Rubiacearum Americanarum Magna Hama Pars IV: New Taxa and Combinations in *Elaeagia* and *Warszewiczia* (Rondeletieae) from Mexico, Central America, and Colombia

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ABSTRACT. The new species *Elaeagia chiriquina* of western Panama and *E. glossostipula* of western Panama and adjacent eastern Costa Rica, described and illustrated here, have been confused with several species of *Elaeagia*, but can be distinguished by details of the stipules, calyx, and corolla. *Elaeagia uxpanapensis* Lorence of Oaxaca, Mexico, is here transferred to *Warszewiczia* based on details of its flower and fruit morphology. This species is also represented by populations disjunct in Costa Rica and northwestern Colombia; these southern populations differ in their larger fruits, and are here separated as *W. uxpanapensis* subsp. *meridionalis*.

RESUMEN. Las especies nuevas *Elaeagia chiriquina* del oeste de Panamá y *E. glossostipula* del oeste de Panamá y el este adyacente de Costa Rica, que se describen e ilustran aquí, se han confundido con varias especies de *Elaeagia*, pero se distinguen por detalles de las estípulas, cáliz y corola. *Elaeagia uxpanapensis* Lorence de Oaxaca, México, aquí se transfiere a *Warszewiczia* basado en detalles de la morfología de las flores y los frutos. Esta especie se encuentra en poblaciones disjuntas en Costa Rica y el noroeste de Colombia; estas poblaciones sureñas se distinguen por los frutos más grandes, y aquí se separan en *W. uxpanapensis* subsp. *meridionalis*.

Key words: Central America, Colombia, *Elaeagia*, Mexico, Neotropics, Rondeletieae, Rubiaceae, *Warszewiczia*.

The neotropical genus *Elaeagia* Weddell (Rondeletieae; Robbrecht, 1993) comprises about 15 species of small to medium-sized trees that grow in regions of wet climate, usually at middle elevations (500–1500 m), from Central America to Venezuela and Bolivia. This genus has not been treated taxonomically as a whole in this century, although Steyermark (1964) provided a summary of the species of northern South America. *Elaeagia* is characterized by its distinctive stipules (see below); its terminal, cymose to paniculate inflorescences that typically are ebracteate or have reduced bracts; its flowers that are homostylous, protrandrous, and diurnal; its calyx limbs that are truncate or sinuate to five-lobed; its campanulate to tubular corollas with their tubes usually shorter than the five lobes, which are convolute to subvalvate (Taylor & Hammel, 1993) in aestivation; its stamens exserted on well-developed filaments that are typically densely pubescent in their lower portions, with this pubescence making the corolla appear barbate in the throat; its two or rarely three linear stigmas; its woody, subglobose to ellipsoidal, capsular fruits that are loculicidal through their tops, usually opening only in the part distal to the insertion of the calyx limb; and its numerous small, angled seeds. In some species, the dehiscent apical portion of the capsule elongates during development to form a beak similar to that of the capsules of some species of *Hedyotis* L., so the fruits appear only partially inferior (Fig. 1E).

The stipules of *Elaeagia* are unusual: on young buds they are complanate and oriented perpendicular to the line formed by the petioles of the subtending leaves, in contrast to the most common stipule arrangement in the Rubiaceae, in which the stipules are oriented parallel to the subtending petioles. In *Elaeagia* the stipules initially are coherent or fused in a completely closed structure (Fig. 1C), and as the leaves emerge this structure splits into two *intra*petiolar portions (Fig. 1H); this condition also contrasts with the most common stipule arrangement in the Rubiaceae, which is to have the stipules *inter*petiolar or separating into two *inter*petiolar portions. (Among neotropical Rubiaceae, only *Capirona* Spruce of the Amazon basin has a stipule arrangement similar to that of *Elaeagia*, with the young stipules of *Capirona* also fused into a closed structure that splits into two interpetiolar portions.) There are two distinct stipule forms within *Elaeagia*: in some species [e.g., *E. myriantha* (Standley) C. M. Taylor & Hammel, *E. nitidifolia* Dwyer, *E. pastoense* Mora] the two stipules are usu-

