

## Hair morphology and systematics of *Physalis* (*Solanaceae*)

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**Abstract:** Hair morphology was examined on developing seedlings and mature plants of ten species from five of seven series in *Physalis*. The taxonomic importance of hair development and the distribution of hair types then was evaluated with respect to other comparative data. Two classes of hair types were observed, as found in earlier investigations of *Solanum* and *Rhododendron*. The first hair class comprises a sequence from unbranched hairs to dendroid-stelliform hairs. Hairs of this class show considerable variability among taxa in size, presence or absence of glandular tips, and presence and degree of branching, and so were useful in making taxonomic comparisons. The second hair class consists of short hairs, each tipped with a multicellular gland. This second hair class was not useful taxonomically because of its lack of variability in morphology and its often rare occurrence on a plant. The taxa studied exhibit distinctive trichome features which serve to distinguish series and, in some cases together with other data, provided new insight into previously enigmatic species relationships.

Comparative trichome morphology has received little attention in systematic studies of the *Solanaceae*, although this type of data has proved useful in analyzing relationships in *Solanum* L. (SEITHE 1962, 1979; SEITHE & ANDERSON 1982). In 1979 SEITHE analyzed the morphology and developmental sequence of eight different hair types from two distinct hair classes occurring in *Solanum*. She described these hair types as well as documenting their topographical and temporal variation in the ontogeny of the plants. From this information, she was able to develop hypotheses concerning the evolutionary trends in *Solanum* hair types, and to evaluate the taxonomic importance of hair morphology in the genus.

In 1982 SEITHE & ANDERSON conducted a detailed analysis of the hair morphology of the members of *Solanum* sect. *Basarthrum*, a species group that has undergone thorough biosystematic investigation (ANDERSON 1975, 1977, 1979 a, b; ANDERSON & GENSEL 1976, ANDERSON & LEVINE 1982). They found pubescence features taxonomically useful at the subsectional level in delimiting both series and species. In some instances their data supported taxonomic conclusions derived from other data, and in other cases pubescence features provided new insights into the relationships among taxa. In addition, their study provided supportive evidence concerning the relationship between *Solanum* sect. *Basarthrum* and *Petota*.

*Physalis* L. is an American genus in subfam. *Solanoideae* of the *Solanaceae* (D'ARCY 1979). Because of recent studies (WATERFALL 1958, 1967; MENZEL 1951, 1957, 1960; HINTON 1970, 1976; HUDSON 1983; SULLIVAN 1984 a, b, 1985) much is known about the biology and systematics of *Physalis*. Paradoxically, pubescence features have not been studied in detail, although such features are often of primary importance in distinguishing among species and subspecific taxa in *Physalis* (WATERFALL 1958, 1967). Thus, a well-documented analysis of trichome morphology in *Physalis* and understanding of the developmental patterns of trichome types found in the genus and their correlation with other features should be invaluable in future systematic and evolutionary studies of the genus.

The *Physalis viscosa* species complex (ser. *Stellatae* of RYDBERG 1896) is an ideal group to use in a detailed analysis of the taxonomic utility of trichome morphology in the genus. A biosystematic analysis of this group has been conducted by SULLIVAN (1984 a, 1985), and the relationships among species based on overall morphology, interbreeding capabilities and analysis of hybrids, transplant studies, foliar flavonoids, and pollen morphology have been thoroughly documented. In addition, some information is available on the relationship of this species group to others in the genus (MENZEL 1951, SULLIVAN 1984 a), so that comparisons can be made at higher taxonomic levels within the genus. Lastly, this species group has traditionally been distinguished from the other members of the genus by the presence of branched hairs on the mature foliage.

The purposes of the present study are to: (1) describe the trichome types for the members of the *Physalis viscosa* species complex and for representative species from other, closely related, species groups; (2) document the developmental sequence of the different trichome types; and (3) evaluate the taxonomic importance of trichomes at different levels in the taxonomic hierarchy based on correlation with data from other types of analyses.

### Materials and methods

Trichome features were examined on ten species from five series in *Physalis* (Tables 1 and 2). Although there has been some argument against the value of nomenclatural recognition of species groups in *Physalis*, (WATERFALL 1958; SULLIVAN 1984 a, 1985) the term series will be used here for convenience in discussing groups of closely-related species. For all taxa except *P. mollis* var. *variovestita* plants were grown from seed for determination of hair morphology on young seedlings, and then herbarium specimens of the same collection number were examined for the hair morphology of mature plants. For *P. mollis* var. *variovestita* only mature plants were analyzed. For most taxa, two different seed collections were examined. Voucher collections are housed in OKL and in JRS' research collection.

