller, averaging only $15\ \mu$ in width; in *A. saccata* they usually measure 20 to $30\ \mu$ in width.

Among North American species *A. saccata* is perhaps most closely allied to *A. palmeri*, a fact to which both Stephani and Howe have called attention. Both are xerophytic species, showing a thallus involute when dry, a rather compact green tissue, and large ventral scales. They agree further in the bluntly conical female receptacles with short and indistinct lobes and in the white pseudoperianths extending almost vertically downward. In most other respects they are amply distinct. In *A. palmeri*, for example, the compactness of the green tissue is due to the small size of the dorsal chambers, the epidermal cells are thin-walled and contain no oil bodies, the peduncle of the female receptacle is naked throughout, and the spores are dark brown and covered over with distinct rounded folds. In *A. saccata*, on the contrary, the compactness of the green tissue is due largely to the subdivision of the dorsal chambers, the epidermal cells show trigones and an occasional cell contains oil bodies, the peduncle of the female receptacle shows a basal cluster of hyaline paleae, and the spores are brownish yellow and usually show no distinct surface folds except the wings along the edges.

With regard to the male inflorescence the statements in the literature are not altogether in accordance, and the limited amount of material at the writer's disposal has made it impossible to decide some of the disputed points. The statements in the description have been taken largely from Bischoff's figures and explanatory text. According to his account the clusters of antheridia occur on both fertile and sterile thalli, forming median subconvex areas on the upper surface, not sharply limited but approximately oval or oblong in outline. According to Nees von Esenbeck's description the species is definitely paroicous; he compares it with *A. ludwigii* in this respect and states that the antheridia are found close to the female receptacle. Stephani describes the antheridia as occurring in small clusters but says nothing about their position with respect to the peduncle, except that the species is monoicous. Müller does not describe the male inflorescence at all, and Massalongo, apparently on the basis of very few observations, states that it occurs on an isolated branch and that the species is therefore not paroicous. The question deserves further study, but according to the evidence at hand both paroicous and autoicous conditions have been demonstrated.

6. *Asterella californica* (Hampe) Underw.

Sauteria limbata Austin, Proc. Acad. Phila. 1869: 229. 1869, in part.

Fimbriaria californica Hampe; Boland. Cat. Pl. San Francisco 40. 1870, nomen nudum; Underw. Bull. Ill. Lab. Nat. Hist. 2: 41. 1884.

Fimbriaria lescurii Austin; Boland. Cat. Pl. San Francisco 40. 1870, as synonym.

Asterella californica Underw. Bot. Gaz. 20: 60. 1895.

Clevea limbata Solms; Stephani, Bull. Herb. Boiss. 6: 773. 1898, in part.

Thallus green above but usually more or less pigmented with purple along the margin and on the ventral surface, mostly 1.5 to 2 cm. long and 7 to 10 mm. wide (rarely only 4 to 7 mm.), plane when moist, more or less incurved when dry, with undulate margins, branching by forking, the keel broad and rounded; epidermis composed of cells with thin walls, sometimes showing minute trigones, averaging about $50 \times 30 \mu$; pores slightly elevated, measuring (with their surrounding cells) mostly 110 to 130 μ in length and 100 to 120 μ in width, surrounded by 6 (sometimes 7 or 8) series of cells with 3 cells in each series, the radiating walls more or less thickened, the cells containing oil bodies as in *A. tenella*; green tissue rather loose, the air chambers in 4 or 5 layers in the median portion, those of the dorsal layer higher and larger than the others but somewhat subdivided by supplementary vertical partitions often reaching nearly or quite to the epidermis; compact tissue occupying from one-fourth to one-third the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about halfway to the margin, composed of cells with thin unpitted walls, an occasional larger cell both here and in the green tissue containing slime; mycorrhiza rarely present in the ventral portion; ventral scales large and imbricate, extending beyond the margin, ovate to lunulate, deeply pigmented throughout or with hyaline appendages, the margin irregularly sinuate or toothed; cells containing oil bodies mostly 10 to 15, scattered; appendages mostly 2 to 4, variable in shape but usually narrowly subulate and acuminate from a broad triangular base, mostly 0.6 to 0.9 mm. long (including the basal portion) and 0.08 to 0.15 mm. wide, sometimes with a sharp tooth or lobe but usually entire, the cells in apical portion mostly 35 to 60 μ long and 25 to 35 μ wide; inflorescence dioicous; antheridia forming an elongated median patch, sometimes forked, at some distance from the apex; ostioles low; a few paleae sometimes present; peduncle straw-colored, sometimes with brownish or purplish pigmentation, naked or nearly so, 1 to 3 cm. high; disk of receptacle green, about 5 mm. across, low-hemispherical, deeply lobed, almost smooth, the lobes mostly 4 (sometimes 5), extending obliquely outward, the margins and the almost bipartite involucre entire or vaguely and irregularly crenate or dentate; pseudoperianth white or rarely purplish, mostly 12 to 16-cleft, the divisions lanceolate, connate at the apex; capsule circumscissile at the middle or above by an irregular line, the operculum breaking up into fragments; spores yellow, mostly 100 to 120 μ in diameter, with wavy wings 12 to 20 μ wide along the edges, the surface covered over more or less completely with a fine and often irregular reticulum with meshes 3 to 4 μ across, formed by delicate, slightly raised lines, the spherical face showing in addition 4 or 5 broad and rounded, irregular ridges lower than the wings, anastomosing but not forming a reticulum, the plane faces with 1 or 2 similar ridges; elaters yellow, variously curved, mostly 240 to 450 μ long and 12 to 16 μ wide, tapering slightly toward the blunt ends, the median portion with 1 or 2 spirals, the ends with 1.

Growing on banks or among rocks; locally abundant in California; known also from Arizona and Guadalupe Island. The following specimens have been examined:

ARIZONA: Bright Angel Trail, bottom of Grand Canyon, 1913, *Nichols* (Y.; listed by the writer, somewhat doubtfully, in *Bryologist* 20: 61. 1917).

CALIFORNIA: Without definite locality or date, *Bolander*, *Bigelow* (C., N. Y., Y.; distributed by Austin, as *Fimbriaria californica*, in *Hep. Bor. Amer.*, no. 135); Oak Run, Shasta County, *Baker & Nutting* (N. Y.); Ukiah and Half Way House, Mendocino County, *Howe* (N. Y.); Murphy, Calaveras County,

Davy (N. Y.); Duncan's Mills, Sonoma County, *Howe* (C. C. H., N. Y.); Olema, Marin County, *Jepson* (Y.); Mill Valley, Marin County, *Howe* (N. Y.); Marin County, *Parsons* (N. Y.); Mount Tamalpais, *Howe* (U. S.); Berkeley, *Howe* (N. Y., U. S.); San Leandro, *Underwood* (N. Y.); Mount Diablo, Contra Costa County, *Howe* (N. Y.); San Francisco and vicinity, prior to 1870, *Bolander* (N. Y.; type), *Rattan* 6452 (U. S.), *T. S. Brandege* 3 (N. Y.), *K. Brandege* (C. C. H.); Stanford University and vicinity, *Campbell* (N. Y., Y.); same locality, *Baker* (N. Y., C. C. H., U. S.; distributed in Pacif. Sl. Bry., no. 763, as *Fimbriaria californica*); Santa Cruz, *Farlow* (N. Y., Y.); Kaweah River Valley, Tulare County, *Coville & Funston* 1304 (N. Y., U. S.; listed by Coville, as *Fimbriaria californica*, in Contr. U. S. Nat. Herb. 4: 230. 1893); Santa Barbara, *Farlow* 12 (N. Y.); Nordhoff, Ventura County, *Newton* (N. Y.); Pasadena, *Underwood* (N. Y.); same locality, *McClatchie* 26, 27 (N. Y.; listed by the collector, as *Fimbriaria californica*, in Fl. Pasadena 624. 1895); same locality, *Teed* (N. Y., U. S., Y.; distributed by Underwood & Cook in Hep. Amer., no. 119, as *Fimbriaria californica*); same locality, *Kingman* 737 (C. C. H.); Millards Canyon, San Gabriel Mountains, *Kingman* 640 (C. C. H.; listed by the collector in Bryologist 14: 34. 1911); Verdugo Canyon, *Warner* (C. C. H.); Santa Monica, *Hasse* (N. Y.); Santa Anita Canyon, *Moxley* 455 (C. C. H., Y.); Santa Ana Hills, San Bernardino Mountains, *Parish* 1728, 1730 (N. Y.); San Diego, *Farlow* 14 (N. Y.); Twin Oaks, San Diego County, *Koch* (N. Y.); Witch Creek, San Diego County, *Alderson* 770, 903, 912 (C. C. H., N. Y.). Many of these specimens have already been listed by Howe (Mem. Torrey Club 7: 50. 1899).

LOWER CALIFORNIA: Guadalupe Island, 1875, *Palmer* 118 (N. Y.; listed by Watson, Proc. Amer. Acad. 10: 121. 1875), *Anthony* 5½ (N. Y.).

Macoun¹ lists the species from the following localities in British Columbia: Lytton, 1889, *J. Macoun*, and Pass Creek, Columbia River, *J. Macoun*. According to a specimen from Lytton in the herbarium of the Canadian Geological Survey, the first of these records was based on *Reboulia hemisphaerica*; in the absence of Pass Creek specimens the second record must therefore be considered as open to suspicion.

Underwood's original description of *Asterella californica* is incomplete but calls attention to the broad and "undulate-lobed" thallus with a brownish purple margin; to the stout, pale purple, and sparingly pilose peduncle; to the subhemispherical and usually 4-lobed receptacle; and to the large, 12 to 16-cleft pseudoperianth. Stephani supplies several additional details, emphasizing among other features the large purple scales with 2 or 3 lanceolate appendages, the distinctly bilabiate involucre, the yellow spores with broad and rough crests, and the unispiral or bispiral elaters. Unfortunately his description includes a few disconcerting statements about the branching and the inflorescence. He makes no mention whatever of branching by forking but describes the thallus as being simple or with apical innovations, and he assigns a monocious inflorescence to the species, with androecia borne on minute ventral branches. These errors are not repeated by Howe, who correctly describes the branching as dichotomous and the inflorescence as dioicous, a full account of the male inflorescence being included. Howe's description and figures,² in fact, are so complete that they leave little to be desired. His discussion of Austin's *Sauteria limbata* is also of much interest. He shows clearly that the species is a composite, being based on male material of *A.*

¹ Cat. Canad. Pl. 7: 3. 1902.

² Mem. Torrey Club 7: 48. pl. 95, 96. 1899.

californica and female material of *Clevea hyalina californica* Howe. He recommends that in order to avoid confusion the specific name* *limbata* be given up altogether, in spite of the fact that *Sauteria limbata* antedates *Fimbriaria californica* by several years.

The slime cells of *A. californica* have apparently been overlooked by previous observers. They occur without definite order in both green and compact tissues and are distinguished by their large size and colorless, highly refractive contents. They are sometimes more numerous in the green tissue, sometimes in the compact tissue, and sometimes equally numerous in both. In exceptional cases they may be very abundant, as many as 50 having been seen in a single section, but they are usually more scantily developed and may be absent altogether. Since slime cells have not been detected in other species of *Asterella*, their presence will sometimes help in the determination of sterile material.

The ventral scales of *A. californica* bear a certain resemblance to those of *Reboulia hemisphaerica* and have perhaps been the cause of confusion. In both plants the scales are characterized by slender and long-pointed appendages, their number varying from 1 to 3 or 4. In the *Asterella*, however, these appendages are subulate, tapering from a broad base, and are separated from one another by sharp sinuses; while in the *Reboulia* the appendages are linear from a very narrow base and are marked off much more sharply from the basal portion of the scale, being separated by a considerable length of margin. In the frequent possession of 3 or even 4 appendages the scales of *A. californica* are distinguished from those of most other species of *Asterella*.

Other unusual features of *A. californica* are the dioicous inflorescence, the deeply lobed female receptacle, and the bipartite involucre. The margins of the last are not always entire, as stated by Stephani. Those studied by the writer show scattered rounded teeth, some of which represent projecting cells, while others are 2 cells in length. The yellow spores, with their distinct marginal wings, fine surface reticulum, and sparsely developed ridges on the faces, are also very distinctive of the species. *A. californica* sometimes grows in company with *A. palmeri* and the two species resemble each other somewhat in a sterile condition, both having a more or less pigmented margin, which becomes incurved when dry, and both developing large purple ventral scales. *A. palmeri*, however, is a somewhat smaller plant, the dorsal air chambers are not subdivided, and the scales rarely have more than one appendage. Of course, if the conical and scarcely lobed female receptacles are present, the species can at once be distinguished.

7. *Asterella lindenbergiana* (Corda) Lindb.

Fimbriaria lindenbergiana Corda; Nees, Naturg. Eur. Leberm. 4: 283. 1838.

Fimbriaria maior Hampe; Nees, loc. cit., as synonym.

Marchantia alpina Schleich.; Nees, loc. cit., as synonym.

Fimbriaria bonjeanii DeNot. Mem. Accad. Sci. Torino II. 1: 335. pl. 1, f. e. 1839.

Asterella bonjeanii Trevis. Rend. Ist. Lombardo II. 7: 777. 1874.

Hypnantron bonjeanii Trevis. Mem. Ist. Lombardo III. 4: 440. 1877.

Asterella lindenbergiana Lindb. Musc. Scand. 1. 1879.

Hypnantron lindenbergianum Kuntze, Rev. Gen. Pl. 1: 89. 1891.

Fimbriaria commutata Stephani, Bull. Herb. Boiss. 7: 209. 1899.

