1995

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A REVISION OF THE EUPHORBIA DIOSCOREOIDES COMPLEX (EUPHORBIACEAE)

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ABSTRACT
A revision of the Euphorbia dioscoreoides complex (subgenus Agaloma) is provided. Euphorbia dioscoreoides ssp. attenuata and E. eglandulosa, both from México, are proposed as new; E. digitata is reduced to synonymy under E. subpeltata. Representative specimens are cited, and distributional and ecological data are provided.

Key words: Euphorbia, subgenus Agaloma, Euphorbiaceae, México, revision.

RESUMEN
Se presenta una revisión taxonómica del Euphorbia dioscoreoides complejo (subgénero Agaloma). Se describen una especie nueva, Euphorbia eglandulosa, y una subespecie nueva, Euphorbia dioscoreoides ssp. attenuata, los dos de México. Se reduce E. digitata como sinónimo de E. subpeltata. Especimenes son citados, y datos ecológicos y distribucionales son proporcionados.

Palabras clave: Euphorbia, subgénero Agaloma, Euphorbiaceae, México, revisión.

Euphorbia L., sensu lato, with as many as 2,000 species, is the largest genus in the family Euphorbiaceae and one of the largest among the flowering plants. The subgenus Agaloma (Raf.) House is one of nine subgenera recognized by Wheeler (1943) and is distinguished from other members of Euphorbia by its involucral appendages and minute, usually glandular stipules. This subgenus comprises about 150 New World species and is most diverse in México and Central America where approximately 85 mostly endemic species occur. The taxa treated in this paper belong to Agaloma and include Euphorbia dioscoreoides Boiss. and its close relatives.

These taxa share the following diagnostic characters, the combination of which distinguishes them from other members of the subgenus Agaloma: leaves with long, slender, peltately attached petioles; cyathia subtended by a pair of linear-filiform opposite leaves; and involucral appendages divided into three to nine segments. The leaf surfaces are essentially glabrous, and with the exception of E. dioscoreoides ssp. dioscoreoides, the proximal margin of the leaf is usually ciliate. The exact phylogenetic relationships between the individual members of the Euphorbia dioscoreoides complex are not yet elucidated, and its relationship to other members of Agaloma is also not obvious, but the long-petiolate leaves, relative lack of bracteoles between the staminate flowers, and deeply pitted seeds warrant its placement in section Cyttarospermum Boiss. [Note: Many authors incorrectly apply the name Adenopetalum (Klotzsch & Garcke) Benth. & Hook.f. (published 1880) to this section. However, at the sectional rank Cyttarospermum (published 1862) has nearly twenty years priority. The type of both sections is the same, namely Euphorbia graminea Jacq.]

The Euphorbia dioscoreoides complex is restricted to México, ranging from Sonora to Tamaulipas south to Chiapas. As here defined it consists of three species, one comprising two subspecies. Of these, one species has gone virtually unrecognized since it was described by Sereno Watson over one hundred years ago; one species and one subspecies are here described as new. These taxa are very similar vegetatively, but can readily be separated from each other on the basis of involucral-appendage characters (Fig. 1–4). Although nearly all of the specimens that I have examined were previously identified as Euphorbia dioscoreoides, the nomenclatural typical taxon, E. dioscoreoides ssp. dioscoreoides, is known only from a relatively small area in the states of México and Michoacán. The following key will distinguish the members of this complex:

1. Cyathia paired (rarely solitary), only 1–2 per cyathium-bearing branchlet; subcyathial leaves usually appearing whorled,
often white; the majority of involucral appendages 5-9-parted; involucral glands lacking or vestigial.

1' Cyathia not paired, usually more than 2 per cyathium-bearing branchlet; subcyathial leaves opposite, green to red but not white; the majority of the involucral appendages 3-5-parted; involucral glands fully developed.

2. Involutional appendages mostly 4-5-parted, the portion extending beyond the gland 1.2 mm or less in length. Euphorbia subpeltata

2' Involutional appendages 3-parted, the portion extending beyond the gland greater than 1.2 mm in length.

