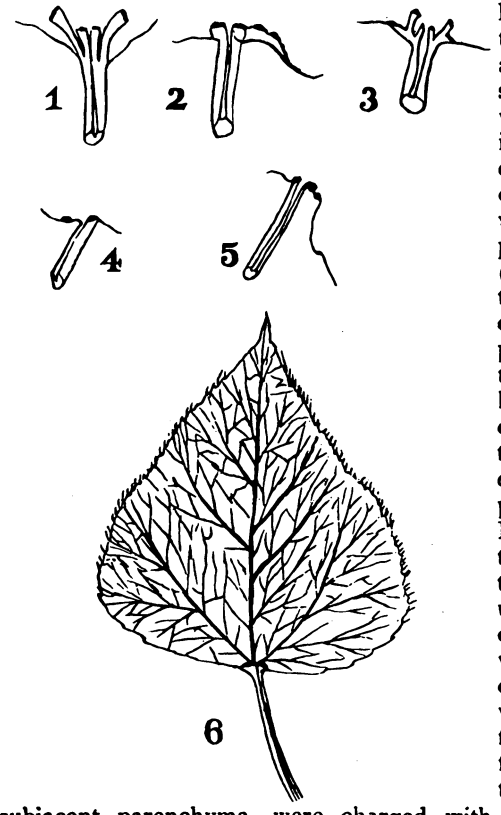
The foliar nectar glands of Populus: by Wm. Trelease.—Early in May, 1880, my attention was drawn to a small aspen (*P. tremuloides*) by the actions of several green bees, belonging to the species known as *Augochlora pura*. At this time the tree was covered with newly expanded foliage; and the bees, flying busily from leaf to leaf, were evidently attracted by something and a moment's observation sufficed to show that they were engaged in collecting nectar, secreted by a double gland at the base of each leaf. These glands were placed on the upper surface of the petiole (Fig. 6) at its union with the blade, appearing, indeed, almost as if the petiole projecting above the upper surface of the blade had been abruptly cut down to the level of the latter, the truncated end being the secreting portion of the gland. Longitudinal sections of the glands showed them to have the structure usually found in members of the sort: the epidermis was transformed into a double layer of thin-walled elongated cells, forming the secreting surface just mentioned; and these cells, as well as the subjacent parenchyma, were charged with saccharine fluids. The homology of the glands, however, was not so readily determined. Each was more or less deeply bilobed and plainly consisted of two confluent glands, and from their similarity, in point of situation, to the



EXPLANATION OF FIGURES.—Fig. 1. Quadrifid gland from base of leaf of *Populus tremula*, var. *pendula*, enlarged.

Fig. 2. Glands from the same plant, borne upon the leaf-margin, enlarged.

Fig. 3. Branched glands from *P. monilifera*, enlarged.

Fig. 4. Base of leaf of *P. monilifera* having one gland displaced and borne on the margin, enlarged.

Fig. 5. Base of leaf of *P. trichocarpa*, showing the gradation of petiolar into serration glands, natural size.

Fig. 6. Leaf of *P. tremuloides*, showing the ordinary form of the double gland, natural size.

twin petiolar glands of various species of *Prunus*, which are known to be marginal outgrowths, representing the tendency to division which has produced the compound leaves of other *Rosaceæ*, it was at once inferred that the glands of *Populus* are of a similar nature; but since the *Salicaceæ* have simple leaves, analogy failed, and actual demonstration was apparently no very easy matter. An examination of other species, though at first yielding no satisfaction, finally solved the problem by affording several series of abnormal cases (Figs 1–5), in which the marginal nature of the glands was clearly shown. Thus, in a cultivated plant of *P. tremula*, var. *pendula*, the glands were found to be usually four in number and quite distinct, the outer pair rising on long stalks, the others being more nearly sessile (Fig. 1); but in one case (Fig. 2), instead of these there were several sessile glands, gradually diminishing in size, arranged along the margin of the leaf-blade—which, it should be added, is distinguishable in most of the species as a double ridge running down the top of the petiole. The paired glands of *P. balsamifera*, var. *candicans* are also quite frequently displaced, so as to terminate rather coarse marginal serrations; and illustrative cases were found in *P. monilifera* (Figs. 3 and 4), *P. ciliata*, *P. Sieboldii*, *P. suaveolens*, and *P. trichocarpa*, in the Gray herbarium at Cambridge. Finally small serration glands of the usual type grading into the petiolar glands, being found in *P. tremula*, var. *pendula*, *P. trichocarpa* (Fig. 5) and other species, left no doubt of the homology of the members in question with those of *Prunus*, *Ricinus*, etc., and their origin is in no wise different from that of the similar outgrowths found on the leaves of certain willows.

