

Flora of Bokor National Park, Cambodia IV: A New Section and Species of *Euphorbia* Subgenus *Euphorbia*

HIRONORI TOYAMA^{1,*}, SHUICHIRO TAGANE¹, PHOURIN CHHANG²,

HIDETOSHI NAGAMASU³ AND TETSUKAZU YAHARA¹

¹Center for Asian Conservation Ecology, Kyushu University, 744 Motoooka, Fukuoka 819-0395, Japan. * htohyscb@kyushu-u.org (author for correspondence); ²Institute of Forest and Wildlife Research and Development, Forestry Administration, 40 Preah Norodom Blvd, Phnom Penh, Cambodia; ³The Kyoto University Museum, Kyoto University, Yoshida-Honmachi, Sakyo-ku, Kyoto 606-8501, Japan

A new section, *Euphorbia* sect. *Bokorenses* under subgenus *Euphorbia* is established for *Euphorbia bokorensis* H. Toyama & Tagane, sp. nov., endemic to Bokor National Park, Cambodia. *Euphorbia* sect. *Bokorenses* is distinguished from related sections *Denisophorbia* and *Goniostema* by unbranched stems and smooth seeds, respectively. Bayesian phylogeny using *matK*, *ndhF*, and ITS regions supports its monophyly from the currently recognized 21 sections. It has a sister relationship with the Malagasy clade, including sections *Denisophorbia*, *Deuterocalli* and *Goniostema*, and to the northeastern African clade, including sect. *Rubellae*. A description, illustration, photographs and preliminary conservation status of the new species, and an updated identification key to the sections of *Euphorbia* subg. *Euphorbia* is provided.

Key words: Bokor National Park, Cambodia, *Euphorbia*, new section, new species

Euphorbia subg. *Euphorbia* (Euphorbiaceae) exhibits the greatest diversity among subgenera in both species richness and growth forms (Horn *et al.* 2012). The last revision of *E.* subg. *Euphorbia* based on comprehensive taxonomic, geographic and phylogenetic studies using 661 species (Dorsey *et al.* 2013) showed revealed four major clades, a New World clade, a Pacific clade, an Old World clade I, and an Old World clade II. Twenty one sections were recognized, including 9 newly described (Fig. 1). According to the classification of Dorsey *et al.* (2013), all of the Asian species are included in *E.* sect. *Pacificae* and *E.* sect. *Euphorbia*. *Euphorbia* sect. *Pacificae* was established by Dorsey *et al.* (2013) and occurs in Australia, Indonesia, New Guinea, and the Pacific islands. It has a unique distribution in the southern Pacific, and is one of the basal lineages

in *E.* subg. *Euphorbia*. *Euphorbia* sect. *Euphorbia* is the largest clade in *E.* subg. *Euphorbia* having over 340 species extending from Africa to Asia, and is a lineage sister to *E.* sect. *Monadenium* of eastern, central, and southeastern Africa.

In Indochina, 10 species of *Euphorbia* subg. *Euphorbia* are known, of which six are cultivated and the other four, *E. antiquorum* L., *E. lacei* Craib., *E. ridleyi* Croizat, and *E. sessiliflora* Roxb., are native (Gagnepain 1931, Dy Phon 2000, Hô 2003, Esser 2005, Newman *et al.* 2007). All species native to Indochina included in *E.* sect. *Euphorbia* generally have succulent stems with a spine shield that is a horny pad of tissue subtending or surrounding each leaf base (Dorsey *et al.* 2013).

In 2011–2013, we investigated the flora in Bokor National Park, Cambodia, and collected ca.

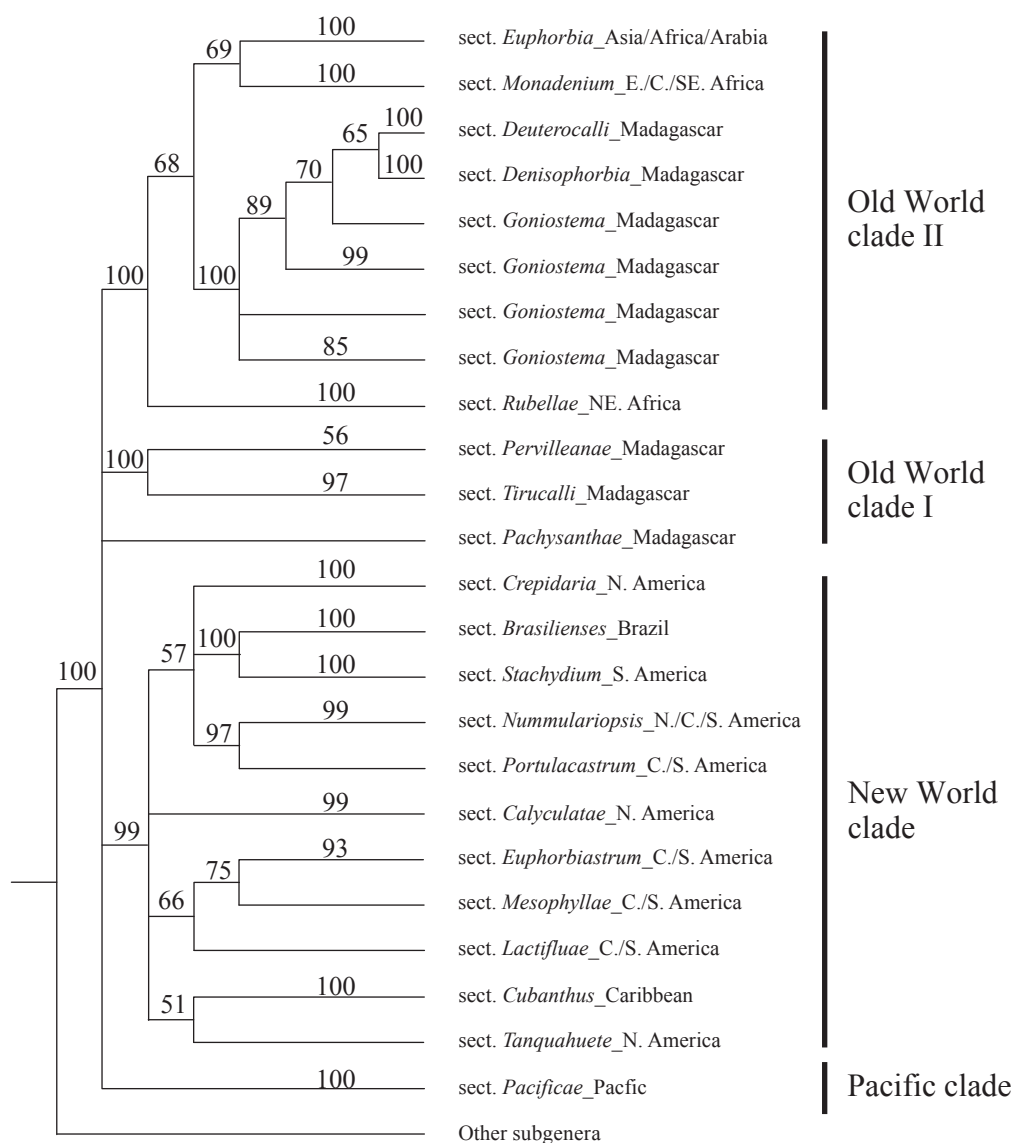


FIG. 1. Schematic phylogeny of *Euphorbia* subg. *Euphorbia* in Dorsey *et al.* (2013) at section level. Branches are labeled with bootstrap support greater than 50. Distribution follows Dorsey *et al.* (2013).