3. Leaf margin ciliate proximally (at least when young); divisions of the involucral appendages narrowed, sometimes abruptly, to an attenuate apex.

3' Leaf margin glabrous; divisions of the involucral appendages not narrowed, the apex obtuse to truncate and frequently irregularly crenate.


Erect, leafy, taprooted annual to 1.3 m, usually 80 cm or less; branchlets slender, glandular-pilose with multicellular trichomes 0.3–1.0 mm long; cauline leaves alternate; stipules inconspicuous, gland-like, 0.1–0.3 mm long, quickly deciduous; petioles mostly longer than the blade, slender 1.9–7.5 cm long, glandular-pilose proximally, glabrous distally, peltately attached; blades entire, membranous, penninerved, lanceolate to ovate to deltoid, 1.8–4.4 cm long, 1.0–3.9 cm wide, acute to mucronulate at the apices, rounded to truncate at the bases, the surfaces essentially glabrous and the margins glabrous or ciliate proximally with multicellular trichomes 0.2–0.4 mm long; cyathia borne in axillary monochasial cymes 1.3–6.1 cm long, axes of the cymes glabrous or distally glandular-pilose; subcyathial leaves opposite, linear filiform, 0.3–1.4 cm long, stipules inconspicuous, ca. 0.2 mm long; peduncle 1–3 mm long, glabrous; involucral obconic-campanulate, 1.0–1.4 mm long excluding the appendages, attenuate to truncate at base; involucral lobes inconspicuous, ca. 0.3 mm long, fimbriate at the apex; involucral appendages 3-parted, white to green and frequently suffused with wine red coloration; involucral glands 5, reniform, often wrinkled, the radial axis (length) 0.1–0.2 mm, the tangential axis (width) 0.3–0.5 mm; bracteoles few per cyathium, filiform and often divided above; staminate flowers ca. 20–30, androphores glabrous; gynophore glabrous or pubescent at its base, elongating to 7.1 mm in fruit; ovary glabrous, rounded 3-lobed; styles 3, biparted, filiform, 0.6–1.1 mm long; capsule strongly 3-lobed, 2.7–3.4 mm long, 3.1–4.0 mm wide; columnella 1.9–2.9 mm long; seeds ecarunculate, ovoid, flattened at the base, 2.0–2.5 mm long, 1.4–1.7 mm in diameter, blackish, with numerous coarse tubercles interspersed with several regular to irregular longitudinal rows of 3–5 shallow isodiametric depressions, the sides of which are beset with numerous minute tubercles and the bottoms of which commonly contain a minute, sharply punctiform pit.
**Euphorbia dioscoreoides** is rather widely distributed along the Pacific slope of México, ranging from Sonora and Chihuahua southward to Michoacán and México (Fig. 5). As here treated, it consists of two geographically segregated subspecies. These are morphologically distinct, and I have seen no intermediates. Both are summer-fall annuals whose growth corresponds with the summer monsoon season.

**Euphorbia dioscoreoides** Boiss. ssp. **dioscoreoides**

- **TYPE:** "Nova Hispánia" (holotype G, not seen; fragment [of the holotype] F!).

**Euphorbia peltata** Sesse & Moçoïno, Fl. Mexic. [in La Naturaleza, ser. 2, vol. 2]: 133. 1894; non E. peltata W. Roxburgh, 1832.

**Euphorbia mocinoi** Oudejans, Phytologia 67: 47. 1989.-**TYPE:** According to the protologue, this species is based on a Mexican Sesse & Moçoïno collection from "Oppido Nandio, prope Zitacuarum [Michoacán]. Floret Augusto." At the Field Museum [#849380!], there is a portion of a Sesse & Moçoïno collection representing *E. dioscoreoides* ssp. *dioscoreoides* that was distributed as *Euphorbia peltata*. This was taken from a Sesse & Moçoïno specimen (MA 1756) at the Real Jardín Botánico Herbarium in Madrid, Spain and presumably represents type material.

