

A NEW FLAGELLIFLOUS SPECIES OF *STENANONA* (ANNONACEAE) FROM MEXICO, WITH A REVIEW OF THE PHENOMENON OF FLAGELLIFLORY

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Abstract: *Stenanona flagelliflora* is described as a new species of small, flagelliflorous tree from deep-soil hill rain forests of the Uxpanapa-Chimalapa region of the Isthmus of Tehuantepec, in Veracruz and Oaxaca, Mexico. In flagelliflory, flowers are borne on essentially leafless modified whip-like branches that trail across the ground; this is the first report of the phenomenon for the flora of Mexico or Central America. The phenomenon of flagelliflory and its worldwide occurrence are reviewed. The Central American genus *Stenanona* is not closely related to other New World annonaceous genera with flagelliflorous species but rather is likely most closely related to the Old World species of *Polyalthia* with superficially inaperturate but internally disulculate pollen. The distribution of *S. flagelliflora* and of its closest relatives, as well as the existence of flagelliflory in Mexican rain forest, provide additional data supporting the persistence of rain forest lineages in Mexico throughout climatically adverse periods of the late Cenozoic. The new species is considered to be Critically Endangered (CR) under the IUCN Red List classification.

Resumen: Se describe *Stenanona flagelliflora* como una especie nueva de arbolito flagelifloro de las selvas de lomerío de la región de Uxpanapa-Chimalapa del Istmo de Tehuantepec en los estados de Veracruz y Oaxaca, México. En el fenómeno de la flagelifloría, las flores, o las inflorescencias nacen de ramitas largas, delgadas y flexibles, más o menos afilas, y rasteras sobre el suelo. En este trabajo se presenta el primer reporte del fenómeno de flagelifloría en la flora de México. Se hace una reseña de la flagelifloría a nivel mundial. *Stenanona*, un género centroamericano, no está muy emparentado con los otros géneros americanos de anonáceas con especies flagelifloras; más bien parece probable que sus relaciones sean más estrechas con un grupo de especies de *Polyalthia* del Viejo Mundo con polen externamente no aperturado e internamente bisulculado. La distribución de *S. flagelliflora* y las de sus congéneres más cercanos, junto con la presencia de flagelifloría en las selvas de México, apoyan a la hipótesis de la persistencia de estirpes selváticas en México a través de periodos climáticos adversos del Cenozoico tardío. La especie nueva se considera en la categoría de "en peligro crítico" (CR) según los criterios de la UICN.

Keywords: Annonaceae, Chimalapa, flagelliflory, flora of Mexico, *Polyalthia*, *Stenanona*, Uxpanapa.

Among the various forms of cauliflory, that known as flagelliflory, in which flowers (usually some shade of reddish) are borne on long whip-like shoots that emerge from the main trunk and then lie upon the soil surface or slightly buried under the leaf litter, is both the most rare and the most spectacular type. Despite contact with the soil, usually no adventitious roots are formed, the shoots functioning purely in a

reproductive capacity. This phenomenon was first made known to the botanical world by Beccari in 1871 in describing the annonaceous species *Unona flagellaris* Becc. (= *Polyalthia flagellaris* (Becc.) Airy Shaw) from Borneo and Sarawak (Beccari, 1871; Airy Shaw, 1939). Flagelliflory has since been documented primarily for a handful of species of Annonaceae in all three major rain forest regions of the World, but it is

also represented by remarkable convergences in species of Achariaceae in Africa, Bignoniaceae in Madagascar, and Rutaceae in the Neotropics. We describe here a new flagelliflorous species of Annonaceae from Mexico in the genus *Stenanona* Standl., unrelated to any of the other known Neotropical flagelliflorous species of Annonaceae. This represents the first report of flagelliflory in the Mexican flora, and indeed the phenomenon has not previously been reported from north of South America.

THE PHENOMENON OF FLAGELLIFLORY

After witnessing cauliflory in its many variations firsthand in Africa, Mildbraed (1922) developed the following terminology (in German) to distinguish among the different types he had observed. "Ramiflory" refers to flowers borne on the leafless portions of small to large branches, whereas "trunciflory" indicates that flowers are borne on the main trunk. He further distinguished "basiflory" as the production of flowers only at the base of the trunk, with the flowers and/or inflorescences either sessile on the trunk or less often borne on perennating brachyblasts. There may also be an elongation of the axis bearing the flowers, in which case Mildbraed applied the term "idiocladanthly," as epitomized by *Couroupita guianensis* Aubl. (Lecythidaceae). Flagelliflory could arise as a further extension of idiocladanthly, with the pendulous flower-bearing axis elongating to the point where it reaches the ground, upon which it continues along the surface horizontally. Mildbraed (1920) had earlier discussed and illustrated flagelliflory in his description of *Paraphyadanthé flagelliflora* (= *Caloncoba flagelliflora* (Mildbr.) Sleumer; Achariaceae, formerly Flacourtiaceae) from Cameroon, Congo, Gabon, and Zaire. He referred to the flowering axes as "Ausläufer," or runners, these emerging from the trunk as high as 30 cm above ground and reaching up to 11.8 m in length. He initially

