

## Studies on the Paleotropical Vernonieae (Asteraceae): additions to the genus *Acilepis* from southern Asia

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*Abstract.*—Thirty-three species are recognized in the genus *Acilepis* with new combinations provided for *A. attenuata*, *A. chiangdaoensis*, *A. divergens*, *A. doichangensis*, *A. fysonii*, *A. gardneri*, *A. heynei*, *A. kingii*, *A. lobbii*, *A. namnaoensis*, *A. nayarii*, *A. nemoralis*, *A. ngaoensis*, *A. ornata*, *A. peguensis*, *A. peninsularis*, *A. principis*, *A. pseudosutepensis*, *A. setigera*, *A. sutepensis*, *A. thwaitesii*, *A. tonkinensis*, and *A. virgata*. *Acilepis belcheri* is described as new. The rhizomiform structure of the pollen muri is discussed and compared with other Vernonieae in Old World Erlangeinae and in New World Lepidaploinae with similar muri.

This study continues a series of papers by the senior author aimed at delimiting monophyletic genera within the tribe Vernonieae (Asteraceae), broadly summarized by Robinson (1999a, 1999b, 2007). The principal result has been the disintegration of the extremely broad and aphyletic concept of the genus *Vernonia* Schreb. The revisions are nearly complete for the Western Hemisphere where the true genus *Vernonia* occurs but are incomplete for many taxa in the Eastern Hemisphere where no species of *Vernonia* sensu stricto occur.

In the first effort to resolve paleotropical members of the tribe (Robinson 1999b), the genus *Acilepis* D. Don was resurrected from synonymy under *Vernonia*, with ten recognized species. Notable characteristics include the herbaceous habit, the simple hairs of the stems, the separated heads, unequal deeply separated cells of the setulae of the achenes, the almost totally deciduous pappus, and the triplicate pollen. Many additional herba-

ceous species in Asia under the name *Vernonia* were insufficiently known at that time to determine their proper placement with regard to *Acilepis*, including *Vernonia attenuata* DC. and *V. divergens* (Roxb.) Edgew. These two species, widespread in southern Asia from India to China, were reviewed but left unassigned by Robinson (1999b). The present study was initiated to place these two species and thereby complete a proper reassignment of all the species that previously had been placed in the genus *Vernonia* in China. In the process, many additional species have been observed from Burma, India, Sri Lanka, and Thailand and are formally transferred here to *Acilepis*, and a new species is described as well. Still other more poorly known species from Burma, the former Indochina, and India undoubtedly belong to the genus but await more complete floristic surveys of those areas.

This study has made extensive use of the treatments of the tribe Vernonieae in India (Clarke 1876, Hooker 1881, Uniyal 1995), the Flora of China treatment by

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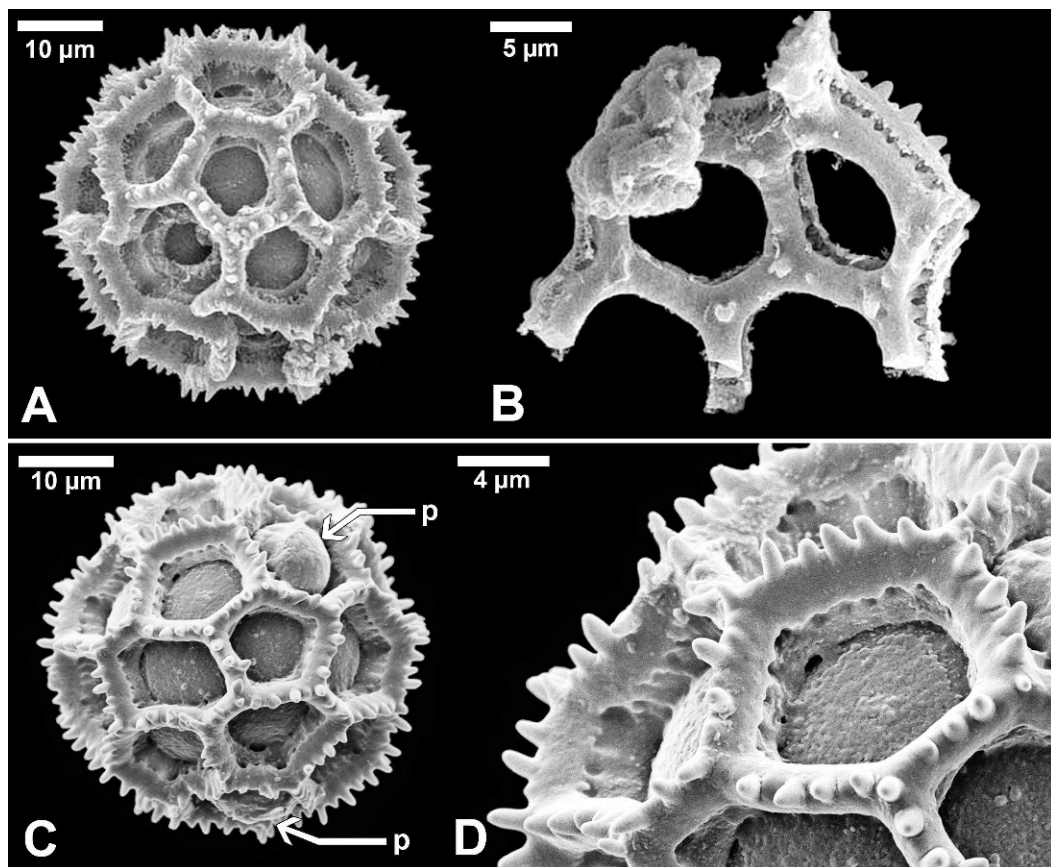


Fig. 1. Scanning electron micrographs of *Acilepis* pollen. A, B. *A. attenuata*, A. Henry 11692 (US). A, Whole grain with distinct pore. B, Rhizomiform structure of easily detached muri. Grains in A and B were acetolyzed. C, D. *A. chiangdaoensis*, M. Tagawa et al. T4038 (KYO). C, Unacetolyzed grain with caps showing positions of pores (p). D, Enlargement of 1C showing columellae and unperforated tectum.

