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Studies on the Gymnantheminae (Vernonieae: Asteraceae) III: restoration of the genus *Strobocalyx* and the new genus *Tarlmounia*

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Abstract.—The genus *Strobocalyx* is resurrected from the synonymy of *Gymnanthemum* and *Vernonia*, and the genus *Tarlmounia* is described. Both of these Asian and Malaysian genera have distinct stylar nodes, blunt stylar hairs and specialized tricolporate, echinate pollen. *Strobocalyx* is typified by the Asian and Indonesian *S. arborea*, and combinations are provided for the 6 other East Asian and Malaysian species: *Vernonia bockiana*, *V. chunii*, *V. esculenta*, *V. solanifolia*, *V. sylvatica* and *V. vidalii*. *Tarlmounia* contains only *Vernonia elliptica*.

A continuing series of papers by the senior author during the last quarter century has segregated many reasonably phyletic units from the old, traditional, aphyletic, core genus *Vernonia* Schreb. and its relatives. The series was summarized up to a point in two papers, Robinson (1999a), making an initial effort at reorganizing genera of the Eastern Hemisphere *Vernoniaeae*, and Robinson (1999b), dealing in more detail with Western Hemisphere members of the tribe. The work is also broadly summarized in less detail in Robinson (2007). These treatments were all based on phenetic studies made prior to the use of DNA sequence data. Partly because of these molecular data, further evaluations of some larger genera have begun. The present series continues to deal with the shrubby or arborescent *Gymnanthemum* Cass. in the subtribe Gymnanthemiae sensu Robinson (1999a), with its woody habit and usually imbricated involucre with rather deciduous inner bracts. The first of these latest studies resurrected the Asiatic genus *Monosis* DC. in Wight (Robinson & Skvarla 2006) which was distinct in its leaf shape and its lophate pollen. This was only a first step in correcting the overly broad concept of *Gymnanthemum*. The present study and a simultaneous study of the somewhat similar Asian and Malaysian genus *Decaneuropsis* (Robinson & Skvarla, 2007) further refine the group.

The present paper deals with the groups that include two Southeast Asian species for which Keeley et al. (2007) have obtained DNA sequences, *Vernonia arborea* Buch.-Ham., a large tree (Fig. 1), and the type of the genus *Strobocalyx* (Blume in DC.) Spach., and *Vernonia elliptica* DC. in Wight, a straggling shrub or sprawling vine. The sequences indicate that the two species are rather close to

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each other, but that they are remote from the mostly African and Madagascan genus *Gymnanthemum* into which *V. arborea* Buch.-Ham. was placed by Robinson (1999a). The distinction of both species from *Gymnanthemum* has been confirmed by study of certain structural features, pollen, sweeping hairs of the style, the basal stylar node, and the absence of a well-developed median shield in the involucral bracts. Revised generic dispositions of the two species and the current understanding of generic limits are presented here. The DNA sequence data (Keeley et al. 2007) offer an extra problem by placing the two Southeast Asian species in close relation to American members of the tribe, a result requiring some discussion.

Materials and Methods

Specimens examined are from the U.S. National Herbarium in Washington, D.C. Examination of microscopic characters involved use of Hoyer’s Solution (Anderson 1954).

Preparation of pollen for scanning electron microscopy (SEM) consisted of acetolysis (Erdtman 1960) followed by the osmium–thiocarbohydrazide repeat procedure (Chissoe et al. 1995) and finally pulse sputter coating with a gold/palladium (60/40) target (Chissoe & Skvarla 1996). Examination was with JEOL 880, Leica 440, and Amray 1810 scanning electron microscopes, all equipped with lanthanum hexaboride (LaB₆) electron sources. The microscopes used were at the University of Oklahoma and in the SEM laboratory of the United States National Museum of Natural History in Washington.

The results of the DNA study and the methods used are reported in Keeley et al. (2007). The phylectic tree included here (Fig. 2) is simplified from the phylogenetic tree of the Vernonieae in the latter paper.

Results

Two genera are accepted in the present treatment, *Strobocalyx* for *V. arborea* and its relatives, and the new genus *Tarlmounia* for *V. elliptica*. The primary characteristics on which the genera are based are as follows.