Leaf margins glabrous; divisions of the involucral appendages 3, 1.4–2.4 mm long, oblong to obovate, obtuse to truncate and frequently irregularly crenate at apex. An excellent illustration of this subspecies can be found in Boissier (1866: table 37).

Tropical deciduous forest and oak woodland in eastern Michoacán and the southwest portion of the state of México. It is replaced in western Michoacán by ssp. *attenuata*. In addition to occupying different geographical ranges, subspecies *attenuata* and *dioscoreoides* also have different elevational preferences; subspecies *dioscoreoides* ranges from 950 m to 1550 m while ssp. *attenuata* primarily ranges from 90 m to 920 m. July to October.

Additional specimens examined.—**MEXICO. MEXICO:** Distr. Temascaltepec, Plaza de Gallos, 950 m, 17 Sep 1932, Hinton 1751 (F, GH, LL, NY, RSA, US); Distr. Temascaltepec, Puerto Salitre, 1300 m, 20 Sep 1932, Hinton 1787 (GH, LL, NY, RSA); Distr. Temascaltepec, Tenayac, 1400 m, 27 Sep 1933, Hinton 4840 (GH, NY, US), 18 Oct 1935, Hinton et al. 8366 (LL, NY, RSA, US); Sto. Tomás, 1100 m, 31 Aug 1952, Matuda et al. 27151 (MEXU), Matuda et al. 27160 (MEXU); Progreso, Luviános, Cerro de La Culebra, 1300 m, 7 Sep 1954, Matuda et al. 31498 (MEXU)[2 sheets]; km 49 S of Temascaltepec on rd to Estanco, 18°55'N, 100°15'W, 1350 m, 3 Sep 1965, Roe et al. 1653 (DAV, F, MICH); 16 km al E de Luviános, sobre la carr. a Tejupilco, 1350 m, 3 Sep 1965, Rzedowski 20751 (DS, MICH, NY); 0.5 km W of Santa Bárbara power plant, 4 mi W of Santo Tomás de los Plátanos, 3500 ft, 11 Sep 1976, Webster 21260 (RSA).—**MICHOACÁN:** Distr. Zitácuaro, Zitácuaro-San José Perla, 1550 m, 22 Aug 1938, Hinton et al. 13132 (ARIZ, GH, LL,


**Euphorbia dioscoreoides** and **E. peltata** are apparently based on the same Sessé and Mocíño collection made over two hundred years ago. The collectors and exact type locality of **E. dioscoreoides** were most likely unknown to Boissier, who described it on the basis of a specimen in Pavón's herbarium from "Nova Hispánia."

This specimen, the holotype, was incorporated into Boissier's herbarium, and according to Dr. Rogers McVaugh (pers. comm., 1994), it bears a printed label "Nueva España Herb. Pavón" and a name added by Boissier, "**E. peltata.**" Although Sessé and Mocíño took part in their Mexican expedition during the late 18th and early 19th centuries, it was not until the late 19th century that their manuscripts on the flora of México were published. In the meantime, their herbarium collections had been disseminated to various people and institutions. Many of the specimens are known to have found their way into Pavón's herbarium (McVaugh, 1961: 173), and, as discussed by McVaugh (1987: 169), it was Pavón's custom to include with the specimen a small ticket containing virtually no information except the name originally given to the plant by Sessé and Mocíño. It seems probable that Boissier added the name from the ticket onto the label, and it is therefore a fair assumption that this is the **Euphorbia peltata** of Sessé and Mocíño. A comparison between a fragment of the holotype of **E. dioscoreoides** and a fragment of a Sessé and Mocíño collection labeled as **E. peltata** (both at F) shows them to be identical in all respects.