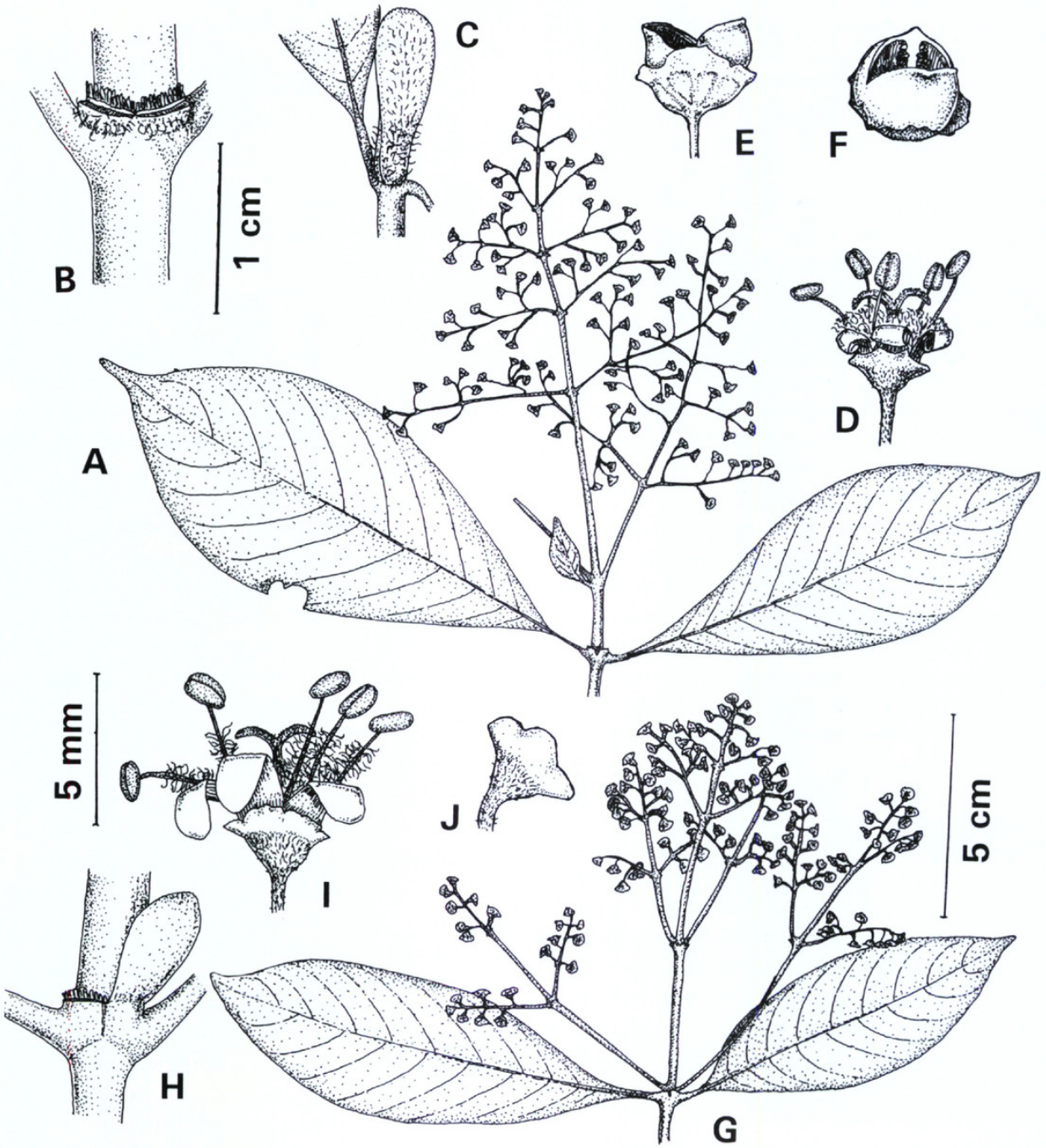

Figure 1. A–F, *Elaeagia glossostipula* C. M. Taylor. —A. Flowering branch. —B. Stem node after stipule limb has fallen. —C. Stem apex with stipule limb still attached. —D. Flower at anthesis. —E. Capsule, side view. —F. Capsule, oblique top view. G–J, *Elaeagia chiriquina* C. M. Taylor. —G. Flowering branch. —H. Stem node with stipule limb partially fallen. —I. Flower at anthesis. —J. Flower after corolla and style have fallen, showing variation in shape of the calyx limb lobing. A, G to 5-cm scale; B, C to 1-cm scale; all others to 5-mm scale. A, based on *McPherson 13557*; B, D, based on *McPherson & Aranda 10075*; C, E, F, based on *Santamaría & Lara 1005*; G, I, J, based on *McPherson 12022*; H, based on *McPherson & Merello 8266*.

ally 1 cm long or shorter and fully persistent after separating, while in other species (e.g., *E. auriculata* Hemsley, *E. karstenii* Standley) the stipules are small to long, to 5 cm long, and after splitting the two portions are then partially caducous (Fig. 1H) with the apical portion falling away leaving two short, persistent, intrapetiolar, truncate bases that often bear well-developed persisting colleters (Fig. 1B).

Another distinctive characteristic of many species of *Elaeagia* is the presence of resin on the apical buds and sometimes coating the young inflorescences. A few species do not appear to have any resin while a few species produce it copiously, in

particular *E. pastoense* Mora of Panama and Colombia and *E. utilis* (Goudot) Weddell of Colombia and Ecuador. Mora-Osejo (1977) documented the anatomy of the secretory structures of *E. pastoense* and the harvest and use of its resin in Colombia, where it is collected from wild trees, heated, stretched into thin sheets, and applied as a wood varnish for handicrafts. Currently the resin is destructively collected from wild plants, but development of sustainable-use harvesting is under study in western Colombia (García S., 1999, pers. comm.).