3,100 specimens, including ca. 770 identified woody species, and 22 new species (Tagane *et al.* 2015a,b, Naiki *et al.* 2015, Tanaka *et al.* 2015, Toyama *et al.* 2016, Yahara *et al.* in press). Additionally, we discovered a spurge with subsucculent stems, gland-like stipules and conspicuous cyathophylls that did not belong in *Euphorbia*

sect. *Euphorbia*. Comparative morphological and phylogenetic studies provided evidence to eliminate its placement within any of the 21 sections recognized by Dorsey *et al.* (2013). Here, we describe a new section, *E. sect. Bokorenses* H. Toyama & Tagane, to accommodate it and a new species, *Euphorbia bokorensis* H. Toyama & Tagane, based on

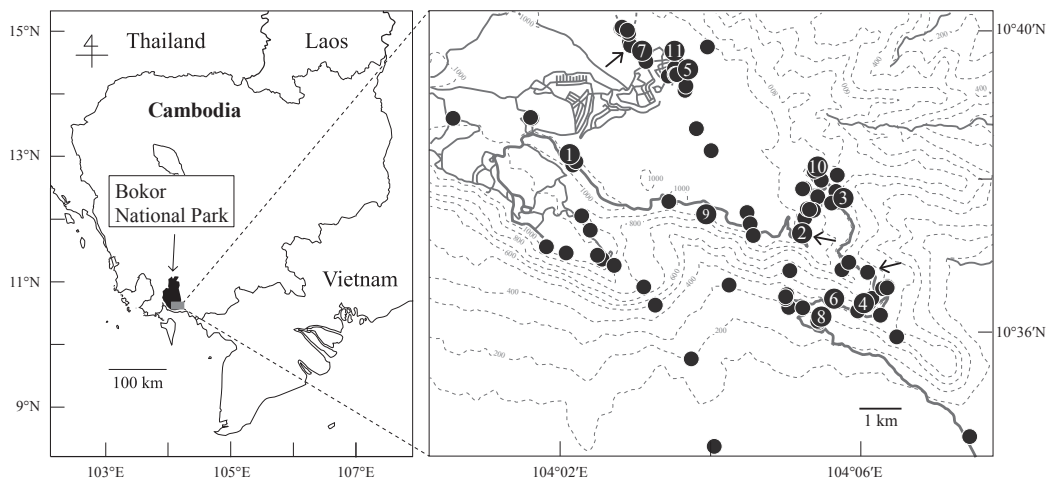


FIG. 2. Location of surveyed sites in Bokor National Park, Cambodia. Surveyed sites are shown by black dots; number above black dot indicates plot ID. Gray line indicates road. Dashed gray lines are contours. Arrows indicate locality where *Euphorbia* was collected.

morphological and phylogenetic evidence.

Materials and methods

Field surveys

We conducted seven field surveys (December 3–23 in 2011; May 8–16, July 14–20, and October 15–26 in 2012; February 16–17, August 6–13, and December 7–12 in 2013) on the southern slope and the top plateau of Bokor National Park, Kam-pot Province, Cambodia (Fig. 2). We recorded the flora by using plot-based surveys and general collections. We placed 21 rectangular plots of $100 \times 5 \text{ m}^2$ along an altitudinal gradient from 266 m to 1,043 m. Data from 11 plots were used in this study; in the other 10 plots we recorded only trees above 4 m tall (Fig. 2, black dots with the number of plot ID). Each plot was divided into 10 subplots of $10 \times 5 \text{ m}^2$, in which we recorded all the species of vascular plants we encountered. In addition, we collected specimens at 94 locations along the whole altitudinal gradient of the park (from 15 to 1,047 m) (Fig. 2, black dots).

Morphological comparison

We also examined dried specimens in the her-

baria BKF, FU, KAG, TI, and VNM, and digitized specimen images on the web (e.g., JSTOR Global Plants). The collections of spurge were also compared with the original descriptions of closely related species and with the taxonomic keys of Dorsey *et al.* (2013).

Molecular phylogenetic analysis

Leaf pieces of the spurge were dried using silica-gel in the field (voucher specimen: Toyama *et al.* 1912, FU). DNA isolation was performed by the CTAB method (Doyle & Doyle 1987) with minor modifications. Before DNA extraction, dried leaf material was milled by QUIAGEN TissueLyser to obtain fine powder. The powder was washed up to five times in a 1 mL buffer (0.1 M HEPES, pH 8.0; 2% Mercaptoetanol; 1% PVP; 0.05 M Ascorbic acid). We sequenced the partial genes for the large subunit ribulose-1,5-bisphosphate carboxylase oxygenase (*rbcL*) and maturase K (*matK*) according to published protocols (Kress *et al.* 2009, Dunning & Savolainen 2010) for DNA barcoding (CBOL Plant Working Group 2009). Each sequence was BLAST searched against GenBank to find species having similar sequences.

In addition to the barcoding regions, we se-

TABLE 1. Summary statistics of datasets used for phylogenetic inference. Chloroplast DNA data set consisted of concatenated *matK* and *ndhF* sequences and indel data. Three-gene dataset consisted of concatenated cpDNA and ITS sequences. *In Dorsey *et al.* (2013), *E. bongensis* is not included in the supplementary Data of “ITS Alignment”, but in the “3-gene Alignment”. Here, we used the ITS sequence of *E. bongensis* in the file of “3-gene Alignment”.