used the term "Rhizanthie" to describe the phenomenon, but two years later rejected it in favor of "flagelliflory" because of the misleading connotation of roots and rooting associated with the former term. It should be noted that a few recent works, such as Balgooy (1997) and Smith et al. (2004), define "flagelliflory" as essentially synonymous with what Mildbraed (1922) and many others term "penduliflory," in which flowers are borne "mid-air" on long pendulous stalks (e.g., *Parkia*, Fabaceae), an inflorescence position often associated with bat pollination. We follow the more traditional terminology, as did for instance Richards (1952) in his classic *The Tropical Rain Forest*.

That there is potentially a progressive series from idiocladanthly to flagelliflory is illustrated by *Hornschurchia* (Annonaceae, tribe Bocageae), a genus of 10 species restricted to the Atlantic coastal forests of eastern and southeastern Brazil (Johnson and Murray, 1995). Among the cauliflorous species, *H. cauliflora* Maas & Setten bears flowers on 0.3–1.3 cm high "knobs" along the trunk (trunciflory); inflorescence axes of *H. leptandra* D. M. Johnson, also arising from the trunk, are (1.5–)5–20 cm long (idiocladanthly); whereas the trunk-borne inflorescence axes of *H. bryotrophe* Nees are sufficiently long (12–63 cm) as to lie on the ground covered by leaf litter (flagelliflory). Inflorescence position in *H. polyantha* Maas is variable, with flowers borne both on flagelliform branches 16–65 cm long and on leaf-opposed inflorescences 2.4–6 cm long. Similar variation in inflorescence position is exhibited by *Erythrochiton fallax* Kallunki (Rutaceae) from Bolivia, Colombia, and Peru (Kallunki, 1992).

In their revision of *Duguetia* sect. *Geanthemum*, which comprises three flagelliflorous species in South America, Maas et al. (1993) further distinguish between two types of flagelliform branches (runners): 1) those that are sympodial branches, consisting of successive lateral shoots each terminating in a rhipidium (the basic inflores-

cence characteristic of Annonaceae; Fries, 1919, 1949), as exhibited by both *D. sessilis* (Velloso) Maas and *D. flagellaris* Huber; and 2) runners formed by the elongation of a single rhipidium, as exhibited by *D. cadaverica* Huber. The flagelliform inflorescence branches of *Hornschuchia* species appear to be elongated rhipidia, as do the flagelliform inflorescences of *Anaxagorea floribunda* Timmerman (Annonaceae) from Colombia and Peru. Similarly, both the previously mentioned *Polyalthia flagellaris*, known from peninsular Malaysia, Sarawak, and Borneo, and the African *Isolona cauliflora* Verdc. (Annonaceae), known from Kenya and Tanzania, also appear to exhibit elongated rhipidia. On the other hand, both *Caloncoba flagelliflora* and the Southeast Asian *Polyalthia hypogaea* King, known from peninsular Malaysia, Sarawak, and Borneo, as well as the new species of *Stenanona* described here, all exhibit sympodial runners. *Goniiothalamus majestatis* P. Kessler (Annonaceae), described in 1996 from Sulawesi (Kessler, 1996), also appears to produce sympodial runners. Branching occurs in both types of flagella, presumably from auxiliary buds in the case of the elongated rhipidia (the rhipidia themselves being determinate).

Although the flagelliform branches usually function solely in a reproductive capacity, reduced leaves are sometimes produced at nodes along the sympodial runners, and those of *Isolona cauliflora* have been reported to form roots. The new species occasionally produces relatively large leaves near the flagellum apex. In a species of *Colea* (Bignoniaceae) in Madagascar, flagelliform inflorescence branches also function in clonal vegetative growth, rooting at their apex following flowering, and then giving rise to a new vegetative shoot (Schatz, pers. obs.). The potential clonal role of flagelliform shoots is especially intriguing in the context of the new flagelliflorous *Stenanona* described below, as its closest relatives appear to be two clonal species (*Stenanona humilis* (Miranda) G. E.

Schatz and an undescribed species [Schatz, in press]) that reproduce vegetatively by short runners.

A NEW FLAGELLIFLOUS SPECIES FROM MEXICO

Stenanona flagelliflora T. Wendt & G. E. Schatz, sp. nov. (Figs. 1–3).