The young seedlings (in most cases, 20 of each seed collection number) were first examined when the cotyledons appeared, and then several times during the development of successive leaves. Living plants were examined under magnifications of  $\times 5-80$ . Representative plant parts (hypocotyl, stem, leaves, calyx) were prepared for microscope slides by heating in a solution of chloralhydrate, glycerine, and water (4:5:5 vol.%). In the case of tightly-standing hairs (all species of ser. *Stellatae* except *P. angustifolia*) it was necessary to tease apart single hairs, as well. Unstained microscope slides were examined under phase contrast at magnifications of  $\times 150$ ,  $\times 300$ , and  $\times 600$ . Approximately 1 000 drawings of the hairs were made from microscope slides with the aid of a drawing prism.

Table 1. Voucher collections of *Physalis* spp. studied. All collections were made by J. R. SULLIVAN (collection numbers listed below)

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- 1) *P. angulata* L.: Mexico: Tabasco, 1239.
  - 2) *P. angustifolia* NUTTALL: U.S.A.: Alabama, Baldwin Co., 1164; Florida, Collier Co., 1207, Pinellas Co., 1185; Mississippi, Jackson Co., 1162.
  - 3 a) *P. cinerascens* (DUNAL) A. S. HITCHCOCK var. *cinerascens*: Mexico: Veracruz, 1234, 1235; Yucatan, 1257, 1258. U.S.A.: Oklahoma, Cleveland Co., 1044.
  - 3 b) Var. *spathulaefolia* (SCHLECHT.) SULLIVAN: U.S.A.: Texas, Chambers Co., 1003; and two collections derived from artificial hybridization studies on material collected in Texas and Louisiana, H-280, H-352.
  - 4) *P. heterophylla* NEES: U.S.A.: Missouri, Barton Co., 1323; Wisconsin, Polk Co., 1341.
  - 5) *P. longifolia* NUTTALL: U.S.A.: Kansas, Rush Co., 1364; Missouri, Dade Co., 1324.
  - 6 a) *P. mollis* NUTTALL var. *mollis*: U.S.A.: Oklahoma, Marshall Co., 1039, 1045; Texas, DeWitt Co., 1123; and one collection derived from artificial hybridization studies on material collected in Louisiana, H-832.
  - 6 b) Var. *variovestita* (WATERFALL) SULLIVAN: U.S.A.: Texas, Aransas Co., 1125.
  - 7) *P. pubescens* L.: U.S.A.: Arkansas, Benton Co., 1314; Missouri, Stone Co., 1319.
  - 8) *P. pumila* NUTTALL: U.S.A.: Missouri, Dade Co., 1325; Oklahoma, Cleveland Co., 1036.
  - 9) *P. virginiana* MILLER: U.S.A.: Wisconsin, Marquette Co., 1339, Polk Co., 1342.
  - 10) *P. walteri* NUTTALL: U.S.A.: Florida, Dade Co., 1210; Georgia, Glynn Co., 1179; North Carolina, Pender Co., 1221; and one collection derived from artificial hybridization studies on material collected in Florida, H-873.

## Results

Two classes of hair types were observed. The first, and most common, hair class consisted of relatively long, branched and unbranched hairs with or without glandular tips (Figs. 1–4, excluding Fig. 1 a); the second hair class comprised short hairs tipped with a multicellular gland (unicellular stalk with 2–4 tiers of small glandular cells; Fig. 1 a). Hairs of both classes have a uniseriate stalk and accordingly begin their development from one epidermal cell. The multicellular glands (second hair class) resembled the “storied” glands of *Solanum* and were not used for comparison among species because of their rare occurrence on a plant (though they are found on nearly every plant) and the little variability in morphology. The variability of the first hair class allowed us to make comparisons among species and series. Hairs in the first class could be categorized into six types: gland-tipped unbranched (Fig. 1 b–f), glandless unbranched (Fig. 1 g–o), gland-tipped branched (Figs. 2, 3, and 4 c–e), glandless branched (Fig. 4 f, g, k, m), stelliform (more than two unbranched rays arising at one point; Fig. 4 l), and dendroid-stelliform (like stelliform but with branched “rays”; Fig. 4 h–j). The general characteristics of the hair morphology for each species investigated are given in Table 2.