The neotropical genus *Warszewiczia* Klotzsch (also Rondeletieae) comprises about five species of medium-sized to large trees that grow in wet lowland to middle-elevation forests from Mexico to Bolivia. *Warszewiczia* is similar to *Elaeagia* in its tree habit, its inflorescence structure and position, its five-lobed calyx limbs and corollas, its stamens that are exserted on pubescent filaments, its linear exserted stigmas, and its woody, similar-sized capsular fruits that open from the top. However, *Warszewiczia* differs from *Elaeagia* by its generally triangular, interpetiolar stipules that are typically convolute in bud and quickly and completely caducous; its protogynous flowers; its imbricate corolla lobe aestivation; and its septicidal fruits. Although *Warszewiczia* is often also characterized by bearing brightly colored calycophylls (i.e., enlarged, petaloid, white or colored calyx lobes that are produced, usually singly, on one or a few flowers in each cymule), these calycophylls are often deciduous before the fruits develop and thus not present on infructescences. The calycophylls appear to be completely absent from some inflorescences, individuals, or populations of calycophyllous species (Taylor, 1997), and the *Warszewiczia* species treated below appears to lack them completely. Another feature of *Warszewiczia* that is not always noted in descriptions is the occasional production of resin at the vegetative apices (Taylor, 1997). *Warszewiczia* has not been treated taxonomically as a whole in this century.

Elaeagia chiriquina C. M. Taylor, sp. nov. TYPE: Panama. Bocas del Toro: vicinity of Cerro Colorado mine above San Felix, along trails N of road along continental divide, 8°35′N, 81°50′W, 1500 m, 26 Jan. 1988, *G. McPherson 12022* (holotype, MO-3635060). Figure 1G–J.

Haec species a congeneris caulium apicibus saepe resinosis, stipularum 6–8 mm longarum caducarum post abscissionem basibus truncatis intrapetiolaribus duabus 1–2 mm altis remanentibus, foliis ellipticis 5–16 × 2.5–5.5 cm acutis vel breviacuminatis, limbo calycino lobato 1–1.2 mm longo atque lobulis corollinis ca. 3 mm longis distinguitur.