Chen (1985), and the treatments of Koyama (2004, 2005) for Thailand. An expanded concept of the genus *Acilepis* is presented here that includes most if not all of both groups treated by Koyama (2004, 2005), as well as the Asian species previously known as *Vernonia attenuata* and *V. divergens*.

#### Materials and Methods

Specimens examined are from the U. S. National Herbarium in Washington, D.C. Examination of all characters with a light microscope involved use of Hoyer's Solution (Anderson 1954). Pollen grains were either treated with acetolysis

[Figs. 1A, B, 2A–C, F: Erdtman (1960)], followed by staining with osmium-thio-carbohydrazide solutions and sputter coating with gold/palladium (Robinson & Skvarla 2006, 2007; Robinson et al. 2008), or rehydrated in water or alcohol directly from herbarium sheets and similarly sputter coated (Figs. 1C, D, 2D, E). Observations were made with a JEOL 880 (Samuel Roberts Microscopy Laboratory at the University of Oklahoma), LEICA 440, and AMRAY 1810 (United States National Museum of Natural History in Washington) scanning electron microscopes (SEM), all equipped with lanthanum hexaboride (LaB<sub>6</sub>) electron sources. Light microscope observations were made

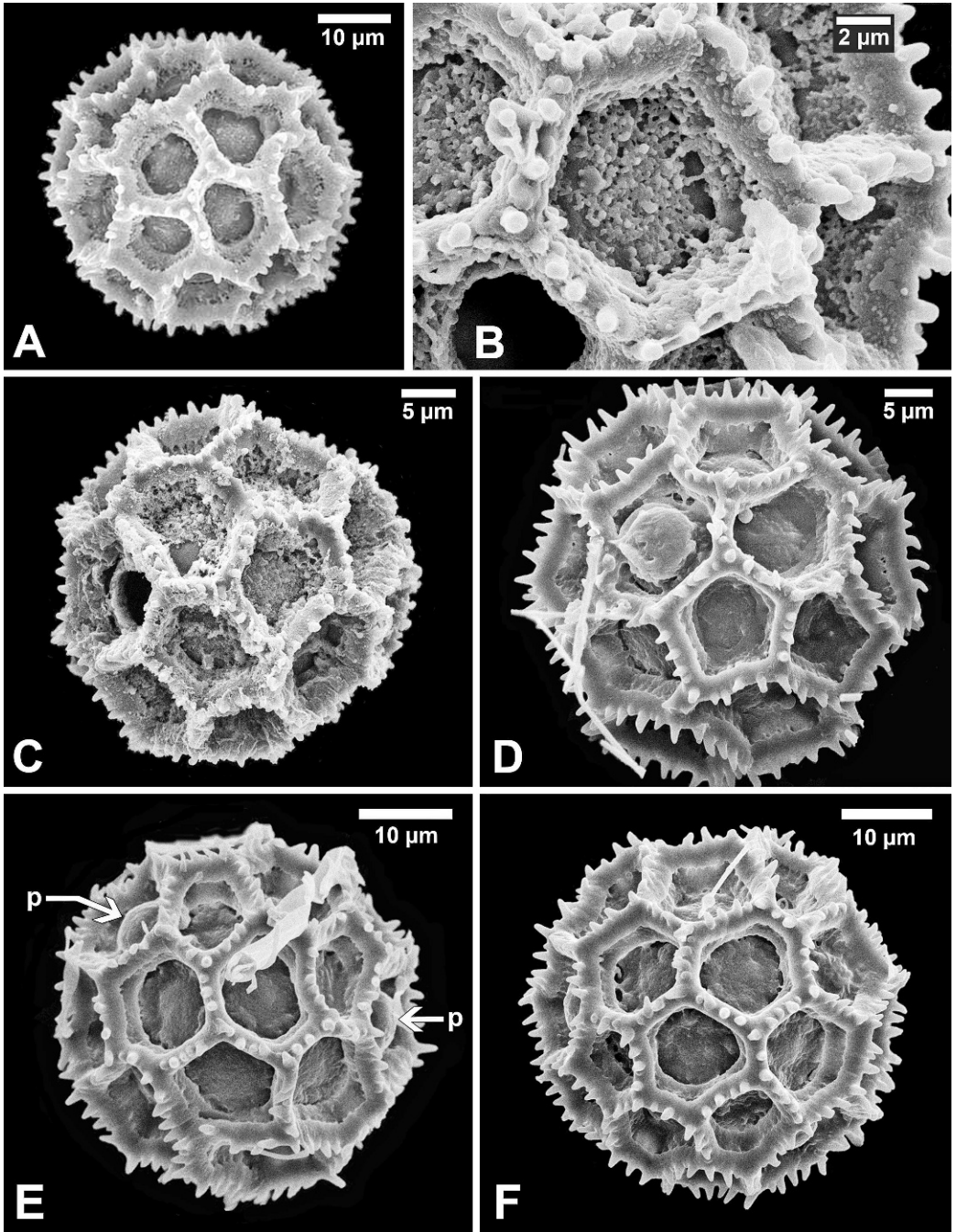


Fig. 2. Scanning electron micrographs of *Acilepis* pollen. A, *A. dendigulensis*, C. J. Saldanha 15785 (KYO). B, C, *A. divergens*, C. J. Saldanha 12357 (US). D–F. *A. saligna*, A. Henry 12714 (US). Figs. A–C, F show acetolyzed pollen; Figs. D, E show unacetolyzed pollen that preserves caps in positions of pores (p).



with a Wild light microscope using 40 $\times$  and oil immersion optics.