Regions	<i>matK</i>	<i>ndhF</i>	ITS*	cpDNA	3-gene
Number of accessions	178	163	283	233	315
Aligned sequence length	2082	1449	669	3531	4200
Variable DNA sites (%)	829 (40)	548 (38)	449 (67)	1377 (39)	1826 (43)
Parsimony-informative sites (%)	490 (24)	357 (25)	404 (60)	847 (24)	1251 (30)
Indels	95	40	125	137	262
Specific variable DNA sites to <i>Toyama et al. 1912</i> (FU)(%)	11 (0.53)	3 (0.21)	2 (0.30)	14 (0.40)	16 (0.38)
Specific indels to <i>Toyama et al. 1912</i> (FU)	0	2	1	2	3
Sequence length of <i>Toyama et al. 1912</i> (FU)	1979	916	623	2895	3518

quenced *matK* including the partial *trnK* intron, NADH dehydrogenase subunit F (*ndhF*) gene, and the internal transcribed spacer region of the nuclear ribosomal DNA (ITS) according to published protocols (Dorsey *et al.* 2013). All three attempts of PCR for *ndhF* region using the primer sets of 536F/1318R, 5F/972R, 536F/1318R, 5F/1318R, and 972F/3R (Lohmann 2006) failed, so we used the primer sets of 972F (Lohmann 2006) and 2110Ri (Steinmann & Porter 2002). We downloaded available sequences from the supplementary data of Dorsey *et al.* (2013) and aligned with our sequences in which we deleted the same regions of the partial *trnK* intron flanking the *matK* following Dorsey *et al.* (2013). The sequence alignment was performed by MAFFT v7.220 (Katoh & Standley 2013), in which the “--auto” option that automatically selects the optimal options was used. MEGA v 6.06 (Tamura *et al.* 2013) was used to check electropherograms and to edit aligned sequences. We used a Bayesian methods implemented in the program BEAST v 1.6.1 (Drummond & Rambaut 2007). We set the GTR + γ model of molecular evolution following a previous study (Dorsey *et al.* 2013) and used an uncorrelated lognormal (UCLN) relaxed-clock model to infer relative divergence times. A random starting tree was used, and a Yule process was set for the tree prior that was useful for species-level analyses (Drummond & Rambaut 2007). Topological constraints include the mono-

phyly of each species for faster calculations. We ran five independent chains of 100 million generations each, sampling every 10,000 generations. The first 1,000 trees were discarded as burn-in from each run, and then 9,000 trees were resampled from all runs using LogCombiner v 1.6.1 (Drummond & Rambaut 2007). Among the posterior distribution of 9,000 trees, the maximum clade credibility tree was identified using TreeAnnotator v 1.6.1 (Drummond & Rambaut 2007) with a posterior probability limit of 0.5 and median node heights.

Results

Field surveys

Among 11 plots, we found fewer than ten individuals of *Euphorbia bokorensis* in one plot (No. 2) placed in an evergreen forest at 888 m alt. (Fig. 2) where *Castanopsis accuminatissima* (Blume) A. DC., *Olea salicifolia* Wall. ex G. Don, *Nephelium hypoleucum* Kurz, *Dracaena gracilis* Wall. *Illicium cambodianum* Hance, *Schima crenata* Korth., and *Xanthophyllum schizocarpon* Chodat dominated. In general collections from 94 locations, we found *E. bokorensis* at only two locations, at 602 m and 912 m alt. (Fig. 2). In each location, we found less than ten individuals. The evergreen forest at 602 m alt. contained *Mallotus paniculatus* (Lam.) Müll. Arg., *Alphitonia incana*

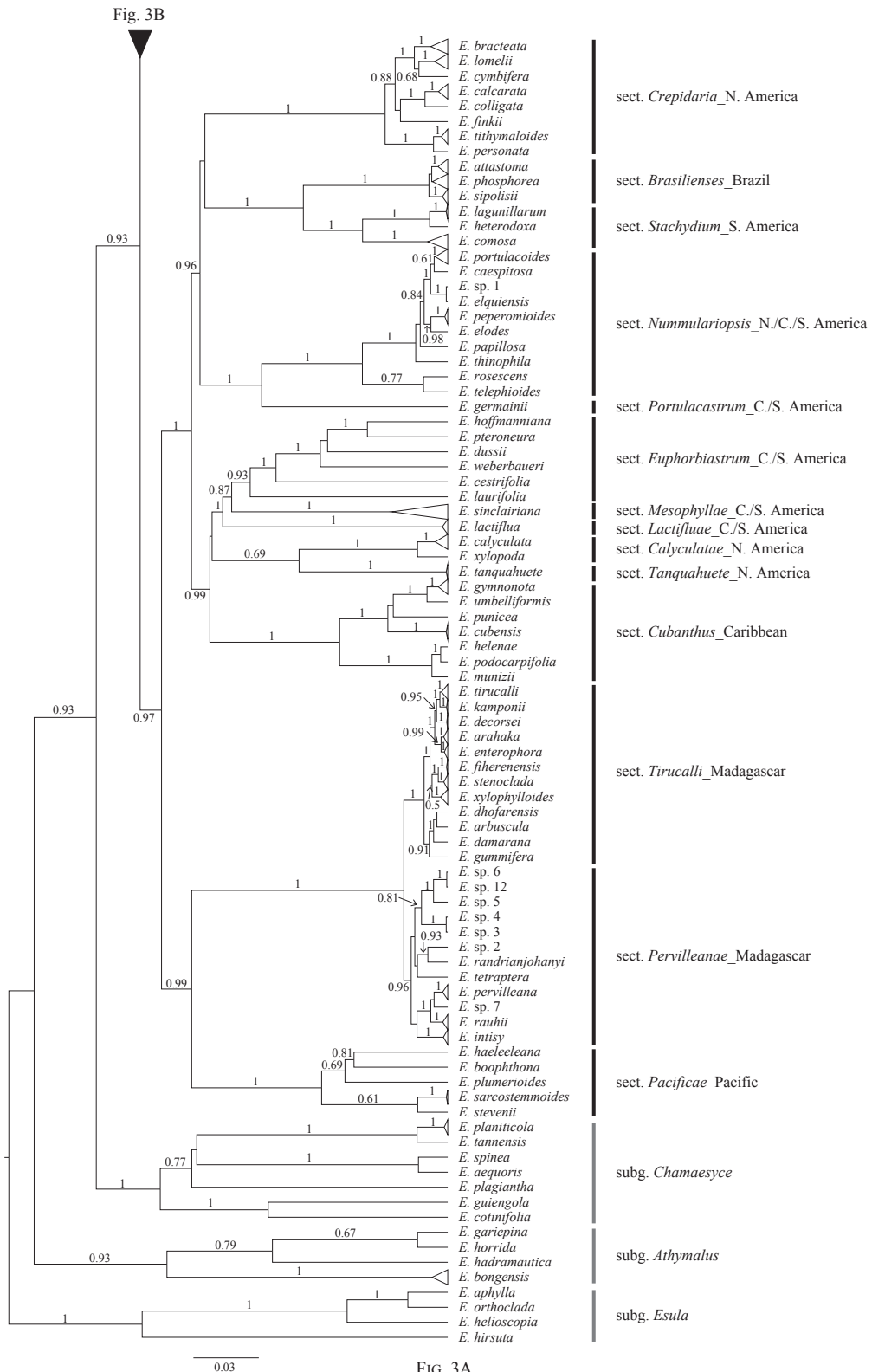


FIG. 3. Bayesian phylogeny of 315 taxa in *E. subgen. Euphorbia* based on *matK*, *ndhF*, and ITS sequences. Multiple accessions of same species are summarized as empty triangles. Clades represented by filled triangles in Fig. 3A are expanded to Figs. 3B and 3C. Branches are labeled with posterior probabilities greater than 0.5.