Thallus sometimes green above but often more or less pigmented with red or purple on both surfaces, mostly 1 to 3 cm. long and 4 to 6 mm. wide, plane or with the undulate-crispate margins somewhat incurved when dry, usually with a shallow and narrow median furrow, branching by forking, the keel narrow and often sharp; epidermis composed of thin-walled cells without trigones, aver-

aging about $35 \times 25 \mu$; pores slightly elevated, measuring (with their surrounding cells) mostly 90 to 120μ in length and 80 to 110μ in width, surrounded by 6 or 7 (rarely 8) series of cells with 3 or 4 cells in each series, the radial walls slightly thickened; cells containing oil bodies as in *A. tenella*; green tissue fairly loose, the air chambers in 3 or 4 layers, those of the dorsal layer sometimes larger than the others but loosely subdivided by supplementary partitions often failing to reach the epidermis; compact tissue occupying from two-thirds to three-fourths the thickness of the thallus in the median portion, gradually thinning out on the sides and extending about two-thirds the distance to the margin, composed of cells with slightly thickened, more or less pitted walls; mycorrhiza not observed; ventral scales large, mostly ovate, sometimes sublunulate, pale purple throughout, marginal slime papillae somewhat persistent; cells containing oil bodies mostly 15 to 20, scattered; appendages mostly 1 or 2 (rarely 3), sometimes approximate or coalescent, lanceolate, scarcely if at all constricted at the base, mostly 0.25 to 0.4 mm. long and 0.08 to 0.12 mm. wide, acute to acuminate, entire or vaguely and minutely crenulate, the cells throughout averaging about $30 \times 20 \mu$; inflorescence parvicous or autoicous, the antheridia occupying an oval irregular median area near the peduncle of the female receptacle or on a separate branch, the ostioles low; peduncle with a loose cluster of lanceolate paleae at base and apex, deeply pigmented, mostly 1.5 to 2.5 cm. long; disk of receptacle mostly 3 to 4 mm. across, bluntly conical, coarsely tuberculate, the lobes mostly 3 or 4, short, extending obliquely downward, the margins and the narrow bilobed involucre entire or nearly so; pseudoperianth usually deep purple, mostly 12 to 16-cleft, the divisions lanceolate, connate at the apex; capsule purple, the method of dehiscence not observed; spores dark purple, mostly 80 to 100μ in diameter, with wavy irregular wings 10 to 14μ wide along the edges, the wings often becoming indistinct through the separation of the outer spore wall layer, the entire surface covered over with a fine reticulum, the meshes 4 to 6μ across, formed by delicate lines or low ridges, darker than the rest of the wall, coarser folds or ridges not present; elaters purple, more or less curved, mostly 100 to 120μ long (rarely up to 200μ) and 12 to 16μ wide, tapering slightly toward the rounded ends, the spirals mostly 2 in the middle and 1 or 2 at the ends, more deeply pigmented than the rest of the wall.

A rare alpine and arctic species, growing on soil among rocks, mostly calcareous; known with certainty only from western North America, Scandinavia, and the higher mountains of central Europe. The following specimens have been examined:

ALASKA: Aats Bay, 1913, *Frye* 921 (Y.; collected on the Kelp Expedition but not previously recorded).

BRITISH COLUMBIA: Selkirk Mountains, 1885, *J. Macoun* (C., U. S.; type collection of *Fimbriaria commutata*); near Kicking Horse Lake, *J. Macoun* (C.).

ALBERTA: Red Earth Creek, Long Lake, south of Pharaoh, 1913, *Brinkman* 983 in part (C. C. H.; mixed with *Bucegia romanica*); valley of Healy Creek, 1913, *Brinkman* 936 (C. C. H.).

WASHINGTON: Queets River Valley, 1907, *Frye* 71 (Y.); Elwha River Valley, *Frye* 33, 58, 63 in part (Y.); Paradise Park, Mount Rainier, *Foster* 1008 (C. C. H.). The first two stations have been reported by Miss Clark (Bull. Torrey Club 36: 300. 1909).

NORWAY: Tromsø amt, Bardodalen, Storfjeld, 1901, *Arnell* (N. Y.); Tromsø amt, Leaviken, Kistelfjeldet, *Kaalaas* (C. C. H.).

SWITZERLAND: "In Alpihus," 1849, *Lesquereux* (N. Y.); between the Riffel and the Gorner Grat, *Mitten* (N. Y.); Col de la Gemmi, *Lacoutre* (C. C. H.).

AUSTRIA: Salzburger Spitze des Unterberges, *Sauter* (N. Y., Y.; distributed in Gottsche & Rabenhorst's Hep. Europ., no. 369, as *Fimbriaria lindenbergi*-

ana); Tatry, *Raciborski* (C. C. H., Y.; distributed in Lillienfeldovna's *Hep. Poloniae Exsic.*, no. 6, as *F. lindenberiana*).

The species has likewise been reported from Sweden, from the Bavarian mountains, from the French and Italian Alps, and from the Austrian provinces of Tirol, Styria, and Carniola.

Two names, *Fimbriaria lindenberiana* Corda and *F. bonjeanii* DeNot., were published almost simultaneously for this distinct and beautiful species. *F. lindenberiana* was based on three specimens, the first from the mountains of Salzburg, the second and third from the Faulhorn and the Gemml, respectively, in Switzerland. The specimen from Salzburg was collected by Funck and should be considered the type of the species, since it was sent to Nees von Esenbeck by Lindenberg. The second and third specimens were collected apparently by Muhlenbeck, although this is not stated in the original description. *Fimbriaria bonjeanii* was based on material collected by Bonjean on Mont-Cenis, in northern Italy. In the *Synopsis Hepaticarum* *F. bonjeanii* is reduced to synonymy.

Underwood¹ has stated, however, that separates of the paper by DeNotaris, *Primitiae Hepaticologiae Italicae*, in which the description of *F. bonjeanii* appeared, were issued in 1838, a year earlier than the Memoir of the Turin Academy, in which the paper was included, was formally published. This being the case, doubt might be thrown upon the priority of *F. lindenberiana*, which also was published in 1838. For a while certain Italian botanists, among whom Trevisan and Massalongo may be mentioned, attempted to maintain *F. bonjeanii* as a species, but when they admitted its identity with *F. lindenberiana* they accepted Corda's specific name without question. Barsall, in fact, in his careful summary of the Italian literature on the Hepaticae,² gives 1839 definitely as the date for the paper by DeNotaris, and Massalongo³ has recently followed his example. The claims of *F. bonjeanii* may therefore be dismissed as baseless.

Asterella lindenberiana was first reported from America by Gottsche, in 1864,⁴ his record being based on two specimens collected by Lindig in the province of Bogotá, Colombia. Schiffner, in 1893,⁵ listed the species not only from Colombia but also from Mexico. None of the specimens referred to have been available for study, and the writer is therefore unable either to verify or to correct these reports. At the same time the occurrence of the species in tropical America must be considered doubtful, in view of its distinctly northern distribution. The first record for northern North America was made by Miss Clark in 1909, on the basis of Frye's Washington material. Macoun's specimens from British Columbia, however, had been collected over twenty years earlier and had been listed by Pearson, in 1890,⁶ under the name *Fimbriaria violacea* Austin, probably on account of their purple pseudoperianths. Macoun repeated this record somewhat doubtfully in 1902,⁷ suggesting that the specimens might be referable to *Asterella fragrans* instead. Meanwhile Stephani, in 1899, had made them the type of his *F. commutata*. Through the kindness of Mr. J. M. Macoun, the writer has been able to make a careful

¹ Mem. Torrey Club 4: 21. 1893.

² Bibl. Epat. Ital. 12. 1902.

³ Atti Ist. Veneto 75: 719. 1916.

⁴ Ann. Sci. Nat. V. Bot. 1: 187. 1864.

⁵ In Engl. & Prantl. Pflanzenfam. 1³: 34. 1893.

⁶ List Can. Hep. 27. 1890.

⁷ Cat. Can. Pl. 7: 4. 1902.

study of the material from British Columbia and has no hesitation in referring it to *A. lindenbergiana*.

Although Stephani's description of the species mentions most of the more important characters, it is not altogether satisfactory. He says nothing, for example, about the characteristic spores and elaters, although Nees von Esenbeck had described them in his original account. Stephani likewise makes no allusion to branching by dichotomy, the usual method, stating that the thallus innovates at the apex or, more rarely, gives rise to ventral outgrowths. In his account of *F. commutata* he makes similar statements about the branching and describes the spores as 68 μ in diameter, yellowish brown, and with coarsely lobed wings, thus giving a somewhat misleading idea of their appearance. In all probability the capsules at his disposal, which he describes as subhyaline, were immature or abnormally developed.

There is little danger of confusing *A. lindenbergiana* with *A. saccata*, although they have certain structural features in common. The thallus of *A. lindenbergiana* is considerably the larger of the two and lacks the apical cluster of hyaline scale appendages, which forms so characteristic a feature of the smaller species. The sharp keel, which is of course seen with especial clearness in cross sections, is a peculiarity which distinguishes the plant not only from *A. saccata* but from most other members of the genus, and the deep purple pseudo-perianths, spores, and elaters are likewise very distinctive.

In the material from Mount Rainier a few ventral tubers were observed, similar to those described and figured by Karsten¹ in the case of *Conocephalum conicum* (L.) Dum. They represent intercalary outgrowths from the side of the keel, which easily become detached, and are in the form of solid spherical or ellipsoidal masses of cells. Scattered over the surface, especially at the apical end, a few narrow paleae can be detected, and the interior cells are gorged with food, some of which is a highly refractive fatty substance staining brilliantly with Sudan III. A small amount of starch also is present. In all probability these tubers serve as organs of vegetative reproduction, but in view of their apparent rarity their efficiency in this respect is doubtful. Bolleter² who has studied the tubers of the *Conocephalum* in some detail, emphasizes the fact that they are poorly adapted to withstand even short periods of dryness. In his experiments he rarely induced them to germinate at all and he suggests that our present *Conocephalum* may have descended from more xerophytic ancestors, in which the tubers played a more important part than they do now. As the habit of the plant gradually grew more hydrophytic the tubers may have lost their xerophytic features, becoming in time vestigial in character. In *Exormotheca tuberifera* Kashyap,³ a species recently described from the Himalayas, ventral tubers are associated with a distinctly xerophytic plant and apparently occur in abundance. No other instances of ventral tubers in the Marchantiaceae are known to the writer, although there are several cases in which the apex of an ordinary branch becomes tuberously thickened and often greatly modified.

8. *Asterella venosa* (Lehm. & Lind.) Evans.

Fimbriaria venosa Lehm. & Lind.; Lehm. Nov. Stirp. Pugill. 4: 29. 1832.

Hypenatron venosum Trevis. Mem. Ist. Lombardo III. 4: 441. 1877.

Thallus very delicate, sometimes thin throughout but not infrequently more or less tinged with purple, the pigmentation occasionally extensive but usually

¹ Bot. Zeit. 45: 649-655. pl. 8. 1887.

² Beih. Bot. Centralbl. 18: 397. 1905.

³ New Phytol. 13: 309. 1914.

restricted to the ventral scales and contiguous portions of the ventral surface, mostly 1 to 2 cm. long and 2.5 to 4 mm. wide, plane or slightly concave above with thin, slightly sinuous-crispate margins, not incurved when dry, branching by forking, apical innovations sometimes present; keel broad and rounded; epidermis composed of cells with thin walls but sometimes with more or less distinct trigones, averaging about $35 \times 25 \mu$ (or a trifle more in shade plants); pores slightly elevated, measuring (with their surrounding cells) mostly 80 to 90 μ in length and 50 to 65 μ in width, surrounded by 7 or 8 (sometimes 6 or 9) series of cells with 2 or 3 cells in each series, the radial walls sometimes thin throughout, sometimes slightly thickened and showing more or less distinct trigones; cells containing oil bodies as in *A. tenella*; green tissue loose, the air chambers in 2 or 3 layers in the median portion, those of the dorsal layer larger than the others and sparingly subdivided by supplementary partitions; compact tissue occupying about one-half the thickness of the thallus in the median portion, thinning out rather abruptly on the sides and extending about one-third the distance to the margin, composed of cells with thin unpitted walls; mycorrhiza sparingly developed; ventral scales small, not overlapping, ovate, colorless or somewhat pigmented with purple, entire; cells containing oil bodies mostly 5 to 10, scattered; appendages borne singly (always, so far as observed), subulate from a broad and unstricted base, mostly 0.25 to 0.4 mm. long and 0.12 to 0.18 mm. wide, acute to acuminate, entire, the cells mostly 40 to 50 μ long and 20 to 25 μ wide, occasional cells with oil bodies in the basal portion; inflorescence parvicous, the antheridia forming a small and irregular median group near the peduncle of the female receptacle, the ostioles low; peduncle with scattered slender paleae and a slightly denser cluster at the apex, usually green but sometimes purple at the base, about 1 cm. high; disk of receptacle mostly 3 to 4 mm. across, flat or nearly so above with a small, slightly elevated center, coarsely tuberculate, with low rounded tubercles, rugose when dry, normally 4-lobed, the lobes spreading almost horizontally, the involucre a thin membrane on the side next the peduncle, not bilobed but vaguely sinuate-crenate on the margin, barely reaching the margins of the lobes; pseudoperianth white or yellow, directed obliquely downward, mostly 8 to 10-cleft, the divisions narrowly lanceolate, connate at the apex; capsule yellow, circumscissile above the base by a very irregular line, the operculum coming off in one piece; spores yellowish brown, translucent, mostly 55 to 65 μ in diameter, with wavy wings 8 to 10 μ wide along the edges, the entire surface (including the wings) covered over with a fine and irregular reticulum formed of wavy and zigzag ridges about 1 μ high slightly darker than the rest of the spore surface, the meshes mostly 1 to 4 μ in diameter (rarely up to 6 μ), coarser folds or ridges not present; elaters pale yellow, variously curved, mostly 180 to 200 μ long and 6 to 8 μ wide, tapering more or less toward their blunt ends, bispiral throughout or unispiral at the ends, the spirals pale and inconspicuous.