### Discussion

The group of species placed here in *Acilepis* possesses triporate pollen and acicular sweeping hairs of the style branches, both characters that are consistent with the large Old World subtribe Erlangeinae (Robinson 1999b). The details of the triporate echinolophate pollen are the most distinctive feature in *Acilepis* (Figs. 1A–D, 2A–F). The pollen is notable for possessing comparatively few lacunae (25–30). The limited number of lacunae results in a less irregular arrangement of lacunae at the poles than in many other Old World genera with triporate pollen. Nevertheless, as observed under the light microscope, sometimes there may be a single polar lacuna and at other times three lacunae meeting at or near the pole, sometimes in the same grain. In polar views of grains, the lacunae over the pores are not perfectly aligned with the pores (Figs. 1C, 2D, E). The irregularity of the lacunar arrangement extends into the intercolpi, where lacunae are staggered relative to each other, and a third lacuna or set of lacunae is sometimes interposed. The latter intercolpar region has been examined with SEM, using unacetolyzed grains in which the caps over the pores are still present to mark those lacunae (Figs. 1C, 2D, E). *Acilepis* resembles other paleotropical Vernoniae with triporate pollen in its irregular lacunae and differs from the tricolporate lophate pollen types that are common in the subtribe Linziinae of the Old World and in many subtribes in the New World. The triporate condition is found in the New World Vernoniae only in the specialized *Acilepidopsis* Group and the subtribe Pacouriinae.

Details of the pollen muri are particularly notable. The margins of the muri have close-set short spines, and have no

evident microperforations. Below the margins, the close-set columellae seem to equal the number of spines (Fig. 1D). The sides below the margin usually have a loose curtain of tectum deposits reaching to near the base (Fig. 2B). The lowest level of the muri under the columellae has a horizontal connector parallel to the muri margins. This basal connector resembles the structure in American Vernoniae termed rhizomiform by Robinson (1999b), where connection to the foot layer seems weak or lacking and muri can strip loose from the core of the pollen grain as a unit (Fig. 1B). A similar condition is observed in the American genera of the subtribe Lepidaploinae, *Echinocoryne* H. Rob. (Robinson 1987), *Chrysolaena* H. Rob. (Robinson 1988), and *Lepidaploa* (Cass.) Cass. (Robinson 1990, 1999b).

The rhizomiform muri of *Acilepis* are grossly similar to those of the American Lepidaploinae, differing in many details such as the closeness of the columellae and the lack of microperforations in the tectum. Many examples of muri partially separated from the foot layer can be seen in Old World Erlangeinae. A spectacular and possibly closely related example is *Phyllocephalum* of Asia and Indonesia (figured in Kirkman 1981; Robinson & Marticorena 1986, Figs. 205–208). SEM studies by the present authors over the last 20 years show that *Cyanthillium* Blume also has muri that are not connected to the foot layer between the baculae at the intersections of the muri. The phenomenon, which needs further study, is thus far known only from the Vernoniae in the Lepidaploinae of the New World and the Erlangeinae of the Old World.

The secondary veins of the leaf provide a somewhat helpful, though not complete, distinguishing feature of *Acilepis*. The veins are generally ascending, usually departing from the midvein at less than 45° angles. With some exceptions, they ascend at least as much as basal margins of the leaf. Vernoniae that have basal

secondary veins strongly directed toward the lower leaf margins do not belong to the genus.

In comparisons with genera in the subtribe Erlangiinae, the simple hairs of the stems, leaves, and inflorescence of *Acilepis* are unlike the T-shaped form seen in genera such as *Cyanthillium* Blume, *Hilliardiella* H. Rob. and *Orbivestis* H. Rob. Of these three genera, the latter two differ by their non-lophate pollen, and *Cyanthillium* differs by its annual or short-lived perennial habit. Three other genera, *Cabobanthus* H. Rob., *Koyamasia* H. Rob., and *Phyllocephalum* Blume, have simple hairs and lophate, triporate pollen. The African *Cabobanthus* was placed in the same group of *Vernonia* to which *Acilepis* belongs (Jeffrey 1988). It differs by possessing a basal tuber and heads clustered at the nodes. The pollen resembles that of *Acilepis*, but it has many more lacunae (over 50). The Asiatic *Koyamasia* lacks a basal node on the style, and has a reduced, deciduous pappus. The Asiatic and Indonesian *Phyllocephalum* also has a reduced deciduous pappus but has obcompressed achenes abruptly narrowed at the top to a narrow corolla insertion, and has subquadrate raphids in the achene walls.

An overview of the genus *Acilepis*, as now circumscribed, shows great variation in the number and shape of the involucre bracts (Figs. 4A–L, 5A–I). The more typical element of the genus, including *A. squarrosa* (Fig. 5I), has up to 200 narrow to long-acuminate bracts in ca. 12 series. Species such as *A. dendigulensis* (Fig. 4F) and *A. divergens* (Fig. 4G) have as few as 50 ovate, short-acute bracts in ca. 5 series. This character, which has been used to define *Vernonia* sections in the past, seems very unreliable within *Acilepis* above the level of species groups. The unreliability of the involucre bracts has already been demonstrated in the New World group Lepidaploinae (Robinson 1999a). The distinctions between the

groups that Koyama (2004, 2005) referred to as *Vernonia* Sect. *Xipholepis* in Thailand (Koyama 2004), and Sect. *Lepidaploa* Subsect. *Paniculatae* (Koyama 2005) seem to be based largely on the involucre bracts that prove to be so unreliable at the generic level. The Sect. *Xipholepis* treatment of Koyama (2004) contains species of the most typical element of *Acilepis*, whereas the group treated as Sect. *Lepidaploa* Subsect. *Paniculata* (Koyama 2005) contains *V. attenuata* and *V. kingii*, which are also members of *Acilepis*.