**Trichomes.**—Hairs on the leaves in *Strobocalyx* vary from the long, simple, uniseriate form with short basal cells and a long nonseptate apical cell in *Strobocalyx arborea* (Fig. 3A) and *S. solanifolia* and in other *Strobocalyx* spp. The latter are sometimes asymmetrical at the base. These differ from the very short-stalked, very long-armed T-shaped form in the apparently closely related *Tarlmounia elliptica* (Fig. 3B). This places *Strobocalyx* and the related *Tarlmounia* among the groups in the Vernonieae with simple- or T-shaped trichomes, in contrast to groups with stellate, spurred, or scale-like trichomes such as the New World Piptocarpinae or Sipolisiinae.

**Inflorescences.**—The shape of the inflorescence in *Strobocalyx* is generally corymbiform with obvious cymose development at the apex. The shape is not strictly pyramidal as in *Monosis* (Robinson & Skvarla, 2006). The length of the peduncles varies from almost none in *S. sylvatica* to elongate in *S. Chunii*. The receptacles may or may not have hairs. In no case does the inflorescence become very dense. The corollas never have elongate slender bases as in *Decaneuropsis* (Robinson & Skvarla, 2007). The achenes of *Strobocalyx* have been traditionally described as 5-ribbed or 5-angled, contrasting with the 10-ribbed condition in most other *Gymnanthemum*-like Vernonieae of the Eastern Hemisphere. Careful examination shows 10 ribs in almost all achenes, but many of these may be faint or totally suppressed. In *Tarlmounia* the inflorescences are elongate and thyrsiform, the achenes are 5-ribbed with little or no evidence of
extra ribs. The pappus in all species examined shows some shorter outer bristles, although these are not in a highly differentiated series.

Style.—In the present study of the Gymnanthemiae, distinctions are emphasized between *Strobocalyx*, *Gymnanthemum* and *Monosis*, all placed in
Gymnanthemum in Robinson (1999a). Two of the useful characters involve the style. In Strobocalyx the base of the style has a distinct expanded node. This is also true of Monosis. Tarlmounia has a conical style base with a narrow basal annulus of thickened cells. In contrast, typical Gymnanthemum, with G. coloratum (Willd.) H. Rob. & B. Kahn and G. amygdalinum (Del.) Sch.Bip. ex Walp., has no evident basal stylar node. Other species of true Gymnanthemum, such as G. myrianthum (Hook. f.) H. Rob. and G. theophrastioidum (Schweinf. ex Oliv. & Hiern) H. Rob., have differentiated cells at the base of the style, but these are few and the node is, at best, scarcely developed.

Sweeping hairs on the upper shaft and branches of the style are blunt in Strobocalyx and Tarlmounia. In contrast, they are pointed in Gymnanthemum and Monosis, and in some other elements that have been placed in the broad concept of Gymnanthemum. The blunt hairs can be seen in a distorted form using SEM, but they are easily observed under the light microscope. This character is not restricted to Strobocalyx and Tarlmounia, which have nonlophate pollen, but also occurs in numerous species of the Eastern
Hemisphere such as Decaneuropsis cumingiana (Benth.) H. Rob. & Skvarla, and in most members of the Piptocarphi- nae in the Western Hemisphere which have ordinary Type A pollen (see discussion below).

**Pollen.**—Strobocalyx and Tarlmounia have tricolporate, echinate, nonlophate
pollen with perforated tectum continuous over the entire surface except the colpi. Such pollen has been called the *Lychnophora* type by Stix (1960) and Type A by Keeley & Jones (1977, 1979) and Jones (1979, 1981). The common Type A pollen is widely distributed in the Vernonieae, sometimes in genera or species where lophate pollen also occurs (Robinson 1987). Still, Type A pollen has stabilized in the subtribes Vernoniiinae sensu stricto, Lychnophorinae, Piptocarphinae, Centratherinae and Sipolisiinae of the Western Hemisphere, and it is common in *Distephanus* Cass., many Erlangeinae, and *Gymnanthemum* sensu stricto of the Eastern Hemisphere. Most species exhibit pollen with irregular disposition of spines on the surface and with large incipient lacunae in the intercolpar region, sometimes with the same pattern of lacunae as in lophate pollen. This type of pollen has been referred to as sublophate (Skvarla et al. 2005). This uneven sublophate pattern can be seen under the light microscope.