TYPE: MEXICO. VERACRUZ: Mpio. Hidalgotitlán [now Mpio. Uxpanapa]. Afluente O del Río Cuevas, ca. 5 horas a pie al S de La Laguna, 17°14'N, 94°31'W, 350 m, 16 Apr 1982 (fl, immature fr), T. Wendt, M. Vázquez, A. Méndez, I. Navarrete & A. García M. 3851 (HOLOTYPE: MEXU!; ISOTYPES: CHAPA!, MO!, WIS!).

Arbor parva 1–4.5-metralis, a specibus aliis *Stenanonae* inflorescentiis flagellaribus et petalis liberis non aristatis differt.

Small TREE 1–4.5 m tall. TRUNK to 5 cm d.b.h. BRANCHES dark brown (drying nearly black) when young, at first finely sericeous with distally directed ascending pale golden hairs mostly 0.2–0.5 mm long, quickly weathering to moderately strigillose, the vegetative buds densely pale-golden pilosulous. LEAF BLADES membranaceous, bright medium glossy green above and paler beneath when fresh, reddish-brown when young, elliptic, to 9–18 cm long and 2.6–6.5 cm wide, 2.2–4.0 times as long as wide, the apex acuminate to abruptly caudate, the acumen mostly 0.8–3.0 cm long and broadly to minutely rounded at the tip, the base acute to cuneate, obviously to minutely rounded at the point of petiole attachment; VENATION brochidodromous, weakly so in the basal portion, with 6–10 lateral veins per side (excluding the acumen), these arising at 60–80° from midrib in distal half of blade, the angle narrower baseward, the tertiary venation subscalariform to reticulate, the finer venation reticulate, the midvein adaxially slightly impressed basally and distally ± plane, abaxially prominently raised,

