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A new Coryphoid palm genus from Madagascar

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Tahina J.Dransf. & Rakotoarinivo, **gen. nov.** (Arecaceae) is described as a new genus from north-western Madagascar, with a single species ***T. spectabilis*** J.Dransf. & Rakotoarinivo, **sp. nov.** *Tahina* is included within tribe Chuniophoeniceae of subfamily Coryphoideae, based on the strictly tubular imbricate rachilla bracts, the flowers grouped in cincinni with tubular bracteoles, and the stalk-like base to the corolla. This position is corroborated by evidence from plastid DNA. Lamina anatomy is discussed in detail, and similarities with and differences from the other members of Chuniophoeniceae are discussed. Based on the ecological characteristics of the single locality, predictions are made on where else it may occur in Madagascar. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **156**, 79–91.

ADDITIONAL KEYWORDS: Arecaceae – *mat*K – palm – palmate – *rbc*L – *rps*16 intron – *trn*L-*trn*F.

INTRODUCTION

Madagascar has a highly diverse palm flora. In their monograph on the palms of the island, Dransfield & Beentje (1995) recognized 170 species, all but six of which were endemic. Since then, a further five species have been described in the genus *Dypsis* (Dransfield & Marcus, 2002; Dransfield, 2003; Hodel & Marcus, 2004; Britt & Dransfield, 2005; Hodel, Marcus & Dransfield, 2005), together with a new species of the charismatic genus *Beccariophoenix* (Rakotoarinivo, Ranarivelo & Dransfield, 2007), a new species of *Ravenea* (Rakotoarinivo, in press (b)), and 20 further new species in *Dypsis* and *Ravenea* (M. Rakotoarinivo & J. Dransfield, pers. observ.). All the new finds are from the humid rainforests of the eastern escarpment and lowlands. In targeting fieldwork on the island, it has been most productive to concentrate efforts in areas in the eastern high rainfall regions where the palm flora is most diverse (Rakotoarinivo, in press (a)), with the particular target of zones where no palm collections have previously been made. The western parts of Madagascar, where studied, carry a numerically much smaller palm flora, with only a few species that can tolerate the strongly seasonal climate. Species such as the endemic *Bismarckia nobilis* Hildebr. & H.Wendl. and *Dypsis madagascariensis* (Becc.) Beentje & J.Dransf., and the non-endemic *Phoenix reclinata* Jacq. and *Hyphaene coriacea* Gaertn., are widespread and abundant throughout the west. This is the last area in Madagascar in which it would have been expected to find a new palm species, let alone a new genus and a representative of an evolutionary line not previously known to exist in Madagascar.

On 5th December 2006, Bruno Leroy, resident in Madagascar and a palm enthusiast, posted photographs of an unidentified palm on PalmTalk, the interactive bulletin board of the International Palm Society (http://www.palms.org). The photographs, taken by Xavier and Nathalie Metz in western Madagascar in September 2006, showed a massive single-stemmed fan-leaved palm with a huge terminal compound inflorescence towering above the leaves, growing in forest at the foot of '*tsingy*' (karst limestone). The Metz family had first seen the palm in August 2005 while on a family picnic but, in the

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*Corresponding author. E-mail: j.dransfield@kew.org absence of inflorescences, assumed it to be *Borassus*. At the resolution at which the photographs were posted, it was not possible to see many details of the inflorescence branches, but the overall impression was highly reminiscent of the Asiatic palm genus *Corypha* (Coryphoideae: Corypheae) (Dransfield *et al.*, 2005). The photographs aroused considerable interest and speculation. On 7th December, John Dransfield was contacted by Matt Patricelli of San Diego, a frequent contributor to the message board, and invited to comment on the identity of the palm in the message thread. Suggestions that it was *Borassus* (two species in Madagascar) were rapidly discounted as the inflorescences in *Borassus* are interfoliar and completely different in structure. Could the palm be a species of *Corypha*, perhaps introduced during colonial days and surviving since? The remoteness of the locality and the palm's occurrence in what appeared to be natural vegetation seemed to negate the idea of introduction. Photographs of the crown in more detail showed that the petioles are unarmed, whereas all species of *Corypha* have spiny petioles, a difference that would not necessarily preclude its belonging to *Corypha*. Thus, the matter rested until, in January, Mijoro Rakotoarinivo visited the site of the palm, together with Bruno Leroy and the Metz family. Here, he was able to make the first scientific collection of the palm, comprising vegetative material including leaf samples in silica gel, and parts of the inflorescence, by this time already in mature fruit. Once the specimens reached Kew, they were examined in detail. Fragments of the petiole and lamina were dispatched to Jack Fisher and Jay Horn in Fairchild Tropical Botanic Garden for anatomical study, and the leaf sample in silica gel was handed over to Ross Bayton for DNA extraction and analysis at the Jodrell Laboratory, Kew.