Observation showed that they do not occur on all of the leaves, but, as a rule, only on the first half dozen or less, which appear on each branch in the early spring; and in summer and autumn, these having fallen, it is sometimes possible to examine several branches without detecting a single glanduliferous leaf, on species which produce them abundantly earlier in the season.

With a view to ascertaining their prevalence through the genus, I examined such species as were found living; and, an opportunity offering, those represented in the herbarium of Dr. Gray, with the following results: In the typical *P. balsamifera* two separate glands were found at the base of the blade, and the serrations of the latter commonly ended in smaller, otherwise similar organs; and in the var. *candicans* the basal glands were always present, though those of the teeth were not so frequent. Those of *P. ciliata* were quite similar. On the broad leaves of *P. Euphratica* two small but well developed glands were found, but none were seen on the narrow leaves of the same species. *P. grandidentata* and *P. heterophylla* have well developed petiolar glands, and the latter has an abundance of serration glands. On *P. monilifera* and *P. anguiata* the basal glands are present, and often stalked and divided (Fig. 3); in the larger leaves they are frequently of large size. In *P. pruinosa* they are large and prominent; in *P. Sieboldii* they are present and frequently remind one of those in *P. candicans*. In *P. suaveolens* they are large, and clearly belong to the leaf-

margin. In typical *P. tremula* they are usually quite similar to those found in *P. tremuloides*, though sometimes more widely separated. Some specimens of this species failed to show any glands; and a cultivated plant of the drooping variety was once examined in early May without the detection of a single gland, though at other times, these organs were found in abundance on the same plant. The glands of *P. trichocarpa* are quite variable, being sometimes large and close together, at other times, small and widely separated. I was never certain that I saw these bodies on *P. alba*, though they may sometimes occur as very small outgrowths concealed by the wool which is so abundant on the leaves. Small serration glands occur on *P. angustifolia*, and the lowest pair—corresponding, doubtless, to those found at the top of the petiole in so many species—are no larger than the others. On *P. Fremontii* very small glands were occasionally seen, but appear to be uncommon. In *P. nigra* serration glands are evident and the lowest pair much as in *P. angustifolia*. No basal glands were seen on the var. *dilatata*; nor were any found on *P. tomentosa*. It appears, therefore, that the greater part of the species examined possess two or more distinct or confluent, well formed glands, situated where the blade and petiole join; and in the few species where none were discovered, I am by no means sure that they may not occasionally be produced; for, as has been previously stated, a careful examination of a plant of the drooping *P. tremula*—which, by the way, was sent out by nurserymen as *P. grandidentata*, *pendula*—in early May, failed to show a single gland, but, a week or two later, after several days of rain, the young branches grew very rapidly for a short time, unfolding many new leaves, and the first three or four of these on each branch bore large and active glands.