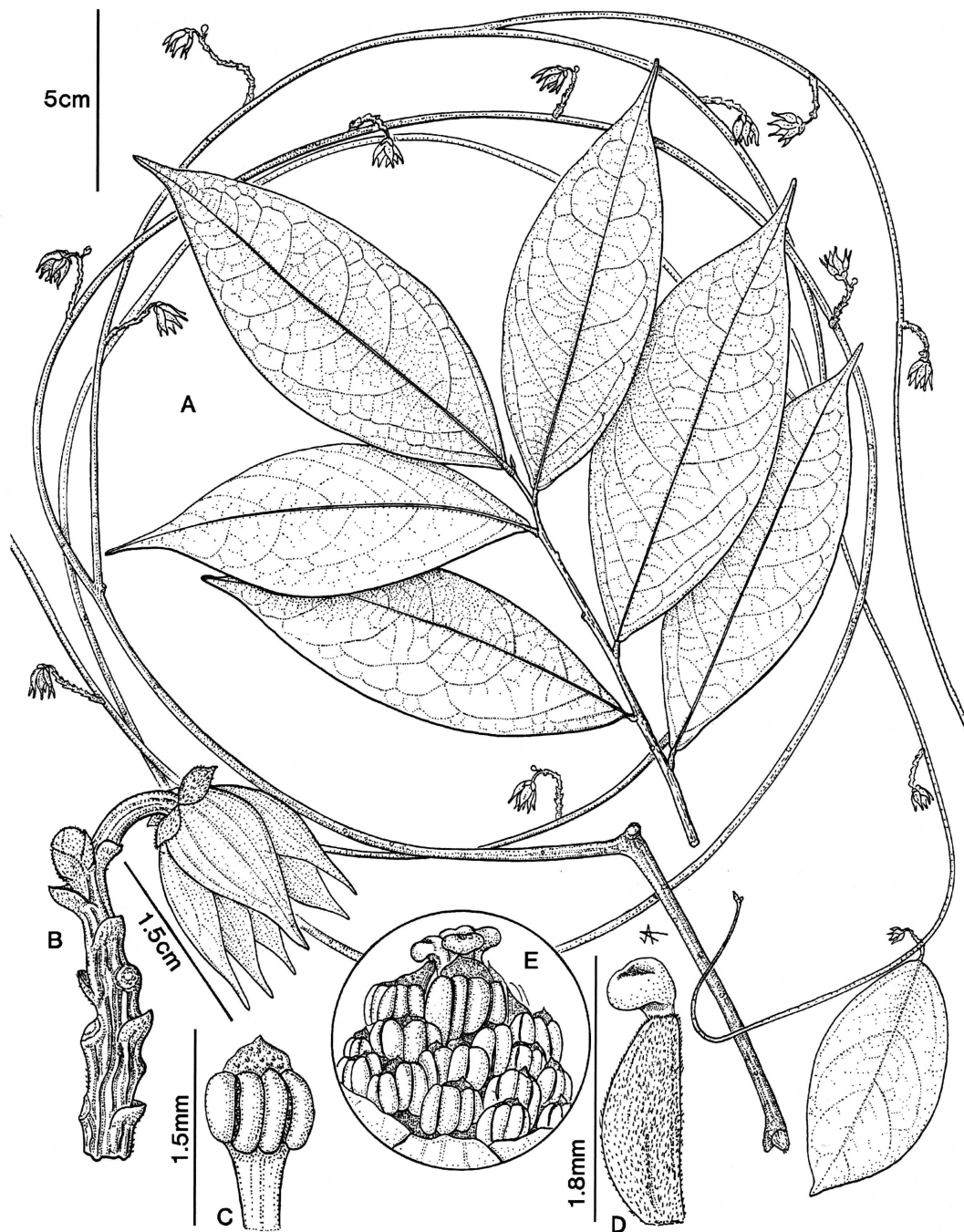


FIG. 1. *Stenanona flagelliflora*. A. Leafy branchlet and flagelliferous branch. B. Rhipidium with anthetic flower. C. Stamen. D. Carpel. E. Androecium surrounding and mostly hiding (except for stigmas) the gynoecium. All drawn from type collection by John Myers.



FIG. 2. *Stenanona flagelliflora*. A. Leaves from sterile upper branches. B. Lower part of trunk, showing flagelliflorous branchlets arising in lower m and drooping to ground, these then coiled on ground by collector to demonstrate length (with Heriberto Hernández G.) C. Rhipidium with late season (October) flower, this apparently not opening further. D. Monocarps. A, B and D from Wendt *et al.* 6686 (photos T. Wendt); C from Ishiki & Rainer 2313 (photo H. Rainer).

the lateral veins slightly raised adaxially and more strongly so abaxially, the finer venation \pm plane adaxially, slightly raised abaxially; VESTITURE of the upper surface lack-

ing except for midrib and extreme bases of lateral veins, these densely beset with erect stout short hairs ca. 0.1 mm long that impart a somewhat scurfy appearance, the

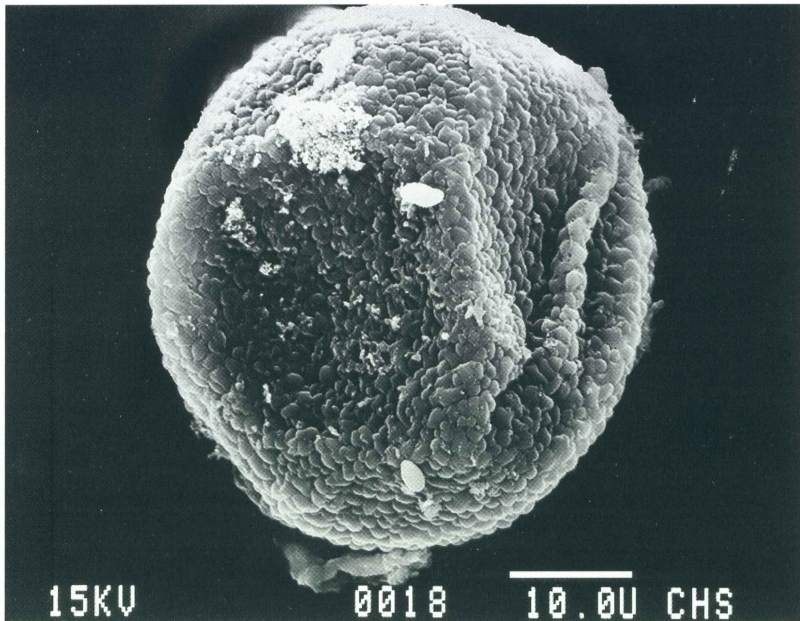


FIG. 3. SEM image of pollen grain of *Stenanona flagelliflora* (type collection, photo G. Schatz.)

lower surface with midrib and larger venation moderately to sparsely beset with hairs like those of branchlets, otherwise glabrate or with very scattered such hairs and usually with numerous minute orange (when dry) pellucid dots. PETIOLES 2–6 mm long, distinctly swollen (and narrowing abruptly to midrib just above blade attachment), 1–2.5 mm thick, canaliculate, with vestiture like that of the branchlets or glabrate. INFLORESCENCES on specialized flagelliflorous branches to >3 m long, these branches arising from the lower 1 m of the trunk and drooping immediately to ground, thence creeping through duff or superficially or pendulous over rocks, frequently branching, sometimes with a few leaves distally, bearing rhipidia typically every 3–12 cm in the distal portions; RHIPIDIA arising sympodially (terminal but appearing lateral), opposite or subopposite a scale or soon-deciduous reduced leaf, the leaf/scale scar usually slightly distal to the inflorescence insertion; PEDUNCLE (the bractless and flowerless basal portion of rhipidium) to 3 cm but generally much reduced or lacking; FERTILE AXIS to 5 (–9) cm long, often much shorter,