The pollen of *Strobocalyx* and *Tarlmounia* differs from most Type A pollen in the Vernonieae in having a much more even distribution of spines and much smaller incipient lacunae in the intercolpar region (Figs. 4A–C, F, 5A, B, 6A–C, 7A–D, 9A–D). The greater density of spines and nearly even spine distribution are visible under the light microscope.

There are additional features of interest in *Strobocalyx* pollen only visible under the SEM. Species such as *S. arborea* (Figs. 4D, E), *S. bockiana* (Fig. 5D), *S. solanifolia* (Figs. 6E, F), *S. sylvatica* (Figs. 8A–D), and *S. vidalii* (Figs. 8E, F) show inward extensions of the columellae of the perforated tectum that often form groups of extra columellae reaching the foot layer (Figs. 4D, 6E, 8A–F). These inward extensions and supplementary columellae are not present in *Tarlmounia* (Fig. 9E).

In *Strobocalyx*, the pollen of *S. bockiana* has a pitted outer surface of the foot layer (Figs. 5C, E) not seen in other species examined under the SEM. The views of the polar region are of interest. *Strobocalyx arborea* (Figs. 4A–C), and *S. bockiana* (Fig. 5A) show a mix of broad raised spinose areas separated by irregular grooves at the poles. *Strobocalyx sylvatica* (Figs. 7B–D) has 1 or 2 spines centered at the pole where the colpi converge. *Strobocalyx solanifolia* (Figs. 6B, C) has an unusual syncolpar condition with a completely open pole. These details have not been surveyed in all species, and their systematic value within the genus is uncertain.

**DNA sequence data.**—Phylogenetically informative DNA sequence data have been obtained for the type species, *Strobocalyx arborea* (Fig. 1), and for the seemingly related *Tarlmounia elliptica* (Keeley et al., 2007). The phylogeny obtained from combining the *trnL-F*, *ndhF*, and ITS data sets placed the two species close together, and distant from typical *Gymnanthemum* (Fig. 2). Rather than coming out close to other Eastern Hemisphere Vernonieae, their closest relatives appear to be in the Western Hemisphere. In fact, they occur nested within one of the subgroups of the large American clade. Accepting the results from molecular studies, there are two possibilities; either the American Vernonieae, in spite of considerable uniformity of some characters, had more than one origin from the ancestral Eastern Hemisphere Vernonieae, or *Strobocalyx* and *Tarlmounia* are some kind of reintroduction of an American lineage of the tribe into the Eastern Hemisphere. This is not resolved at this point, and the authors do not all agree which is more likely. Resolution will need sequences from many additional Southeast Asian Vernonieae.

Another genus in the Western Hemisphere that comes out close to *Strobocalyx* and *Tarlmounia* in the molecular study (Keeley et al. 2007), is *Eremosis*
(DC.) Gleason, which shows some similar Piptocarphinae-type characters, woody habit, imbricated involucres with deciduous inner bracts, and blunt sweeping hairs on the style. Such characters are also found in the apparently less closely related *Critoniopsis* of South America. All groups involved have sufficient structural distinctions to negate any really close relationship.

Fig. 4. SEM of *Strobocalyx arborea* pollen (Sumatra, Rahmat Si Toroes 3264 US). A–C, Whole grains in near polar views, showing density of spines with small intercolpar lacunae, continuous perforated tectum between colpi, and deep grooves near poles; D, E, Broken grains showing numerous intrusions or supplementary columellae from inner surface of perforated tectum; F, Whole grain, colpar view.
The two genera in the present study share blunt sweeping hairs of the style, and a non-sublophate variant of type A pollen. They differ in the simple versus T-shaped hairs, the broadly corymbiform versus thyrsiform inflorescences, the triangular versus oblong apical appendages of the anther, the basically 10-ribbed versus 5-ribbed achenes, the short and broad versus the narrower stopper-shaped carpopodium, and the extra columnellae under the spines of the pollen versus no extra columnellae. The group of Gymnanthemine genera that have been treated in this series of papers can be distinguished by the following key:

1a. Plants scandent or scrambling shrubs; inflorescences elongate-thyrsoid; sweeping hairs of the style branches blunt .................. 2a

1b. Erect shrubs or trees; sweeping hairs of style branches acute or blunt ...... 3a

2a. Hairs of the stems and leaves simple, not T-shaped; corollas slender-stalked, with bases elongate and filiform; bases of styles without nodes; achenes