Trees to 11 m tall; stems glabrous, with vegetative apices frequently resinous. Leaves 5–16 × 2.5–5.5 cm, elliptic, chartaceous, glabrous, at base cuneate to acute, at apex acute to shortly acuminate; secondary veins 9 to 10 pairs, not looping to interconnect, without domatia, adaxially costa plane to prominulous and secondary and minor venation plane, abaxially costa and secondary veins plane to prominulous and minor venation plane; petioles 5–12 mm long; stipules 6–8 mm long, ligulate to obovate, rounded, glabrous except hirtellous in lower half, caducous leaving persistent and truncate intrapetiolar bases 1–2 mm high. Inflorescences 8–11 × 5–10 cm, pyramidal, puberulous to hirtellous, ebracteate, with secondary axes branched to several orders; peduncles 3; pedicels 1.5–3.5 mm long. Flowers with hypanthium ca. 1 mm long, turbinate; calyx limb 1–1.2 mm long, glabrous, 5-lobed for ca. half its length, lobes rounded to obtuse; corolla white, externally puberulous at least near base, tube ca. 1 mm long, lobes 5, ca. 3 mm long, ligulate, rounded; filaments densely villosulous in lower portion, anthers ca. 1 mm long; stigmas 2, ca. 1.2 mm long. Fruits not seen.

Distribution, habitat, and phenology. Wet forest at 1500–1750 m in western Panama; collected with flowers in January, with flower buds in February.

This new species is distinguished by the combination of its vegetative apices that are frequently resinous, stipules that are 6–8 mm long and caducous leaving truncate bases 1–2 mm high, elliptic leaves 5–16 × 2.5–5.5 cm and acute to shortly acuminate at apex, calyx limbs 1–1.2 mm long and lobed for about half their length, and corolla lobes ca. 3 mm long. The size, shape, and caducous limb of the stipules distinguish *E. chiriquina* from the other *Elaeagia* species known from Central America. The specific epithet refers to the known geographic distribution of this species, in the Chiriquí region of western Panama.

Paratypes. PANAMA. **Chiriquí:** along trail to Cerro Pate Macho, 8°49′N, 82°24′W, *McPherson & Merello 8266* (MO, PTBG).

Elaeagia glossostipula C. M. Taylor, sp. nov. TYPE: Panama. Bocas del Toro: along old pipeline road from continental divide, 8°48′N, 82°15′W, 900 m, 27 Dec. 1986, *G. McPherson & J. Aranda 10172* (holotype, MO-3618289; isotype, PTBG-7037). Figure 1A–F.

Haec species a congeneris caulium apicibus saepe resinosis, stipularum 18–40 mm longarum caducarum post

abscissionem basibus truncatis intrapetiolaribus duabus 1.5–2 mm altis remanentibus, foliis ellipticis 8–27 × 2.5–11 cm acutis vel breviacuminatis, limbo calicino lobato 0.8–1 mm longo atque lobulis corollinis 2–2.2 mm longis distinguitur.

Trees to 15 m tall; stems puberulous, with vegetative apices frequently resinous. Leaves 8–27 × 2.5–11 cm, obovate to oblanceolate, papyraceous, adaxially glabrous, abaxially puberulous to hirtellous, at base cuneate to acute, at apex acute to shortly acuminate; secondary veins 9 to 17 pairs, not looping to interconnect, without domatia, adaxially costa plane to prominulous, secondary veins plane, and finely reticulated minor venation prominulous, abaxially costa plane to prominulous and secondary and minor venation prominulous; petioles 5–15 mm long; stipules 18–40 mm long, ligulate to oblanceolate, rounded, glabrous except puberulous to villosulous and usually also hirsute near base, caducous leaving truncate intrapetiolar bases 1.5–2 mm high. Inflorescences 13–20 × 12–20 cm, pyramidal, hirtellous, with secondary axes branched to several orders; peduncles 3; bracts reduced; pedicels 1.5–5 mm long. Flowers with hypanthium 0.8–1 mm long, turbinate to cupuliform; calyx limb 0.8–1 mm long, puberulous to glabrous, 5-lobed for about half its length, lobes obtuse to truncate; corolla white, externally glabrous, tube 0.5–0.8 mm long, lobes 5, 2–2.2 mm long, ligulate, rounded; flaments densely villosulous in basal portion, anthers ca. 1 mm long; stigmas 2, ca. 1.2 mm long. Fruits 3.5–4 mm diam., subglobose, beak (i.e., apical portion above insertion of calyx limb) enlarged after anthesis, eventually longer than persistent calyx limb.