eventually bearing up to 20(–40) flowers but only 1(2) at a time, older inflorescences thus with a long bracteose axis and 1(2) flowers distally, the flowers arising opposite bracts (inflorescence sympodial), the internodes short, 1–2 mm; BRACTS triangular to at length broadly and bluntly triangular (due to thickening of inflorescence axis), 1–2 mm long; PEDICELS 4–7 mm long in flower, to >10 mm in fruit, minutely strigillose, bearing a minute bracteole in the lower one-third. FLOWERS nodding (all measurements refer to liquid-preserved or rehydrated material); SEPALs 3, each one oval-ovate, 2.8–3.6 mm long, 1.5–2.2 mm broad, acute to narrowly rounded at apex, strigillose and ciliate abaxially, glabrous adaxially, at anthesis either strongly re-trorsely oriented with its apex strongly reflexed toward the pedicel, or spreading more or less at a 90 degree angle to the pedicel with its apex not reflexed, concave in profile and cupping the base of the adjacent inner petal, thus cucullate, drying light tan and contrasting markedly with the dark petals; PETALS 6, free, in 2 moderately differentiated series, dark salmon-red to

purple-red; OUTER PETALS each with a thick, fleshy, retrorsely directed basal claw that distally abruptly curves nearly 180° into the antrorsely directed blade, the blade narrowly triangular-ovate from a rounded base, 13–14 mm long, 5–6 mm wide, fleshy, abaxially strigillose distally and in the center proximally, apically acuminate to a finely rounded tip, with 3–7 faint longitudinal veins sometimes discernable abaxially in dried material; INNER PETALS with same general form as outer petals, differing in the shape of the claws, which extend laterally into broadly and deeply concave, pouch-like bases, in the shape and size of the blades, which are more broadly triangular-ovate, 12.5–13 mm long, and 6–7 mm wide, and in the blade vestiture, which is restricted to the distal portion; STAMENS ca. 35, variable in size and form, 1.2–2.6 mm long, the filaments 0.2–1.7 mm long, fleshy, the inner longer than the outer, the anther thecae 0.6–1.0 mm long, the connective either barely developed or (especially in distal [interior] stamens) prolonged into a horizontal to nearly vertical, deltoid, tuberculate appendage up to 0.6 mm long; POLLEN solitary, apolar, radiosymmetric, globose, 42–45 μ diam., inaperturate, the exine surface verrucate; CARPELS 6, each ovary prismatic-ellipsoid, 1.5 mm long, sparsely short setaceous, each stigma globose, 0.3 mm diam., the ovule solitary. Mature MONOCARPS (fruit segments) obliquely ellipsoid (flatter in outline on the side toward floral axis), short-stipitate to nearly sessile, with 1–3 typically maturing per flower, when dry 15–21 mm long and 7–8 mm thick, the surface glabrous, orange-red, the fruit wall ca. 2 mm thick, yellow. SEED solitary, covered with remnants of the fruit wall, rugose; TESTA thin, light brown; ENDOSPERM ruminant.

PHENOLOGY: Collected with abundant flower in April; in fruit with very few more or less closed flowers (Fig. 2C) in August and October. The leaves are evergreen; young flushing leaves were noted in April.

DISTRIBUTION AND HABITAT: Very locally common at 200–350 m elevation, in evergreen rain forest on hills with deep soils (“hill forest” or *selva de lomerío*, see Wendt, 1997) in the southern part of the Uxpanapa region of extreme southern Veracruz and the adjacent part of the Chimalapa region of eastern Oaxaca, on the Gulf slope of the Isthmus of Tehuantepec. The new species appears to prefer very mesic canyon bottoms and lower slopes, where associated canopy trees include *Dialium guianense* (Aubl.) Sandwith, *Guatteria anomala* R. E. Fr., *Guarea grandifolia* DC., *Virola guatemalensis* (Hemsl.) Warb., *Warszewiczia uxpanapensis* (Lorence) C. M. Taylor, *Terminalia amazonia* (J. F. Gmel.) Exell, *Poulsenia armata* (Miq.) Standl., *Sterculia xolocotzii* T. Wendt & E. L. Taylor, *Dussia mexicana* (Standl.) Harms, *Tapirira chimalapana* T. Wendt & J. D. Mitch., diverse Lauraceae, and many others.