Fig. 3C

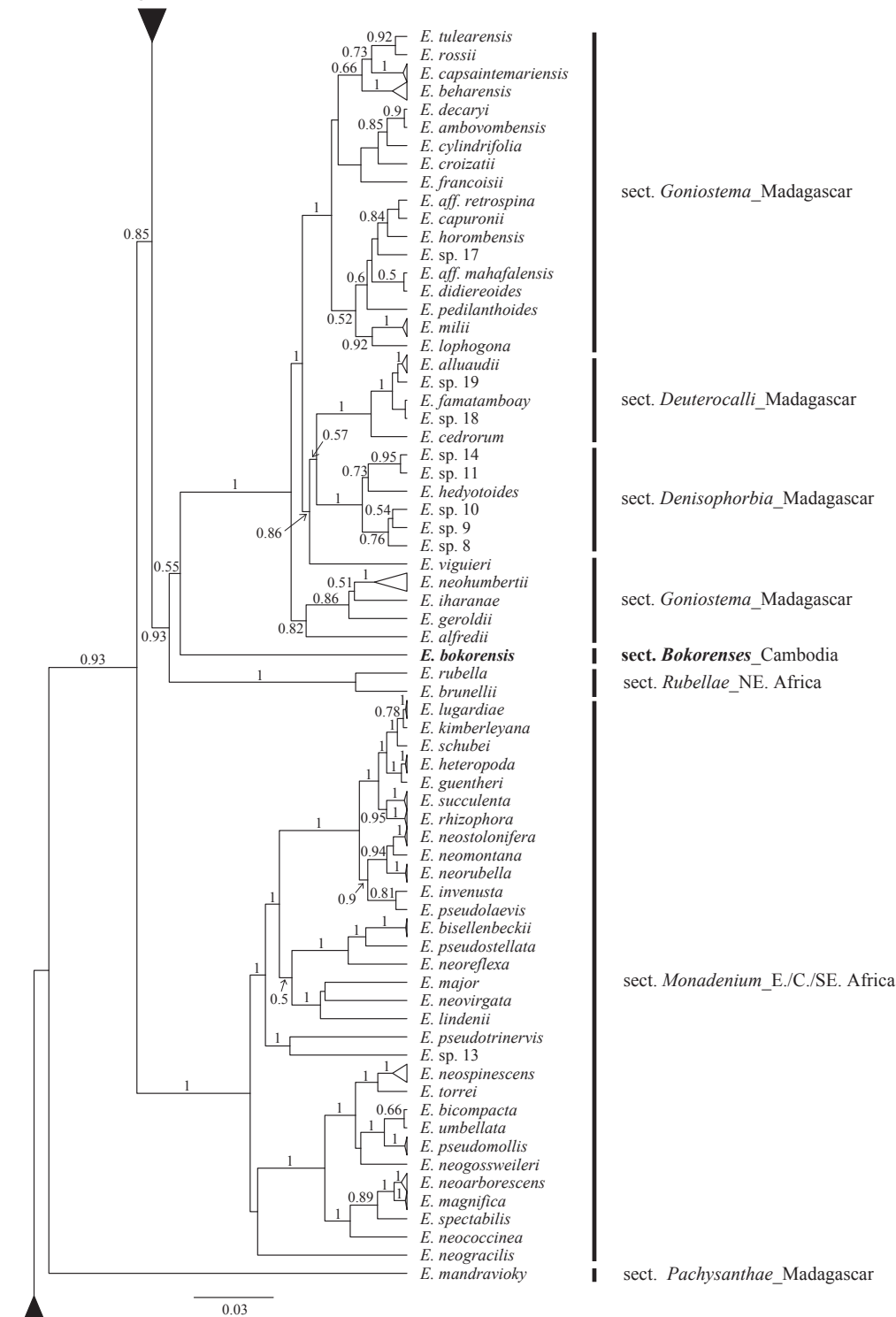


Fig. 3A

Fig. 3B

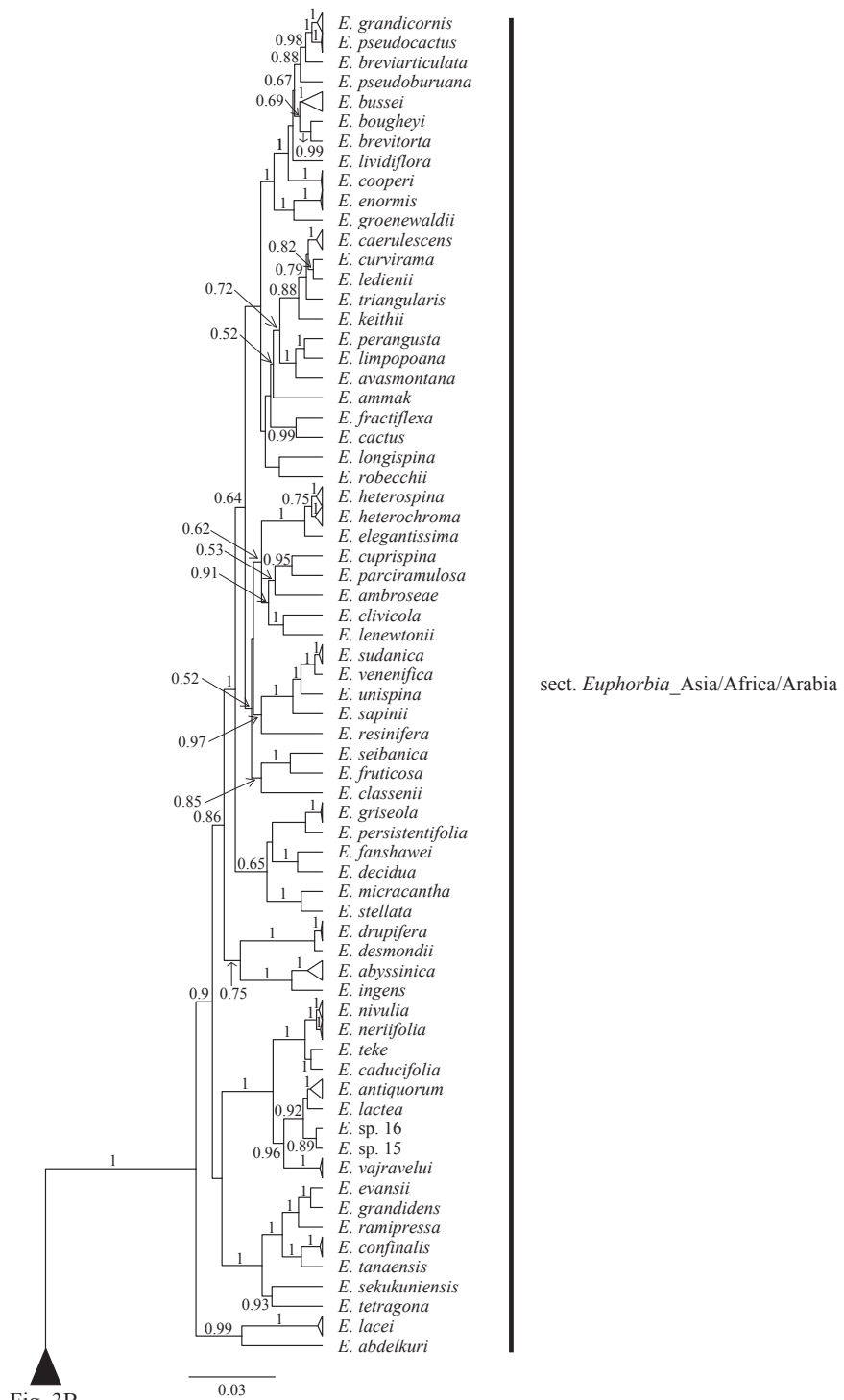


FIG. 3C

(Roxb.) Teijsm. & Binn. ex Kurz, *Archidendron quocense* (Pierre) I. C. Nielsen, *Phoebe lanceolata* (Nees) Nees, and *Gironniera subaequalis* Planch.; the site at 912 m contained *Macaranga andamanica* Kurz, *Beilschmiedia penangiana* Gamble, *Illicium tenuifolium* (Rindl.) A. C. Sm., *Ardisia sanguinolenta* Blume, and *Antidesma laurifolium* Airy Shaw.

Sequence variation and molecular phylogeny

Summary statistics for each dataset are given in Table 1. The aligned sequences of *matK*, *ndhF*, and ITS were 2082, 1449, and 669 base pairs long, respectively, of which 490, 357, and 404 base pairs were parsimony-informative. Three specific indels and 16 specific variable sites were in *Euphorbia bokorensis*. DNA sequences of the barcoding regions of *E. bokorensis* are the most similar to *Euphorbia abyssinica* (accession no. AY794824, *rbcL* identity: 566/567) and *E. cactus* (accession no. KF408914, *rbcL* identity: 565/566) of sect. *Euphorbia*, and *E. ambarivatoensis* (accession no. JQ951981, *matK* identity: 763/775) of sect. *Goniostema*.

The Bayesian phylogeny supports the monophyly of *Euphorbia* subg. *Euphorbia* (with 93% posterior probability) and comprising three major clades and one unplaced section (Fig. 3). *Euphorbia bokorensis* was in one of the major clades, but clearly separate from the other sections and showed a sister relationship with the Malagasy clade, including *Denisophorbia*, *Deuterocalli*, and *Goniostema*; this group is sister to the north-eastern African section, *Rubellae* (Fig. 3).

Discussion

Morphology, phylogeny, and taxonomy of *Euphorbia bokorensis*

Euphorbia bokorensis was not assignable to any of the sections recognized by Dorsey *et al.* (2013). Based on the key of Dorsey *et al.* (2013), *E. bokorensis* is included in *E. sect. Euphorbia* or in *E. sect. Monadenium*, but is distinguished from the former by its spineless stems and conspicuous cyathophylls, and from the latter by the