The two groups under which Koyama (2004, 2005) treated members of *Acilepis* represent potential subgroupings within the genus. The typical group, treated as *Vernonia* Sect. *Xipholepis* by Koyama (2004), with large heads, and narrow sometimes reflexed tips on the involucre bracts, may include *A. aspera*, *A. belcheri*, *A. clivorum*, *A. doichangensis*, *A. nannaoensis*, *A. nantcianensis*, *A. nayarii*, *A. ngaoensis*, *A. peninsularis*, *A. scariosa*, *A. silhetensis*, *A. spirei*, and *A. squarrosa*. The group treated by Koyama (2005) as *Vernonia* Sect. *Lepidaploa* Subsect. *Paniculatae*, with smaller heads and shorter acute involucre bracts seems to include *A. attenuata*, *A. chiangdaoensis*, *A. kingii*, *A. lobbii*, *A. nemoralis*, *A. peguensis*, *A. principis*, *A. pseudosutepensis*, *A. saligna*, *A. sutepensis*, *A. tonkinensis*, and *A. virgata*. Two additional groups may include species with large heads and abrupt, long, awn-like or strap-shaped tips on the involucre bracts such as *A. gardneri*, *A. setigera*, and *A. thwaitesii*, and another group with ovate essentially sessile leaves, smaller heads and mucro-tipped involucre bracts such as the non-tomentose *A. divergens* and the tomentose *A. dendigulensis*, *A. fysonii*, and *A. heynei*.

The generic name, *Acilepis*, derives from the long-pointed, sometimes reflexed tips of the involucre bracts, but the group of species, including *A. dendigulensis*, and *A. divergens* has only short-acute slightly apiculate tips on the bracts.

**Acilepis** D. Don, Prodr. Fl. Nepal 169  
(1825)

*Type species.*—*Acilepis squarrosa* D. Don.

Erect herbs or subshrubs, 1–3 m tall, without basal tubers; stems pentangular, with ascending branches in the inflorescence; hairs of stems, leaves and inflorescence simple, unbranched, multiseptate at base, often with long subfusiform apical cell, sparse or in dense tomentum. Leaves alternate, ovate or obovate to oblong or oblanceolate, venation pinnate, secondary veins mostly ascending, angle from midvein mostly less than 45°. Inflorescence of single heads, or racemiform, spiciform, or with branches corymbiform, with few to many heads; peduncles short. Heads 7–17 mm long, 3–23 mm wide; involucre bracts 50–200 in 5–12 series, chartaceous, mostly persistent, glabrous to wooly, ovate and very reduced below, median and inner mostly oblong to oblong-lanceolate, apices short-obtuse, short-apiculate, or long-awned; receptacle epaleate, alveolate, often spiculiferous, glabrous, pilose, or fimbriate. Florets 4–80 in a head; corollas lavender, basal tube long and slender, gradually broadened near top into short throat, throat half or less as long as anther thecae, lobes narrowly oblong, narrowed only near tips, with scattered narrowly capitate glands outside; anthers without glands, thecae spurred, without tails, apical appendage narrowly oblong-ovate, with thin-walled cells; base of style with distinct, sclerified, stopper-shaped node; style branches with appressed acicular sweeping hairs. Achenes 8–10-ribbed, usually with scattered glands and numerous idioblasts, with or without setulae, setulae when present with slender deeply divided cells of unequal length, raphids oblong with rhomboid tips; pappus with both series rather easily deciduous, inner series of capillary bristles, as long as corolla, long-exserted beyond involucre bracts, whitish or yellowish to reddish,

with slender tips, rarely broader distally, outer series of shorter setae or narrow squamae. Pollen 37–45  $\mu\text{m}$  in diameter in fluid, echinolophate, triplicate, with lacunae slightly irregularly arranged at poles, muri with unperforated tectum marginally, with curtain of loose tectum over bases of muri; spines and their underlying columellae close-set along the muri, with bases of muri rhizomiform, easily detaching from foot layer.

Chromosome numbers of seven species of *Acilepis* have been counted (Mehra et al. 1965; Mathew & Mathew 1976, 1983, 1988; Koyama 2004, 2005), *A. attenuata* ( $n = 9$ ), *A. chiangdaoensis* ( $n = 54$ ), *A. dendigulensis* ( $n = 9$ ), *A. divergens* ( $n = 9$ ), *A. doichangensis* ( $n = 54$ ), *A. ngaoensis* ( $n = 36$ ), *A. squarrosa* ( $n = 18$ ). The base number of the genus is evidently  $n = 9$  but includes species that are diploid ( $n = 18$ ), octoploid ( $n = 36$ ) and duodecaploid ( $n = 54$ ).

The 33 currently recognized species of *Acilepis* are listed below. One species that falls in the genus, *Vernonia kradungensis* H. Koyama, is reduced to synonymy under *A. peguensis* (C. B. Clarke) H. Rob. & Skvarla, and one species, is described as new.

*Acilepis aspera* (Buch.-Ham.) H. Rob.,  
Proc. Biol. Soc. Wash. 112:226 (1999).

Fig. 4A

*Vernonia aspera* Buch.-Ham. pro parte,  
Trans. Linn. Soc. London 14:219  
(1824).

*Eupatorium pyramidale* D. Don, Prodr.  
Fl. Nepal 170 (1825).

*Vernonia roxburgii* Less., Linnaea 6:674  
(1831).

*Xipholepis aspera* (Buch.-Ham.) Steetz in  
Peters, Naturw. Reise Mossab. 345  
(1864).

*Vernonia thorelii* Gagnep., Bull. Mus.  
Hist. Nat. (Paris) 492 (1919).

*Vernonia pyramidalis* (D. Don) Mitra,  
Indian J. Forest. 99:100 (1973).

