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VEGETATIVE ANATOMY AND FAMILIAL PLACEMENT OF *TOVARIA*

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ABSTRACT

Leaf, stem, node, and wood anatomy are examined for *Tovaria pendula* collections from Peru. Features claimed to separate *Tovaria* from Capparaceae have hitherto included exstipulate nodes and paracytic stomata. However, the presence of stipules and of anomocytic stomata is demonstrated, together with occurrence of probable myrosin cells in leaves and stems. The nodal type is one reported from Capparaceae. This leaves features of gynoecium and fruit, chiefly, as means of distinguishing *Tovaria* from Capparaceae: ovary nonstipitate, 6–8 loculate, with axile placentation; fruit a berry; ovules with two nucellus layers; endosperm well developed. These features are considered insufficient to maintain recognition of Tovariaceae. Placement in a monogeneric subfamily, Tovarioideae, of Capparaceae seems advisable. Wood anatomy of *Tovaria* is essentially capparaceous. Pits on vessels are apparently nonvestured, but nonvestured pits may be found in Capparaceae. Vessels increase in diameter and decrease in density with age. Vessel elements are larger in roots than in stems. Wood anatomy is mesomorphic. The fact that there is no discrepancy between wood anatomy and habitat is held to be correlated with presence of drought-deciduous leaves in *Tovaria,* as opposed to presence of a foliar apparatus more resistant to transpirational loss.

Key words: *Tovaria,* Capparaceae, Capparales, vegetative anatomy, wood anatomy.

INTRODUCTION

Tovaria consists of two species: *Tovaria pendula* R. & P., which ranges from Bolivia and Peru to Venezuela; and *T. diffusa* Fawcett & Rendle, native to Mexico, Central America, and the West Indies. *Tovaria* is considered as the sole genus of Tovariaceae by some recent authors, such as Cronquist (1981), Dahlgren (1980), Heywood (1978), and Takhtajan (1980). Others, such as Thorne (1983), regard *Tovaria* as a genus of Capparaceae; Thorne places *Tovaria* in its own subfamily, Tovarioideae.

If one compares a detailed description of Tovariaceae with one of Capparaceae, one finds the following features are claimed to separate *Tovaria* from Capparaceae (data from Cronquist 1981 and Mauritzon 1935). *Tovaria* is cited as having nodes exstipulate, trichomes absent except on stamens (variously present in Capparaceae), flower parts in each whorl 6–8 (sepals 2–4, commonly 6, petals 2–6, commonly 4, stamens 6 to many in Capparaceae), placentation axile, locules 6–8 (placentation parietal in the bicarpellate ovary of Capparaceae, which is sometimes subdivided by a false septum), nucellus two cells thick (4–5 in Capparaceae), fruit a berry with soft flesh inside a papery shell (fruit a capsule of various kinds in Capparaceae).

Little information has been published on vegetative anatomy of *Tovaria.* Metcalfe and Chalk (1950) mentioned only that centric arrangement of chlorenchyma