MATERIAL AND METHODS

Herbarium material (*Rakotoarinivo RMJ337*) was collected following the recommended procedure of Dransfield (1986). Mature fruit was collected in 70% alcohol. Lamina material was collected in silica gel for subsequent DNA extraction.

Geographical information systems

In order to define the bioclimatic requirements and potential distribution of the new palm, its current occurrence was analysed with Maxent 2.2 using ecological variables, including different parameters such as temperature, precipitation, topography and geology. As a statistical program for species distribution modelling, Maxent calculates the probability of occurrence (from 0 to 100) of one species in each pixel of 30 × 30 m resolution throughout the study area. At the same time, it identifies the most important factors governing the distribution of one taxon by giving a training gain for each variable selected; one factor is considered as important if the species displays a strong sensibility in relation to it, i.e. a high value of the test gain (Phillips, Anderson & Schapire, 2006). The variables having the most influence in the model are then hypothesized to be the most significant for the distribution of the palm.

Anatomy

All material investigated was derived from the single herbarium specimen: *Rakotoarinivo RMJ337* (K). Lamina anatomy was examined from a portion of dried leaf segment collected *c*. 2–3 cm distal to the base of the sinus of a medially positioned fold. Petiole anatomy was taken from the distal region near the lamina. All material was rehydrated in a 5% solution of Contrad 70 (Decon Laboratories, King of Prussia, PA, USA) for 24 h at 60 °C (Schmid & Turner, 1977), and subsequently fixed in formalin–acetic acid–alcohol (FAA) for 1 week. Prior to sectioning, all lamina material was desilicified in a 25% HF solution for 12–16 h, scraped or sectioned, stained with aqueous toluidine blue O, and mounted in Karo (high fructose corn) syrup. Other sections were stained for lignin using the phloroglucinol test, or for cutin using Sudan IV (Ruzin, 1999). Whole mounts of lamina pieces, not treated with HF, were cleared in a 5% NaOH solution at 70 °C, stained with safranin, dehydrated, and mounted in Permount (Fisher Scientific, Fair Lawn, NJ, USA).

Molecular study

DNA sequence data were gathered to match the study of Asmussen *et al*. (2006), the most comprehensive phylogenetic account of palms published to date. DNA was extracted from silica gel-dried material of the new palm (*Rakotoarinivo 337*, K) using standard protocols (Doyle & Doyle, 1987). Four plastid DNA regions (*mat*K, *rbc*L, *rps*16 intron, *trn*L-*trn*F) were sequenced following Asmussen *et al*. (2006).

The DNA sequences (EMBL accession numbers AM779614, AM779615, AM779616, AM779617) were incorporated into the four-gene alignment of Asmussen *et al*. (2006). Our analyses were focused on a subset of taxa in the alignment comprising subfamily Coryphoideae and an appropriate choice of outgroups from the remaining four subfamilies, following the current classification of palms (Dransfield *et al*., 2005). The data were analysed using maximum parsimony as implemented in PAUP* version 4.0b10 (Swofford, 2002) following a conventional search strategy [heuristic search, 100 replicates, random taxon addition sequence, characters unordered and equally weighted, tree bisection–reconnection (TBR) branch swapping, zero length branches collapsed when their maximum length equals zero]. Support values were estimated by analysing 1000 bootstrap replicates [one heuristic search per bootstrap replicate, simple taxon addition sequence, subtree pruning–regrafting (SPR) branch swapping, saving up to five trees per replicate, other options as above].