Confusion has arisen from the evident mixture of two species in Buchanan-Hamilton's original material, part being the species treated here as *Acilepis divergens* (Hooker, 1881). Further confusion has arisen from attempt by Hooker (1881) to treat *Vernonia aspera* of Candolle (1836) as a different species from *V. aspera* of Buchanan-Hamilton even though the Candolle entry cites Buchanan-Hamilton as a source.

*Acilepis attenuata* (DC.) H. Rob. & Skvarla, comb. nov.  
Figs. 1A, B, 4B

*Conyza attenuata* Wall., Numer. List [Wallich] n. 3030, comp 130, nom. nud.  
*Vernonia attenuata* Wall. ex DC., Prodr. 5:33 (1836).

The type in Geneva, as seen in microfiche, has a much more diffuse branching than the specimens seen at the US National Herbarium and those illustrated from China (Chen 1985).

*Acilepis belcheri* H. Rob. & Skvarla, species nov.  
Figs. 3, 4C

*Type:* Upper Burma. Myitkyina region, 21 mi.-mark, Myitkyina-Sumprabum road, rare on open roadside, to 4' tall; 16 Oct 1945; U.S.A. Typhus Commission; *R. O. Belcher* 822 (holotype US, isotype K).

*Ad Acilepis namnaoensis similis sed in inflorescentibus late corymbiformibus differt.*

Subshrubs to 1.3 m high, unbranched between base and inflorescence; stems brown, terete to rather pentagonal, pilose, with short, reddish, multicellular, uniseriate hairs and scattered yellowish glandular dots. Leaves alternate, subsessile; petioles 1–3 mm long, densely puberulous; blades oblong-lanceolate, mostly 5–7 cm long, 1.2–2.4 cm wide, base subacute, rounding into remotely serrulate margin, more serrate distally, apex sharp-

ly acute, upper surface scabridulous, lower surface puberulous mostly on veins, with glandular dots in areoles; secondary veins 4 or 5 on each side of midvein, arched upward from bases spreading at 45° angles or less. Inflorescence broadly corymbiform to slightly cymiform, with branches widely spreading at nearly 45° angles; bracteoles 1.5–4.5 cm long, 0.5–1.4 cm wide, acute at base and apex; peduncles 0.8–1.4 mm long, hispidulous. Heads to 1.4 cm high, 0.6 cm wide; involucre campanular; involucre bracts mostly persistent, 75–80 in ca. 7 series, lower bracts subulate with erect-spreading tips, with many glandular dots, puberulous, median and inner bracts oblong with pale bases and purple tips and upper margins, apices progressively shorter above, from awned to apiculate, cluster of glandular dots outside below erect tips; receptacles densely pilosulous. Florets ca. 15 in a head; corollas lavender, ca. 10 mm long, with narrowly capitate glands sparse on basal tube and throat, dense distally on lobes, basal tube slender, ca. 7 mm long, throat less than 1 mm long, linear-lanceolate lobes ca. 3 mm long; anther thecae 2.7 mm long, apical appendages ca. 0.4 mm long. Achenes ca. 2.5 mm long, 10-ribbed, with numerous glands between ribs, with sparse, deeply divided setulae with unequal cells; pappus of ca. 35 very caducous, white, slender bristles ca. 7 mm long, outer series of slender bristle ca. 2 mm long. Pollen grains in fluid ca. 57 µm in diameter.

The new species is named for the collector, Robert O. Belcher, at East Michigan University in Ypsilanti, known more recently for his work on Senecioeae of the Australian region.

The holotype at US was annotated by Koyama in 1993 as *Vernonia roxburgii* Less., and the specimen resembles the specimen illustrated by Koyama (2004) that has elongate branches in the inflorescence. However, *Vernonia roxburgii*, treated here as a synonym of *Acilepis*





Fig. 3. Herbarium sheet of *Acilepis belcheri* H. Rob. & Skvarla, n. sp., Burma, Belcher 822 (holotype US).

*aspera*, is described by Koyama (2004) as having a compound racemose inflorescence and heads 20–25 mm across with ca. 30 florets. Specimens seen at US also

seem to have larger heads without spreading inflorescence branches. *Acilepis belcheri* seems closer to *Vernonia namnaoensis* Koyama from northern