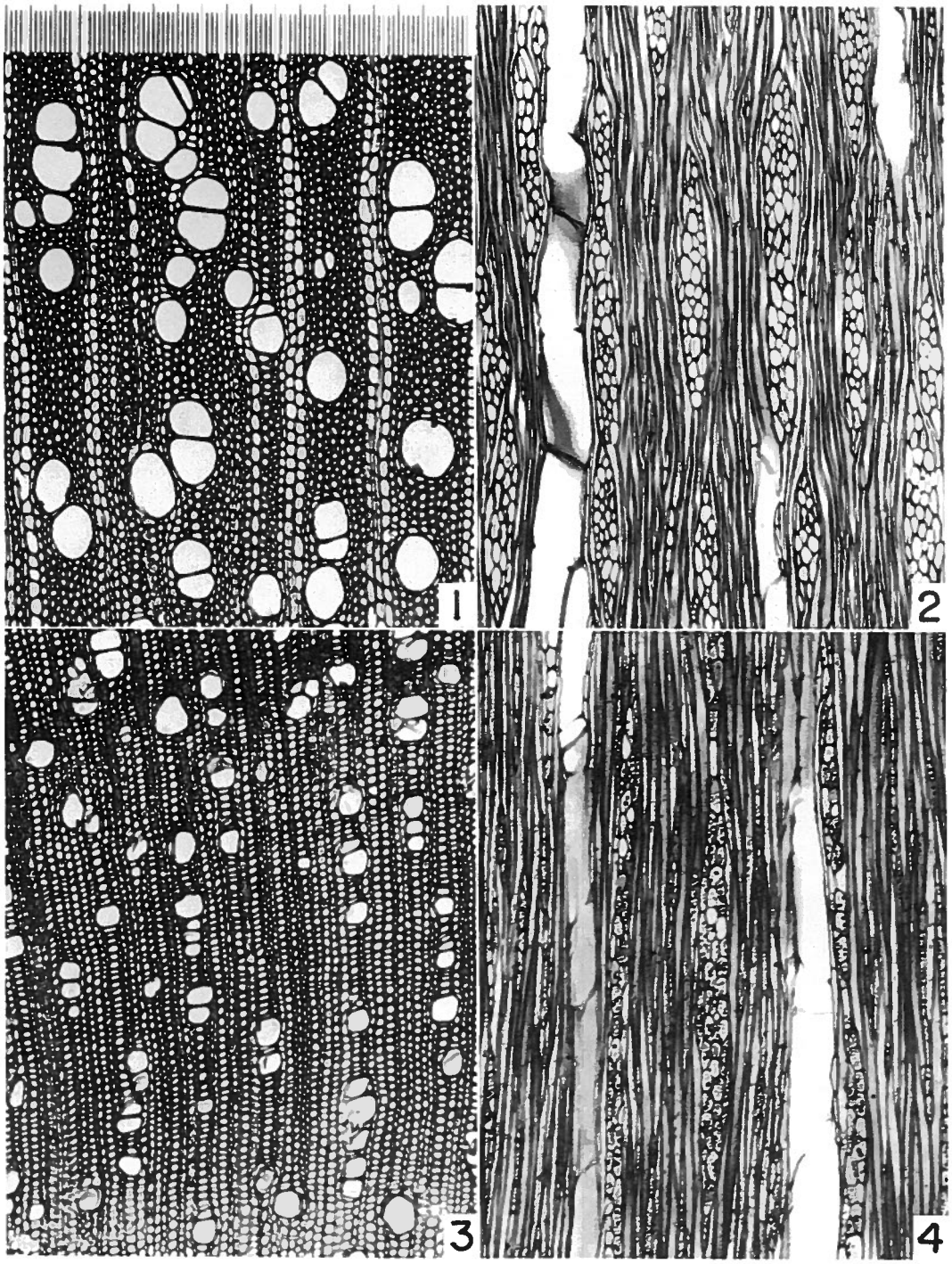

Fig. 1–4. Wood sections of *Tovaria pendula*.—1–2. Wood from *Carlquist 7156*, large stem.—1. Transection, illustrating large vessels, about half of which are grouped.—2. Tangential section; rays are relatively wide, short.—3–4. Wood from *Carlquist 7099*, young stem.—3. Transection; pores narrow.—4. Tangential section; rays tall, slender. (Fig. 1–4, magnification scale above Fig. 1 [finest divisions = 10 μm].)

has been found in the leaves of *Tovaria.* Wood anatomy has not been described hitherto, although *T. pendula* is woody and can be a shrub with a stem to about 6 cm in diameter. Suitable material for anatomical studies was collected by the writer during a visit to Peru in 1982. *Tovaria pendula* is common on scree areas in the cloud-forest zones of Peru. It can be an erect shrub where plants are solitary; where it occurs on steep slopes among other vegetation, it often leans outward and downward. Study of these plants revealed some features different from those ascribed to *Tovaria* above. These can be used as new evidence for including *Tovaria* in Capparaceae or segregating it as its own family.