Growing on banks; known only from Brazil and Mexico. The following specimens have been examined:

FEDERAL DISTRICT OF MEXICO: Amecameca, 1908, *Barnes & Land* 339 in part (Y.; mixed with *Targionia hypophylla* L.); Cañada Santa Magdalena, *Barnes & Land* 441 (Y.).

PUEBLA: Banks along Avenida Hidalgo and path to barranca, Teziutlán, *Barnes & Land* 555 (Y.).

BRAZIL: Without definite localities or dates (N. Y.; two specimens, one collected by Klotzsch, the other by an unknown collector.)

The type specimens of this fragile species have not been studied by the writer. They were collected in Brazil by Sellow, no more definite locality being men-

tioned. In the Synopsis Hepaticarum the species is placed in the subgenus *Brachyblepharis*, being accepted without question, and no specimens except Sellow's are listed. Two years later, however, Lindenberg¹ reported it from Java, and this record was accepted by other writers on Javan liverworts, including Gottsche, Zollinger, and Sande-Lacoste. In 1898, Schiffner² still accepted this Javan record, expressing the opinion that *Fimbriaria khasiana* (Griff.) Mitt. and *F. leptophylla* Mont. of India might be synonyms of *F. venosa*. The following year Stephani, in his monograph, separated the Javan specimens from *F. venosa* and described them as a new species under the name *F. zollingeri*. Schiffner³ soon accepted this new species, changing the name to *Hypenantron zollingeri* and transferring to it as probable synonyms the two Indian species mentioned above. The range of the true *F. venosa* was thus again restricted to Brazil, and its discovery in Mexico marks an interesting extension. The Mexican plants have been carefully compared with the two Brazilian specimens in the herbarium of the New York Botanical Garden and agree in all essential respects.

The original description of *A. venosa* says little or nothing about the histological features or the spores and elaters, but emphasizes the usual green color and the extreme delicacy of the thallus, stating that the surface is covered over with anastomosing veins, visible to the naked eye. It notes also the orbicular disk of the female receptacle and the short pseudoperianths, these not reaching the margins of the disk. Perhaps the most serious errors are those connected with the male inflorescence, which is said to be on a distinct plant, the inference being that the species is dioicous. The receptacle is said further to be borne on a short peduncle and to be provided below with white follicles. It is, of course, obvious that these statements must have been based either on young female receptacles or on plants belonging to some other genus. In the Synopsis the male inflorescence is said to be unknown, but the description repeats most of the other statements made by the original authors. It gives additional details, however, about the size of the plant, the occasional lobing of the receptacle, the yellowish green, margined and reticulated spores, and the bispiral elaters.

Stephani supplies many other details and corrects the earlier statements about the inflorescence, showing that the antheridia are situated close to the peduncle of the female receptacle. His account of the epidermal pores, which states that the surrounding cells are in only 4 or 5 series, with 2 cells in each series, does not agree with the writer's observations, and the entire disk which he describes is evidently not a constant feature of the species. At the same time his description is trustworthy in most respects. The Javan *Fimbriaria zollingeri* is certainly a close relative of *A. venosa*, rivaling it in delicacy. The spores, however, will at once serve to distinguish it. In addition to a fine and delicate reticulum the spherical face shows a coarse reticulum, with meshes 20 to 30 μ across, formed by high ridges similar to the marginal wings.

Lehmann and Lindenberg compare their *F. venosa* with *F. tenella* and state that it differs sufficiently in its more delicate thallus, green both above and below and veiny on the upper surface; in the presence of slender paleae at the apex of the peduncle; and in the shorter divisions of the pseudoperianth, coherent at the apex. It might be added that the dorsal air chambers are subdivided, that the epidermal pores have more radiating series of cells around them, that the appendages of the ventral scales are smaller and apparently

¹ Meissner, Bot. Zeit. 6: 463. 1848.

² Consp. Hep. Arch. Ind. 43. 1898.

³ Fl. Buitenzorg 4: 23. 1900.

always entire, that the disk of the female receptacle is flat or nearly so, and that the spores lack a coarse reticulum on the spherical face. Among Mexican species *A. pringlei* bears a certain resemblance to *A. venosa*, in spite of its more xerophytic tendencies; but its undivided dorsal chambers, its smaller epidermal pores, the large and toothed appendages of its ventral scales, its autoicous inflorescence, its 12 to 16-cleft pseudoperianth, and its darker, almost opaque spores are distinctive characteristics.

9. *Asterella rugosa* Evans, sp. nov.

Thallus sometimes green throughout but usually with some purple pigmentation, especially along the margin and on the ventral surface, mostly 1.5 to 2 cm. long and 8 to 10 mm. wide, plane above or with a shallow median groove, the margins mostly crenate and closely undulate-crispate, not incurved when dry, branching normally by forking but sometimes by apical innovations or lateral intercalary outgrowths, the keel narrow but rounded; epidermis composed of cells with thin walls and small but very distinct trigones, averaging about $30 \times 25 \mu$; pores slightly elevated, measuring (with their surrounding cells) mostly 80 to 110 μ in length and 60 to 90 μ in width, surrounded by 6 (sometimes 5 or 7) radiating series of cells with 3 or 4 cells in each series, the radial walls more or less thickened and showing distinct trigones; cells containing oil bodies not abundant, much as in *A. tenella*; green tissue loose, the air chambers in 3 or 4 layers, those of the dorsal layer sparingly subdivided by supplementary partitions extending to the epidermis; compact tissue occupying about one-half the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about one-fourth the distance to the margin, composed of cells with thin unpitted walls; mycorrhiza present; ventral scales small, narrowly to broadly ovate, usually purple throughout or with the tips of the appendages hyaline, the marginal slime papillae more or less persistent but inconspicuous; cells containing oil bodies mostly 15 to 20, scattered; appendages mostly borne singly but sometimes in pairs, not constricted at the base and not distinctly marked off from the basal portion, subulate from a broad base, mostly 0.45 to 0.6 mm. long and 0.15 to 0.2 mm. wide at the base, usually entire but sometimes with 1 or 2 coarse and irregular teeth, acuminate, the cells averaging $50 \times 20 \mu$; inflorescence dioicous (apparently); male inflorescence borne on a leading branch and not limiting its growth, consisting of a narrow elongated median group of antheridia without marginal paleae; ostioles long; female inflorescence borne on a similar branch; peduncle with a loose apical cluster of slender paleae, otherwise naked or nearly so, not pigmented, about 1 cm. long; disk of receptacle 3 to 4 mm. across, the upper surface slightly convex, covered with low and coarse tubercles, rugose when dry, scarcely or not at all lobed; involucre narrow, its features not clearly made out; pseudoperianths normally 4, extending almost vertically downward, white or brownish, mostly 12 to 14-cleft, the divisions lanceolate and coherent at the apex; capsule brown, its method of dehiscence not observed; spores brown, mostly 80 to 90 μ in diameter, with pale yellowish brown, wavy and vaguely crenulate wings 8 to 10 μ wide along the edges, the wings marked by narrow and low irregular and darker ridges, extending outward but growing narrower and paler toward the wing margins, the spherical face covered over with a fine and irregular reticulum, with meshes about 10 μ in diameter, inclosed by a system of anastomosing ridges similar to those on the wings, the plane faces with similar but lower and often indistinct ridges, sometimes almost smooth, coarser folds or ridges not present; elaters brown, more or less curved, mostly 140 to 200 μ

long and 12 to 18 μ wide, tapering slightly toward the blunt ends, usually with 2 spirals in the median portion for a variable distance and 1 at each end, sometimes with 1 to 4 rings instead of spirals at the ends, the walls between the turns of the spiral unpigmented or pale brown.

A mountain species, growing on shaded banks; known only from the following collections:

FEDERAL DISTRICT OF MEXICO: La Cima, alt. 3,000 meters, October 14, 1908, *Barnes & Land* 413 (Y.; type); same locality, July 17, 1908, *Pringle* 10682 in part (distributed in Pl. Mex., in admixture with *Plagiochasma crenulatum* Gottsche, under the name *P. muenchianum* Steph.).

The material of this new species is unfortunately so scanty that it has been impossible to determine the inflorescence with certainty. Three clusters of antheridia were observed, all on a single plant, and a female receptacle was present on a neighboring thallus, but it was impossible to demonstrate any connection between them. The male inflorescence bears a strong resemblance to that of the dioicous *A. californica*, which perhaps adds to the probability that *A. rugosa* also may be dioicous. The species derives its name from the finely crinkled appearance of the thallus along the margin. In typical cases this is distinctly fluted and stands in sharp contrast to the smooth surface of the thallus throughout the remainder of its extent.

In addition to the elongated male inflorescence, *A. rugosa* shares certain other features with *A. californica*, such as the large size of the thallus, the dichotomous branching, the green tissue with subdivided dorsal chambers, and the compact tissue with unpitted walls. There are, however, important differential characters. In *A. rugosa* the epidermal cells have distinct trigones; the green tissue is very loose, the dorsal chambers being sparingly subdivided; the ventral scales show only 1 or (rarely) 2 appendages; the disk of the receptacle is scarcely lobed; and the spores are brown, with the meshes of the fine surface network about 10 μ across, and without coarse folds or ridges of any kind (except the marginal wings). In *A. californica*, on the other hand, the epidermal cells are thin-walled throughout or show very minute trigones; the green tissue is somewhat more compact, the dorsal chambers being more abundantly subdivided; the ventral scales show 2 to 4 appendages; the disk of the receptacle is deeply lobed; and the spores are yellow, with the meshes of the network only 3 to 4 μ across, and with additional coarse ridges on the spore faces.

Among Mexican species it will be sufficient to compare *A. rugosa* with *A. pringlei* and *A. venosa*, both of which are distinctly smaller. In *A. pringlei* the green tissue, although somewhat more compact, shows no subdivision of the dorsal air chambers, each being clearly provided with an epidermal pore; the pores, moreover, are smaller, the appendages of the ventral scales are larger and usually more toothed, and the female receptacle is distinctly lobed. In *A. venosa*, which is perhaps the closest known ally of *A. rugosa*, the thallus is even more delicate; the inflorescence is parolcous; the disk of the receptacle is flatter, looser in texture, and usually lobed; the pseudoperianth is only 8 to 10-cleft (instead of 12-cleft or more); the spores are paler and show a finer surface network, the meshes being mostly only 1 to 4 μ wide; and the elaters are only 6 to 8 μ in diameter (instead of 12 to 18 μ).

10. *Asterella elegans* (Spreng.) Trevis.

Fimbriaria elegans Spreng. Syst. Veg. ed. 16. 4¹: 235. 1827.

Marchantia physocarpa Bertero; Spreng. loc. cit., as synonym.

Fimbriaria cub[an]ensis Lehm.; Mont. in Sagra, Hist. Cuba 9: 489. pl. 19, f. 3. 1845.

Fimbriaria elegans γ *cubensis* Gottsch., Lind. & Nees, Syn. Hep. 565. 1846.

Asterella elegans Trevis. Rend. Ist. Lombardo II. 7: 785. 1874.

Hypenantron elegans Trevis. Mem. Ist. Lombardo III. 4: 441. 1877.

Asterella cubensis Underw. Bot. Gaz. 20: 63. 1895.

Asterella austini Underw. op. cit. 64. 1895.

Asterella wrightii Underw. loc. cit.

Fimbriaria wrightii Stephani, Bull. Herb. Boiss. 7: 97. 1899.

Fimbriaria austini Stephani, op. cit. 203. 1899.

Thallus green above, usually more or less pigmented with purple on the ventral surface and along the margin, sometimes with scattered dots or splotches of purple on the upper surface, mostly 1 to 3 cm. long and 2 to 4 mm. wide (rarely up to 6 mm.), plane or slightly concave, with undulate and often crispate margins, often scarious when old and scarcely or not at all incurved when dry, rarely branching by forking, usually by means of apical innovations and ventral outgrowths, the keel broad and rounded; epidermis composed of cells with slightly thickened walls and sometimes with minute trigones, averaging about $50 \times 30 \mu$; pores distinctly elevated, measuring (with their surrounding cells) mostly 100 to 130 μ in length and 70 to 100 μ in width, surrounded by 6 to 8 (rarely only 5) radiating series of cells with 3 or 4 cells in each series, the radial walls slightly thickened; cells containing oil bodies scattered and few in the epidermis, otherwise as in *A. tenella*; green tissue compact, the air chambers mostly in 2 to 4 layers in the median portion, those of the deeper layers small, those of the dorsal layer higher and larger but subdivided by crowded vertical supplementary partitions failing to reach the epidermis in the vicinity of the pores; compact tissue occupying nearly or quite two-thirds the thickness of the thallus in the median portion, thinning out more or less abruptly on the sides and extending from one-third to one-half the distance to the margin, composed of cells with more or less thickened and distinctly pitted walls; mycorrhiza often abundant in the lower part; ventral scales ovate to lunulate, usually with purple pigmentation, the cells containing oil bodies mostly 6 to 15, scattered, tending to be more numerous in the acropetal portion; appendages usually borne singly but not infrequently in pairs, narrowly lanceolate or subulate, slightly or not at all constricted at the base, mostly 0.6 to 0.9 mm. long (rarely down to 0.35 mm.) and 0.09 to 0.15 mm. wide, the margin entire or vaguely crenulate from projecting cells, rarely bearing a single spinelike or cilium-like tooth near the base, the apex acuminate, the cells mostly 100 to 120 μ long and 30 to 40 μ wide; inflorescence autoicous; male inflorescence in the form of a clearly defined and slightly raised oval to emarginate disk, containing usually 15 to 30 antheridia and surrounded by a fringe of narrow paleae, terminal on a short or more or less elongated branch but sometimes with an apical innovation; ostioles distinctly elevated; female inflorescence borne on a similar branch; peduncle more or less pigmented with purple, bearing scattered lanceolate paleae along its entire length (at least when young) and a denser cluster at the apex, mostly 1 to 1.5 cm. high; disk of receptacle green or somewhat purple, mostly 3 to 4 mm. across, coarsely tuberculate, hemispherical in the center, normally 4-lobed, the lobes short but distinct, extending obliquely downward and outward, the margins crenate, the involucre rather broad, entire or sinuate, scarcely or not at all bilobed; pseudoperianth usually white to brownish but sometimes more or less purple, usually 8 but sometimes 9 or 10- (rarely 12) cleft, the divisions lanceolate, coherent at the apex; capsule brown, circumscissile above the middle by an irregular line, the operculum coming off in one piece; spores pale to dark brown, mostly 80 to 100 μ in diameter (rarely as low as 60 μ or as high as 120

μ), with wavy wings 8 to 20 μ wide along the edges, the margins of the wings broadened out and more deeply pigmented, marked with irregular points and lines, the surface of spore minutely and irregularly punctulate, the spherical faces showing in addition a coarse and usually regular reticulum, the meshes mostly 15 to 20 μ wide, inclosed by a system of high and thin ridges similar to the wings and usually involving the wings themselves, the plane faces covered by similar reticula; reticula sometimes irregular and incomplete, especially on the plane faces; elaters pale to dark brown, more or less curved, mostly 150 to 300 μ long and 12 to 14 μ wide, tapering slightly toward the blunt ends, sometimes unispiral or bispiral throughout but usually bispiral in the median portion for a variable distance and unispiral at the ends.