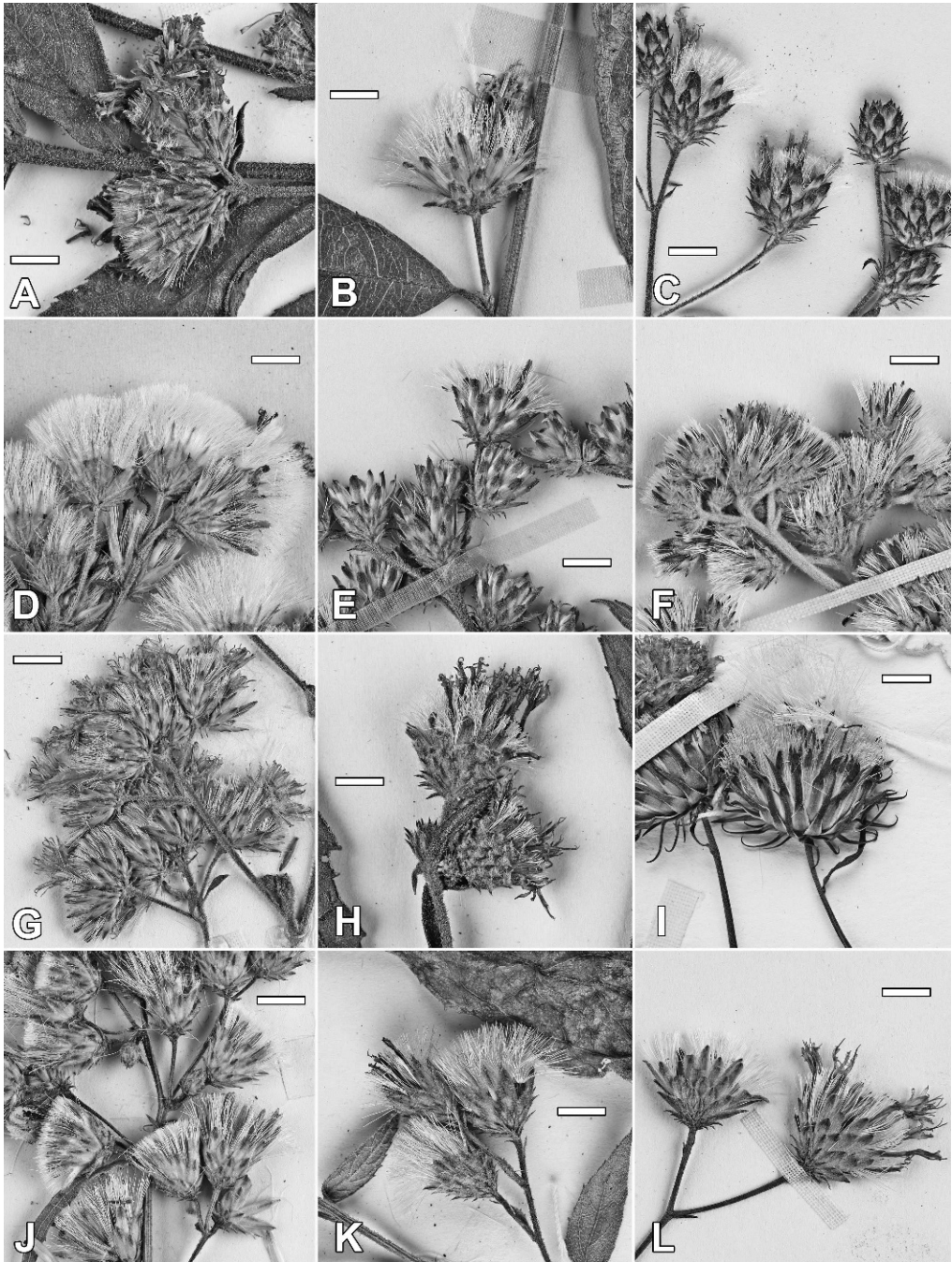


Fig. 4. Photographs of heads and involucre bracts of *Acilepis*. A, *A. aspera*, W. J. Kress et al. 97-5991 (US). B, *A. attenuata*, A. Henry 11692 (US). C, *A. belcheri*, R. O. Belcher 822 (holotype, US). D, *A. chiangdaoensis*, M. Tagawa et al. T-4038 (holotype, KYO). E, *A. clivorum* A. Henry 9131 (US). F, *A. dendigulensis*, C. J. Saldanha 15785 (US). G, *A. divergens*, C. J. Saldanha 16113 (US). H, *A. doichangensis*, T. Shimizu et al. T-20693 (holotype, KYO). I, *A. gardneri*, L. H. Cramer 5147 (US). J, *A. kingii*, Iwatsuki & N. Fukuoka 3556 (KYO). K, *A. namnaoensis*, H. Koyama et al. T-31840 (holotype, KYO). L, *A. nemoralis*, A. Grierson 1154 (US). Scale bars = 5 mm.

Thailand with ca. 23 florets in the heads. Neither of these related species, nor the other close relatives, show the widely spreading inflorescence branching seen in the holotype of *A. belcheri* or in the scan of the isotype at Kew. The setulae of the achenes of the new species are sparse and small, nearly hidden among the glands, and they might not be noticed under a dissecting microscope.

*Acilepis chiangdaoensis* (H. Koyama)

H. Rob. & Skvarla, comb. nov.

Figs. 1C, D, 4D

*Vernonia chiangdaoensis* H. Koyama, Bull. Natl. Sci. Mus., Tokyo, Ser. B. 31(2):68 (2005).

*Acilepis clivorum* (Hance) H. Rob., Proc.

Biol. Soc. Wash. 112:226 (1999).

Fig. 4E

*Vernonia clivorum* Hance, J. Bot. 7:164 (1869).

*Aster coriaceiformis* H. Lév & Vaniot, Repert. Spec. Nov. Regni Veg. 8:358 (1910).

*Acilepis dendigulensis* (DC.) H. Rob.,

Proc. Biol. Soc. Wash. 112:226 (1999).

Figs. 2A, 4F

*Conyza indica* Wall., Numer. List [Wallich] n. 3042, comp. 152, nom. nud.

*Decaneurum dendigulense* DC. in Wight, Contr. Bot. Ind. 7 (1834).

*Lysistemma dendigulense* (DC.) Steetz in Peters, Naturw. Reise Mossambique 341 (1864).

*Vernonia indica* Wall. ex C. B. Clarke, Compos. Ind. 16 (1876).

*Acilepis divergens* (Roxb.) H. Rob. &

Skvarla, comb. nov.

Figs. 2B, C, 4G

*Conyza divergens* Wall., Numer. List [Wallich] n. 3027A, comp. 137, nom. nud.

*Conyza multiflora* Wall., Numer. List [Wallich] n. 3032q, comp. 142, nom. nud.

*Conyza lanceolata* Wall., Numer. List [Wallich] n. 3059, comp. 169, nom. nud.

*Eupatorium versicolor* Wall., Numer. List [Wallich] n. 3167, comp. 277, nom. nud.

*Eupatorium polyanthemum* Wall., Numer. List 3171, comp. 281, nom. nud.

*Eupatorium divergens* Roxb., Fl. Ind. (Roxburgh) 3:414 (1832).

*Decaneuron divergens* (Roxb.) DC. in Wight, Contr. Bot. Ind. 8 (1834).

*Vernonia nilgheryensis* DC., Prodr. 5:32. (1836).

*Vernonia divergens* (Roxb.) Edgew., J. Asiat. Soc. Bengal 2:172 (1853).