MATERIALS AND METHODS

Stem, leaves, wood, and other portions of *T. pendula* (*Carlquist 7099*) were preserved in the field in a formalin solution prepared by adding paraformaldehyde powder to water. This fixative, although not suitable for some histological purposes, was adequate for the present study. Wood samples of a larger plant (*Carlquist 7156*) were prepared by drying.

Sections of leaves and stems were prepared by ordinary paraffin techniques and stained with safranin and fast green. Both transections and paradermal sections of leaves were prepared.

Wood of *Tovaria* is too soft to be sectioned on a sliding microtome with good results, but too hard for ordinary paraffin techniques. A recently devised method (Carlquist 1982) proved ideal for sectioning this wood. Wood sections were stained with safranin. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Seedlings were grown from seeds (*Carlquist 7156*) collected in the field. These served for studying nodal anatomy (fresh material hand sectioned and observed with a dissecting microscope) and for demonstrating the presence of stipules. Herbarium vouchers were deposited in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL DESCRIPTIONS

Wood

A full description is given below for the wood of a *T. pendula* stem (*Carlquist 7156*). The descriptions of the other wood samples contain data only where features differ significantly from those of the *Carlquist 7156* stem.

Carlquist 7156 *stem* (Fig. 1–2).—Growth rings absent. Pores circular. Perforation plates simple. Mean number of vessels per group, 1.77. Mean number of vessels per mm^2, 40. Mean vessel diameter, 68 μm. Mean vessel-element length, 305 μm. Mean vessel wall thickness, 1.4 μm. Vessel-vessel pitting alternate, pits oval, 4 × 5 μm. Vessel-ray and vessel-axial parenchyma pitting chiefly scalariform. No vesturing evident on pits as seen by means of a light microscope. All imperforate tracheary elements are libriform fibers with very small sparse pits on radial walls. Some fibers septate. Mean diameter of libriform fibers, 28 μm. Mean length of libriform fibers, 761 μm. Mean wall thickness of libriform fibers, 3.0 μm. Axial parenchyma scanty vasicentric, in strands of 2–3 cells. Vascular rays both multiseriate and uniseriate, the former more abundant. Mean height of