The type locality of **Euphorbia peltata** is reported as "**Oppido Nandio, prope Zitacuarum.**" This location is about 6 km south–southwest of Zitacuaro, Michoacán. McVaugh (1977: 190) states that Sessé and another member of his expedition, Castillo, probably visited this area in August of 1792, and it is likely that the type was collected then. Modern collections of **E. dioscoreoides** ssp. **dioscoreoides** from the vicinity of Zitacuaro are known (e.g., **Soto Núñez & Cortés A. 2345** and **Hinton et al. 13132**).

**Euphorbia dioscoreoides** Boiss. ssp. **attenuata** V.W. Steinmann, ssp. nov.—**TYPE:** México, Chihuahua, Río Mayo, Guasarames, 20 Aug 1936, **Gentry 2401** (holotype ARIZ [#313757]; isotypes ARIZ [ #70037]!, GH!, MEXU!, US!)

Annua erecta; **Euphorbiaceae** dioscoreoidi affinis, a qua folis ad basim ciliatis et segmentis involucralibus attenuatis differt.

Leaves ciliate proximally; divisions of the involucral appendages 3(–4), 1.3–3.1 mm long, generally lanceolate, attenuate at apex.

This subspecies occurs in deciduous and semideciduous tropical forests (with a single Sonoran pine-oak woodland record) from Sonora and Chihuahua to western Michoacán from 90 to 1220 m. Frequently in mesic and shady habitats. Gentry (1942: 171) says of this subspecies (misidentified as **E. uniglandulosa**), "a slender, turgescent summer annual, almost hydrophytic in character, withering quickly under the noontday suns."

**May to November.**
Euphorbia eglandulosa V.W. Steinnann, sp. nov.—

TYPE: México, Guerrero, limestone ledges of mountains above Iguala, 2500–3000 ft, 10 Oct 1900.

Pringle 8393 (holotype MEXU[118410]); isotypes FJ[2 sheets!], GH!, MEXU[18408!], MICH!, MO!, NY!, POM!, UC[2 sheets!], US!.

Annua erecta: Euphorbia dioecoroidi affinis, a qua foliis ad basim ciliatis, segmentis involucralibus linearis-filiformibus, et glandulis involucralibus multihis vel redactis differt.

Erect, leafy, taprooted annual to ca. 1 m tall; stems to 4 mm thick and unbranched at the base; stems and branchlets densely glandular-pilose with multicellular trichomes up to 1.1 mm; cauline leaves alternate; stipules 0.2–0.4 mm long, glanduliform, quickly deciduous; petioles longer than blades, slender, 2.1–4.3 cm long, densely glandular-pilose, peltately attached; blades entire, membranous, penninerved, broadly ovate, 1.9–3.2 cm long, 1.6–2.8 cm wide, mucronulate at the apices, truncate at the bases, the surfaces essentially glabrous and the margins ciliate proximally with multicellular trichomes 0.2–0.5 mm long; cyathia borne in pairs at the ends of axillary branchlets 1.0–1.3 cm long, the axes of the branchlets glandular-pilose at least along the proximal half; leaves of the cyathium-bearing branchlets 4 (rarely 2 by reduction of one pair), pseudowhorled, green or white, linear-filiform, 3.4–6.2 mm long, stipules filiform, 0.2–0.5 mm long; peduncles 2–3 mm, glabrous or glandular-pilose; involucral abscission-campanulate, usually wider than long, 1.3–2.0 mm long, 1.5–2.9 mm wide, white and tinged with purple or pink, rounded to truncate at base, glabrous or sparsely strigose without, glabrous within; involucral lobes white, conspicuous, to 1.1 mm, filiform at apex; involucral glands absent or vestigial; involucral appendages 5, white, divided into 5–7(–9) linear segments 1.6–1.9 mm long, these often dilated at the apex; bracteoles several per cyathium, generally united proximally and divided into filiform divisions distally; staminate flowers ca. 30–40, androphores glabrous; gynophores glabrous, elongating to 4.0 mm in fruit; ovary glabrous, roundly 3-lobed; styles 3, biparted, filiform, 1.6–2.2 mm long; capsule strongly 3-parted, 2.6–3.1 mm long, 3.6–4.2 mm wide; columna l.8–2.5 mm long; seeds ecarunculate, ovoid, flattened at the base, 2.1–2.5 mm long, 1.6–1.8 mm in diameter, brown to blackish, with numerous coarse tubercles interspersed with several regular to irregular longitudinal rows of 3–5 shallow isodiamic depressions, the sides of which are beset with numerous minute tubercles and the bottoms of which commonly contain a minute, sharply punctiform pit.