*Lysistemma divergens* (Roxb.) Steetz in Peters, Naturw. Reise Mossambique 341 (1864).

*Lysistemma multiflorum* Steetz in Peters, Naturw. Reise Mossambique 341 (1864).

*Gymnanthemum metzianum* Sch. Bip. ex Hook.f., Fl. Brit. Ind. 3:234 (1881), nom. nud.

*Vernonia metziana* Sch. Bip. ex Hook.f., Fl. Brit. Ind. 3:234 (1881), nom. nud.

The species is distributed throughout southeast Asia from India to Thailand and China. The admixed material in the Buchanan-Hamilton type of *Vernonia aspera* was this species.

*Acilepis doichangensis* (H. Koyama)

H. Rob. & Skvarla, comb. nov.

Fig. 4H

*Vernonia doichangensis* H. Koyama, Bull. Natl. Sci. Mus. Tokyo, Ser. B. 30(1):22 (2004).

Described (Koyama 2004) from Thailand and China (Yunnan), seen in this study from Vietnam (Tonkin; Hoa Binh, Nov 1926, *Petelot s.n.*, USNM 1507342).

*Acilepis fysonii* (Calder) H. Rob. &

Skvarla, comb. nov.

*Vernonia fysonii(i)* Calder, Rec. Bot. Surv. India 6:343 (1914).

- Acilepis gardneri* (Thwaites) H. Rob. & Skvarla, comb. nov.  
Fig. 4I
- Vernonia gardneri* Thwaites, Enum. Pl. Zeyl. (Thwaites) 161 (1860).
- Acilepis heynei* (Bedd. ex Gamble) H. Rob. & Skvarla, comb. nov.
- Vernonia heynei* Bedd. ex Gamble, Kew Bull. 1920:340 (1920).
- Acilepis kingii* (C. B. Clarke) H. Rob. & Skvarla, comb. nov.  
Fig. 4J
- Vernonia kingii* C. B. Clarke, Compos. Ind. 12 (1876).  
The species was treated as a synonym of *Vernonia clivorum* by Hooker (1881) but was recognized as a distinct species by Koyama (2005).
- Acilepis lobbii* (Hook.f.) H. Rob. & Skvarla, comb. nov.
- Vernonia lobbii* Hook.f., Fl. Brit. Ind. 3:231 (1881).  
A scan of the type provided by the Royal Botanic Gardens at Kew shows the characteristic short-petiolate lower leaves with broadly obovate blades.
- Acilepis namnaoensis* (H. Koyama) H. Rob. & Skvarla, comb. nov.  
Fig. 4K
- Vernonia namnaoensis* H. Koyama, Bull. Natl. Sci. Mus. Tokyo, Ser. B. 30(1):22 (2004).
- Acilepis nantcianensis* (Pamp.) H. Rob., Proc. Biol. Soc. Wash. 112:226 (1999).
- Vernonia bracteata* var. *nantcianensis* Pamp., Nouvo Giorn. Bot. Ital, n. s. 18:98 (1911).
- Vernonia silhetensis* var. *nantcianensis* (Pamp.) Hand.-Mazz., Symb. Sin. 7:1084 (1930).
- Vernonia nantcianensis* (Pamp.) Hand.-Mazz., Notizbl., Bot. Gart. Berlin-Dahlem 13:608 (1937).
- Acilepis nayarii* (Uniyal) H. Rob. & Skvarla, comb. nov.
- Vernonia nayarii* Uniyal, Indian J. Forest. 11(2):171 (1988).
- Vernonia recurva* Bedd. in Moore, J. Bot. 63:171 (1925) [non *Vernonia recurva* Gleason, Bull. New York Bot. Gard. 4:222 (1906)].
- Acilepis nemoralis* (Thwaites) H. Rob. & Skvarla, comb. nov.  
Fig. 4L
- Vernonia nemoralis* Thwaites, Enum. Pl. Zeyl. (Thwaites) 161 (1860).
- Acilepis ngaoensis* (H. Koyama) H. Rob. & Skvarla, comb. nov.  
Fig. 5A
- Vernonia ngaoensis* H. Koyama, Bull. Natl. Sci. Mus., Tokyo, Ser. B. 30(1):25 (2004). Cited by Koyama (2004) as endemic to Thailand.
- Acilepis ornata* (Talbot) H. Rob. & Skvarla, comb. nov.
- Vernonia ornata* Talbot, J. Bombay Nat. Hist. Soc. 11:691 (1898).
- Vernonia dalzelliana* J. R. Drumm. & Hutch., Kew Bull. 1909:261 (1909).
- Acilepis dalzelliana* (J. R. Drumm. & Hutch.) H. Rob., Proc. Biol. Soc. Wash. 112(1):226 (1999).
- Acilepis peguensis* (C. B. Clarke) H. Rob. & Skvarla, comb. nov.  
Fig. 5B
- Vernonia peguensis* C. B. Clarke, Compos. Ind. 13 (1876).





Fig. 5. Photographs of heads and involucral bracts of *Acilepis*. A, *A. ngaoensis*, T. Shimizu et al., -27543 (holotype, KYO). B, *A. peguensis*, H. Koyama & T. Wongprasert T-31211 (holotype of *Vernonia kradungensis* H. Koyama, KYO). C, *A. principis*, H. Koyama & C. Phengkhai T-39209 (KYO). D, *A. saligna*, J. F. Rock 1912 (US). E, *A. scariosa* var. *crassa*, A. Grierson 1109 (US). F, *A. setigera*, D. B. Sumithraarachchi et al., DBS 60 (US). G, *A. silhetensis*, A. Henry 12498A (US). H, *A. spirei*, M. Poilane 2228 (US). I, *A. squarrosa*, Banerjee et al., 3039 (US). Scale bars = 5 mm.

*Vernonia kradungensis* H. Koyama, Bull. Natl. Sci. Mus., Tokyo, Ser. B. 31(2):72 (2005).