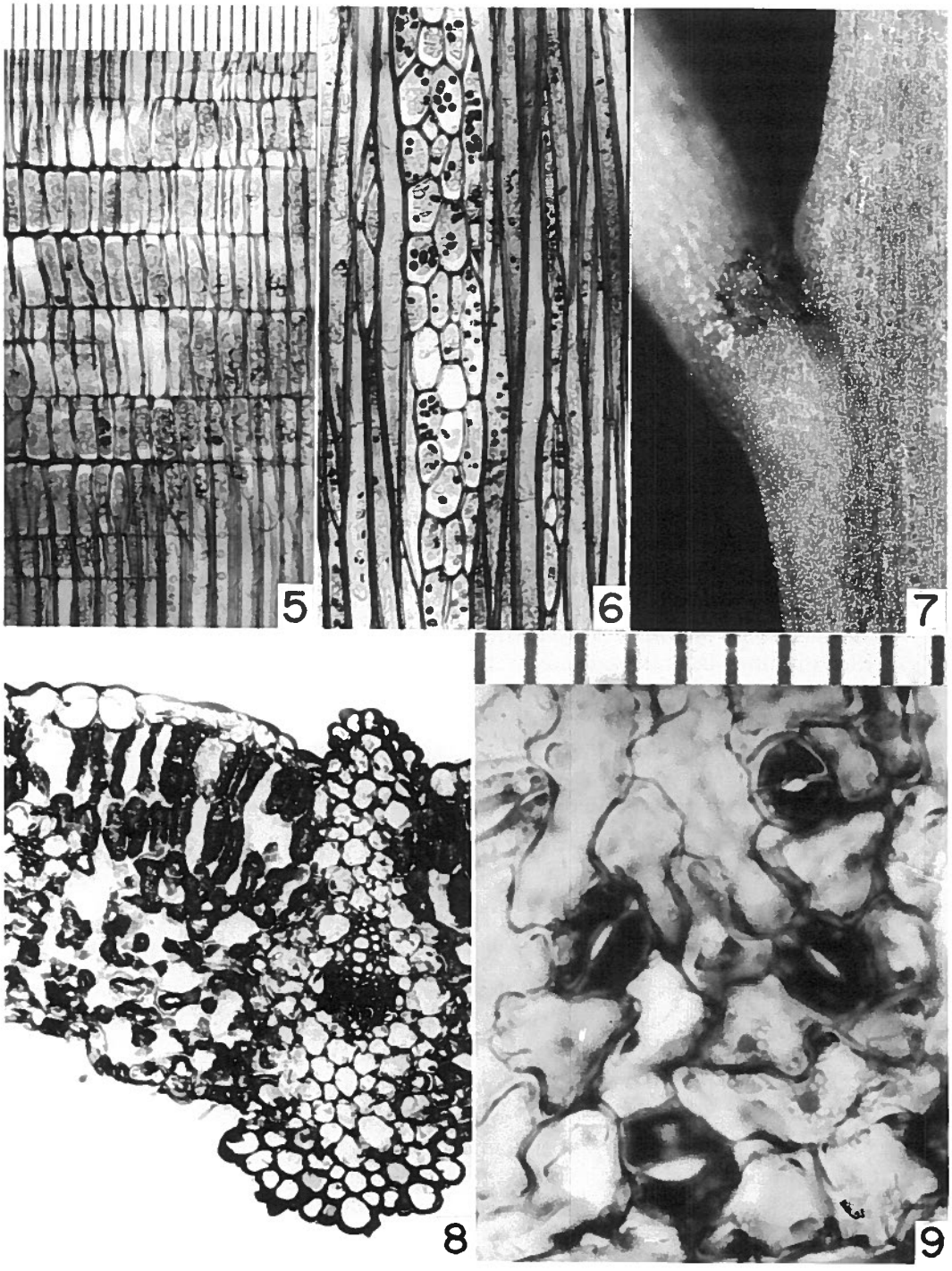

Fig. 5–9. *Tovaria pendula.*—5–6. Wood sections of young stem, *Carlquist 7099.*—5. Radial section; ray cells are all upright.—6. Tangential section portion; starch visible in ray cells and libriform fibers.—7. Node from seedling, showing stipule near petiole base.—8–9. Leaf sections, *Carlquist 7099.*—8. Transection, vein with bundle-sheath extension at right.—9. Paradermal section, showing anomocytic

multiseriate rays, 536 μm. Mean height of uniseriate rays, 111 μm. Mean width of multiseriate rays, 57 μm or 3.8 cells. Ray cells predominantly upright (Fig. 2), but a few procumbent cells present in central portions of rays. Ray cell walls thin but lignified. Wood nonstoried. Starch present in ray cells, libriform fibers, and axial parenchyma cells. Crystals absent.

Carlquist 7156 *root.*—Features like those of the stem except for the items given. Mean number of vessels per mm^2, 41. Mean diameter of vessel elements, 88 μm. Mean vessel-element length, 336 μm. Mean wall thickness of vessel elements, 1.4 μm. Mean diameter of libriform fibers, 25 μm. Mean length of libriform fibers, 737 μm. Mean wall thickness of libriform fibers, 2.5 μm. Mean height of multiseriate rays, 454 μm. Mean height of uniseriate rays, 84 μm. Mean width of multiseriate rays, 71 μm or 4.9 cells. Upright, square, and procumbent cells about equally frequent in rays.