five similar glands and ecarunculate seeds (Figs. 4 & 5). *Euphorbia bokorensis* is morphologically similar to *E. boivinii* Boiss. (*E. sect. Denisophorbia*) and *E. boissieri* Baill. (*E. sect. Goniostema*) in its monoecious sexuality, shrub-like habit and well-developed oblanceolate leaves. *Euphorbia boivinii* has sympodial branching (vs. unbranched), smaller leaves (to 10 by 4 cm vs. 13–24 by 3–6 cm), attenuate leaf base (vs. cuneate base), and reduced (vs. conspicuous) cyathophylls. *Euphorbia boissieri* has larger leaves (34 by 6 cm), attenuate leaf base, fewer cyathia (to 4) per cyme (vs. to 8), reduced cyathophylls, and verrucose (vs. smooth) seeds.

Euphorbia bokorensis is morphologically and phylogenetically (Fig. 3) distinct from the species of all known sections. We therefore propose a new section, *Bokorenses*, to accommodate *E. bokorensis*.

Molecular phylogeny of *Euphorbia* subg. *Euphorbia*

Our molecular phylogenetic analysis recognized three major clades and one unplaced section in *Euphorbia* subg. *Euphorbia* (Fig. 3). The first clade with 100% posterior probability includes 11 sections, *Brasilienses*, *Calculatae*, *Crepidaria*, *Cubanthus*, *Euphorbiastrum*, *Lactifluae*, *Mesophyllae*, *Nummulariopsis*, *Portulacastrum*, *Stachydium*, and *Tanquahuete*, and corresponds to the New World clade of Dorsey *et al.* (2013). The second clade with 93% posterior probability includes six sections, *Denisophorbia*, *Deuterocalli*, *Euphorbia*, *Goniostema*, *Monadenium*, and *Rubellae*, and corresponds to the Old World clade II of Dorsey *et al.* (2013). The third clade with 99% posterior probability includes three sections, *Pacificae*, *Pervilleanae*, and *Tirucalli*, which correspond to the Pacific Clade and part of the Old World clade I of Dorsey *et al.* (2013). One unplaced section is *Pachysanthae*, which corresponds to part of the Old World clade I in Dorsey *et al.* (2013). Each section recognized by Dorsey *et al.* (2013) was monophyletic except for *Goniostema* (Fig. 3).