The topographical variability of hairs found in the genera *Rhododendron* (SEITHE 1960, 1980) and *Solanum* (SEITHE 1962) was not expressed so distinctly in *Physalis*. However, the hairs of the lower leaf surface usually represented a more advanced developmental stage than those of the upper leaf surface or they differed in size (those of the upper surface sometimes being slightly larger). On taxa characterized by branched trichomes the hairs of the leaf margin, especially on young seedlings,

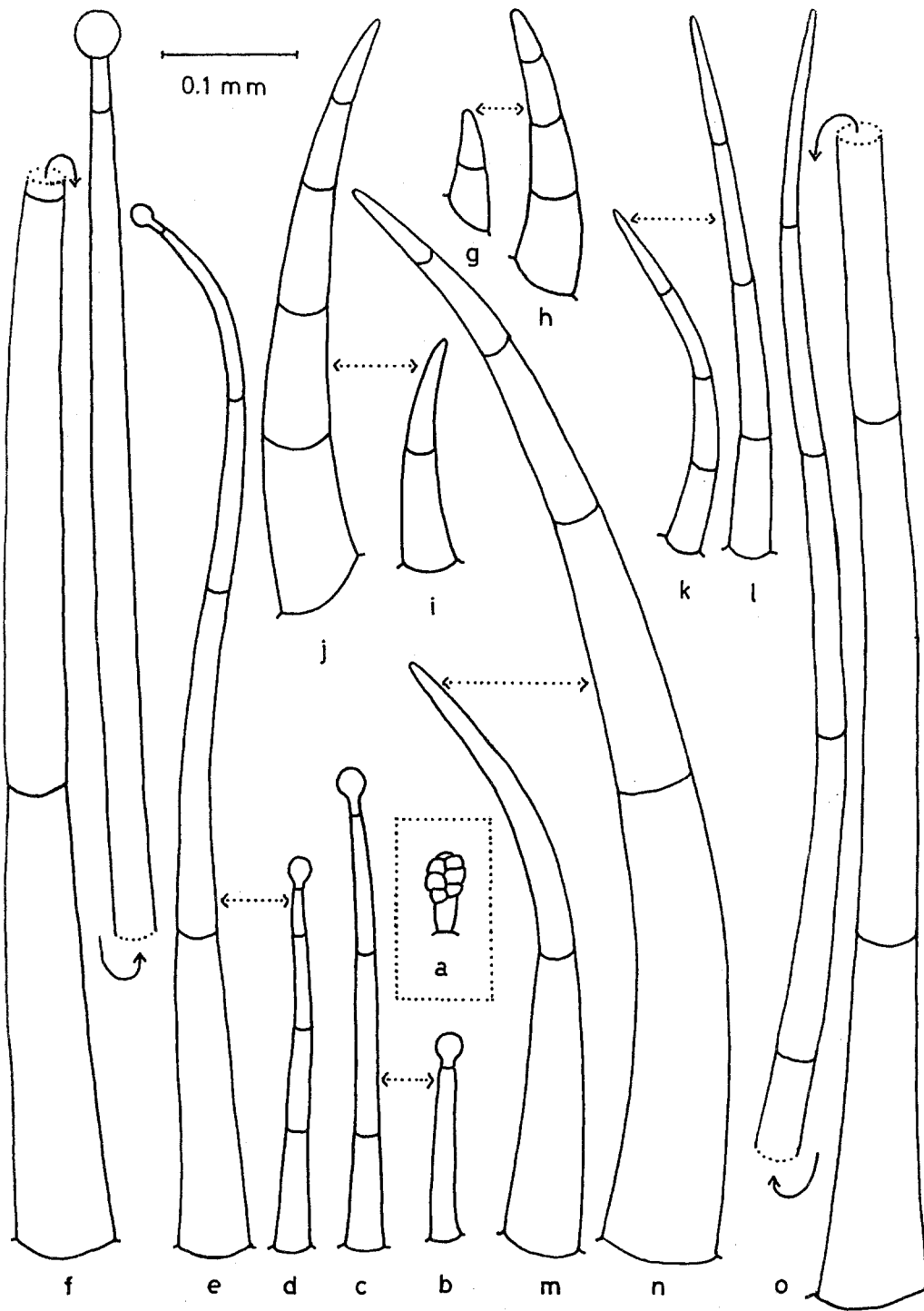
Table 2. General characteristics of the hair morphology for each *Physalis* species investigated. Abbreviations for trichome types: *unbr* glandless unbranched; *gl unbr* gland-tipped unbranched; *br* glandless branched; *gl br* gland-tipped branched; *st* stelliform; *de st* dendroid-stelliform. The second hair class (short hairs tipped with a multicellular gland) was found on every species examined and is not listed. <sup>1</sup> Up to the 8th leaf (except on *P. mollis*, up to the 15th leaf); <sup>2</sup> hairs of class I only on calyx margin and a few on young leaf apex; <sup>3</sup> coll. #1258 on hypocotyl also with *unbr* and *br*, on mature plant with larger *de st*; <sup>4</sup> hairs of about 8th to 15th leaf (transitional indumentum); <sup>5</sup> young seedlings not examined