CONSERVATION ASSESSMENT: Following the IUCN (The World Conservation Union) Red List guidelines (IUCN, 2001), it seems likely that *Stenanona flagelliflora* meets the criteria for a Critically Endangered (CR) species, although clearly there are many unknowns concerning its population parameters. Within the Uxpanapa-Chimalapa rain forests, the species is restricted to a small area of high-precipitation, deep-soil forests at the northern foot of the Sierra de Tres Picos at 200–350 m elevation. The known Extent of Occurrence (EO) is 60 km²; total potential EO is probably no more than double that figure, with 100 km² a reasonable estimate, based on topographical, climatological, and substrate considerations. The Area of Occupancy (AO) within the EO is probably no more than 5%, given the restricted nature of the habitat on the floors and lower slopes of certain steep-sided valleys of small creeks; AO is thus rather generously estimated at 5 km². There are 4 known subpopulations (3 represented by the cited collections). The area is under intense settlement pressure, especially on the Veracruz side of the state

line, and, in addition, escaped fires in dry years such as 1998 have burned significant areas with potentially appropriate habitat. We therefore anticipate a dramatic loss of habitat for the species in the next two decades (approximately three generations), and thus feel that it qualifies as Critically Endangered [CR A3c+4ac;B1ab(i,ii)+2ab(i,ii)].

ADDITIONAL SPECIMENS EXAMINED: MEXICO.

OAXACA. Mpio. Sta. María Chimalapa: Parte superior del Arroyo Garrobo, ca. 5 km en línea recta al SE de Rancho Alegre, Ver. (ca. 15 km en línea recta al SSE de La Laguna, Ver.), en las faldas N de la Sa. de Tres Picos, 17°08'55"N, 94°28'21"O, 210–260 m, 16 Aug 1995 (fr, scarce fl), *T. Wendt et al.* 6686 (CHAPA, MEXU, MO, NY, TEX), 7 Apr 1996 (fl), *T. Wendt et al.* 6842 (CHAPA, MEXU, TEX, MO), 17 Apr 1995 (fl), *T. Wendt et al.* 6882 (MEXU). **VERACRUZ. Mpio. Uxpanapa:** Lomería al S del Poblado Dos, por el camino a La Paz, ca. 5–6 km por camino y brecha al S de la terracería Sarabia-Uxpanapa, 17°11'30"N, 94°38'39"O, 230 m, 28 Oct 1998 (fr, scarce fl), *M. Ishiki & H. Rainer* 2313 (ECOSUR, WU), 2314 (ECOSUR, WU). [ECOSUR = herbarium of the Colegio de la Frontera Sur, San Cristobal, Chiapas, Mexico.]

The new species is clearly not closely related to any of the other Neotropical flagelliflorous Annonaceae, exhibiting none of the following diagnostic characters of their genera. *Anaxagorea* has been definitively established as basal within the family, and is characterized by its laminar stamens, inner staminodes, granular monosulcate pollen, and dry, explosively dehiscent monocarps (Doyle et al., 2000; Maas et al., 1984). *Duguetia* possesses stellate and/or lepidote indumentum and pseudosyncarpus fruits (Maas et al. 2003). *Hornschuchia* has septate anthers, with pollen borne in polyads of 8 or 16, and dehiscent monocarps, each seed bearing a fibrous caruncle (Johnson and Murray, 1995). The new species can be placed in *Stenanona* on the basis of its: simple indumentum; brochidodromous leaf venation; distinctly swollen petiole with the leaf base rounded at the point of attachment with the petiole; valvate sepals that dry light tan in contrast to the dark petals; moderately fleshy petals that often exhibit

longitudinal venation when dry; stamens with the apical connective prolonged into a deltoid appendage; globose, inaperturate pollen (Fig. 3); and seeds with a crustaceous, rugose seed coat covered with remnants of the endocarp (Schatz, 1987, in press). *Stenanona* is a genus of 13 species distributed from Veracruz, Mexico, to western Colombia (Schatz, in press). The new species is anomalous within the genus not only in its flagelliflorous nature, but also in lacking the long, drawn-out petal-apex tapering to an aristate tip that is characteristic of all other species. This is presumably a phylogenetic loss related to the position of flowers at or near the surface of the ground. Within *Stenanona*, *S. flagelliflora* appears to be most closely related to *S. humilis* and a related undescribed species with which it shares free, somewhat differentiated petal whorls (the general shape of these very similar with the exception of the drawn-out apex of the latter two) and a single ovule per carpel. It is tempting also to speculate on the possible homologous nature of the reproductive, inflorescence-bearing flagella in the new species and the vegetative stolons that give rise clonally to new ramets in the two related species, as previously noted.