Our phylogeny (Fig. 3) had two topological conflicts with the phylogeny previously presented

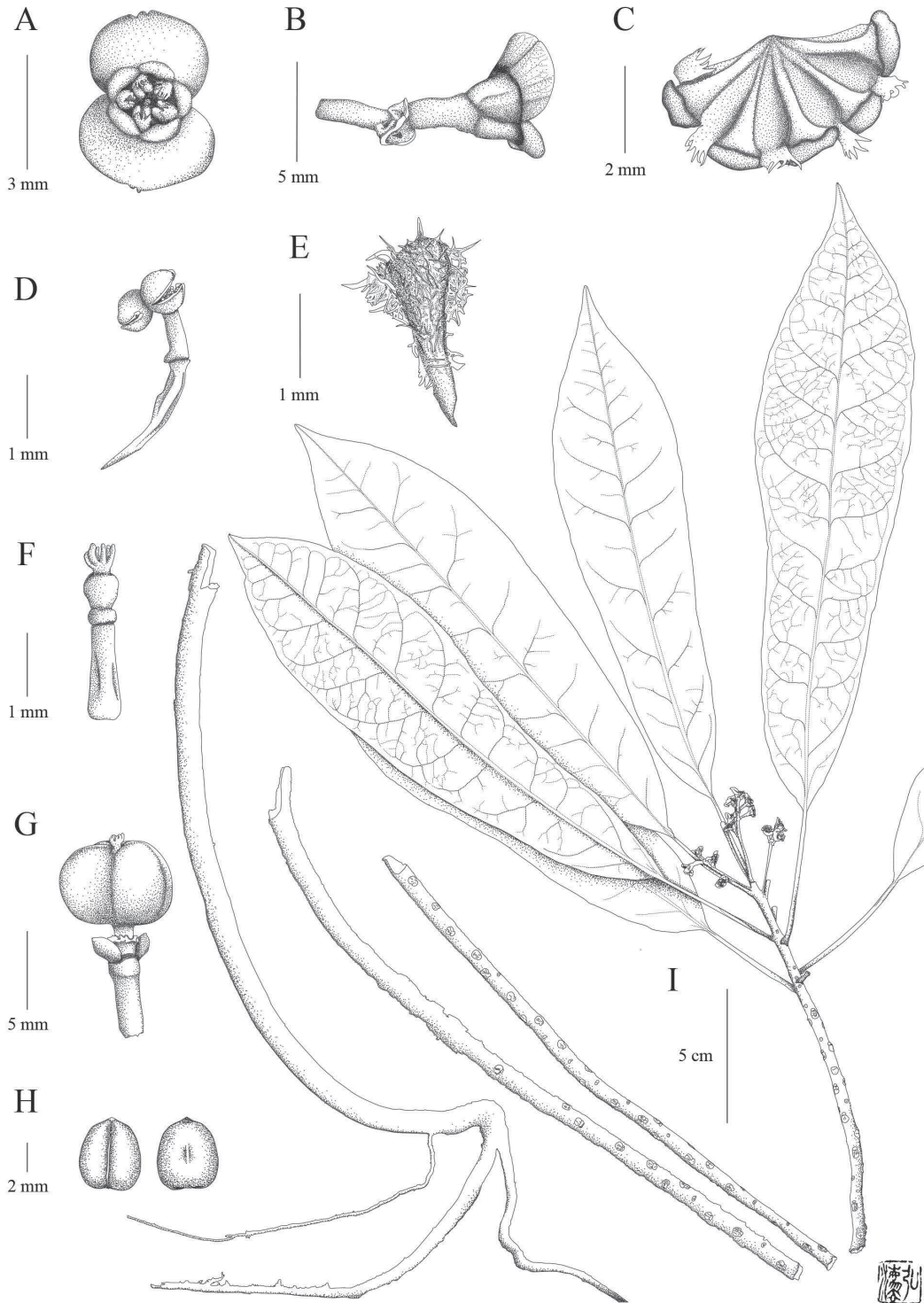


FIG. 4. *Euphorbia bokorensis* H. Toyama & Tagane, sp. nov. A & B, cyathium; C, glands and lobes of involucre; D, staminate flower; E, filamentous structure; F, pistillate flower; G, immature fruit; H, seeds; I, flowering plant (A & G from *Fuse* 6192, FU; B, C, D, E & F from *Toyama et al.* 1912, FU; H & I from *Toyama et al.* 4583, KYO. Drawn by H. Toyama).

(Dorsey *et al.* 2013). First, sect. *Monadenium* is the basal lineage of the Old World clade II, including sections *Bokorenses*, *Denisophorbia*, *Deuterocalli*, *Euphorbia*, *Goniostema*, and *Rubellae*, but is treated as a monophyletic clade with sect. *Euphorbia* in Dorsey *et al.* (2013). Second, sect. *Tanquahuete* was sister to sect. *Calyculatae*, but was sister to sect. *Cubanthus* in Dorsey *et al.* (2013). These conflicts might be due to our use of MAFFT v 7.220 (Katoh & Standley 2013), which is known as one of the best performers for alignments (Pervez *et al.* 2014).

Phytogeography of E. bokorensis and perspectives for future research

The phylogenetic relationship among sections close to *Bokorenses* (Fig. 3) suggests long-distance dispersal from Africa or Madagascar to Southeast Asia. The sister relationship of African and Southeast Asian clades has been observed in 15 taxonomic groups and is explained by the out of India hypothesis (Datta-Roy & Karanth 2009), which proposed that rafting of India carried Gondwanan forms to Asia after the break-up of the Gondwana super continent. However, continental drift occurred 160–40 Ma (Datta-Roy & Karanth 2009), while the oldest fossil of *Euphorbia* are 37.2–33.9 Ma (Behrensmeyer & Turner 2013). It is therefore more likely that the relationships among the sections close to *Bokorenses* are the result of a more recent trans-oceanic dispersal rather than continental drift. Alternatively, *E. bokorensis* may be a relic species that was distributed more extensively in the past (but after 37.2–33.9 Ma), and thereafter retreated to Bokor National Park. In our floristic survey of this area, we found 34 endemic species and 11 widely distributed species from Africa to Asia (Tagane *et al.* in prep.). Comparative phylogeography and population genetics among these species, and further botanical surveys in Indochina, will help in understanding the phytogeography and history of *E. bokorensis*.

Euphorbia bokorensis provides an interesting opportunity for studying the evolution of morphological character and phylogeography of *E.* subg. *Euphorbia* (Fig. 3). In morphology, it shows

the presumed ancestral character states of the clade including sect. *Denisophorbia*, *Deuterocalli*, and *Goniostema* in having alternate leaves, five glands lacking appendages and ecarunculate seeds, but shows differences in having a shrub-like habit and terminal and axillary synflorescences (Horn *et al.* 2012). Phylogeographically, *E. bokorensis* may link Southeast Asia to Madagascar. Further phylogeographic studies may help us to understand the evolutionary history of subgenus *Euphorbia*.