	Hypocotyl	Young seedling <sup>1</sup>	Mature plant	Remarks (mature plant)
Ser. <i>Stellatae</i>				
<i>P. angustifolia</i>	gl unbr	gl unbr, unbr	br <sup>2</sup>	small to medium
<i>P. cinerascens</i>				
var. <i>cinerascens</i>	gl unbr <sup>3</sup>	gl unbr, unbr, gl br, br	de st	medium (to large <sup>3</sup> )
var. <i>spathulaefolia</i>	gl unbr	gl unbr, unbr, gl br, br	st, de st	medium
<i>P. mollis</i>				
var. <i>mollis</i>	gl unbr	gl unbr (& unbr, gl br, br) <sup>4</sup>	de st	medium, much-branched
var. <i>variovestita</i>	— <sup>5</sup>	— <sup>5</sup>	gl unbr, unbr, gl br	very large
<i>P. walteri</i>	gl unbr	gl unbr, unbr, gl br, br	st, de st	small
Ser. <i>Lanceolatae</i>				
<i>P. longifolia</i>	gl unbr	gl unbr, unbr	unbr	short to long
<i>P. pumila</i>	gl unbr	gl unbr, unbr, gl br, br	unbr, gl br, br	medium to large
<i>P. virginiana</i>	gl unbr	unbr	unbr	short to long
Ser. <i>Heterophyllae</i>				
<i>P. heterophylla</i>	gl unbr	gl unbr, unbr	gl unbr, unbr	medium to long
Ser. <i>Pubescentes</i>				
<i>P. pubescens</i>	gl unbr	gl unbr	gl unbr, unbr	short to long
Ser. <i>Angulatae</i>				
<i>P. angulata</i>	gl unbr	unbr	unbr	short

showed a tendency to be unbranched. Hairs on other organs of the plant (stem, calyx) were more similar to those on the upper leaf surface.

As in *Rhododendron* and *Solanum*, *Physalis* spp. with branched trichomes exhibited more complex branching on mature foliage than on the cotyledons and first leaves. Seedlings of all *Physalis* spp. examined began with gland-tipped unbranched hairs (Fig. 1 b, c) on the hypocotyl (the two collections of *P. cinerascens*

Fig. 1. *Physalis*: unbranched hairs. *a* Second hair class; example of a multicellular gland. *b–o* First hair class, variability of gland-tipped hairs (*b–f*) and of glandless hairs (*g–o*). The arrows between two hairs indicate that they are connected by intermediate forms. *a* *P. angustifolia* (JRS 1185: upper leaf surface). *b–e* *P. mollis* var. *mollis* (JRS 1045: *b, c* hypocotyl; *d, e* 12th petiole). *f* *P. mollis* var. *variovestita* (JRS 1125: petiole). *g, h* *P. angulata* (JRS 1239: leaf margin). *i, j* *P. virginiana* (JRS 1339: lower leaf surface). *k, l* *P. pubescens* (JRS 1314: lower leaf surface). *m, n* *P. heterophylla* (JRS 1323: lower leaf surface). *o* *P. mollis* var. *variovestita* (JRS 1125: petiole)