Mostly tropical deciduous forest, Morelos and northern Guerrero and one disjunct locality in Chiapas (Fig. 5), often in rocky areas, the substrate frequently referred to as limestone, 600 to 2100 m. August to October.

Paratypes.—MEXICO. CHIAPAS: Mpio. Chiapa de Corzo, slope above El Chorreadero, 860 m, 26 Sep 1988, Breedlove 70137 (CAS); 31 Oct 1988, Breedlove 70833 (CAS).—GUERRERO: Taxco Viejo, 18 Sep 1937, Abbott 413 (GH); 16 km (by rd) from Iguala on rd to Taxco, 1260 m, 1 Oct 1983, Anderson 12924 (DAV); Mpios. Iguala & Buenavista, Cañón de la Mano, entre Los Amates y El Naranjo, 10 km al N de Iguala por el ferrocarril, 900–1000 m, 13 Sep 1986, Catalán H. 172 (MEXU); 4 km S of Acuítlapan, 21 Aug 1943, Clausen et al. 6044 (MEXU); on rd from Iguala to Telolopan, 8 Sep 1954, Dresler 1799 (GH); along Guanavaca-Telolopan Rd, ca. 10 mi from Taxco, 5500 ft, 19 Aug 1935, Ma-Daniels 109 (F); Iguala Canyon, 2500 m, 21 Sep 1905, Pringle 13066 (ARIZ, CAS, F, GH, MICH, TEX, US); Achota, 500 m, Sep 1926, Reko 4983 (US); 8 km al NW de Iguala, carr. Iguala-Taxco, 920 m, 14 Oct 1981, Soto Núñez & Silva R. 3326 (MEXU); Telolopan, Xalostoc 30 km al NW de Iguala, carr. a Telolopan, 1420 m, 25 Aug 1982, Tenorio L. 1491 (MEXU, MO); W of Iguala, Los Sabinos Canyon, 16 Sep 1945, Turner 1773 (NY); mountainside
This species is unusual in that the involucres are frequently wholly glabrous, though in some collections (e.g., Reko 4983) vestigial glabres are present. Many species of the subgenus Agaloma have involucres on which the gland number is reduced, sometimes to one, but in these instances the accompanying involucral appendage is also lacking. This species is unique among the Euphorbia known to me in lacking glabres while possessing well-developed involucral appendages.