Distribution, habitat, and phenology. Wet forest at 900–1300 m in western Panama and adjacent eastern Costa Rica; collected with flowers in January, March, November, and December, with fruits in January, March, September, and December.

This new species is distinguished by the combination of its vegetative apices that are frequently resinous; its stipules 18–40 mm long, usually hirsute near the base, and caducous leaving truncate intrapetiolar bases 1.5–2 mm high; its elliptic leaves 8–27 × 2.5–11 cm and apically acute to short-acuminate; its calyx limbs 0.8–1 mm long and 5-lobed for about half their length; and its corolla lobes 2–2.2 mm long. The form, size, and caducous limb of the stipules together with the leaves that are acute to cuneate at the base distinguish this from the other species of *Elaeagia* known from Central America, except *E. karstenii* Standley. The specific epithet refers to the distinctive shape of the stipules. *Elaeagia karstenii* differs from *E. glossostipula* by its longer corolla lobes (2.5–4 mm long), its stipules that are hirtellous to villosulous throughout but never hirsute near the base, and its obovate leaves 13–38.5 × 6.5–21 cm.

Paratypes. COSTA RICA. **Limón:** región sureste del Lago Dabagri, cruzando las filas hacia Telire (Laguna Tiestos y Fila de Los Aguacatillos), *L. D. Gómez et al. 23196* (MO). **Puntarenas:** cantón de Parrita, cuenca del Naranjo y Paquetá, fila Chonta, La Virgen, 9°35′N, 84°09′W, *Morales & Abarca 6284* (INB, MO). PANAMA. **Bocas del Toro:** Fortuna Dam region, along road to Chiriquí Grande, 8°48′N, 82°10′W, *McPherson 8670* (MO, PMA); Fortuna Dam region, along continental divide trail bordering Chiriquí, 8°45′N, 82°15′W, *McPherson & Aranda 10075* (MO); trocha que comunica con la cima de Cerro Guabo, *Santamaría & Lara 1005* (MO, PMA). **Bocas del Toro-Chiriquí Border:** Fortuna Dam region, along continental divide trail, 8°45′N, 82°15′W, *McPherson 13550* (MO, PTBG), *13557* (MO). **Chiriquí:** NE del campamento de Fortuna (Hornito), sitio de presa, después de caseta de excavaciones geológicas, 8°45′N, 82°15′W, *Correa et al. 2885* (MO, PMA); NE del campamento de Fortuna (Hornito), sitio de presa, 8°45′N, 82°15′W, *Garibaldi et al. 2885* (MO, PMA); road from Fortuna Lake to Chiriquí Grande, 5 km along track to just S of continental divide, 8°49′N, 82°12′W, *Hampshire & Whitefoord 428* (BM, F, MO, PMA); vicinity of Fortuna Dam, along trail near Río Hornito, 8°45′N, 82°15′W, *McPherson 9902* (BM, DUKE, MO).

Warszewiczia uxpanapensis (Lorence) C. M. Taylor, comb. nov. Basionym: *Elaeagia uxpanapensis* Lorence, Bol. Soc. Bot. México 46: 66, fig. 1. 1983. TYPE: Mexico. Oaxaca: municipio de Matías Romero (Zona de Uxpanapa), a 2 km SE del aserradero La Floresta sobre el camino a Río Verde, a 15 km S de Esmeralda, 250 m, 25 May 1981, *T. Wendt, S. Koch, A. Villalobos & J. García 3299* (holotype, MEXU; isotypes, CHAPA not seen, MO-3273136).