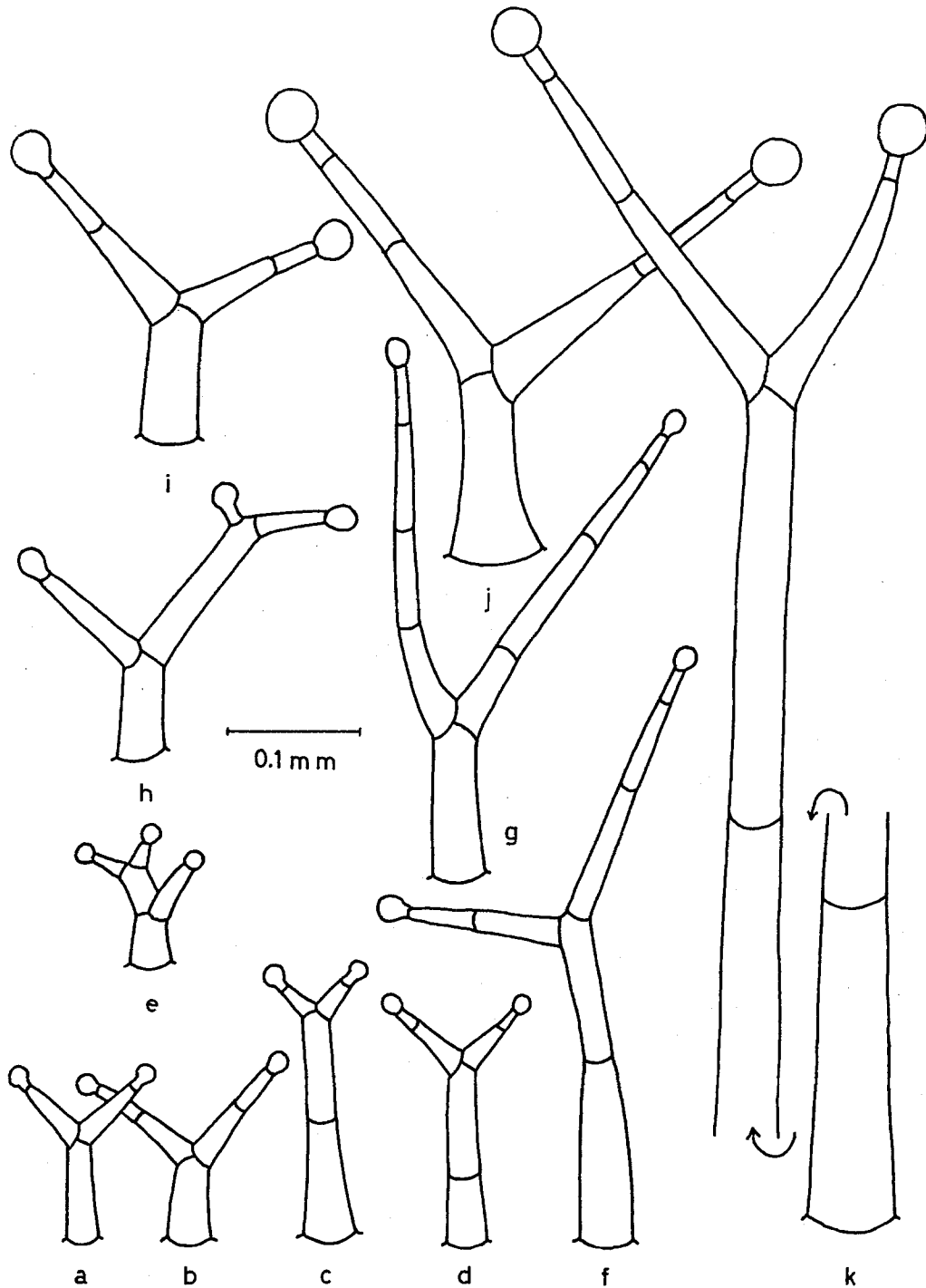


Fig. 2. *Physalis*: first hair class. Variability of gland-tipped, branched hairs. *a-e* *P. cinerascens* var. *spathulaefolia* (JRS H-280: *a, c* 2nd petiole; *b* 3rd internode; *d, e* 4th internode). *f, g* *P. pumila* (JRS 1325: 7th petiole). *h* *P. walteri* (JRS 1221: 1st petiole). *i-k* *P. mollis* var. *variovestita* (JRS 1125: *i* lower leaf surface; *j, k* petiole)