On rocks and banks, sometimes on coral formations; apparently restricted to the West Indies and especially abundant in Cuba. The following specimens have been examined:

CUBA: Without definite localities or dates, *Wright* (N. Y., U. S., Y.; one specimen, the type of *A. austini*, distributed in Austin's Hep. Bor. Amer., no. 136c, as *Fimbriaria elegans*; another specimen, the type of *A. wrightii*, distributed in Wright's Hep. Cub., as *F. tenella*; a third specimen, distributed in Hep. Cub., as *F. elegans*, and listed by Underwood, as *A. cubensis*, in Bot. Gaz. 20: 63. 1895); Monte Verde, Yateras, 1860, *Wright* (H., Y.); Arroyo de Piedra, 1858, *Wright* (H., Y.); Matanzas and vicinity, *Underwood* 2087 (N. Y.; listed by Underwood, as *A. cubensis*), *Britton, Britton & Shafer* 326, 352 (N. Y., Y.); Caverns of Thermopylae, Monte Libano, Oriente, *Maxon* 4262 (N. Y., U. S., Y.; also distributed, as *Hypenantron elegans*, in Crypt. Exsic. Mus. Vinden., no. 1689); Arroyo Trinitario (Río Negro) and Arroyo Grande, Trinidad Mountains, Santa Clara, *E. G. Britton* 5204, 5483 (N. Y., Y.); Ranchuelo, Santa Clara, *Cuesta* 989, 991 (N. Y., Y.); Rincón to Banaó, Santa Clara, *Shafer* 12325 (N. Y., Y.); vicinity of Mal Paso, Río San Miguel, Pinar del Río, *Wilson* 9301, 9363 (N. Y., Y.); between Bahía Honda and Baños Aguacate, Pinar del Río, *Wilson* 9217 (N. Y., Y.); Río Mestanza, Pinar del Río, *Britton, Britton & Cowell* 10160 (N. Y., Y.); Bahía Honda to El Rosario, *Shafer* 12048 (N. Y., Y.); Ripreso del Guaso, *Hioram & Batiste* 1507 (N. Y., Y.); Caracusey Valley, Bana Mountains, Santa Clara, *León & Roca* 8349.

HISPANIOLA: Santo Domingo, 1871, *Wright, Parry & Brummell* (U. S., Y.).

PORTO RICO: El Yunque, 1902, *Evans* 87 (N. Y., Y.); Río Prieto and vicinity, Sierra de Naguabo, *Shafer* 3695 (N. Y., Y.).

JAMAICA: Chestervale, 1903, *Underwood* 1143 (N. Y.); Mabess River, *Evans* 288 (Y.).

The following West Indian specimens, cited from the literature, are also of interest:

CUBA: Banks of the Carima River, 1839, *Otto* (type of *Fimbriaria cub[an]ensis*).

HISPANIOLA: Without definite locality, date, or collector's name (type of *F. elegans*); Santo Domingo, *Eggers* (listed by Stephani, as *F. elegans*, in Bull. Herb. Boiss. 7: 199. 1899).

The original material of *Fimbriaria elegans* came from the island of Hispaniola, no further data being supplied. In all probability it was collected by the Italian botanist Bertero, who visited the West Indies in 1821, since one of his manuscript names is quoted by Sprengel as a synonym. This original material is not represented in any of the herbaria consulted by the writer. In its absence it has seemed justifiable to associate the name *A. elegans* with the commonest and most widely distributed of the West Indian species, more especially since this agrees in all essential respects with the original diagnosis

and with the longer description of Lehmann and Lindenberg,¹ drawn up from the type material. This species, as the writer understands it, has not yet been found on the American mainland or in the Old World, although *A. elegans* has been reported from several widely separated localities in both hemispheres, most of the records (in the writer's opinion) being based on incorrect determinations. As a matter of fact, the species is exceedingly variable and has a number of close allies, some of which are distinguished with difficulty.

Among the features emphasized by Sprengel the tuberculate, 4-lobed female receptacle and the pilose peduncle are especially worthy of mention. Lehmann and Lindenberg, without alluding in any way to the histological features or the male inflorescence, add a few important details about the thallus and the female receptacle. They estimate the size of the thallus as 0.6 to 1.2 cm. × 3 mm., and describe the upper surface as glaucous green with white dots (the epidermal pores) and the margin and lower surface as purple; they allude also to the occurrence of apical innovations. They describe the pseudoperianths as hyaline or purple, with 6 to 8 linear divisions, coherent at the apex; the spores as purple and marginate; and the elaters as simple and purplish, each in a narrow tube, thus implying a unispiral condition.

Among the suspicious or incorrect records the one made by DeNotaris² in 1839 should be particularly mentioned. On the basis of a specimen collected by Thomas on the island of Corsica he reported the species as European. Corsica has since been bryologically explored with considerable care, especially by Camus,³ but no additional material of *A. elegans* has come to light, and nobody has reported it from other parts of Europe. In spite of this meager evidence the species has been quoted as European by Underwood, Stephani, Müller, Massalongo, and other recent writers. Boulay,⁴ however, refers rather vaguely to certain old reports of *F. elegans* in France and states that they were based on *Grimaldia fragrans*. Whether this statement applies to the Corsican record is not definitely brought out. It is to be hoped that European botanists may take the trouble of studying the specimens in the DeNotaris Herbarium at Turin and of determining their true status.

In proposing *F. cub[an]ensis* Lehm. as a new species Montagne compared it with *F. elegans*, describing the thallus as shorter, broader, and not convolute from ascending borders, and the receptacle as barbate below. The illustrations, drawn by Gottsche, show, among other details, female receptacles with the disks covered over with low tubercles; peduncles bearing scattered paleae with a denser tuft at the apex; both male and female receptacles borne on more or less elongate branches, broadening out from a stalklike base and thus implying a ventral origin; ventral scales not crowded, ovate and gradually narrowed to a subulate acuminate appendage; dark brown spores showing a paler wing and (in the case of a crushed spore) a fairly regular reticulum; and 3 short elaters, 2 with a single spiral each and the third with more than 1 spiral. It will be seen at once that these characters are hardly sufficient to separate a species, a conclusion which was reached by the authors of the Synopsis Hepaticarum and afterwards by Montagne⁵ himself.

In the Synopsis, *F. elegans* is again described but no very important character is added except that the ventral scales sometimes show two appendages. The authors recognize, however, 5 distinct forms or varieties and assign to

¹ Lehm. Nov. Stirp. Pugill. 4: 28. 1832.

² Mem. Accad. Sci. Torino II, 1: 335. 1839.

³ Bull. Soc. Bot. France 48: cli-clxxiv. 1902.

⁴ Musc. France 2: 190. 1904.

⁵ Syll. Crypt. 92. 1856.

the species certain Mexican and Indian specimens. These forms, with their respective ranges, are as follows: α (with no special name), from Hispaniola and Corsica; β *beyrichiana*, from Mexico; γ *cubensis* (based on Lehmann's species), from Cuba; δ *orientalis*, from Nepal; and ϵ *obtusata*, from Mexico. The writer suspects that the forms β and ϵ represent *A. lateralis*, to be discussed later on, but can make no positive statements in the absence of specimens; the form δ would probably now be referred to one of the recognized Indian species, although here again the matter must be left in doubt.

In 1851 Mitten¹ listed *F. elegans* from Ecuador, but this record, according to specimens in the Mitten Herbarium, was based on *Fimbriaria macropoda* Spruce. In 1856 Sullivant² listed it from Texas, a record based on *A. echinella*, as Underwood has since shown. In the same year Gottsche³ listed the species from Australia and in 1863⁴ added a new station for Mexico, but neither of these records can be accepted. The Australian plant would undoubtedly be referred to one of the many species of that region and the new Mexican record, as will be shown, was based on *A. lateralis*. In 1885 Spruce⁵ doubtfully referred to *F. elegans* additional material from Ecuador. His description is accurate but makes no mention of the male inflorescence or the capsule. Fortunately mature spores and elaters are present in the specimens which he afterwards distributed in his *Hepaticae Spruceanae* and show that they represent *A. lateralis*.

When Underwood revised the North American species of *Asterella* in 1895 he published a new description of *A. elegans*, citing it from Mexico, but not from the West Indies, and noting its occurrence in Europe and South America. The variety *cubensis* of the Synopsis he again elevated to specific rank and, further, proposed as new, under the names *A. austini* and *A. wrightii*, two other species based on Cuban material. Stephani, in his monograph of 1899, accepts *A. wrightii*, *A. cubensis*, and *A. austini* without question, transferring them to *Fimbriaria*, and quotes *F. elegans* from Santo Domingo and Cuba, as well as from Costa Rica, Mexico, Ecuador, and California (the last probably meaning Lower California). The writer, however, after a careful study of Underwood's descriptions and of the specimens upon which his Cuban species were based, has regretfully reached the conclusion that they represent forms of *A. elegans* and that they must therefore be reduced to synonymy.

In Underwood's descriptions little or nothing is said about the branching, the stomata, the green tissue, the ventral scales, or the male inflorescence, and the differences brought out are based on variable characters. To all three of the Cuban species which he recognizes he assigns a tuberculate female receptacle, an 8-cleft pseudoperianth (sometimes 9-cleft in *A. cubensis*) with coherent divisions, a peduncle about 1 cm. high and pilose at the apex, bispiral elaters, and a more or less marked purple pigmentation, the extent of which is sometimes left uncertain. His most important differences are derived from the spores: in *A. cubensis* these are said to be 95 to 105 μ in diameter, brown or purplish brown, opaque, and with a paler margin; in *A. austini*, 110 to 118 μ in diameter, yellow, distinctly reticulated, and broadly winged; in *A. wrightii*, dark yellow, otherwise as in *A. austini*. In his description of *A. elegans*, which was probably drawn from Mexican specimens, the spores are said to be 100 to

¹ Journ. Bot. Kew Misc. 3: 361. 1851.

² In A. Gray, Man. ed. 2. 688. 1856.

³ Linnaea 25: 561. 1856.

⁴ Dansk. Vid. Selsk. Skrivt. V. 6: 368. 1863.

⁵ Trans. Bot. Soc. (Edinburgh) 15: 563. 1885.

135 μ in diameter, dark purple or nearly black with a reddish border, reticulated when young and opaque when old; the pseudoperianth is described as 8 to 12-cleft with coherent divisions, the peduncle as 1 to 1.5 cm. high and pilose (especially at the apex), the elaters as bispiral, and the receptacle as convex, no tubercles being mentioned.

In recognizing Underwood's Cuban species Stephani discusses some of the features not alluded to in the original descriptions but brings out few additional differential characters. To all three species (as well as to *F. elegans*) he assigns apical innovations and ventral branches, a photosynthetic tissue with hairs in the chambers, at least under the pores (but see, in this connection, p. 252), and a female receptacle with high tubercles or papules. The pores are said to be surrounded by 6 radiating series of cells, with 3 cells in each series in *A. wrightii* and *A. austini*, 4 or 5 in *A. elegans*, and 5 in *A. cubensis*. In *A. cubensis* the spores are described as 90 μ in diameter, brownish red, with narrow papillate wings; in *A. wrightii* as 102 μ in diameter, orange-colored, with broad and rough yellow wings; and in *A. elegans* as 100 μ in diameter, reddish brown, with narrow and rough, entire wings; in *A. austini* the spores are not described. With regard to the appendages of the ventral scales, Stephani states that 1 or 2 may be present in *A. cubensis*, implying a single appendage in the other cases. In all four species the appendages are said to be long and narrowly lanceolate or filiform, a single marginal spine being occasionally present in *A. wrightii*. The position of the male inflorescence at the apex of a ventral branch—short in *A. elegans*, short or long in the three Cuban species—is likewise noted.

In order to show that the differences brought out by Underwood and Stephani are too slight and too inconstant, in the case of the Cuban species, to be considered specific, it will perhaps be justifiable to discuss the characters of *A. elegans*, as understood by the writer, in some detail. The thallus varies greatly in size and general appearance according to the environment. In dry localities it is usually only 2 to 3 mm. in width and may be even less; in moist and shaded localities it sometimes attains a width of 6 mm. The broader forms are often thin and delicate, but the narrower forms may be equally so, although they tend to be firmer and more compact. The amount of pigmentation also is subject to great variation. At one extreme the plants are green throughout; at the other the pigmentation involves the ventral scales, the spaces between the scales, the marginal portions of both surfaces, the peduncles and disks of the female receptacles, and the pseudoperianths. Even the dorsal surface of the thallus may be spotted or blotched with purple. The margins tend to become scarious with age but are not strongly incurved when dry, so that the species never presents a xerophytic appearance.