Fig. 5. SEM of Strobocalyx bockiana pollen (China, Rock 6225 US). A, B, Whole grains in near-polar and near-colpar views, showing density of spines, continuous perforated tectum between colpi, and deep grooves near poles; C–E, Broken grains showing some inward intrusions from perforated tectum and essential lack of supplementary columnellae; also showing pitting of inner exine covering the foot layer.
strongly 10-ribbed; pollen sublophate, with perforated tectum continuous over incipient lacunae . . Decaneuropsis
2b. Hairs of the stems and leaves T-shaped with long arms, short-stalked and pressed against stems or leaf surface, sericeous; corollas without long slender bases; style with distinct basal node; pollen nonlophate, densely spinulose, without incipient lacunae but with perforated tectum continuous over noncolpar surfaces . . . . . . . . Tarlmounia
3a. Leaves strongly obovate, with basal secondary veins spreading nearly
straight toward leaf margins; inflorescence pyramidal thyrsoid; sweeping hairs stout and pointed; pollen tricolporate, echinolophate with 3 or 4 equatorial lacunae in each intercolpus, tectum lacking obvious perforations, tectum absent in centers of lacunae

3b. Leaves ovate to elliptic, with basal secondary veins curved and often subparallel with basal leaf margins; inflorescence corymbiform to somewhat cymiform; sweeping hairs pointed or blunt

4a. Corollas with slender bases; achenes strongly 10-ribbed; style base without large node; sweeping hairs of style branches pointed; pollen sublophate with continuous perforated tectum over incipient lacunae, columellae centered under spines

4b. Corollas widening from near base; achenes 5-ribbed to weakly 10-ribbed; style base with large distinct node; sweeping hairs of style branches blunt; pollen nonlophate, with crowded spines and without distinct incipient lacunae, with more than one columella or projection from perforated tectum under spines

Monosis

Gymnanthemum


Vernonia sect. Strobocalyx Blume ex DC., Prodr. 5:21 (1836). Type: Vernonia arborea Buch.-Ham.
Trees or small shrubs; stems and branches rather rounded, pith solid; leaves alternate, petiolate, hairs uniseriate, with a long apical cell symmetrical or slightly asymmetrical at base; blades ovate or oblong to obovate, with cuneate to obtuse bases, with lower secondary veins ascending toward margins. Inflorescence somewhat sympodial, corymbiform with slightly cymiform tip. Involucres campanulate to ovoid; bracts to obtuse bases, with lower secondary veins ascending toward margins. Inflorescence somewhat sympodial, corymbiform with slightly cymiform tip. Involucre campanulate to ovoid; bracts appressed, rather chartaceous, without median thickened shield, graduate in 4–5 series, inner bracts rather deciduous, tips rounded to short-acute; receptacles epaleaceous, glabrous to puberulous, alveolate. Florets 5–30 in a head; corollas whitish, narrowly funnelform from near base; apical anther appendage triangular with blunt tip; style base with prominent sclerified node; upper shaft and branches with blunt sweeping hairs. Achenes 5–10-angled, often only 5 clearly evident, surface with few or no setulae, with many idioblasts in surface layer, few or no small rectangular raphids.

Fig. 8. SEM of Strobocalyx pollen. A–D, S. sylvatica (China, Rock 2468 US), broken grains showing inward intrusions from perforated tectum and supplementary columellae; E, F, S. vidali pollen (Philippines, Ramos 324 US), broken grains, showing inward intrusions from perforated tectum and supplementary columellae.
in wall. Pappus of many long capillary bristles, slightly to distinctly enlarged distally, with few shorter bristles at base not forming distinct outer series. Pollen ca. 37–45 μm in diameter in fluid, tricolporate, echinate, nonlophate, spines crowded without large lacuna-like depressions in intercolpi, not sublophate, with well developed perforated tectum; inner surface of tectum with many downward projections, often with supplementary columellae in addition to major columellae under the spines, rarely with perforations evident on surface of foot layer. Chromosome number \( n = \) ca. 30 (Jones 1982).

Etymology.—The name is from the Greek στροβός for twisted and καλέχω for cup, in reference to the imbrication pattern of the bracts of the involucre.

Geography.—From Southeast Asia in India and southern China to Vietnam, Malaysia, and Indonesia including New Guinea.