Carlquist 7099 *small stem (about 9 mm in diameter)* (Fig. 3–6).—Mean number of vessels per group, 1.90. Mean number of vessels per mm^2, 58. Mean vessel diameter, 53 μm. Mean vessel-element length, 419 μm. Mean vessel wall thickness, 2.0 μm. Mean diameter of libriform fibers, 25 μm. Mean length of libriform fibers, 679 μm. Mean wall thickness of libriform fibers, 1.8 μm. Mean height of multiseriate rays, 1804 μm. Mean height of uniseriate rays, 166 μm. Mean width of multiseriate rays, 53 μm or 3.20 cells. Ray cells predominantly erect (Fig. 5, 6), and only a few square cells and no procumbent cells present.

Stipules

Although descriptions of the genus *Tovaria* claim absence of stipules, a pair of small green stipules, irregular in shape and with erose margins, may be found at least on younger plants at the base of each petiole (Fig. 7). These are consistently present, and do not contain any of the features of petiolar glands and thus must be considered stipules.

Node

At each node, a single trace departs into the petiole. The trace is in the form of a broad arc of vascular tissue. No vascular tissue enters the stipules.

Stem

The epidermis of the stem consists of cells with dome-shaped outer epidermal walls. The outer wall is covered by a discrete cuticle about 2 μm thick. Beneath the epidermis lie about seven layers of chlorenchyma. Within the chlorenchyma occasional large cells which are tentatively identified as myrosin cells are scattered. These cells are more than twice the diameter of the chlorenchyma cells. As seen in longitudinal section, two to several of these presumed myrosin cells may be grouped in vertical files. Primary phloem fibers may be found on the bundles, but no fibers are formed in the secondary phloem. Parenchyma cells that occur

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stomata. (Fig. 5, 6, 8, magnification scale above Fig. 5 [divisions = 10 μm]. Fig. 9, magnification scale above Fig. 9 [divisions = 10 μm].)

between the primary phloem fiber strands of adjacent bundles remain thin walled, but their walls may become lignified. Starch occurs in all parenchyma cells within the xylem. The pith consists of spherical cells with moderately thick lignified walls; cells near the periphery of the pith contain starch.

Leaf

A transection of the lamina is illustrated in Fig. 8. The upper epidermis is composed of cells with slightly convex outer walls, not truly dome shaped except above the bundle-sheath extensions. These cells are polygonal in outline as seen in surface view (from a paradermal section). No distinct cuticle is evident, although some cutinization of the outer wall is apparent from staining reactions. The mesophyll is differentiated into two layers of palisade and 5–6 layers of spongy cells. No centric arrangement of chlorenchyma cells was observed in this material. The lower epidermis consists of cells that have flat outer tangential walls. Seen in face view, as in a paradermal section, cells of the lower epidermis have wavy outlines. Cuticular striae occur on the outer walls of some abaxial epidermis cells. No subsidiary cells are associated with the guard cells; thus, an anomocytic condition is present (Fig. 9). Bundle-sheath extensions occur on the larger veins (Fig. 8, right). Both upper and lower epidermises of the bundle sheaths are composed of cells that are markedly dome shaped; a few may be said to extend far enough to be termed unicellular trichomes. Beneath the epidermis of the bundle-sheath extensions lie about two layers of lamellar collenchyma. Within the bundle-sheath extensions of some veins may be found myrosin cells. One to three (often two) may be found either adaxially, abaxially, or both, midway between the vein and the epidermis. A few myrosin cells were seen in positions lateral to some smaller veins also.

ONTOGENETIC AND ORGANOGRAPHIC CORRELATIONS

The vessel dimensions of the three samples of *T. pendula* are probably not sufficient for generalizations. However, the trends they show are common ones. In mesic shrubs, one expects increase in vessel diameter, with corresponding decrease in vessel density, over time. This trend could be extracted from the data of a number of studies, but attention was called to it in a recent study (Carlquist 1985), which attempted to relate these changes to a tendency for a plant to develop wider vessels concomitantly with progressive increase in root system and the increase in foliage permitted by the larger root system. The vessel elements appear to be larger in roots than in stems of *T. pendula,* but the number of vessels per mm^2 is about the same in the two organs.