Branching by forking occurs occasionally but is infrequent, especially after the formation of the sexual organs has begun. The branching then is almost invariably intercalary, sometimes by means of apical innovations, but usually by means of ventral outgrowths. The sexual branches themselves vary greatly in length and in width, but their growth is always brought to an end by the development of the receptacles, whether male or female. A sexual branch, however, especially if elongated, may give rise to an apical innovation or to lateral branches, these in turn bearing new receptacles. A sexual branch if elongated is usually relatively broad; if abbreviated, relatively narrow. In one observed instance a long branch bore a female receptacle and 6 lateral branches, 4 of which (2 male and 2 female) were very short, while the other 2 (1 male and 1 female) were more elongated, though less than half the length of the original branch; one of the longer branches bore 2 short lateral branches

(one male and the other female), while the other bore a single short (female) lateral branch. In another instance a long branch bore a male receptacle, a short apical innovation (also male), and 5 short lateral branches (4 female and 1 male). These examples will give some idea of the variability encountered.

In its histological features the thallus shows a delicate epidermis with slightly thickened walls and sometimes with minute trigones, the cells with oil bodies being few and scattered. The pores have a broad membrane around the opening and each is usually surrounded by 6 to 8 radiating series of cells with 3 or 4 (rarely only 2) cells in each series. The writer has not yet observed 5 cells, although Stephani gives this number as characteristic of *A. austini*. The green tissue shows much uniformity, although its thickness may vary from 0.15 mm. to 0.3 mm. in different specimens. The crowded supplementary partitions in the dorsal chambers often give the effect of filaments, in cross sections of the thallus, especially beneath the pores, where they fail to reach the epidermis. The compact tissue, composed of cells with numerous minute pits in the walls, occupies a strand, plane or slightly convex above; in the latter case the green tissue is a little thicker over the sides of the strand than over the middle, and the more deeply situated air chambers in this region are distinctly larger than elsewhere. Mycorrhiza seems to be almost invariably present. The cells containing the hyphae tend to form a definite strand in the compact tissue, elliptical in section and variable in size. Their walls may be quite colorless but are usually purple, even in plants which are otherwise colorless. They are distinctly thinner than the walls of the cells without hyphae.

The ventral scales never extend beyond the margins, except in the apical region, but show great variation in size and in extent of pigmentation. Each scale contracts gradually into 1 or 2 appendages without showing a sharp line of demarcation. In the basal portion the marginal cells are slightly smaller than the median cells, and the slime papillae are usually short-lived and inconspicuous, especially on deeply pigmented scales. The appendages are long-subulate or lanceolate, running out into slender cuspidate or filiform points. In most cases their margins are entire; they may, however, be vaguely crenulate, and occasionally a marginal spine or cilium is present at the base (as Stephani described for *A. wrightii*). But even in plants where such spines occur they seem to be exceptional, many of the appendages being without them, so that they can not be considered of specific importance.

The male receptacle is much more clearly defined than in the preceding species and is further distinguished by the fact that it always limits the growth of the male branch. It consists of a slightly elevated oval or circular disk, sometimes with an apical notch, and is surrounded by a fringe of slender paleae which shrivel with age and are sometimes difficult to detect. The number of antheridia varies but is usually rather large, and the ostioles are distinctly elevated, especially on young receptacles.

The peduncle of the female receptacle varies in length and the size of the disk also varies somewhat, according to the vigor of the plant and the number of fertilized archegonia. The disk shows a central, strongly convex area and, in typical cases, 4 lobes extending obliquely downward and about as long as the diameter of the central area; sometimes the number of lobes is reduced to 3, 2, or even 1. The upper surface of the disk is covered over with coarse tubercles, each with an apical pore, these tubercles being especially prominent in the central area. The paleae of the peduncle are scattered except in the apical region and become much less conspicuous with age. The disk is usually green but sometimes shows a little purple pigmentation; the peduncle, on the

other hand, is almost always purple throughout the greater part of its length. The involucre, which consists of a fairly wide membrane without a special indentation next the peduncle, is continuous with the outer margin of a lobe, a tubular sheath being thus formed around each capsule. The margin of the involucre is entire or nearly so. The pseudoperianths, varying in color from white or yellowish white to purple, are inconspicuous and are usually 8-cleft, although pseudoperianths with as many as 12 clefts exceptionally occur. The segments are rather broadly lanceolate and cohere at the apex.

The operculum of the brown capsule, although coming off in one piece, has an exceedingly irregular outline. It leaves behind a broad urn with a coarsely dentate or crenate margin. The cells of the operculum have conspicuous trigones and the same thing is true of the teeth of the urn, but the remaining cells of the capsule wall are rather thin and without trigones.

The spores yield some of the most important characters of the species, in spite of the range in the amount of pigmentation and in size which they exhibit. Their color is usually some shade of brown; it may be a pale yellowish brown, a deep blackish brown, or some intermediate shade. The paler spores show the surface markings clearly, but the dark spores are sometimes so opaque that the markings are distinguished with difficulty. The diameter of the spores is usually 80 to 100 μ , but spores as small as 60 μ or as large as 130 μ in diameter occur. In one instance the spores from a single capsule varied from 80 μ to 110 μ in diameter. The surface of the spore is minutely punctulate; it shows in addition distinct wings along the 6 edges and a system of anastomosing ridges similar to the wings on the 4 faces, in typical cases forming regular networks in which the wings take part. The meshes of these networks, however, are often incomplete, the networks in consequence being irregular. The wings around the spherical face are 10 to 20 μ wide, those separating the plane faces mostly 8 to 10 μ wide, while the ridges are mostly 8 to 15 μ wide. When the networks are regular there are usually 6 or 7 meshes across the spherical face and about 4 meshes across each plane face from base to apex. The wings and ridges are not only wavy, crenulated, and more deeply pigmented (in the case of pale spores) on their margins, but broaden out distinctly and show an irregular system of fine dots and lines when seen on edge.

The elaters vary considerably in length and in diameter; most of them are 150 to 300 μ in length and 12 to 14 μ in diameter, but extremes of 100 μ and 400 μ in length and of 10 μ and 18 μ in diameter have been observed. The majority of the elaters show 2 spirals in the median portion for a variable distance and 1 spiral at each end, but elaters unispiral or bispiral throughout exceptionally occur.

It has already been noted that the most important characters of Underwood's three Cuban species were drawn from the spores. In the Matanzas material of *A. cubensis*, from which his description was probably drawn, the spores show the deep coloration and opacity which he assigns to them, but they show in addition, after soaking in glycerin, a distinct and regular reticulum formed of wings and ridges, essentially like the regular reticulum found in typical *A. wrightii* and the more irregular reticulum found in typical *A. austini*. The spore differences, therefore, easily come within the range of variation which the writer associates with *A. elegans*. Since the same thing is true of the slight differences in the epidermal pores and ventral scales, to which Stephani has called attention, the claims of the species for recognition clearly break down. In the writer's opinion, as will be shown later, most of the specimens which Underwood and Stephani have referred to *A. elegans* belong rather to *A. lateralis*, a close relative of the mainland.

11. *Asterella echinella* (Gottsche) Underw.

Fimbriaria echinella Gottsche, Dansk. Vid. Selsk. Skrivt. V. 6: 367. 1863.

Astcrella echinella Underw. Bot. Gaz. 20: 62. 1895.

Thallus essentially like that of *A. elegans* and the branching of the same type; epidermis composed of cells with slightly thickened walls but without trigones (so far as observed), averaging about $50 \times 25 \mu$; pores slightly elevated, measuring (with their surrounding cells) mostly 80 to 100 μ in length and 70 to 90 μ in width, surrounded usually by 6 to 8 series of cells with 3 cells in each series; green and compact tissues, in relative amount and in structure, as in *A. elegans*; ventral scales ovate to narrowly lunulate, the appendages borne singly or sometimes in pairs, narrowly subulate, acuminate, entire or nearly so, mostly 0.6 to 0.9 mm. long and 0.07 to 0.12 mm. wide, the cells usually 75 to 110×25 to 30μ ; inflorescence autoicous; male inflorescence terminal on a more or less elongated branch, sometimes innovating at the apex, in the form of an oval to obcordate, slightly elevated disk, surrounded by a fringe of slender paleae, the antheridia (according to Gottsche) 50 to 60; female inflorescence borne on a short or more or less elongate branch; peduncle mostly 1 to 1.5 cm. high, not pigmented (so far as observed), bearing long scattered paleae especially at the apex; disk of receptacle 0.5 to 1 mm. long, hemispherical in the center, normally 4-lobed as in *A. elegans*; pseudo-perianth white or somewhat tinged with purple, mostly 8 to 10-cleft, the divisions lanceolate, coherent at the apex; capsule as in *A. elegans*, the operculum separating by an irregular line and coming off in one piece; spores pale to dark brown, mostly 60 to 100 μ in diameter (rarely as low as 50 μ or as high as 110 μ), with wings 8 to 10 μ wide on the edges, the margins of the wings broadened out and more deeply pigmented, marked with irregular dots and lines; surface of spore minutely and irregularly punctulate, the spherical face showing in addition a coarse and usually regular reticulum, the meshes mostly 15 to 20 μ wide, inclosed by a system of narrow ridges 6 to 8 μ high and similar to the wings, and usually by the wings as well, the plane faces with similar reticula; reticula often incomplete or irregular, especially on the plane faces; elaters pale to dark brown, more or less curved, mostly 140 to 200 μ long and 12 to 14 μ wide, often unispiral throughout but not infrequently bispiral in the middle for a variable distance and unispiral at the ends.

On rocks and banks, Arkansas to Mexico. The following specimens have been examined:

TEXAS: Without definite locality, 1849, *Wright* (H., N. Y., Y.; listed as *Fimbriaria elegans* by Sullivant in A. Gray, Man. ed. 2. 688. 1856; listed also by Underwood in Bot. Gaz. 20: 62. 1895); without definite locality, *McAllister* (N. Y., Y.).

VERACRUZ: Orizaba, 1853 and 1855, *Müller* 2245, 2285 in part, 2327 (N. Y., U. S.; including the type of *F. echinella*); along Mexican Railway above Fortín, Orizaba, *Barnes & Land* 630 (Y.); Huantica, *Ervendberg* (H., Y.).

The following record is quoted from Stephani's monograph:

ARKANSAS: Without definite locality or date, *Trécul*.

Gottsche's original description of *Fimbriaria echinella* is so full and accurate that the writer has been able to add very little to our knowledge of the species. In addition to the long tubercles of the female receptacle, which give the species its name, Gottsche mentions, among other important features, the lateral branches and apical innovations and associates the receptacles with them, noting that the sexual branches may be elongate. He gives, further, unusually good descriptions of the spores with their reticulate markings and of

the elaters, noting the frequent occurrence of 2 spirals in the middle and 1 at each end.

Stephani, in his description, adds details about the epidermis and green tissue, which were not considered in the original account. As in the case of *A. elegans* and certain other species, he alludes to filaments in the air chambers, but describes them as very short, often reduced to a single cell. In a few cases, where he deviates from Gottsche's description, he introduces incorrect or at any rate misleading statements. He states definitely, for example, that the male branches are short, thus giving no idea that they vary in length. He states further that the elaters are bispiral and that the spores are reddish, 63μ in diameter, and lobate-cristate. He thus tells us nothing about the unispiral and partially unispiral elaters or about the conspicuous reticulations on the surface of the spores, although these features were clearly brought out by Gottsche and are well shown by the type material, which Stephani doubtless examined. The size of the spores is also far more variable than he implies.

The writer feels considerable hesitation in accepting *A. echinella* as a valid species, on account of its very close relationship to *A. elegans*. Except for the fact that the tubercles of the female receptacle are longer in *A. echinella* than in *A. elegans*, the two species are essentially alike. This is indicated by the descriptions. Even when the features of *A. echinella* are considered in detail for the sake of completeness, no other important differences are brought out. Whether it is justifiable to base a species on a single character and especially on a character subject to variation is perhaps questionable. It may be noted, however, in support of such an action, that the very long tubercles of *A. echinella* certainly give the plants a distinctive appearance and that the known ranges of *A. echinella* and *A. elegans* do not overlap. There occurs in Mexico, moreover, another species, *A. lateralis*, which is likewise very close to *A. elegans* but which has shorter tubercles. There is no evidence that this species intergrades with *A. echinella*, and the three species might well be considered as forming a series with *A. elegans* in the middle. Of course later investigations may prove the instability of these ideas.

12. *Asterella lateralis* Howe.

? *Fimbriaria elegans* β *beyrichiana* Gottsch., Lind. & Nees, Syn. Hep. 565. 1846.

? *Fimbriaria elegans* ϵ *obtusata* Gottsch., Lind. & Nees, loc. cit.

Fimbriaria quitensis Spruce, Trans. Bot. Soc. (Edinburgh) 15: 563. 1885, as synonym.

Asterella lateralis Howe, Bull. Torrey Club 25: 189. 1898.

Fimbriaria lateralis Stephani, Bull. Herb. Bolss. 7: 201. 1899.