This species from wet forest at 170–430 m in southern Mexico was originally described based on specimens with inflorescences bearing only flower buds and infructescences with only young fruits. The flower buds on the collections studied by Lorence have the lobes nearly open in aestivation, so their arrangement in bud is not clearly evident, and the open flowers variously have the anthers and stigmas equally well developed, the stigmas better developed than the anthers, or the anthers relatively more developed than the stigmas, so that most or all of the buds appear to have opened prematurely as the specimens were dried. The young capsules of the fruiting collections are dehiscent, apparently loculicidally, through a small apical opening, and the stipules are caducous and lacking on the specimen except those at the bases of some of the inflorescences. The stipules produced at the

bases of the inflorescences are atypical in many plants of Rubiaceae and thus not taxonomically informative.

In general aspect the plants seen by Lorence resemble several species of *Chimarrhis, Warszewiczia schwackei* K. Schumann of the Amazon basin, and *Elaeagia myriantha*; without more information, the placement of this species in *Elaeagia* was not counterindicated. However, more collections of this species are now available and show that its stipules are interpetiolar, triangular, and convolute in aestivation, that its flowers are strongly protogynous, and that its capsules are primarily septicidal and apparently only secondarily and shortly loculicidal. As noted above, these features all characterize *Warszewiczia* and distinguish it from *Elaeagia*; therefore, *E. uxpanapensis* is here transferred to *Warszewiczia*. The arrangement of the corolla lobes in bud is difficult to discern but apparently open, though the lobes overlap weakly on their sides in a manner consistent with a convolute arrangement.

Within *Warszewiczia, W. uxpanapensis* is similar in general aspect and inflorescence arrangement to *W. schwackei* of the Amazon basin; *W. schwackei* can be distinguished from *W. uxpanapensis* by its white calycophylls (though these apparently are not produced in all inflorescences), its calyx limbs 0.2–0.3 mm long, its corolla lobes 0.6–1 mm long, and its distribution at low elevations in the central and western Amazon basin. (The corresponding characters of *W. uxpanapensis* are presented below.)

Recent exploration has expanded the known range of *Warszewiczia uxpanapensis* to central Costa Rica and northwestern Colombia. The plants of all these regions occupy comparable habitats and cannot be distinguished by their vegetative organs, inflorescences, and flowers, and thus are here considered conspecific. Several species of *Psychotria* L. subg. *Psychotria* show similarly large range disjunctions without marked morphological differentiation; in some cases the disjunct populations have been treated as a single wide-ranging species, and in other cases some morphological differences are evident and infraspecific taxa have been recognized (Hamilton, 1989). Based on the lack of collections of *W. uxpanapensis* from northern Central America and an apparent difference in fruit size between Mexican plants and those of Costa Rica and Colombia, two subspecies are recognized here. The rank of subspecies is chosen because these two populations are distinct in one quantitative feature and fully allopatric (Stuessy, 1990).

Warszewiczia uxpanapensis subsp. **meridionalis** C. M. Taylor, subsp. nov. TYPE: Costa Rica. Alajuela: Reserva Forestal de San Ramón, laderas al este de la estación, 10°13′N, 84°36′W, 2 May 1987, *G. Herrera Ch. 600* (holotype, MO-429761; isotypes, COL-394796, F).

Haec subspecies a subspecie typica capsula 2.5–3 mm [vs. 1.5–2 mm] longa distinguitur.