Though of such frequent occurrence, these glands have been generally overlooked or considered of little value by systematic botanists, probably because of their limitation to the earlier leaves, and their occasional entire suppression. The elder Michaux, speaking of this genus[1], says: "Glandulæ basi folionum nihil valent ad distinguendas species, quidpe quae, in eadem specie, aut desunt aut adsunt." In his descriptions of the species he mentions these organs only in *P. grandidentata*. The younger Michaux figures them in *P. angulata*[2] and *P. monilifera*[3] without making mention of them while they are figured and mentioned under *P. canadensis* (*P. monilifera*)[4]. Wesmael,[5] speaking of *P. Candicans*, says "Petiole * * * portant 2 glandes dans le jeune age." Bigelow[6] and Loudon[7] mention the glands of *P. grandidentata;* and Pursh[8] describes them in *P. lævigata* (*P. monilifera*), and *P. monilifera*. Loudon[9] also

[1] Flora boreali Americana, II, 243.
[2] Arbres, III Pl. XI; N. Am. Sylva, II, Pl. 94.
[3] Arbres, III, Pl. X; N. Am. Sylva, II. Pl. 96.
[4] Arbres, III, pp. 298, 299. Pl. XI; N. Am. Sylva II, p. 117, Pl. 95.
[5] Monographie de toutes les especes connues du genre Populus, 1869, p. 68.
[6] Plants of Boston, 1824, p. 370.
[7] Arboretum, III, p. 1650.
[8] N. Am. Flora, 1814, p. 618 and 619.
[9] l. c. pp. 1655 and 1657.

speaks of their occurrence on the latter species, and Wesmael,[10] speaking of this species under its synonym of *P. Canadensis*, also mentions these bodies; and elsewhere[11] makes the following surprising statement: "Communement sur les feuilles des femelles on recontre deux glandes petiolaires tres-voisines de la base du limbe. Toutefois, ce caractere n'a rien de constant sur toute des feuilles d'un meme rameau, et quelquefois meme on les observe sur les feuilles de l'autre sexe." Pursh[12] also noted the glands of *P. trepida* (*P. tremuloides*). As I have said, the secreting and subjacent tissues in these organs are charged, while young, with syrup, the sugar being doubtless derived from the transformation of starch which is of abundant occurrence in the adjacent parenchyma. A study of glands at the beginning of their activity showed the process of secretion to be the following: The slight cuticle which covers the modified epidermis becomes separated from the balance of the cell-wall, probably by the transformation of a thin layer of the latter into one of the gums, which by its osmotic power causes transudation of saccharine fluid from the interior of the cell. This constantly increasing quantity of fluid swells the loosened cuticle out in the form of a delicate bladder, which soon bursts and allows the nectar to appear on the surface. Evaporation is constantly going on, so that, if the plant is supplied through its roots with an abundance of water the cell wall separates a denser external, from a less dense internal syrup and a continuation of the osmotic action keeps up the secretion of nectar for a considerable length of time. At times the evaporation predominates, and crystals of sugar may then be found upon the gland, in a dense, uncrystallized syrup; at other times the secretion is so plentiful as to collect in drops which occasionally flow upon the surface of the leaf. Carefully washing the glandular surface with pure water always lessened its power of secretion, and, if repeated several times, so as to remove the last trace of sugar, completely prevented further activity. The addition of a small drop of syrup, however, always caused a renewal of the secretion, in glands which had been thus washed.[13]

Although the presence of apparently perfect glands was noticed in the species previously enumerated, I was able to prove their activity by examination of living plants only in *P. tremuloides; P. balsamifera, candicans; P. grandidentata; P. monilifera;* and P. *tremula, pendula.*

The nectar which accumulates at the surface of the glands is largely gathered by numbers of small insects, chiefly Hymenoptera and

[10] l. c. p. 63.
[11] l. c. p. 27.
[12] l. c. p. 618.
[13] These experiments, which appear to show conclusively the osmotic nature of the secreting process, were suggested by, and are but repetitions of, some of those performed by Dr. W. P. Wilson in Pfeffer's laboratory, the results of which were communicated to the writer last winter, and have just been published in *Untersuchungen aus d. bot. Inst. in Tuebingen*, as I learn from an abstract of Dr. Wilson's article by Francis Darwin (*Bot. Zeitung*, 1881, p. 545).