Thallus much like that of *A. elegans* but more xerophytic in habit, the margins more or less incurved when dry and the ventral pigmentation usually more intense, mostly 1 to 2 cm. long and 2 to 4 mm. wide, rarely forking, almost always ventrally branched, the sexual branches (with rare exceptions) very short; epidermis composed of cells with somewhat thickened walls but rarely with trigones, averaging about $55 \times 28 \mu$; pores distinctly elevated, measuring (with their surrounding cells) mostly 120 to 160 μ in length and 90 to 110 μ in width, surrounded usually by 8 (sometimes 9 or 10, rarely 4 to 7) radiating series of cells with 3 or 4 cells in each series, the radial walls slightly thickened; cells containing oil bodies as in *A. elegans*; green tissue compact, the air chambers mostly in 3 or 4 layers, similar to those of *A. elegans*; compact tissue occupying from one-half to two-thirds the thickness of the thallus in the median portion, thinning out gradually on the sides and

extending about halfway to the margin, composed of cells with distinctly thickened and pitted walls; mycorrhiza often present; ventral scales ovate to lunulate, deeply pigmented throughout or with hyaline borders, in the latter case often with more or less persistent slime papillae; cells containing oil bodies mostly 15 to 20, scattered, tending to be more numerous in the acropetal portion; appendages borne singly or in pairs, sometimes bleached out, slightly or not at all contracted at the base, narrowly lanceolate or subulate, mostly 0.8 to 1 (rarely only 0.5) mm. long and 0.13 to 0.18 (rarely only 0.1) mm. wide, acuminate, entire or nearly so, the cells mostly $70 \times 40 \mu$; inflorescence autoicous; male inflorescence borne on a very short and slightly expanded ventral branch, consisting of a small and not clearly defined cluster of antheridia with occasional narrow paleae at the edge; ostioles short but distinct; female inflorescence borne on a very short (rarely slightly elongated) ventral branch, more expanded than the male branch and often obcordate; peduncle more or less pigmented with purple, pilose in the upper part, especially at the apex, becoming naked below, mostly 1 to 2 cm. high; disk of receptacle mostly 2.5 to 3.5 mm. across, covered with low tubercles, those of the lobes often larger and more conspicuous than those of the hemispherical disk, the lobes mostly 4, distinct, spreading obliquely downward, the margins crenate, the involucre rather broad, entire or sinuate, slightly indented in the middle but scarcely bilobed; pseudoperianth white or rarely purplish, mostly 8 to 10-cleft (rarely up to 12-cleft), the divisions extending about halfway to the base, lanceolate, connate at the apex; capsule as in *A. elegans*; spores pale yellowish brown to dark purplish brown, mostly 90 to 120 μ in diameter, with wavy wings 10 to 20 μ wide along the edges, the margins of the wings often more deeply pigmented and very minutely crenulate; the entire surface of spore minutely and densely punctulate but nowhere with distinct lines, the spherical face showing in addition a coarse and sometimes regular reticulum, the meshes mostly 18 to 20 μ across, inclosed by a system of thin ridges similar to the wings but only 6 to 8 μ wide, very rarely involving the wings, the plane faces with similar reticula; reticula often very irregular and incomplete, especially on the plane faces; elaters brown, the color sometimes affecting the thin parts of the wall, variously curved, mostly 200 to 240 μ long and 12 to 14 (sometimes up to 22) μ wide, scarcely tapering toward the blunt ends, usually with 2 spirals in the median portion for about one-third the length of the elater and 1 spiral at each end.

On banks, Mexico, Costa Rica (?), and Ecuador. The following specimens have been examined:

FEDERAL DISTRICT OF MEXICO: Near Toluca, 1903, *Rose & Painter* (Y.); Amecameca, *Pringle* 10674 (Y.; distributed by Pringle in Pl. Mex. as *Fimbriaria austini*), *Barnes & Land* 340 (Y.); Cañada Santa Magdalena, Contreras, *Barnes & Land* 429.

JALISCO: Río Blanco, 16 kilometers from Guadalajara, 1908, *Barnes & Land* 220 (Y.).

LOWER CALIFORNIA: Without definite locality, 1890-92, *T. S. Brandege* 3, 5, 8 (N. Y.; listed as *F. echinella* by Brandege in Proc. Calif. Acad. II. 3: 182. 1891; also, as *A. elegans*, by Underwood in Bot. Gaz. 20: 63. 1895).

MORELOS: Pasque, near Cuernavaca, 1908, *Pringle* 15320 (Y.; distributed by Pringle in Pl. Mex. as *Fimbriaria bolanderi* Aust. ?).

PUEBLA: Santa Barbara, near Puebla, 1909, *Frère Nicolás* 1 (Y.).

SAN LUIS POTOSÍ: Without definite localities, *Parry & Palmer* (N. Y.); in 1876, *Schaffner* 4 (N. Y.).

SINALOA: Colomas, foothills of the Sierra Madre, 1897, *Rose* (N. Y.; type).

TEPIC: Tepic, Sierra Madre, 1897, *Rose* (N. Y.; listed by Howe).

VERACRUZ: Orizaba, 1853, Müller 2285 in part (N. Y.; listed by Gottsche in Dansk. Vid. Selsk. Skrivt. V. 6: 272. 1863, as *F. elegans* γ *obtusata*); same locality, J. G. Smith (N. Y.); along the Coatepec road and railroad, Barnes & Land 557 (Y.); Córdoba, Farlow 15 (N. Y.; listed as *A. elegans* by Underwood).

ECUADOR: Near Baños, Spruce (listed by Spruce as *F. elegans* (?) and distributed under the same name in Hep. Spruceanae).

The following records for *F. elegans* in literature should probably be transferred to *A. lateralis*:

OAXACA: Near Comaltepec, Liebmann (listed in Syn. Hep. as ϵ *obtusata*).

VERACRUZ: Near Jalapa, Beyrich 64, Schiede & Deppe 110; Orizaba, Liebmann (all listed in Syn. Hep. as β *beyrichiana*).

COSTA RICA: Without definite locality, Wendland (listed by Stephani in Bull. Herb. Boiss. 7: 199. 1899).

ECUADOR: Canelos, Spruce.

The type material of *A. lateralis* is not in very good condition and the female receptacles are so dried and shriveled that they fail to give a very convincing idea of their true features. Even the spores and elaters give an impression of rather poor development. The second specimen which Howe cites, collected at Tepic, shows immature female receptacles, but the surface tubercles are distinct, those of the lobes being more pronounced than those of the central portion of the disk. In spite of his unsatisfactory material Howe has given a full and clear description of the species and the writer has been able to add very little to it. Howe's account of the spores, however, deserves some amplification, and his description of the elaters as "bispiral" does not bring out the fact that they are commonly unispiral at the ends.

Through the study of the rather extensive series of specimens listed above the writer has reached the conclusion that *A. lateralis* is not uncommon in Mexico, but that it has been confused with *A. elegans*. Whether the two varieties, *beyrichiana* and *obtusata*, of the Synopsis actually represent *A. lateralis* must of course remain doubtful in the absence of specimens, although Müller's plants from Orizaba, referred by Gottsche to the variety *obtusata*, are clearly the same as Howe's species.

According to the original description the spores are "brown, opaque, 75 to 90 μ , very minutely granulose papillate, the angles with a narrow concolorous margin, the faces exhibiting a few low ridges, these often uniting to form 2 to 4 shallow rather irregular areolae across each face, the more mature and opaque spores appearing simply warty-rugose in outline or subentire." When the spores are well developed, however, they are larger than this account indicates and show a more regular reticulum. The fact that the reticulum rarely involves the marginal wings will serve to distinguish the spores from those of *A. elegans* and other allied species. The wings in consequence appear homogeneous in texture except for the slightly darker margin, the entire surface being covered with crowded dots. Occasionally one of the ridges extends partly across a wing, giving the appearance of a dark line, but it usually thins out and disappears before reaching the margin. The wings and ridges do not show the marked broadening out on their edges which is so characteristic a feature in *A. elegans*, and there are usually no linear markings in this region.

The close relationship existing between *A. lateralis* and *A. elegans* has already been noted and has been brought out further by the descriptions. On the whole, however, the claims of *A. lateralis* for recognition as a species are considerably firmer than those of *A. echinella*. Aside from the differences in the spores and in the tubercles of the female receptacle, there are interest-

ing differences in the male branches. In *A. lateralis* these seem to be invariably short, extending but slightly beyond the margin of the thallus and not broadening out to any marked extent. Upon these branches the antheridia form a small group in a rather vaguely defined median area and show very few marginal paleae or none at all. In *A. elegans* the male branches vary greatly in size, some of them being 1 cm. long or more and correspondingly wide, and the numerous antheridia are situated on a clearly defined and slightly raised receptacle, surrounded by a fringe of paleae. The differences in the female branches, although less constant, are sometimes striking. In *A. lateralis* these are usually almost as short as the male branches, although they broaden out a little more; in *A. elegans* they vary in length to the same extent as the male branches. In exceptional cases, unfortunately, a female branch in *A. lateralis* may be somewhat elongated, so that this distinction must be used with caution.

13. *Asterella reticulata* Evans, sp. nov.

Thallus green above, usually more or less pigmented with purple on the ventral surface and along the margin, sometimes with scattered dots or splotches on the upper surface, mostly 1 to 3 cm. long and 2.5 to 5 mm. wide, plane or slightly concave with undulate, scarcely crispate, margins, often scarious when old and somewhat incurved when dry; branching (so far as observed) ventral, sometimes lateral, sometimes by means of apical innovations, in the latter case occasionally soon repeated, thus giving rise to a jointed appearance, the keel broad and rounded; epidermis composed of cells with somewhat thickened walls but without distinct trigones, averaging about $50 \times 25 \mu$; pores distinctly elevated, measuring (with their surrounding cells) mostly 110 to 140 μ in length and 80 to 120 μ in width, surrounded by 6 to 8 radiating series of cells with 3 or 4 cells in each series, the radial walls slightly thickened; cells containing oil bodies, green tissue, and compact tissue all as in *A. elegans*; mycorrhiza often abundant; ventral scales much as in *A. elegans*, the appendages usually borne singly but sometimes in pairs, narrowly subulate or lanceolate, mostly 0.75 to 0.9 mm. long and 0.12 to 0.15 mm. wide, the margin sometimes bearing a spinelike tooth near the base, the apex acuminate; cells as in *A. elegans*; inflorescence doubtful but probably autoicous; male inflorescence (only 2 cases observed) as in *A. elegans*, terminal on a more or less elongated branch; female inflorescence borne on a more or less elongated branch; peduncle pigmented with purple (except in the apical portion), bearing scattered lanceolate paleae with a denser tuft at the apex, mostly 1 to 1.5 cm. high; disk of receptacle purple (so far as observed), mostly 2.5 to 3 mm. across, covered with coarse but low tubercles, hemispherical in the center, normally 4-lobed, the lobes short but distinct, extending obliquely downward and outward, the margins and involucre as in *A. elegans*; pseudoperianth brownish, not pigmented with purple, mostly 8 to 10-cleft with lanceolate divisions coherent at the apex; capsule brown, circumscissile above the middle by an irregular line, the operculum coming off in one piece; spores rather dark brown, mostly 70 to 80 μ in diameter, with a wavy wing 3 or 4 μ wide and often 4 to 8 μ thick around the spherical face and much broader but otherwise similar wings along the other edges, the whole surface (except sometimes close to the wings) covered over with an irregular and fairly coarse reticulum, with meshes mostly 8 to 12 μ wide, inclosed by a system of narrow and thick ridges, these mostly 3 to 4 μ wide and equally thick, the broad edges of both wings and ridges marked by darker irregular lines and occasional lighter interstices, the surface otherwise smooth or vaguely and minutely punctulate; elaters pale brown, variously curved, mostly 200 to 250 μ long and 12 to 14 μ wide, tapering slightly toward the blunt

ends, usually bispiral in the middle for a variable distance and unispiral at the ends, rarely unispiral throughout.

On rocks; known only from the following locality:

CUBA: Monte Verde, Yateras, March 18, 1860, *Wright* (H., Y.).

It is with considerable hesitation that the writer proposes a new species on a single collection, more especially since this new species is closely allied to the variable *A. elegans*. There is, however, so marked a difference in the spore markings that this course appears justifiable. In *A. elegans* the wings and ridges of the spores are thin and wide and inclose a fairly regular reticulum with the meshes mostly 15 to 20 μ wide; in *A. reticulata* the wings (except those along the edges of the pyramid) are thick and narrow and inclose an irregular reticulum with smaller meshes, mostly 8 to 12 μ wide. The margins of the wings and ridges are marked by very irregular fine lines which tend to run parallel around the meshes but often deviate from one another and leave minute spaces or interstices of varying sizes. It has already been pointed out that the wings and ridges in *A. elegans* show a tendency to broaden out on their edges, but the condition is even more striking in the new species. In addition to the differences derived from the spores, the female receptacle of *A. reticulata* is covered over with shorter tubercles than that of *A. elegans*, approaching in this respect the Mexican *A. lateralis*.

The inflorescence of the new species has not been determined with certainty. The two male inflorescences observed were borne on elongated branches but, although female receptacles were present in the vicinity, it was impossible to demonstrate a connection between them. If the species could be proved dioicous, this would afford another important character, helping to distinguish it from *A. elegans*; it is more probable, however, that the species is autoicous and that the male inflorescences become difficult to detect by the time the capsules are mature.

Aside from the differences already noted, *A. reticulata* and *A. elegans* are strikingly alike. In general appearance, in the minute structure of the thallus, in the form of the ventral scales and their appendages, in the male inflorescence, in the pseudoperianths, and in the elaters no differences of any significance have been detected. The new species, to be sure, presents a somewhat xerophytic appearance, the margins of the thallus tending to be incurved when dry, but this feature is too inconstant to be emphasized, since the margins of the thallus in *A. elegans* are sometimes incurved to a slight degree.

14. *Asterella bolanderi* (Austin) Underw.

Fimbriaria bolanderi Austin, Proc. Acad. Phila. 1869: 230. 1869.

Fimbriaria violacea Austin, loc. cit., as a synonym of *F. echinella*; Bull. Torrey Club 3: 17. 1872.

Asterella bolanderi Underw. Bot. Gaz. 20: 61. 1895.

Asterella violacea Underw. loc. cit.