Figs. 1, 3A, 4A–F

Vernonia celebica DC., Prodr. 5:21 (1836).
Vernonia javanica DC., Prodr. 5:22 (1836).
Vernonia blumeana DC., Prodr. 5:22 (1836).


Strobocalyx bockiana (Diels) H. Rob., S. C. Keeley, Skvarla & R. Chan, comb. nov.


Strobocalyx chunii (Chang) H. Rob., S. C. Keeley, Skvarla & R. Chan, comb. nov.

Vernonia chunii Chang, Sunyats. 3: 272, pl. 35 (1937).

Strobocalyx esculenta (Hemsl.) H. Rob., S. C. Keeley, Skvarla & R. Chan, comb. nov.


Strobocalyx sylvatica (Dunn) H. Rob., S. C. Keeley, Skvarla & R. Chan, comb. nov.

Strobocalyx vidalii (Merr.) H. Rob., S. C. Keeley, Skvarla & R. Chan, comb. nov.


Species excluded:


Tarlmounia H. Rob., S. C. Keeley, Skvarla & R. Chan, genus nov.

Plantae scandentes alternifoliae in caulibus et superfulcibus abaxialibus foliorum argenteo-sericeis aspectu elaeagnoidis, pilis T-formibus, in ramis longis et tenuis. Inflorescentiae anguste pyramidales in bracteis decrescentes; ramulis saeppe defractis; involucris imbricatis mediocriter persistentibus, bracteis distaliter obtusis vel rotundatis; flores ca. 5 in capitulo; corollae albae vel albo-violescens tenues epilosiæ parce glanduliferae e basem
anguste infundibulares; thecae anther-arum base paucе caudataе, appendices apicales anguste oblongae; basi stylorum annulate nodati, rami stylorum in pilis obtusis obstiti. Achaenia 5-angulata, glandulifera; carpopodia anguste obturaculiforma; setae pappi base tenues distaliter latioribus. Grana pollinis in typis A subtypis Strobocalyces.

Plants scandent, with slender stems, pith solid; stems, undersides of leaves, and peduncles densely silvery sericeous with long-armed T-shaped hairs. Leaves alternate, short-petiolate; blade oblong to obovate, base obtuse, margins entire to remotely denticulate, apex rounded to apiculate, upper surface green, nearly glabrous, with few scattered hairs, undersurfaces densely sericeous with slender, appressed T-shaped hairs, secondary veins pinnate, 4–6, irregularly arching toward tip. Inflorescences terminal on branches, narrowly pyramidal with usually short, lateral corymbose branches and branchlets, mature branches usually deflected at nodes; heads in small rather dense clusters; involucral bracts imbricated in ca. 5 series, broadly obtuse to rounded at tip, inner bracts tardily deciduous; receptacle glabrous. Florets ca. 5; corollas white or pale purple in bud and becoming white, ca. 6 mm long, texture of corolla wall thin, funnelform from ca. 1.5 mm above base, without hairs, with scattered glands; anther thecae with minimal basal fringe, apical appendage narrowly oblong; style base broadened with annulus of sclerified cells; upper shaft and branches of style with blunt sweeping hairs. Achenes 5-sided, rarely with extra angle, without hairs, with glandular dots, with numerous idioblasts on surface, with scattered small rhombic or short oblong raphids in wall; carpodium narrowly stopper-shaped, nearly cylindrical, longer than wide; pappus of numerous slender bristles, narrow near base, broadened distally, somewhat fragile, with few short bristles interspersed.

Pollen 37–40 μm in diam., Type A subtype like Strobocalyx not sublophate, with distinct micropores in tectum, differing from Strobocalyx by lack of extra columnellae under the spines and lack of inward projections from the inner surface of the tectum.

The generic name is based on the local name for the species cited on two specimens in the U.S. National Herbarium, distributed by the Royal Forestry Department of Thailand. The names on the two specimens differ slightly, Tarlmoun, and Tarnmoun. The former of the two is chosen here.

Type species.—Vernonia elliptica DC. in Wight

Tarlmounia elliptica (DC. in Wight) H. Rob. S. C. Keeley, Skvarla & R. Chan, comb. nov. Figs. 3B, 9A–E

Vernonia elaeagnifolia DC., Prodr. 5:22 (1836).

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