In a broader sense, *Stenanona flagelliflora* and the genus *Stenanona* in general appear to be far more closely related to a group of Old World (especially Southeast Asian) species currently referred to the genus *Polyalthia*—which includes flagelliflorous species—than to any of the New World flagelliflorous annonaceous species noted above. Combined morphological and molecular phylogenetic analyses strongly suggest that *Polyalthia* as currently circumscribed is polyphyletic (Doyle et al., 2000). A group within *Polyalthia* has been identified with superficially inaperturate globose pollen that nevertheless exhibits two areas of intine thickening that correspond to germination zones (Waha and Hesse, 1988). This "*Polyalthia* disulcate" group falls within the *Miliusa* clade (Doyle et al., 2000), which also includes *Sapranthus*

(Central America) and *Ancana* (Australia), both of which have been hypothesized as being allied to *Stenanona* (van Heusden, 1992; van Setten and Koek-Noorman, 1992). Overall floral morphology of *Stenanona* remarkably resembles a number of *Polyalthia* species, including *P. stenopetala* Ridl., *P. cinnamomea* Hook. f. & Thomson, and *P. angustissima* Ridl. (Sinclair, 1955), the latter of which was cited by Waha and Hesse (1988) as among the disulcate species. According to Heimo Rainer (personal communication), transmission electron microscopy of pollen of *S. flagelliflora* (and of an additional species of *Stenanona*) reveals the characteristic intine structure of the "*Polyalthia* disulcate" group. Evidence is thus strong that the relationship of *Stenanona* is with this Southeast-Asian-centered group. The essentially Central American distribution of the genus is common (but by no means universal, see Davis et al., 2002) in New World rain forest genera thought to demonstrate this type of boreotropical relationship (Wendt, 1993). More in-depth molecular studies on *Stenanona*, *Polyalthia*, and related genera are needed on this point. Within this context it is nevertheless interesting to note that, based on floral morphology, the flagelliflorous species *P. flagellaris* and *P. hypogea* likely fall within the "*Polyalthia* disulcate" group, and that these Southeast Asian species may well be the closest relatives to share this unusual trait with *S. flagelliflora*.

The new species is biogeographically interesting in several other respects. It represents yet another new species from the rain forests of the Isthmus of Tehuantepec (the Uxpanapa-Chimalapa region; see Wendt, 1997). This area has yielded numerous species new to science and apparently endemic (summarized in part in Wendt, 1989, 1993, 1997). The wetter areas of rain forest of the region (Uxpanapa and portions of Chimalapa) form the western terminus of a crescent-shaped lowland area of high precipitation (averaging over 3000 mm/year) that stretches eastward through extreme south-

ern Tabasco and northern Chiapas to northeastern Chiapas (the "crescent area" or *el área del arco* of Wendt, 1989). This area has been proposed as a region in which rain forest plant lineages persisted during adverse climatic periods of the later Cenozoic (a "floristic refuge;" Wendt, 1989). Elevated endemism is one criterion used in supporting this argument. While a new species apparently endemic to the area is useful evidence, two more facts are even more notable. First, the entire 3-species complex of related species comprising *Stenanona flagelliflora*, *S. humilis*, and the undescribed species is endemic to the crescent area, with the last restricted to essentially the same range as *S. flagelliflora* and *S. humilis* occurring allopatrically on karst habitats from northern Uxpanapa to northern Chiapas (Schatz, in press). Second, at a worldwide level the phenomenon of flagelliflory is restricted to lowland rain forests. It is unclear how long such an adaptation would take to evolve in a small tree lineage, but it seems unlikely that it has developed in *Stenanona* since the end of the Pleistocene, 10,000 years ago. This reinforces the hypothesis that rain forest habitat persisted in at least some parts of the crescent area during the Pleistocene. The fact that a second flagelliflorous species of Annonaceae also occurs in the Uxpanapa-Chimalapa area (Schatz, Wendt, and Rainer, in prep.), one that is clearly not sister to *Stenanona flagelliflora*, only bolsters this argument. Obviously, molecularly-supported and dated phylogenies in these groups would provide fascinating insight into the problem.