Thallus much like that of *A. lateralis*, green or yellowish green above, the margins and ventral surface usually more or less pigmented with purple, the margins strongly incurved when dry, mostly 1 to 2 cm. long and 2 to 4 mm. wide, rarely forking, almost always with ventral branches and apical innovations, the sexual branches ventral and very short, rarely if ever innovating; epidermis composed of cells with somewhat thickened walls and sometimes with minute trigones, averaging about $40 \times 28 \mu$; pores distinctly elevated, measuring (with their surrounding cells) mostly 110 to 150 μ in length and 70 to 110 μ in width, surrounded usually by 7 or 8 (rarely 6 or 9) radiating series of cells with 3 (sometimes 2 or 4) cells in each series, the radial walls slightly thickened; cells con-

taining oil bodies as in *A. elegans*; green and compact tissues as in *A. lateralis*; ventral scales ovate to broadly ovate or lunulate, deeply pigmented throughout or with hyaline borders and appendages, the slime papillae inconspicuous and usually short-lived; cells containing oil bodies usually 15 to 30, mostly scattered but sometimes in pairs or small groups, tending to be more numerous in the acropetal portion; appendages usually borne singly but sometimes in pairs, slightly or not at all constricted at the base, narrowly lanceolate or subulate, mostly 0.5 to 0.75 mm. long and 0.1 to 0.15 mm. wide, acuminate, entire or vaguely and irregularly crenulate; cells mostly 70 to 80 \times 30 to 40 μ ; inflorescence autoicous; male inflorescence borne on a very short, subclavate, scarcely expanded branch, consisting of a vaguely defined median group of about 10 antheridia with short ostioles, marginal paleae wanting (so far as observed); female inflorescence borne on a short and expanded, emarginate or obcordate branch; peduncle more or less pigmented with purple except in the upper part, loosely or densely pilose and with a more persistent apical cluster, mostly 1 to 3 cm. high; disk of receptacle mostly 2.5 to 4 mm. across, covered with very low tubercles or essentially smooth, becoming rugose when dry; lobes mostly 4, short but distinct, extending obliquely downward, the central portion hemispherical to bluntly subconoidal; pseudoperianth white or more or less pigmented with purple, mostly 10 to 12- (or sometimes up to 16 or 18) cleft, with lanceolate divisions connate at the apex; capsule pale brown, circumscissile by an irregular line, the operculum coming off in fragments; spores yellow to brown, mostly 65 to 100 μ in diameter, with wavy wings 8 to 12 μ wide along the edges, the margins of wings a little darker; entire surface of spore minutely and irregularly punctulate but without distinct lines, the spherical face showing in addition a coarse regular reticulum, the meshes mostly 12 to 20 μ across, inclosed by a system of thin ridges similar to the wings, the plane faces with similar reticula; elaters yellow to brown, mostly 160 to 220 μ long and 8 to 12 μ wide, tapering slightly toward the blunt ends, mostly bispiral in the middle and sometimes throughout but usually unispiral at the ends for a variable distance.

On banks, sometimes shaded; known only from California. The following specimens have been examined:

CALIFORNIA: Without definite localities, *Coulter* 841 (N. Y.), 1864-70, *Bolander* (N. Y., U. S., Y.); Ukiah, Mendocino County, *Howe* 794 (N. Y.); Hoods Peak, Sonoma County, *Bioletti* (N. Y.); Howell Mountain, Napa County, *Setchell* (N. Y.); Olema, Marin County, *Jepson* (N. Y., U. S.); Mill Valley, Marin County, *Howe* (C. C. H., N. Y., U. S., Y.; also distributed by Underwood & Cook in Hep. Amer., no. 158, as *Fimbriaria bolanderi*); same locality, *Blasdale* (C. C. H., N. Y.); San Rafael, 1865, *Bolander* (N. Y., Y.; type; also distributed by Austin in Hep. Bor. Amer., no. 136d, as *F. bolanderi*); Auburn, *Bolander* (N. Y., Y.); same locality, *Pulsifer-Ames* (N. Y.); Jackson, Amador County, *Hansen* 1615, 2101, etc. (N. Y.); Middle Fork, Amador County, *Hansen* 1020 (N. Y., U. S.); White Bar, Amador County, *Hansen* (C. C. H.); Antioch, Contra Costa County, *T. S. Brandegee* (C. C. H.); Fruitvale, Alameda County, *Howe* (N. Y.); near Stanford University, *Baker* (C. C. H., N. Y., U. S.; distributed in Pacif. Sl. Bry., no. 629, as *Fimbriaria violacea*); Los Burros Trail, Santa Lucia Mountains, Monterey County, *Eastwood* (N. Y.); Pasadena, *McClatchie* (N. Y.); Twin Oaks, San Diego County, *Koch* (N. Y.). Many of these specimens have already been recorded by Howe under either *A. bolanderi* or *A. violacea* (Mem. Torrey Club 7: 52, 54. 1899).

Austin, in his original description of *F. bolanderi*, emphasized the short ventral branches bearing the male and female inflorescences as one of the distinctive features of the species. According to his statements it shared this

feature with only one other species known to him, the plant which he afterwards described as *F. violacea*. Except for the fact that he assigned three or four spirals to the elaters, his account is clear and accurate, although he naturally paid but little attention to histological details. When he published *F. violacea* three years later he again compared it with *F. bolanderi*, but brought out several differences, among them the following: the larger size; the densely areolate thallus, not margined and with a broadened ventral keel; the thicker and blackish purple peduncle; the larger female receptacle, not umbonate upon drying, usually tricarpous, and very long-barbate below; the semipendent pseudoperianths, 12 to 16-cleft and violet. To *F. bolanderi* he had ascribed an indistinctly porous thallus, with a membranous margin; a pale purple peduncle (toward the base); a female receptacle umbonate upon drying; subradiately spreading pseudoperianths, usually 10-cleft and white. He admitted that his specimens of *F. violacea* were immature and of course said nothing about the spores and elaters.

The validity of *Asterella violacea* has been recognized by Underwood, Stephani, and Howe. Underwood's description¹ is largely based on Austin's, and makes no mention of the spores and elaters; these structures are described, however, by Stephani and by Howe, the latter author² giving detailed figures of both *A. violacea* and *A. bolanderi*. In accepting *A. violacea* as a species he notes its occasional approach to *A. bolanderi* but regards it as "usually very distinct," emphasizing "the violet, 12-18-cleft pseudoperianth, the larger more conical ♀ receptacle with less spreading lobes and more abundantly paleaceous-barbate beneath, and the commonly larger spores and elaters." He adds that "the violet coloration sometimes disappears from the pseudoperianth," but that under these circumstances the lobes of the receptacle often show a trace of purple.

Stephani places *F. violacea* and *F. bolanderi* ten numbers apart in his monograph, on account of differences in the ventral scales, *F. violacea* being included in a group with lanceolate appendages and *F. bolanderi* in a group with setaceous appendages. In his detailed descriptions he speaks of the appendages of *F. violacea* as single and narrowly lanceolate; of those of *F. bolanderi* as filiform, 2 cells wide below, and long-setaceous at the apex. As a matter of fact these differences are both vague and inconstant. Stephani's statements about the spores also might seem to imply differences, but this is owing largely to their incompleteness. In *F. violacea* he speaks of the spores as lobate-crested with thin rough crests; in *F. bolanderi*, as having narrow, remotely crenulate wings. One other difference which he indicates was based on a misconception. In *F. violacea* he describes filaments reaching the epidermis in the narrow spaces of the green tissue; in *F. bolanderi* he describes narrow spaces without filaments. Stephani's description of *F. violacea* is drawn from Jepson's specimens, and he notes that the pseudoperianths are not violet but hyaline, a deviation which he regards as unimportant.

The writer has had the privilege of studying a large series of specimens, some labeled *A. bolanderi* and some *A. violacea*, from the herbarium of the New York Botanical Garden and from other collections. Although the differences emphasized by Howe and in part by Austin are often apparent, they are nevertheless, in the writer's opinion, too subject to variation to offer a secure basis for specific separation. The differences in the pseudoperianths, for example, are hardly greater than those shown by *A. tenella*, where the color varies from

¹ Bull. Ill. Lab. Nat. Hist. 2: 41. 1884.

² Mem. Torrey Club 7: pl. 97, 98. 1899.

white to purple and the number of divisions from 8 to 12. With regard to the shape of the female receptacle the difference between "subconoidal" and "sub-hemispherical" is certainly slight; Stephani, in fact, speaks of the receptacle in *A. violacea* as having an "alte rotundato" center and of that in *A. bolanderi* as being "hemisphaerica," and thus seems to imply an even slighter difference. The difference in the direction of the lobes is sometimes striking but by no means constant. In Howe's plate 98, figure 4, the typical condition of *A. violacea* is seen, the lobes being directed downward rather than outward, but in figures 5 and 6 the lobes spread about as much as in plate 97, figure 7, where a typical receptacle of *A. bolanderi* is depicted. On the whole, these slight differences in color and in shape, as well as in the size of the receptacle, are paralleled by other species and might easily be caused by differences in environment.

The difference in the size of the spores is perhaps deserving of more consideration and is usually accompanied by a difference in the width of the marginal wings. In a series of specimens labeled *A. violacea* the spores measured 80 to 110 μ in diameter, and the wings were 10 to 16 μ or even as much as 20 μ in width; in a series labeled *A. bolanderi*, the spores were mostly 65 to 70 μ (rarely 80 μ) in diameter, and the wings were rarely 12 μ in width. The difference in the width of the elaters was less apparent: in *A. violacea* it was usually 10 to 12 μ , although sometimes only 8 μ ; in *A. bolanderi*, it was mostly 8 to 10 μ . At the same time, it should be emphasized that the spore markings, as shown by Howe's descriptions and figures (*pl. 97, f. 21; pl. 98, f. 13*), are essentially the same, whatever the size of the spores. Even the difference in size of the spores, however, is insufficient to be considered specific, since it is unsupported by other trustworthy characters. An equally great variation in size is found in other species of *Asterella* and also in other genera of the Operculatae. In *Reboulia hemisphaerica*, for example, Schiffner¹ distinguishes a variety *microspora*, in which the spores have a diameter from one-fifth to one-fourth smaller than those of the typical form. Associated with this difference in size he finds a difference in color, the spores of the variety being much paler, and he finds similar variations in color in the spores of *Targionia*, *Grimaldia*, and *Neesiella*. Without attempting to explain these variations in all cases he suggests that a small size and a pale color may sometimes be due to immaturity, and he warns against the practice of placing too much reliance on such deviations from type in the proposal of new species. The writer therefore feels justified in regarding *A. violacea* as a synonym of *A. bolanderi*.

When Howe published *A. lateralis* as a new species he regarded it as an ally of *A. bolanderi*, largely on account of its short ventral sexual branches. In distinguishing it he emphasized the spore differences, the somewhat smaller female receptacle, the 8-cleft pseudoperianth (10 to 12-cleft in *A. bolanderi*), and the shorter and broader elaters. If *A. lateralis* is defined in the broad sense indicated in the present paper, the spore differences are not very striking, the markings being much alike in the two species, except that in *A. lateralis* the wings rarely take part in the formation of the reticula and the meshes tend to be a little larger. The differences in the size of the receptacles is likewise slight, if well-developed specimens are compared. The other differences mentioned by Howe are more significant, and it may be added that the elaters of *A. lateralis* tend to be unispiral for a longer distance than those of *A. bolanderi*. The longer tubercles on the receptacle of *A. lateralis* afford another distinctive feature; in *A. bolanderi* the tubercles are very short or even lacking altogether, the surface appearing smooth. In some respects *A. lateralis* occupies an inter-

¹ Oesterr. Bot. Zeitschr. 58: 228. 1908.

mediate position between *A. bolanderi* and *A. elegans*. Possibly the careful study of these closely related species in the field will bring to light differential characters which the study of preserved material has failed to show.

15. *Asterella versicolor* Evans, sp. nov.

Thallus green above, deeply pigmented with purple on the ventral surface and along the margin, mostly 0.5 to 1 cm. long and 1.5 to 3 mm. wide, more or less concave, especially when dry, the slightly crispate margins often becoming more or less incurved; branching ventral, sometimes by apical innovations, some of the branches growing out into narrow subterete processes with reduced green tissue; keel broad and rounded; epidermis composed of cells with slightly thickened walls and scarcely evident trigones, averaging about $45 \times 30 \mu$; pores somewhat elevated, measuring (with their surrounding cells) mostly 100 to 140 μ in length and 70 to 90 μ in width, surrounded usually by 6 (rarely 5 or 7) radiating series of cells with 2 or 3 cells in each series, the radial walls slightly thickened; cells with oil bodies as in *A. tenella*, usually forming an irregular row in the lower epidermis near the margin; green tissue compact, the air chambers in 3 or 4 layers, those of the dorsal layer larger than the others but subdivided by crowded vertical supplementary partitions extending nearly or quite to the epidermis except in the vicinity of the pores; compact tissue occupying about two-thirds the thickness of the thallus in the median portion, thinning out rather abruptly on the sides and extending from one-third to one-half the distance to the margin, composed of cells with thickened pitted walls; mycorrhiza abundant (so far as observed); ventral scales ovate, often pigmented throughout but sometimes with paler margins and appendages; cells containing oil bodies mostly 10 to 20, scattered but more abundant in the acropetal portion; marginal slime papillae usually persistent; appendages borne singly or (rarely) in pairs, narrowly subulate, not constricted at the base but usually sharply marked off, mostly 0.4 to 0.6 mm. long and 0.05 to 0.07 mm. wide, entire, acuminate, the cells mostly 60 to 100 μ long and 30 to 35 μ wide; inflorescence autoicous; male inflorescence (so far as observed) borne on a very short expanded branch, the antheridia forming an irregular median group without marginal paleae, the ostioles distinct; female inflorescence borne on a similar but sometimes more elongate and more expanded branch, the peduncle purple, with scattered slender paleae and a denser apical cluster, mostly 1.5 to 2 cm. long; disk of receptacle mostly 2 to 3 mm. across, mostly green or brownish, covered with short crowded tubercles, the center flattened-hemispherical, normally 4-lobed, the lobes short but distinct, extending obliquely outward, the margin crenate; involucre broad, white to purple, entire or nearly so; pseudo-perianth white to purple, mostly 10 to 12-cleft, the divisions lanceolate, coherent at the apex; capsule reddish brown, circumscissile above the middle by an irregular line; spores purplish black, becoming semiopaque, 110 to 120 μ in diameter, with paler, translucent, wavy, and minutely crenulate wings 10 to 12 μ wide along the edges, the entire surface (inclusive of the wings) covered over by a fine and very irregular reticulum, the meshes mostly 2 to 8 μ in diameter, inclosed by low and more deeply pigmented ridges 2 to 3 μ high, the periphery of the faces appearing irregularly roughened in profile view; elaters (especially the spirals) pigmented with purple and sometimes deeply so, variously curved, mostly 220 to 240 μ in length and 14 to 16 μ in diameter, tapering slightly toward the ends, sometimes unispiral throughout but usually bispiral in the median portion for a variable distance and unispiral at the ends, the spirals sometimes difficult to observe in deeply pigmented elaters.