Diptera. On *P. tremuloides* I observed the following visitors: *Augochlora pura*, *Selandria Rubi*, *Microgaster* sp., *Phytodietus vulgaris*, *Halictus* sp. (identified by Mr. Cresson), and numerous small flies which have not been determined, beside a multitude of ants, of which Mr. McCook kindly identified *Formica exsectoides*, *F. fusca*, *F. gagates*, *Crematogaster lineolata*, and *Dorymyrmex pyramicus*. The common two-spotted *Coccinella* was also frequently seen to feed upon the secretion of these glands. Many of these insects were also found upon *P. grandidentata* and *P. monilifera*, and in addition I noticed one species of *Andrena* upon the former. The first thing that strikes one in studying the insects which feed upon the extrafloral nectar of our poplars is their variety:—Coleoptera, Diptera, and both parasitic and imparasitic Hymenoptera are found, the most numerous being ants, and ichneumonid parasites. As is usual in such cases, the ants as a rule show a disposition to fight, rather than give up their places by the glands, over which they sometimes remain for hours; and some species are so pugnacious that the slighest jar to the branch upon which they are is sufficient to cause them to assume the offensive, and, with mandibles open, they rush about in search of the cause of the disturbance. On presenting my finger to them on such an occasion I have usually found them manifesting a sufficiently strong desire to bite it, but, as when in attendance upon aphides, they are not generally disposed to leave the plant. Whether it be on account of its greater quantity, or because it possesses a more agreeable flavor, I am unable to say, but the honey-dew of aphides is far more attractive to all of the ants observed than the nectar from extrafloral glands, not only in this, but in other genera of plants; and Belt[14] has found the same to be true of the honey dew of coccids. In 1880 the poplars about Ithaca, N. Y., were badly infested with plant-lice which I referred to *Chaitophorus populicola*; and it was noticeable that after these insects became established on a tree the ants, previously very abundant about the foliar glands, soon transferred their attention to the aphides, so that as a rule the only visitors to the glands were small bees, flies, and Microgasters. Besides the *Chaitophorus*, one other plant-louse was found upon the leaves of *P. tremuloides*, but it was not identified. Both these insects were found suffering from the attacks of some parasite, and large numbers were to be seen greatly swollen and either dead or dying. Observation showed that, in the case of the *Chaitophorus*, one of the Microgasters found about the nectar-glands of the plant was the cause of this; and several times one of the parasites, after feasting upon the secretion of these glands, was seen to begin a search for suitable candidates for its favor. Carefully examining the aphides with its antennæ, as it moved through them, the Microgaster rejected all beyond a certain size, knowing that they would have reached maturity before its own offspring had attained its full development; but when one of the right age was discovered, her ovipositor was quickly brought forward under her body, and a single thrust lodged the egg

[14] Naturalist in Nicaragua, p. 225.

within the body of the victim, there to undergo its further development and transformations. These plant-lice were also destroyed in considerable numbers by the larvæ of the two-spotted lady-bird, which also feeds upon the nectar of the plant. Thus it appears that the secretion of nectar by extrafloral glands on poplars attracts to the plants many insects, of which at least three kinds—ants, ichneumonids, and lady-birds—are of benefit to them, the first rendering it unsafe for lepidopterous larvæ or other herbivorous insects to frequent the plant, and making contact with it undesirable for larger animals, while the other two destroy one of its insect enemies in large numbers.

After reaching maturity, the leaves of poplars are quite coriaceous and being for this reason less liable to attack than when younger, no longer require the protection secured by their glands; hence it happens that these organs are found actively secreting only on young leaves, and only on those produced early in the season, when the foliage, young fruit, and tender branches most require protection; and, being no longer required, they are not produced by the later formed leaves. A somewhat similar case is afforded by some of the *Smilaceæ*, where Prof. Delpino[15] has shown that the young plants are protected by a bodyguard of ants, maintained by the production of nectar by foliar glands, while the older plants, being protected against grazing animals, etc., by their thorns, have no glands.