Taxonomic Treatment

***Euphorbia* sect. *Bokorenses* H. Toyama & Tagane, sect. nov.**

This section is the most similar to Sect. *Denisophorbia* in having spineless stems with gland-like stipules, cyathia with usually 5 glands, and ecarunculate smooth seeds. It differs in having unbranched (not sympodially branching) stems.

Typus. *Euphorbia bokorensis* H. Toyama & Tagane

Description. Shrubs, monoecious. Stems subsucculent, smooth, usually unbranched. Stipules gland-like. Leaves alternate, spirally arranged. Synflorescences terminal and axillary, pedunculate, simple or compound cymes. Cyathia bisexual; cyathophylls conspicuous, fused basally, surrounding the involucre; involucre lobes triangular, with feathery tips; glands 5, entire, typically elliptic, without appendages. Capsules smooth. Seeds smooth, ecarunculate.

Species included. *Euphorbia bokorensis* H. Toyama & Tagane

***Euphorbia bokorensis* H. Toyama & Tagane, sp. nov.** —Figs. 4 & 5.

Euphorbia bokorensis resembles *E. boivinii* Boiss. (*E.* sect. *Denisophorbia*) and *E. boissieri* Baill. (*E.* sect. *Goniostema*) in its monoecious cyathia, shrub-like habit, and well-developed oblanceolate leaves, but differs from the former in having unbranched (vs. sympodially branching) stems, larger leaves (13–24 by 3–6 cm vs. to 10 by 4 cm),

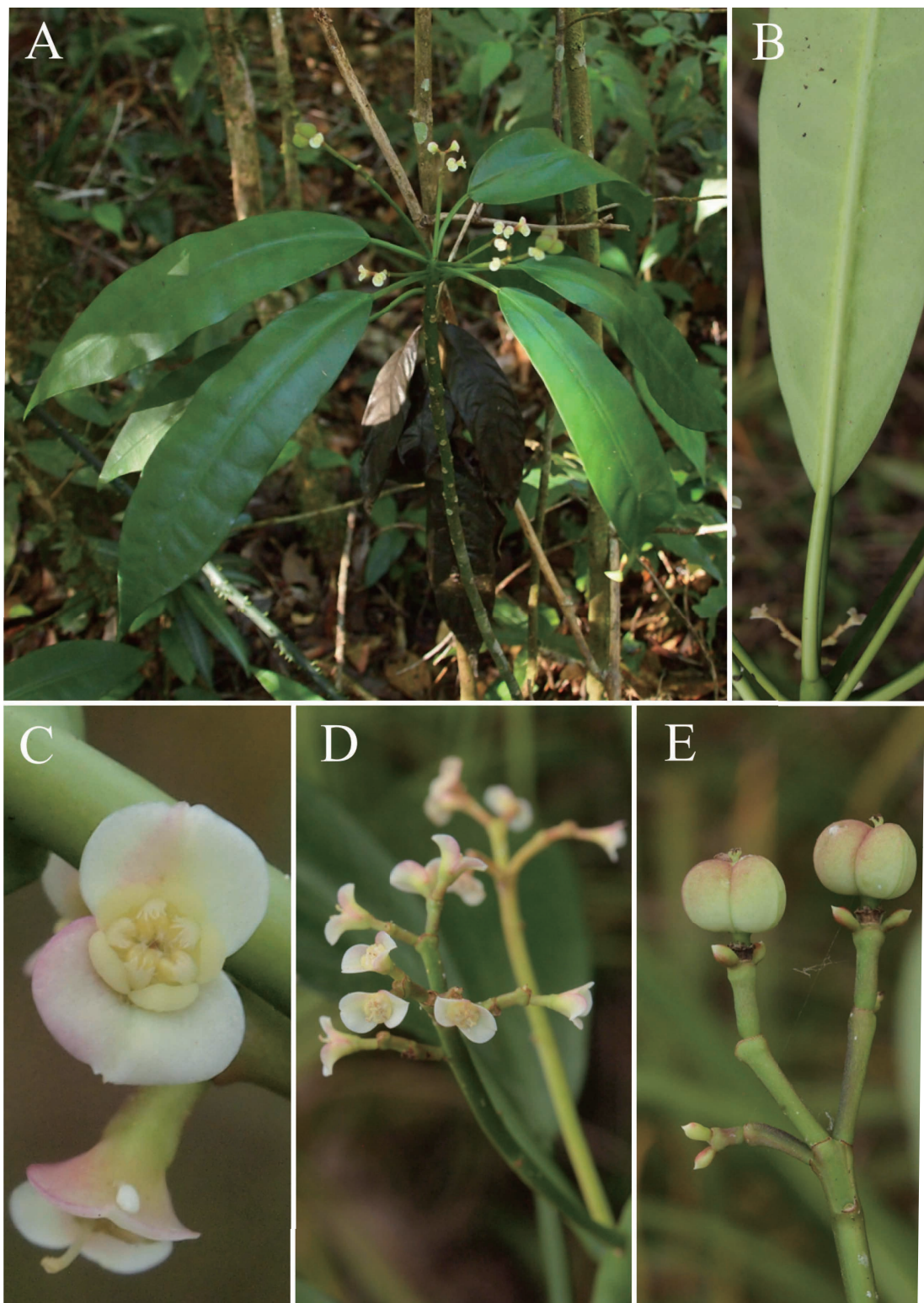


FIG. 5. *Euphorbia bokorensis* H. Toyama & Tagane, sp. nov. A, branch with cyathia; B, abaxial surface of leaf; C, cyathium; D, synflorescence; E, fruits [Photographs by S. Tagane & K. Fuse on 10 December 2011 (A) or 9 December 2013 (B–E)]

cuneate leaf base (vs. attenuate base), and conspicuous (vs. reduced) cyathophylls; from the latter in having smaller leaves (vs. 34 by 6 cm), cuneate (vs. attenuate) leaf base, to 8 cyathia per cyme (vs. to 4 cyathia per cyme), conspicuous (vs. reduced) cyathophylls, and smooth (vs. verrucose) seeds.

Typus. CAMBODIA, Kampot Province: Bokor National Park, evergreen forest near Popokvik waterfall, 917 m alt., 10°39'30.82"N and 104°03'05.14"E, 25 October 2012, Toyama H., Tagane S., Ide T., Chhang P., Nagamasu H. & Yahara T. 4583 [fl. & fr.] (holo- KYO. iso- FU, herbarium of the Forest Administration in Cambodia).