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LITERATURE CITED

- Airy Shaw, H. K. 1939. Additions to the flora of Borneo and other Malay islands. XII. Annonaceae of the Oxford University Expedition to Sarawak, 1932. *Bull. Misc. Inform.* 1939: 275–290.
- Balgooy, M. M. J. van. 1997. *Malesian Seed Plants. Volume 1—Spot-characters. An Aid for Identification of Families and Genera*. Leiden: Rijksherbarium/Hortus Botanicus.
- Beccari, O. 1871. Illustrazione di nuove o rare specie di piante Bornensi—Anonaceae. *Nuovo Giorn. Bot. Ital.* 3: 177–193.
- Davis, C. C., C. D. Bell, S. Mathews, and M. Donoghue. 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proc. Natl. Acad. Sci. U.S.A.* 99: 6833–6837.
- Doyle, J. A., P. Bygrave, and A. Le Thomas. 2000. Implications of molecular data for pollen evolution in Annonaceae. Pp. 259–284 in *Pollen and Spores: Morphology and Biology*, eds. M. M. Harley, C. M. Morton, and S. Blackmore. Kew: Royal Botanic Gardens.
- Fries, R. E. 1919. Studien über die Blütenverhältnisse bei der Familie Anonaceae. *Acta Horti Berg.* 6(6): 3–48.
- . 1949. Sobre la caulifloría en la familia de las Anonáceas. *Lilloa* 16: 251–261.
- IUCN. 2001. *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland, and Cambridge, U.K.: ICUN Species Survival Commission.
- Johnson, D. M., and N. A. Murray. 1995. Synopsis of the tribe Bocageae (Annonaceae), with revisions of *Cardiopetalum*, *Froesiodendron*, *Trigynaea*, *Bocagea*, and *Hornschurchia*. *Brittonia* 47: 248–319.
- Kallunki, J. A. 1992. A revision of *Erythrochiton sensu lato* (Cuspariinae, Rutaceae). *Brittonia* 44: 107–139.
- Kessler, P. 1996. *Goniotalamus majestatis*, a new species of Annonaceae from Sulawesi, Indonesia. *Blumea* 41: 27–28.
- Maas, P. J. M., and L. Y. Th. Westra. 1984/1985. Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A. St. Hil. *Bot. Jahrb. Syst.* 105: 73–34; 145–204.
- , L. Y. Th. Westra, N. A. J. Meijdam, and I. A. V. van Tol. 1993. Studies in Annonaceae. XV. A taxonomic revision of *Duguetia* A. F. C. P. de Saint-Hilaire sect. *Geanthemum* (R. E. Fries) R. E. Fries (Annonaceae). *Bol. Mus. Paraense Emilio Goeldi, N. S., Bot.* 9(1): 31–58.
- , L. Y. Th. Westra, L. W. Chatrou, & collaborators. 2003. *Duguetia* (Annonaceae). *Fl. Neotrop. Monogr.* 88: 1–274.
- Mildbraed, J. 1920. *Paraphyadanthé* Mildbr. nov. gen. Flacourt. Ein interessanter Fall von “Rhizanthie” aus Kamerun. *Notizbl. Bot. Gart. Berlin-Dahlem* 7: 399–405.
- . 1922. *Wissenschaftliche Ergebnisse der zweiten deutschen Zentral-Afrika-Expedition, 1910–1911, unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg*. Leipzig: Verlag von Klinkhardt & Biermann.
- Richards, P. W. 1952. *The Tropical Rain Forest. An Ecological Study*. Cambridge: Cambridge University Press.
- Schatz, G. E. 1987. Systematic and ecological studies of Central American Annonaceae. Ph.D. dissertation. Madison: University of Wisconsin.
- . in press. Synoptic revision of *Stenanona* Standl. (Annonaceae). *Novon*.
- Smith, N., S. A. Mori, A. Henderson, D. W. Stevenson, and S. V. Heald. 2004. *Flowering Plants of the Neotropics*. Princeton: Princeton University Press.
- Sinclair, J. 1955. A revision of the Malayan Annonaceae. *Gard. Bull. Singapore* 14: 149–516.
- van Heusden, E. C. H. 1992. Flowers of Annonaceae: Morphology, classification and evolution. *Blumea*, suppl. 7: 1–218.
- van Setten, A. K., and J. Koek-Noorman. 1992. Fruits and seeds of Annonaceae. Morphology and its significance for classification and identification. *Biblioth. Bot.* 142: 1–101.
- Waha, M. & M. Hesse. 1988. Aperture types within

- Sapranthus* and *Polyalthia* (Annonaceae). *Pl. Syst. Evol.* 161: 135–146.
- Wendt, T.** 1989. Las selvas de Uxpanapa, Veracruz-Oaxaca, Mexico: evidencia de refugios florísticos cenozoicos. *Anales Inst. Biol. Univ. Nac. Autón. México, Bot.* 58: 29–54.
- . 1993. Composition, floristic affinities, and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. Pp. 595–680 in *Biological diversity of Mexico: origins and distribution*, eds. T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa. New York: Oxford University Press.
- . 1997. Uxpanapa-Chimalapa Region, Mexico. Pp. 130–134 in *Centres of Plant Diversity. A Guide and Strategy for their Conservation. Vol. 3. The Americas*, eds. S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-lobos, and A. C. Hamilton. Cambridge, U.K.: IUCN Publications Unit.