Vessel-element length is greater in the small stems than in the large stems of *T. pendula.* This would be in accordance with the progressive decrease with age shown in instances of paedomorphosis (Carlquist 1962). Presence of erect cells exclusively in rays of younger stems also suggests this. Woods with these characteristics may be suspected of having herbaceous ancestry. Herbaceous ancestry can by hypothesized for some groups of Capparaceae. The fact that rays in *Tovaria* become shorter and wider with age is in accordance with the findings of Barghoorn (1941) for dicotyledons at large.

ECOLOGICAL CONCLUSIONS

If one computes the ratio Mesomorphy (Carlquist 1977) for *T. pendula* woods, the results are: larger stem (*7156*), 518; root, 721; smaller stem (*7099*), 383. These figures are in accord with an interpretation of *Tovaria* as clearly mesic. This is also in accord with the habitat of *Tovaria pendula,* which can be characterized as a cloud-forest element.

The leaf of *Tovaria pendula* is of a drought-deciduous type. When a species has drought-deciduous leaves, the wood anatomy tends to be an accurate reflection of the habitat. When the foliar apparatus tends to resist desiccation (e.g., succulent leaves), the wood of a dicotyledon may be more mesomorphic than the habitat of the plant would suggest.

All of my material of *T. pendula* showed normal bifacial mesophyll construction. Metcalfe and Chalk (1950) report centric palisade for *Tovaria* (species not given). Centric palisade, as cited in earlier literature, can usually be equated with what is now called Kranz syndrome (Brown 1975), which generally occurs in less mesic (warmer, and therefore drier in temperate climates) habitats than do species with normal leaf construction (e.g., Teeri and Stowe 1976). Obviously this situation should be investigated further in *Tovaria.*

FAMILIAL STATUS OF *TOVARIA*

There seems to be little doubt about the relationships of *Tovaria*: the genus clearly belongs to Capparales. One strong indication is the presence of apparent myrosin cells in stems and leaves. These were reported as "mucilage cells" for *Tovaria* by Lagerheim (quoted in Solereder 1908), but my material did not show mucilaginous contents. The strong glucosinolate scent of the leaves is certainly very suggestive of the identity of these cells, although the Millon test was not undertaken. In addition, numerous other features offer evidence of affinity to Capparaceae: hexamery or octomery of floral parts, imbricate nature of sepals and petals, trifoliolate nature of leaves, many details of embryology (Mauritzon 1935), pollen morphology, pollen-grain wall stratification (Erdtman 1953), and some features of lesser significance because they are widespread in dicotyledons (alternate leaves, terminal racemes, hypogynous chorisepalous and chirpetalous flowers.

Features by which *Tovaria* is claimed to differ from Capparaceae include (data from descriptions in Cronquist 1981): paracytic stomata, exstipulate nodes, nonstipitate ovary, axile placentation, six locules, barrate fruit with papery shell, endosperm well developed, and nucellus two cells thick.

The present study has revealed presence of stipules and of anomocytic stomata in *Tovaria.* Thus, two features used to separate *Tovaria* from Capparaceae have been eliminated. The nodal and petiolar anatomy of *Tovaria,* not hitherto described, agree with the conformation reported by Metcalfe and Chalk (1950) for '*Capparis linearis* Jacq.' This nodal anatomy can thus be added to the list of resemblances between *Tovaria* and Capparaceae. Vestured pits were not observed in my material of *Tovaria,* but vestured pits are not uniformly present in Capparaceae.

As a consequence of the present study, few major structural differences between *Tovaria* and Capparaceae can be identified. These residual differences relate mostly

to locule number in the ovary, placentation type, and fruit type. If Capparaceae were a uniform family, one might possibly be able to contrast *Tovaria* with it. However, the diversity of Capparaceae is such that discontinuities within Capparaceae are of the same order of magnitude as those which separate the family from *Tovaria*. Consequently, the treatment of Thorne (1983), who places *Tovaria* in a monogeneric subfamily, Tovarioideae, of Capparaceae is accepted.

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