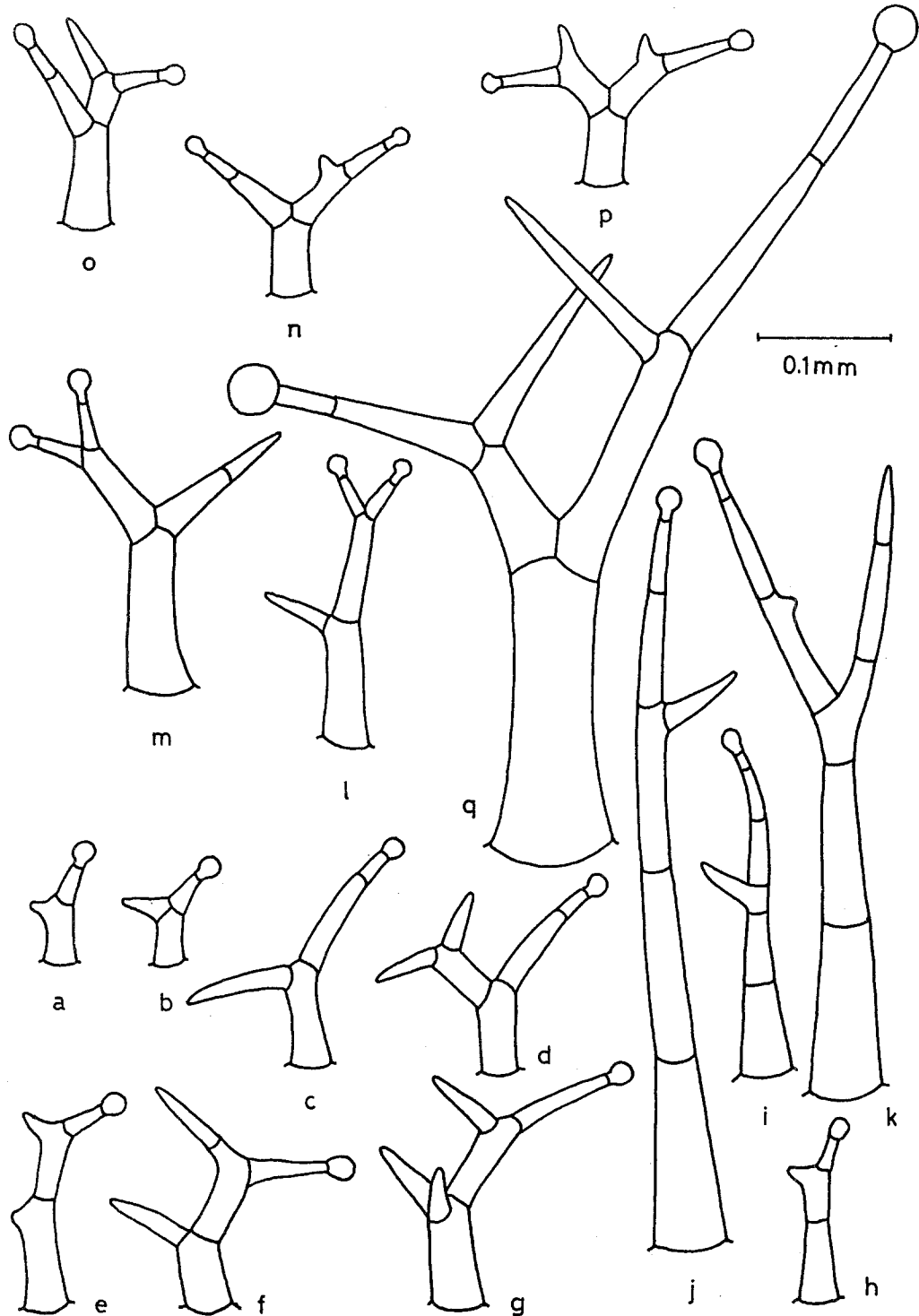


Fig. 3. *Physalis*: first hair class. Variability of partly gland-tipped, branched hairs. *a-g* *P. walteri* (JRS 1210: *a, b* 4th petiole; JRS 1221. *c, d* 3rd petiole; *e-g* 1st petiole). *h* *P. cinerascens* var. *spathulaefolia* (JRS H-280: 3rd petiole). *i-k* *P. pumila* (JRS 1325: 7th petiole). *l-p* *P. cinerascens* var. *spathulaefolia* (H-280: *l, m* 2nd petiole; *n, o* 3rd petiole; *p* 3rd internode). *q* *P. mollis* var. *variovestita* (JRS 1125: petiole)