On rocks; known only from central Mexico. The following specimens have been examined:

JALISCO: West end of the Sierra de San Esteban, near Guadalajara, alt. 1,600 meters. September 28, 1908, *Barnes & Land* 192 (Y.; type).

MORELOS: Near Cuernavaca, October 18, 1908, *Pringle* 10667 (Y.; distributed in Pl. Mex. as *Fimbriaria echinella*).

A wide range in color is found in many species of *Asterella* but is particularly striking in the present species. The upper surface of the thallus is usually green, sometimes with a glaucous cast, but the lower surface with its ventral scales and the peduncles of the female receptacles are deeply pigmented with purple. The greatest variety in color is shown by the receptacles themselves. The upper tuberculate portion seems to be pretty constantly green when young, becoming yellow or brownish when old, but the involucre and pseudoperianths show all gradations from a pure white to a clear reddish purple, the amount of pigmentation varying in both extent and degree, although always less than that of the thallus and peduncles.

The slender branches mentioned in the description are almost as thick as broad, and represent a striking and interesting condition. Apparently an ordinary vegetative thallus grows out directly into a process of this character, the keel becoming strongly rounded, the upper surface concave, and the thin marginal portions very narrow and incurved. The branch thus takes on the appearance of a narrow purple cylinder, the upper surface being more or less completely inclosed. In all probability these branches may be looked upon as a xerophytic adaptation, this idea being supported by the incurved margins of the normal flat thallus under conditions of dryness and by the compactness of the green tissue.

In the structure of the thallus, in the method of branching, and in the restriction of the inflorescences to ventral branches, *A. versicolor* shows a close relationship to *A. elegans*. Even the ventral scales have much in common, although the slime papillae tend to be more persistent in the Mexican species and the appendages are usually smaller. Further resemblances are to be noted in the tuberculate female receptacles, with their short, obliquely spreading lobes, broad and undivided involucre, and pseudoperianths with coherent, lanceolate segments. The most striking differential characters are those derived from the male inflorescences and the spores. In *A. versicolor* the male branch is very short, the antheridia form a small, indefinite group without marginal paleae, and the spores are covered over with a fine and very irregular reticulum. In *A. elegans*, on the other hand, the male branch varies greatly in length, the antheridia are in a larger and more clearly defined group with a fringe of marginal paleae, and the spores, which are usually paler, are covered over with a coarse and usually regular reticulum. The tubercles on the female receptacle are about as long as those of *A. elegans*, averaging perhaps 0.3 mm. in length, and are therefore appreciably shorter than those of *A. echinella*, with which the new species has been confused.

The dark spores and purple elaters of *A. versicolor* have much in common with those of *A. lindenbergiana*, although the relationship between the species is exceedingly remote. Even the spore markings, which consist of a delicate network formed by low anastomosing ridges, are much the same. It is not difficult, however, to detect differences in the spores. The reticulum in *A. versicolor*, for example, is more irregular than that of *A. lindenbergiana*, the meshes showing a wider range of variation in size, and the wings are more conspicuous and distinct, owing largely to the tendency of the outer spore wall to become separated in *A. lindenbergiana*. The spores, moreover, are a trifle larger, and the elaters are usually longer.

DOUBTFUL SPECIES.

Five North American species, proposed by Stephani under the generic name *Fimbriaria*, still remain to be considered. Unfortunately the types of these species, which are presumably in the Boissier Herbarium, are inaccessible at the present time; and the published descriptions, even when full, fail to throw light on all their important features. It is therefore impossible to reach definite conclusions regarding their validity, and the writer can do nothing more than call attention to their probable position in the genus. Since, however, Stephani's two new Canadian species, *F. commutata* and *F. macounii*, have had to be reduced to synonymy, being based on variable and insufficient characters, and since many of his descriptions include incorrect or misleading phrases, it is natural to look upon his species and upon his descriptions with a good deal of suspicion, until they have been subjected to critical investigation. The five species were all based, at least in part, on Mexican material.

1. *FIMBRIARIA ARSENI* Stephani, Sp. Hep. 6: 11. 1917.

MEXICO: Without definite locality, *Frère Arsène*.

The species described in the sixth volume of Stephani's extensive *Species Hepaticarum* are treated with unusual brevity, important and even essential characters being often omitted. In the present instance nothing is said about the epidermis or the spores, except that the latter were immature in the material studied. The ventral scales are said to be large and deeply bifid, with the laciniae, or appendages, a little shorter than the basal portion, but the shape of the appendages and the peculiarities of their margins and apices are not alluded to. The air chambers are said to be low and "filiferous" and the inflorescence is described as monoicous. The antheridia are stated to be grouped on lateral male branches, and the disk of the female receptacle to be umbonate and 5-lobed, with short rounded lobes. In the case of the pseudoperianth the ovate and somewhat elongated form and the hyaline character are the only features mentioned, the number of divisions present not being stated. This last omission, however, is made by Stephani throughout his treatment of the genus.

Without studying the actual type material it would be quite impossible to determine specimens from this brief and vague description or to decide the taxonomic status of the species. The situation of the antheridia on lateral branches might perhaps indicate a relationship with *A. elegans*, and a guess might be hazarded that *F. arsenii* was a synonym of *A. lateralis*. Unfortunately it would be nothing more than a guess, since *A. lateralis* is distinguished from its allies largely by its spore characters.

2. *FIMBRIARIA ATRISPO* Stephani, Bull. Herb. Boiss. 7: 93. 1899.

MEXICO: Without definite localities, *Schaffner, Maury*.

The most important characters assigned to the present species are the following: ventral floral branches; narrow air chambers without "filaments"; large epidermal pores, each surrounded by 6 radiating series of cells with 4 or 5 cells in a series; large purple ventral scales, each bearing 1 or 2 long, lanceolate appendages, often ending in long-linear apices (2 cells wide); a monoicous inflorescence; a very small androecium, the number of antheridia

often reduced to two; a slender peduncle with narrowly linear paleae in the upper part; a disciform receptacle, coarsely tuberculate and scarcely convex, the lobes confluent throughout, the receptacle thus appearing without lobes; an involucre extending to the margin of the disk; an ovate, hyaline, horizontal pseudoperianth, scarcely extending beyond the disk; almost black spores, 108μ in diameter, with narrow rough wings; bispiral elaters, 230μ long.

Although nothing is said in the description about the length of the sexual branches, the fact that they are ventral in position would seem to indicate that this species, as well as the preceding, was related to *A. elegans*. In fact, the vegetative characters of *F. atrispora* agree in all essential respects with those of *A. lateralis*, except that the air chambers are said to be without "filaments." If this means that no supplementary partitions are present, it might indicate a relationship with the *A. tenella* group, where the dorsal chambers remain undivided; but the phrase by no means demands this interpretation and may simply mean that the supplementary partitions extend to the epidermis and do not look like free filaments in section view. Unfortunately the characters assigned to the female receptacle—the almost flat and scarcely lobed disk—would seem to remove the species definitely from *A. lateralis*. These characters, however, may be due to a poor development of the female plants. In *A. elegans*, for example, the lobes are often indistinct, even when ripe capsules are present, if the conditions have been unfavorable for full development; and the upper surface is not necessarily very convex, if the tubercles are left out of consideration. The writer would therefore suggest that *F. atrispora* be considered a possible synonym of *A. lateralis*, until its status can be adequately determined.

3. FIMBRIARIA MEXICANA Stephani, Sp. Hep. 6: 15. 1917.

MEXICO: Without definite locality, *Frère Nicolás*.

The description of *F. mexicana* is open to the same criticism as that of *F. arsenii* and leaves the reader in much doubt regarding the essential features of the species. Here again the epidermis and the spores are completely neglected, and nothing is said about the air chambers except that the compact ventral tissue (costa) is much thicker than the green tissue (stratum anticum). In fact, the measurements given for thickness lead to curious deductions. According to these the thickness of the ventral tissue in the middle is 1 mm. while the entire thickness of the thallus in the same position is likewise 1 mm., thus leaving nothing at all for the green tissue and the epidermis. The thallus of *F. mexicana* is described as large, 2.5 cm. long and 10 mm. wide, and the ventral scales are said to be large and purple, each with a single unusually large appendage, measuring 3×3 mm., the apex being obtuse and the margin irregularly repand. The branches are stated to be lateral, rarely appearing as apical innovations, and the inflorescence is given as monoicous, with the antheridia borne on slender branches. The more important features associated with the female receptacle are the very large disk, measuring 10 mm. in width, with a minutely umbonate apex and 4 lobes; an obovate involucre, with a papulose cuticle; and an ovate pseudoperianth, equaling the involucre in length.

In its large size *F. mexicana* is comparable with *A. californica* and *A. rugosa*, but the description gives little evidence of relationship with these species, in both of which a dichotomous type of branching prevails. Among the North American species characterized by a prevalingly ventral branching, *A. elegans* and its allies at once come to mind. In these species, however, with rare exceptions, neither the thallus nor the disk of the female receptacle exceeds 5 mm. in width. The remarkable appendages of *F. mexicana* also, with their obtuse apices, are very different from anything in the *A. elegans* group, and in their

unusual size they seem to be unique. In all the other North American species the length of the appendages apparently never exceeds 1 mm., and such a length seems to be always associated with narrow and sharp-pointed appendages. The true relationships of *F. mexicana* thus remain obscure.

4. *FIMBRIARIA PRINGLEI* Stephani, Rev. Bryol. 36: 139. 1909.

MEXICO: Without definite locality, *C. G. Pringle*.

Most of the important collections of Hepaticae made by Pringle in Mexico were sent to Stephani for determination, and *F. pringlei* is one of the nine new species which he proposed in his first report on the material.¹ Now the name *F. pringlei* is untenable on account of the older *F. pringlei* Stephani, of 1899, based on *Asterella pringlei* Underw., of 1895, a species discussed at length in the present report. There is also evidence that Stephani himself had little confidence in the validity of this new species, since he makes no allusion to it in the sixth volume of his Species Hepaticarum, where several of the other novelties in Pringle's collection are again proposed as new. Under the circumstances further comment is perhaps unnecessary. Stephani refers to the species, however, certain sterile plants in which the thallus is slender and decurved, appearing hornlike on account of the incurved margins; and since these features are very unusual in *Asterella*, a few words about them may not be out of place. Among the North American species studied by the writer the only one showing branches of this type is *A. versicolor*. Specimens of this species from the Pringle collection, referred by Stephani to *A. echinella*, are in the writer's possession and arouse a strong suspicion that *F. pringlei* Stephani 1909, is a synonym of *A. versicolor*. Unfortunately Stephani describes the spores as yellow and 54 μ in diameter, while those of *A. versicolor* are purplish black and 110 to 120 μ in diameter. It is quite possible, however, that he did have this species before him when he drew up his description, and that his account of the spores was drawn from poorly developed capsules or from the capsules of some other species in accidental admixture.

5. *FIMBRIARIA STAHLII* Stephani, Bull. Herb. Boiss. 7: 201. 1899.

MEXICO: Without definite locality, *Bourgeau, Stahl*.

GUATEMALA: Without definite locality, *Bernouilli*.

Stahl's specimens should, of course, be considered the type. Whether the species is identical with the Mexican "*Fimbriaria stahliana*," investigated by Kamerling² in 1897, does not appear. Kamerling's observations, however, refer simply to the epidermal pores of the female receptacle, so that his account can not be regarded as the publication of a species in the taxonomic sense.

In Stephani's monograph *F. stahlII* directly precedes *F. lateralis*, but the characters which he emphasizes by no means indicate a close relationship. In his description of the thallus he speaks of thin-walled epidermal cells; of narrow air chambers, the roof of nearly every one occupied by an almost bullate pore, the opening surrounded by 6 radiating series of cells with 4 or 5 cells in each series; and of large ventral scales, each with a single long-linear appendage. He doubtfully assigns a monocious inflorescence to the species, and states that the antheridia are in elongated groups on narrow branches. He notes further that the peduncle of the female receptacle is naked; that the disk (known only from imperfect examples) is globose and covered over with numerous papilliform

¹ Hepaticae mexicanae novae recoltées par le Dr. Pringle de Burlington. Rev. Bryol. 36: 138-140. 1909.

² Flora 84: Erg. Bd. 52. pl. 1, 2, f. 14-17. 1897.

pores; that the lobes are delicate, veiny, and spreading; and that the spores are almost black, 85μ in diameter, and covered with low crenulate crests.

The undivided air chambers which Stephani emphasizes apparently show that *F. stahlii* is a relative of *A. tenella*, and the long androecia, borne on special branches, point pretty definitely to *A. pringlei*. Unfortunately there are a few marked discrepancies. The epidermal pores, for example, are far more complex than those of *A. pringlei*, where the number of cells in each radiating series is almost invariably two. The appendages, moreover, give no indication of variability, and it would hardly seem possible that the curious marginal teeth so often found in *A. pringlei* could have escaped Stephani's attention, if *F. stahlii* and *A. pringlei* are actually the same. Even if they are not the same, however, they are evidently closely allied.