Shrubs, monoecious, ca. 0.7 m tall; stems subsucculent, terete, smooth, usually unbranched (branched when cut), ca. 0.8 cm in diam. bark green when young, greenish-gray when old, glabrous. Stipules ca. 0.2 mm long, gland-like. Leaves alternate, spirally arranged; petioles 2–6 cm long, glabrous; leaf blades carnosae, oblanceolate, (4.5–)13–24 by (1.5–)3–6 cm, base cuneate, margin entire, apex acuminate, membranous when dry, glabrous; venation brochidodromous, secondary veins 10–14 pairs, abaxially slightly prominent when dry, tertiary veins obscure on both surfaces, but becoming faintly visible when dry. Synflorescences terminal and axillary, pedunculate, simple and compound cymes. Cyathia to ca. 8 per cyme, bisexual, 7–10 mm long; peduncle glabrous, 1–4 mm long; cyathophylls 2, conspicuous, orbicular, ca. 4 by 5 mm, fused basally, surrounding the involucre, white or with pink gradation; two axial cyathium buds between cyathophylls and involucre; involucre lobes triangular, ca. 1 mm long, with feathery tips; glands 5, entire, typically elliptic, cream, ca. 0.5 by 1.5 mm, without appendages. Staminate flowers 10, glabrous; pedicels 1–2.5 mm long, filaments ca. 1 mm long, anther lobes yellow, ca. 0.4 mm long. Filamentous structures 5, liner-cuneate, at base of staminate flowers, 2–3 mm long. Pistillate flowers glabrous; pedicel 1.4–2 mm long; reduced perianth forming an annular protuberance at base of gynoeceum, 0.2–0.3 mm long; ovary 3-locular, glabrous; stigma 6-lobed, ca. 0.3 mm long, jointed at base. Capsules obtusely 3-lobed, smooth, ca. 8 mm in diam., greenish red. Seeds 3 per fruit, ca. 5 by 4 mm, ovoid to subglobose, smooth, eca-

runculate.

Distribution. Cambodia (known only from Bokor National Park).

Other specimens examined. CAMBODIA, Kampot Province: Bokor National Park, evergreen forest, 888 m alt., 10°37'15.48"N and 104°05'10.71"E, 10 December 2011, Toyama H., Tagane S., Ide T., Chhang P., Nagamasu H. & Yahara T. 1912 [fl. & fr.] (FU, Forest administration of Cambodia); 602 m alt., 10°36'44.87"N and 104°06'0.79"E, 9 December 2013, Fuse K. 6192 [fl. & fr.] (BKF, FU, Forest Administration of Cambodia).

Phenology. Flowers and fruits were observed in October and December.

Preliminary conservation status. *Euphorbia bokorensis* is known from three localities between 600–900 m alt. Less than 10 mature individuals were observed at each site in moist evergreen forests. It is qualified as critically endangered (CR) using the criterion D of the Red List Categories (IUCN 2012), although additional individuals may be discovered by more through surveys.

Mt. Bokor is considered to be one of the biodiversity hotspots in Southeast Asia. In our field survey, we collected ca. 3,100 specimens including ca. 770 identified species and 22 new species (Tagane *et al.* 2015a,b, Naiki *et al.* 2015, Tanaka *et al.* 2015, Toyama *et al.* 2016, Yahara *et al.* in press). However, recent development for tourism (e.g., construction of a casino and hotels) has threatened biodiversity of the area (Kosterin 2012). *Euphorbia bokorensis* occurs in the understory of moist evergreen forests along and close to the main road from the bottom to the resort to the plateau on the summit. To conserve *E. bokorensis*, as well as other endemic and rare species in Bokor National Park, eliminating habitat destruction by logging and land use change is needed.

Vernacular name. Champa Phnom.

GenBank accession Nos. Toyama *et al.* 1912: AB936028 (*rbcL*), AB936029 (*matK*), LC054296 (*ndhF*), LC054297 (ITS).

Key to the sections of *E. subg. Euphorbia*

Based on the key to the sections of *Euphorbia* subg. *Euphorbia* in Dorsey *et al.* (2013), *Euphorbia bokorensis* is included in *E. sect. Euphorbia* and *E. sect. Monadenium*. However, *E. bokorensis*

is distinguished from those two sections by its spineless stem, 5 similar glands and ecarunculate seeds (Figs. 4 & 5). The revised key is as follows. The numbers shown in the key are same as in Dorsey *et al.* (2013).

Key to the sections of *Euphorbia* subg. *Euphorbia*

- 11. Plants varied in habit, but if geophytic then with glands fused into a horseshoe shape, or with 5 similar glands; widespread (Africa, southern/eastern Asia) 12a
- 12a. Stems usually succulent, angled or tuberculate, generally with distinctive spine shields composed of a horny pad and associated spines; cyathophylls reduced, scale-like..... *E. sect. Euphorbia*
- 12a. Stems spineless or with spines of stipular origin, but without spine shields; cyathophylls conspicuous..... 12b
- 12b. Cyathia with one large horseshoe-shaped or circular gland; seeds carunculate *E. sect. Monadenium*
- 12b. Cyathia with 5 similar glands; seeds ecarunculate..... ***E. sect. Bokorenses***

11 is revised from the lower key of 11 in Dorsey *et al.* (2013) p. 304. 12a & 12b are revised from the upper and lower keys of 12 in Dorsey *et al.* (2013) p. 304.

Euphorbia sect. *Bokorenses* is closely related to *E. sect. Denisophorbia*, *E. sect. Deuterocalli*, *E. sect. Goniostema*, and *E. sect. Rubellae* (Fig. 3). The following is the key to sections.

Key to sections of *Euphorbia* sect. *Bokorenses*, *E. sect. Denisophorbia*, *E. sect. Deuterocalli*, *E. sect. Goniostema*, and *E. sect. Rubellae*

- 1a. Cyathia with 4 equal-sized glands and 2 smaller glands produced by division of a single gland; seeds carunculate *E. sect. Rubellae*
- 1b. Cyathia usually with 5 glands (or 4 or 6); seeds ecarunculate 2
- 2a. Stipules spine-like, papery or comb-like, more or less branched, diversely colored; seeds verrucose *E. sect. Goniostema*
- 2b. Stipules glandular or punctiform, never spiny or papery; seeds smooth 3
- 3a. Stem unbranched; cyathophylls conspicuous; cyathia bisexual *E. sect. Bokorenses*
- 3b. Stem branched; cyathophylls inconspicuous to well developed; cyathia unisexual (rarely bisexual in *E. sect. Denisophorbia*) 4
- 4a. Plants essentially leafless (leaves very small, soon caducous); stipules modified as a waxy or glandular ring around leaf insertion *E. sect. Deuterocalli*
- 4b. Plants with leaves spirally arranged; stipules reduced to glandular dots *E. sect. Denisophorbia*

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