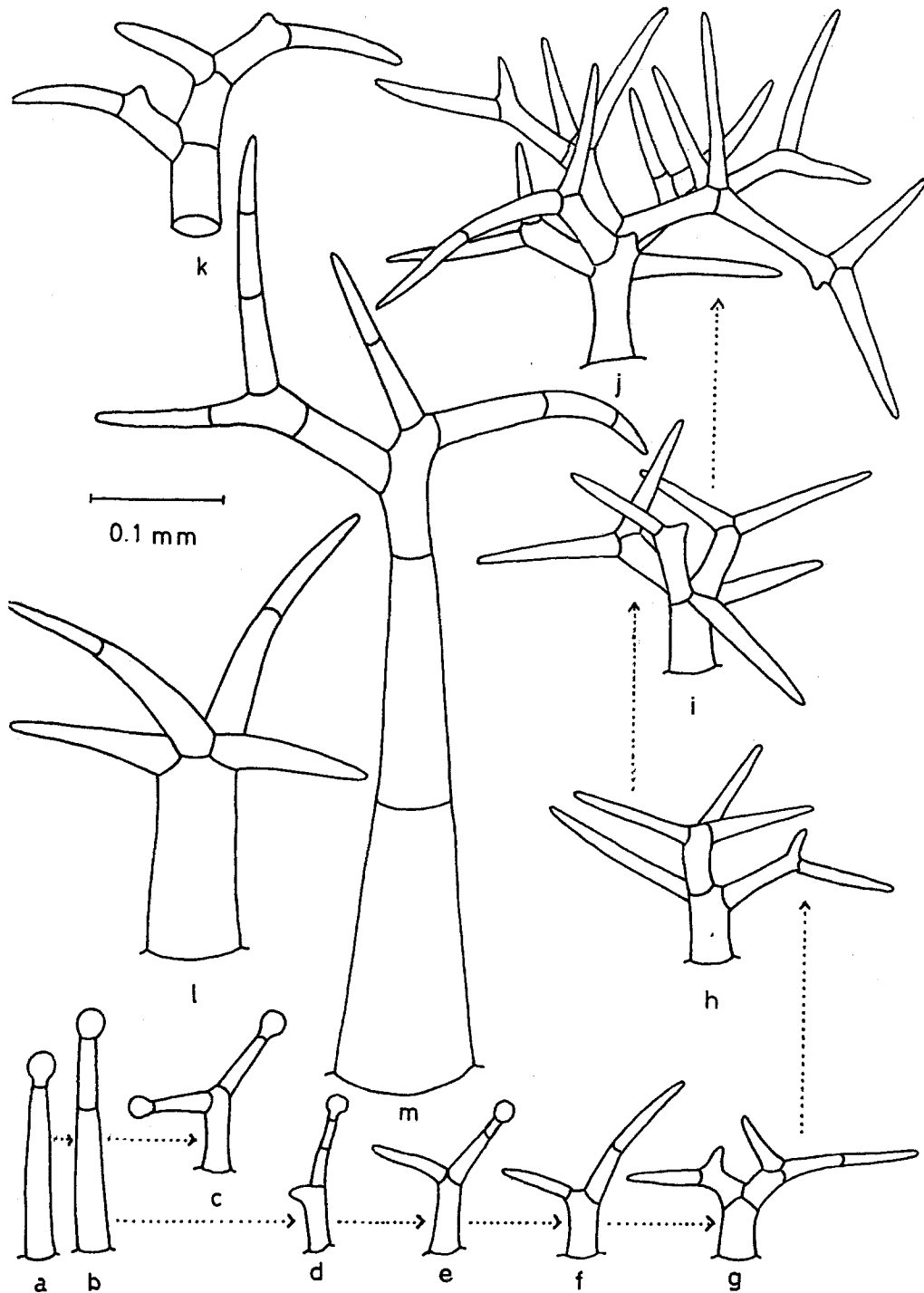


Fig. 4. *Physalis*: first hair class. *a-j* Example of a sequence from gland-tipped unbranched hairs on hypocotyl to glandless multi-branched hairs on leaf of mature plant. *f-m* Some examples of the variability of glandless branched hairs; "stelliform" hair type (*l*), "dendroid stelliform" hair type (*i, j*). *a-j* *P. mollis* var. *mollis* (JRS 1045: *a, b* hypocotyl; *c* 8th petiole; *d-f* 12th petiole; *g* 14th petiole; *h, i* 19th lower leaf surface; JRS 1039: *j* lower leaf surface). *k* *P. angustifolia* (JRS 1185: calyx). *l* *P. cinerascens* var. *spathulaefolia* (JRS 1003: lower leaf surface). *m* *P. pumila* (JRS 1325: stem)



var. *cinerascens* from the Yucatan also had glandless hairs on the hypocotyl), and on the following leaves and internodes progressed through a series of intermediate hair forms (e.g., Figs. 2 a–h, 3 a–p, and 4 c–i; hairs like 3 a and 3 e also occur without glands) to the indumentum typical of the mature foliage (e.g., Figs. 2 i–k, 3 q, and 4 j–m). More specifically, the earliest leaves have not only the gland-tipped unbranched hairs found on the hypocotyl, but also glandless unbranched hairs and hairs with small outgrowths (Fig. 3 a, e, h; these may be either glandular or glandless). On the following leaves, some hairs have small outgrowths that are separate cells (Fig. 3 b, c). On the next leaves, furcate hairs begin to dominate (Fig. 3 n, p), then hairs with 3 arms begin to dominate (on the earliest of these, the outgrowths are not separate cells, such as in Fig. 4 g). This manner of increased branching complexity continues until the hair type typical of the mature foliage of the species or variety is reached. The range of variation of hairs on each leaf includes hair forms from the previous leaf, but these diminish in occurrence on the subsequent leaves.

Within this sequence of hair types two trends can be recognized. One is a progression from unbranched to few-branched to multi-branched hairs. The other trend is from glandular to glandless hairs. The two trends appear to be independent, because in some cases the branching begins earlier than the appearance of glandless hairs, and in other cases the reverse is true. Also, some species retain unbranched hairs or gland-tipped hairs on the mature foliage (Table 2).

## Discussion

The indumentum of *Physalis*, like that of *Solanum* (SEITHE 1962, 1979; SEITHE & ANDERSON 1982) shows differences among series and species that are of use in evaluating relationships. There are trichome features that serve to distinguish series in the genus. For example, ser. *Stellatae* is characterized by mature foliage with predominantly dendroid-stelliform hairs, while serr. *Heterophyllae* and *Pubescentes* bear leaves with a mixture of glandular and non-glandular unbranched hairs. While both serr. *Lanceolatae* (with the exception of *P. pumila*) and *Angulatae* are characterized by having only non-glandular unbranched hairs on the mature foliage, size differences exist between the two series (compare Fig. 1 i, j, and g, h).