Shrub, perennial herb, or annual, 20–150 cm tall, the root often thickened and tuberous; branches slender, glabrous or glandular-pilose; cauline leaves alternate; stipules inconspicuous, ca. 0.3 mm long, gland-like, quickly deciduous; petioles mostly longer than the blades, slender, 0.9–5.7 cm long, peltately attached; blades entire, membranous to subcoriaceous, pinnernerved, nearly orbicular to ovate to lanceolate, 0.9–4.6 cm long, 0.7–2.4 cm wide, acute to obtuse at the apices, rounded to truncate (rarely cordate) at the bases, the surfaces essentially glabrous and the margins glabrous or ciliate proximally with puberulent trichomes 0.1–0.2 mm long; cyathia borne in axillary monoehacial or partially dichasial cymes 1.5–6.1 cm long, the axes of the cymes glabrous or distally glandular-pilose; subcylindrical leaves opposite, linear-subulate to filiform, 0.5–1.9 cm long, with minute filiform stipules 0.2–0.5 mm long; peduncles 1–3 mm long, glabrous; involucral campanulate, 0.9–1.3 cm long excluding the appendages, green to red-tinged, the base generally attenuate when young and becoming rounded to truncate in age, glabrous or sometimes sparsely strigose distally outside, strigose on the distal half inside; involucral lobes inconspicuous, ca. 0.3 mm long, fimbriate at the apex; involucral appendages (2–)3–5–6)-parted, glabrous, the divisions resembling fingers, oblong, rounded-obtuse at the apex, 0.4–1.0(–1.2) mm long; involucral glands 5, reniform, the radial axis (length) 0.2–0.3 mm, the tangential axis (width) 0.5–0.6 mm; bracteoles several per cyathium, divided into filiform divisions above; stamine flowers ca. 20–30, androphores glabrous; gynophore glabrous or rarely distally glandular-pilose, elongating to 10 mm in fruit; ovary glabrous, roundly 3-lobed; styles 3, biparted, filiform, 0.6–1.0 mm long; capsule strongly 3-lobed, 2.3–3.0 mm long, 3.2–4.1 mm wide; columnella 1.7–2.2 mm long; seeds echinate, spheroidally ovoid, 1.7–2.1 mm long, 1.3–1.6 mm in diameter, brown to grayish-black, with numerous coarse tubercles interspersed with several regular to irregular longitudinal rows of 3–5 shallow isodiametric depressions, the sides of which are beset with numerous minute tubercles and the bottoms of which commonly contain a minute, sharply punctiform pit.

Tropical forest, oak woodland, and pine-oak woodland, commonly in disturbed habitats and frequently on limestone substrates. This species ranges from central Coahuila to southwestern Tamaulipas, southward through San Luis Potosí to Guanajuato, Querétaro, and Hidalgo; it also occurs in Morelos, Guerrero, and Oaxaca (Fig. 6). Reproductive from April to November and in February, so far as is known, 250–1600 m.

Fig. 6. Distribution of *Euphorbia subpeltata*.

A comparison between the type material of *Euphorbia digitata* and *Euphorbia subpeltata* reveals no differences of taxonomic merit between them, and the two are here considered synonymous. The leaves of *Pringle 3272* (the type of *E. subpeltata*) are nearly orbicular and obtuse to mucronulate (Fig. 7). *Pringle 3525* (the type of *E. digitata*) possesses leaves that are ovate-lanceolate and acute (Fig. 10). Although the two collections are superficially rather different, and it is understandable why Watson named them as separate species, the numerous collections now available illustrate the thorough continuum in leaf shape and provide evidence that the two entities cannot be maintained as distinct. The leaves of this species are highly variable (Fig. 7-10), and the types merely represent extremes in leaf morphology and are otherwise very similar. The only collection that I have seen with
leaves closely matching the type of *E. subpeltata* is Stanford et al. 1031.

The plants in Morelos, Guerrero, and Oaxaca differ from plants throughout the northern range of this spe-

cies in that they are densely glandular-pilose and consistently summer–fall annuals. The northern plants are nearly always perennial herbs or shrubs, and although frequently glandular-pilose, this is never to such an extent as in the southern plants. The significance of these differences is not yet apparent, and the plants from Morelos, Guerrero, and Oaxaca are here referred to *Euphorbia subpeltata*.

**ACKNOWLEDGMENTS**

Drafts of this paper were reviewed by J. Travis Columbus, Mark H. Mayfield, Rogers McVaugh, J. Mark Porter, Timothy S. Ross, Grady L. Webster, and one anonymous reviewer; their criticism is greatly appreciated. Luis R. Lozoya assisted with the Spanish abstract. For the privilege of access to their collections I am indebted to the curators and staffs at A, ARIZ, ASU, CAS, DS, DAV, F, GH, HUMO, LL, MEXU, MICH, MO, NY, POM, RSA, TEX, UC, UCR, and US.

**LITERATURE CITED**