Some light is thrown on the conditions upon which the development of these organs depends, by the drooping aspen already mentioned, turgidity and active growth being evidently the immediate requisites; but the primary reason for their existence, bringing in the much-vexed questions, of heredity and first causation, is not so easily cleared up. On the whole it appears probable that these organs are protective, as those of *Passiflora*, *Gossypium* and other plants are supposed to be; and we have been able to show that this protective function is, at the present time and in our own climate, of some positive value.[16] It is not unlikely, however, that in the Cretaceous and Tertiary periods, in the youth of the genus, protection was far more needed than now, and these glands may then have been efficient in maintaining upon the plant a body-guard of pugnacious ants that served to repel other species which, like the leaf cutting ants against which *Pteris*, *Acacia*, etc., are now similarly protected in tropical America, would have been very destructive to the plants if left to themselves.

It having been suggested that the glands of *Populus* may have been of great use in the earlier geological ages, the question naturally

[15] Atti R. Universita di Genova, IV, Pt. I, p. 26.

[16] Although of considerable protective value to-day, these glands by no means prevent the plant from suffering defoliation at times. I recollect seeing the cottonwoods (*P. angulata*) almost entirely stripped of their foliage in Alabama in May, 1879, by a chrysomelid beetle, *Plagiodera scripta*. Knowing nothing of the leaf-glands at that time, I can not say whether they were actively secreting; but I do not recollect seeing ants about the trees, and as I was then carefully studying phenomena of this sort, their presence would scarcely have gone unnoticed.

arises whether they have not been preserved in fossil leaves. From their occurrence on so small a percentage of the leaves, this is less probable than in many other plants where glands are produced the season through; and an examination of such specimens and figures as I had access to failed to show me a single instance of their preservation. Prof. Lesquereux, however, writes me that they are of regular occurrence in varying numbers and position, on the tertiary *P. glandulifera* Heer; in which they have been figured by Heer.[17] Whether this is an autonomous species, or merely based on the early, glanduliferous leaves of some other species, I am unable to say, but one might almost expect the latter to be the case.

A Large Puff-Ball.—On the morning of October 18 some unknown friend placed in my yard a specimen of the Giant Puff-ball (*Lycoperdon giganteum*), which had attained unusual proportions during the long continued rains. It was depressed-globular, its circumference in a horizontal plane being fifty-eight inches, and the line reaching from the ground on one side over the top and down to the ground again was thirty-two inches. In Mr. Peck's "U. S. Species of Lycoperdon," I find but one larger specimen noted, and that was over eight feet in circumference, unless those mentioned by Schweinitz may have been larger —J. M. C.

Alopecurus saccatus, n. sp.—Culms 5 to 10 inches high, erect or slightly geniculate below, simple; the radical leaves short, cauline about 3, the lower sometimes extended into a long filiform point, upper ones short, the sheath inflated and generally enclosing the base of the panicle; upper ligules deltoid, acute, about 2 lines long; panicle spike-like, oblong, 1 to 1½ inches long, comparatively loosely flowered; spikelets 2 lines long, the outer glumes narrowly oblong, obtuse, scarious at the apex, slightly united at the base, lateral nerves obscure, the keel and margins fringed with silky hairs, otherwise nearly smooth; flowering glume (lower palet) oblong, obtuse, smooth, equaling the outer glumes, the margins united more than half the length, forming a sack and enclosing the oblong seed which is one tenth of an inch long; awn stout twice or thrice as long as the glume, inserted near the base; spikelets about 60 on an inch of the panicle.

This species is remarkable forthe large size of the spikelets, and for the saccate flowering glume. Found in Eastern Oregon by T. J. Howell. —GEO. VASEY.

Potamogeton Hillii, n. sp.—This plant, a fragment of which I noticed in the collections of the Phila. Acad., without name or locality given, and a few specimens of which are among the miscellaneous sheets of Dr. Robbins, and named by him provisionally, P. *pauciflorus*, larger form," now proves to be a distinct species.

Imperfect specimens, sent by Rev. E. J. Hill, were noticed in this Journal for May, 1880, as a possible var. of *P. zosterifolius*, and

[17] Flor. foss. Helvet. II, Pl. LVIII, f. 5–10.