The hair morphology of *P. pumila* is somewhat of an enigma. In a biosystematic analysis HINTON (1976) considered *P. pumila* to be closely related to the members of ser. *Lanceolatae* in overall morphology, flavonoid chemistry, and cross-compatibility. However, the trichomes of *P. pumila* (Figs. 2 f, g, 3 i–k, 4 m; also less branched to unbranched hairs on the stem and more branched on lower leaf surface, and a few with a glandular tip on the upper leaf surface) more closely resemble those of ser. *Stellatae* than those of ser. *Lanceolatae*. In a biosystematic study of the members of ser. *Stellatae*, SULLIVAN (1984 a, 1985) tested, to a limited extent, the relationship between *P. pumila* and the members of ser. *Stellatae*. She found a low degree of cross-compatibility between *P. pumila* and *P. mollis* (resultant hybrid plants appeared stunted), but obtained no hybrid plants when crossing *P. pumila* with *P. mollis* var. *variovestita*. She also demonstrated that *P. pumila* has some macromorphological similarities with the members of ser. *Stellatae*, although the phenetic distance between the two is relatively large as compared with the similarity of the members of ser. *Stellatae* to one another. Lastly, *P. pumila* has

the same foliar flavonoids as some populations of *P. angustifolia* (in ser. *Stellatae*), but shares only one flavonoid compound with either variety of *P. mollis*, and that compound is common to most species of *Physalis* assayed (SULLIVAN 1984 a, 1985). Thus, trichome morphology does not correlate with data from other types of analyses in the case of *P. pumila*.

The similarities in trichome morphology between *P. mollis* var. *variovestita* (Figs. 1 f, o, 2 i–k, and 3 q) and the transitional indumentum of *P. mollis* var. *mollis* (Fig. 1 d–e, also glandless, and hairs similar to Figs. 3 a–h and 4 c–g), especially the very long unbranched hairs with an understratum of short few-branched hairs on the petioles up to about the 15th leaf, provide some additional evidence bearing on the relationship between these two taxa. WATERFALL (1958) described *P. variovestita* when he revised the N. American members of *Physalis*. He noted that this new species intergraded with *P. mollis* and *P. cinerascens* in overall morphology. MENZEL (1960) thought she had a clue as to the relationships of *P. variovestita* when she discovered a population in southeastern Texas that appeared to be the result of hybridization between *P. mollis* and *P. macrophysa*. The suspected hybrids resembled *P. variovestita*.

In a detailed analysis of the relationships among *P. cinerascens*, *P. mollis*, and *P. variovestita*, SULLIVAN (1984 a, 1985) found that the latter two were, indeed, closely related genetically, chemically, and morphologically. She was not, however, able to determine whether *P. variovestita* was of hybrid origin, as suspected by MENZEL (1960). Because *P. variovestita* shared morphological and chemical characteristics with *P. mollis*, and because the two were interfertile, SULLIVAN (1984 a, 1985) treated the two as conspecific. The trichome morphology of *P. mollis* var. *mollis* and var. *variovestita* confirms a close relationship between the two varieties.

In the species of *Physalis* examined, two trends are evident in the first hair class (relatively long, branched or unbranched hairs). In the one trend, unbranched hairs give rise to few-branched hairs and later to multi-branched hairs. The other trend is from glandular to glandless hairs. These two trends appear to be independent of one another. Two species (*P. angustifolia* and *P. angulata*) exhibit only few hairs, but a sequence of hair types is yet to be seen.

It is likely that branched hairs have evolved more than once in the *Solanaceae*, because the dendroid-stelliform hair type found in *Physalis* is not the same as the stellate hairs of *Solanum*. Therefore, the term “stellate hairs” as previously applied to *Physalis* by all authors is here changed to “stelliform” or “dendroid-stelliform hairs”. In *Solanum*, all the rays of the star (branches) arise simultaneously from the same point and remain unicellular and unbranched (SEITHE 1962, 1979). In *Physalis*, the rays arise one after the other, each below the cell wall in a preceding ray (compare the small outgrowths in hairs like in Fig. 4 g–k). If this occurs two or more times at the same point, a star-like appearance results (Fig. 4 l), but the often different lengths of the rays indicate that they did not arise simultaneously. The hairs can bear additional “stars” at the ends of the rays (Fig. 4 h, j) and/or can be irregularly branched (Fig. 4 k–m). Stelliform hairs are not found alone but always together with dendroid-stelliform hairs. The second hair class found on *Physalis* (short hairs, each tipped with a multicellular gland; Fig. 1 a) resemble the “storied glands” found on *Solanum* (SEITHE 1962, 1979; SEITHE & ANDERSON 1982). It is interesting to note that the gland-tipped unbranched hairs are a “connecting link” in *Physalis*, as they are in *Solanum*, i.e., they occur on nearly all species, while branched hairs can be found only in some.

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