Comparison of the Koyama type from northern Thailand, loaned by KYO, with a scan of the Clarke type from northern Burma, provided by Kew, shows the same relatively large leaves with tapering atten-

uate bases of the blades and the same form of inflorescence.

*Acilepis peninsularis* (C. B. Clarke)  
H. Rob. & Skvarla, comb. nov.

*Vernonia bracteata* Wall. ex DC. var. *peninsularis* C. B. Clarke, Compos. Ind. 18 (1876).



- Vernonia peninsularis* (C. B. Clarke) C. B. Clarke ex Hook. f., Fl. Brit. India 3:233 (1881).
- Acilepis principis* (Gagnep.) H. Rob. & Skvarla, comb. nov.  
Fig. 5C
- Vernonia principis* Gagnep., Bull. Mus. Hist. Nat. (Paris) 25:490 (1919).
- Acilepis pseudosutepensis* (H. Koyama) H. Rob. & Skvarla, comb. nov.
- Vernonia pseudosutepensis* H. Koyama, Bull. Natl. Sci. Mus. Tokyo, Ser. B. 31(2):74 (2005).
- Acilepis saligna* (DC.) H. Rob., Proc. Biol. Soc. Wash. 112:226 (1999).  
Figs. 2D–F, 5D
- Conyza saligna* Wall., Numer. List [Wallich] n. 3061, comp. 171, nom. nud.
- Eupatorium longicaule* Wall., Numer. List [Wallich] n. 2169, comp. 279, nom. nud.
- Vernonia saligna* DC., Prodr. 5:33 (1836).
- Vernonia longicaulis* DC., Prodr. 5:33 (1836).
- Vernonia martinii* Vaniot, Bull. Acad. Int. Geogr. Bot. 12:124 (1903).
- Vernonia sequinii* Vaniot, Bull. Acad. Int. Geogr. Bot. 12:24 (1903).
- Acilepis scariosa* (DC.) H. Rob., Proc. Biol. Soc. Wash. 112:227 (1999).  
Fig. 5E
- Vernonia scariosa* Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18:346 (1836), hom. illeg., non *V. scariosa* Poir. 1808.
- Decaneurum scariosum* DC., Prodr. 7:264 (1838).
- Gymnanthemum scariosum* (DC.) Sch.Bip. ex Walp., Repert. Bot. Syst. (Walpers) 2:949 (1843).
- Centratherum scariosum* (DC.) C. B. Clarke, Compos. Ind. 4 (1876).
- Vernonia lankana* Grierson, Ceylon J. Sci., Biol. Sci. 10:43 (1972).
- Acilepis setigera* (Arn.) H. Rob. & Skvarla, comb. nov.  
Fig. 5F
- Vernonia setigera* Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18:345 (1836).
- Acilepis silhetensis* (DC.) H. Rob., Proc. Biol. Soc. Wash. 112:227 (1999).  
Fig. 5G
- Eupatorium glabrum* Heyne ex Wall., Numer. List [Wallich] n. 3283, comp. 393, nom. nud.
- Vernonia? bracteata* Wall., Numer. List [Wallich] n. 2921, comp. 31, nom. nud.
- Decaneurum silhetense* DC., Prodr. 5:67 (1836).
- Decaneurum glabrum* DC., Prodr. 5:67 (1836).
- Gymnanthemum glabrum* (DC.) Sch.Bip. ex Walp., Repert. Bot. Syst. (Walpers) 2:948 (1843).
- Gymnanthemum silhetense* (DC.) Sch.Bip. ex Walp., Repert. Bot. Syst. (Walpers) 2:948 (1843).
- Xipholepis silhetensis* (DC.) Steetz in Peters, Naturw. Reise Mossambique 2:344 (1864).
- Vernonia bracteata* Wall. ex C. B. Clarke, Compos. Ind. 17 (1876).
- Vernonia silhetensis* (DC.) Hand.-Mazz., Symb. Sin. 7(5):1084 (1936).
- Acilepis spirei* (Gandog.) H. Rob., Proc. Biol. Soc. Wash. 112:227 (1999).  
Fig. 5H
- Vernonia spirei* Gandog., Bull. Soc. Bot. France 54:194 (1907).
- Acilepis squarrosa* D. Don, Prodr. Fl. Nepal. 169 (1825).  
Fig. 5I
- Vernonia squarrosa* (D. Don) Less., Linnaea 6:627 (1831).

*Vernonia rigida* Wall., Numer. List [Wall-ich] n. 2925, comp. 35, nom. nud.

*Vernonia teres* Wall., Numer. List [Wall-ich] n. 2926, comp. 36, nom. nud.

*Vernonia rigiophylla* DC., Prodr. 5:15 (1936).

*Vernonia teres* Wall. ex DC., Prodr. 5:15 (1836).

The species has the pappus bristles broader at the tips than in other members of the genus.

*Acilepis sutepensis* (Kerr) H. Rob. & Skvarla, comb. nov.

*Vernonia sutepensis* Kerr., Bull. Misc. Inform. Kew 1935:329 (1935).

*Acilepis thwaitesii* (C. B. Clarke) H. Rob. & Skvarla, comb. nov.

*Vernonia thwaitesii* C. B. Clarke, Compos. Ind. 11 (1876).

*Vernonia gardneri* var. *nervosa* Thwaites, Enum. Pl. Zeyl. (Thwaites) 161 (1860).

*Acilepis tonkinensis* (Gagnep.) H. Rob. & Skvarla, comb. nov.

*Vernonia tonkinensis* Gagnep., Bull. Mus. Hist. Nat. (Paris) 25:492 (1919).

*Acilepis virgata* (Gagnep.) H. Rob. & Skvarla, comb. nov.

*Vernonia virgata* Gagnep., Bull. Mus. Hist. Nat. (Paris) 25:493 (1919).

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