Trees to 40 m tall; stems hirtellous to glabrescent. Leaves 6.5–21 × 3.2–12 cm, elliptic to obovate or oblanceolate, chartaceous, adaxially glabrous, abaxially glabrous except with a line of pilose pubescence along each side of costa, at base cuneate to obtuse, at apex obtuse to acute; secondary veins 7 to 9 pairs, not looping to interconnect, with pilosulous domatia in axils, adaxially costa plane to a little sulcate, secondary veins plane, and reticulated minor venation plane to prominulous, abaxially costa prominent, secondary veins prominulous, and minor venation plane to prominulous; petioles 1–2 cm long; stipules 9–13 mm long, interpetiolar, triangular to ovate, acute, glabrous, caducous. Inflorescences 6–15 × 5–15 cm, terminal and sometimes also produced in distalmost leaf axils, hirtellous to glabrescent, paniculate with higher-order axes spiciform; peduncles 1.5–3.5 cm long; bracts to 0.5 mm long. Flowers sessile in glomerules of 2 to 7; hypanthium ca. 1 mm long, turbinate, hirtellous to glabrous; calyx limb 0.8–1 mm long, glabrous, sinuate to shallowly lobed, lobes deltoid, without calycophylls; corolla funnelform, green, externally glabrous, tube ca. 0.8 mm long, lobes 5, ca. 2 mm long, ligulate, obtuse to rounded; anthers ca. 0.5 mm long, exserted; stigmas ca. 1 mm long, oblong. Fruits 2.5–3 × 2.5 mm; seeds 0.2–0.5 mm long.

Distribution, habitat, and phenology. Wet forest at 600–1300 m, central Costa Rica and northwestern Colombia; collected in flower in March and May, in fruit in March through May, July, and September through November.

The specific epithet refers to the relatively southern range of this subspecies. These plants have been confused in Costa Rica and Colombia with *Elaeagia myriantha*; *E. myriantha* can be distinguished quickly from *Warszewiczia uxpanapensis* by its stipules that are complanate in bud and persistent as two rounded to truncate, intrapetiolar segments. This new subspecies can be distinguished from the typical subspecies as follows:

KEY TO THE SUBSPECIES OF *WARSZEWICZIA UXPANAPENSIS*

1. Capsules 1.5–2 mm long; plants of Oaxaca, Mexico, growing at 170–430 m . . . subsp. *uxpanapensis*
1′. Capsules 2.5–3 mm long; plants of Costa Rica

and Colombia, growing at 600–1300 m . . . . . subsp. *meridionalis*

Paratypes. COLOMBIA. **Antioquia:** municipio de San Luis, Autopista Medellín–Bogotá, sector Río Samaná-Río Claro, *J. J. Hernández et al. 522* (HUA, MO); municipio de San Luis, quebrada La Cristalina, 6°N, 74°45′W, *J. G. Ramírez & Cárdenas L. 754* (JAUM, MO), *844* (JAUM, MO), sector SE, *J. G. Ramírez & Cárdenas L. 1886* (JAUM, MO). COSTA RICA. **Alajuela:** San Carlos, Peñas Blancas, *Haber & Bello C. 1928* (MO); Monteverde Reserve, Peñas Blancas river valley, Atlantic slope, 10°20′N, 84°43′W, *Haber ex Bello C. 5687* (F, MO), *Haber & Bello 7088* (F, MO); Reserva Biológica Monteverde, Río Peñas Blancas, Finca Beto, 10°29′N, 84°44′W, *Haber & Bello 7592* (CR, MO); cantón de San Ramón, Reserva Forestal San Ramón, Cedral de Miramar, 2.5 km O, en el límite de la Reserva, 10°14′N, 84°39′W, *Q. Jiménez et al. 1534* (CR, MO). **Heredia:** Parque Nacional Braulio Carrillo, sendero del transecto, immediately to right of trail one half hour below refugio at 1070 m, 10°17′N, 84°05′W, *Boyle 1315* (F, MO). **Limón:** Parque Internacional La Amistad, quebrada Crori, Croriña, 9°25′N, 82°59′W, *A. Chacón 252* (CR, F, MO). **San José:** cantón de Tarrazú, Faja Costeña del Valle de Parrita, Concepción de Tarrazú, en la Fila San Isidro, camino a San Isidro, 9°34′N, 84°05′W, *Morales & Ureña 3754* (CR, F, MO).

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