MORPHOLOGY

It was instantly obvious that the palm did not belong to the genus *Corypha*. The structure of the rachillae, the flower-bearing branches, was completely different, with tightly sheathing, completely tubular imbricate rachilla bracts, highly reminiscent of the Asiatic genus *Chuniophoenix* (Coryphoideae: Chuniophoeniceae) (Dransfield *et al*., 2005), whereas, in *Corypha*, the rachillae are naked, bearing minute non-tubular bracts that subtend a cincinnus of flowers. Unfortunately, the only flowers present in the single collection were mummified and may represent old buds, just preanthesis. However, there was sufficient structure visible to show that the flowers were arranged in a cincinnus of two or possibly more flowers, included within the subtending rachilla bract, each flower enclosed by a tubular bracteole, an arrangement very similar to that of *Chuniophoenix*. Furthermore, the receptacle and corolla base were adnate to form a stalk on which the free corolla lobes, six stamens, and gynoecium sat. Such pedicelliform corolla bases are known in all genera of Chuniophoeniceae and Boraseae. The fruit structure was also very different from that of *Corypha*, with basal embryo and ruminate endosperm as opposed to the apical embryo and homogeneous endosperm of *Corypha*. The leaf blade was unlike any other fan palm known to us, having a hierarchy of folds (see Figs 1E, 3C), rather than the usual arrangement of folds of equal size.

All morphological evidence indicates that the palm represents a hitherto undescribed genus belonging to Chuniophoeniceae. Differences between the new palm and other members of Chuniophoeniceae are presented in Table 1.

DESCRIPTION OF THE NEW GENUS AND SPECIES

TAHINA J.DRANSF. & RAKOTOARINIVO, **GEN. NOV.**

Diagnosis: Palma grandis hapaxantha, foliis costapalmatis, petiolo inerme, basin fissure triangulare, lamina induplicate, plicatis aliquot ordinium; inflorescentia terminalis suprafoliaris, numerosis inflorescentiis lateralibus composita, rachillis bracteas tubulosas, imbricatas ferentibus, cincinnos florum subtendentibus; flores hermaphroditi; calyx membranaceus, tubulosus, trilobus, lobis brevibus; corolla basin ad receptaculum connata, distale petalis imbricatis; stamina 6; gynoecium syncarpum, tricarpellatum, triovulatum; fructus vestigio stigmatum apicali, epicarpio laeve, mesocarpio carnoso, fibroso, endocarpio membranaceo; endospermium ruminatum, embryone subbasali.

Table 1. The genera of Chuniophoeniceae compared

	Tahina	*Nannorrhops*	*Kerriodoxa*	*Chuniophoenix*
Habit	Massive solitary tree palm	Moderate, clustering shrubby palm	Moderate solitary tree palm	Slender clustering shrubby palm
Stem	Erect, unbranched	Erect or procumbent, dichotomously branched	Erect, unbranched	Erect, unbranched except at base
Petiole base	Split	Split	Entire	Split or entire
Hastula	Adaxial and abaxial present	Absent	Adaxial present	Absent
Plications	Hierarchy of plications	Uniform	Uniform	Uniform
Indumentum	Blade ± concolorous	Blade ± concolorous	Blade strongly discolorous	Blade ± concolorous
Flowering behaviour	Hapaxanthic	Hapaxanthic	Pleonanthic	Pleonanthic
Inflorescence branching	3 orders	4 orders	4 orders	Spicate or up to 2 orders
Endosperm	Ruminate	Homogeneous	Ruminate	Homogeneous or ruminate
Embryo position	Basal	Basal	Sub-basal	Basal
Germination	Remote tubular			
Eophyll	Palmate	Entire lanceolate	Entire lanceolate	Entire lanceolate

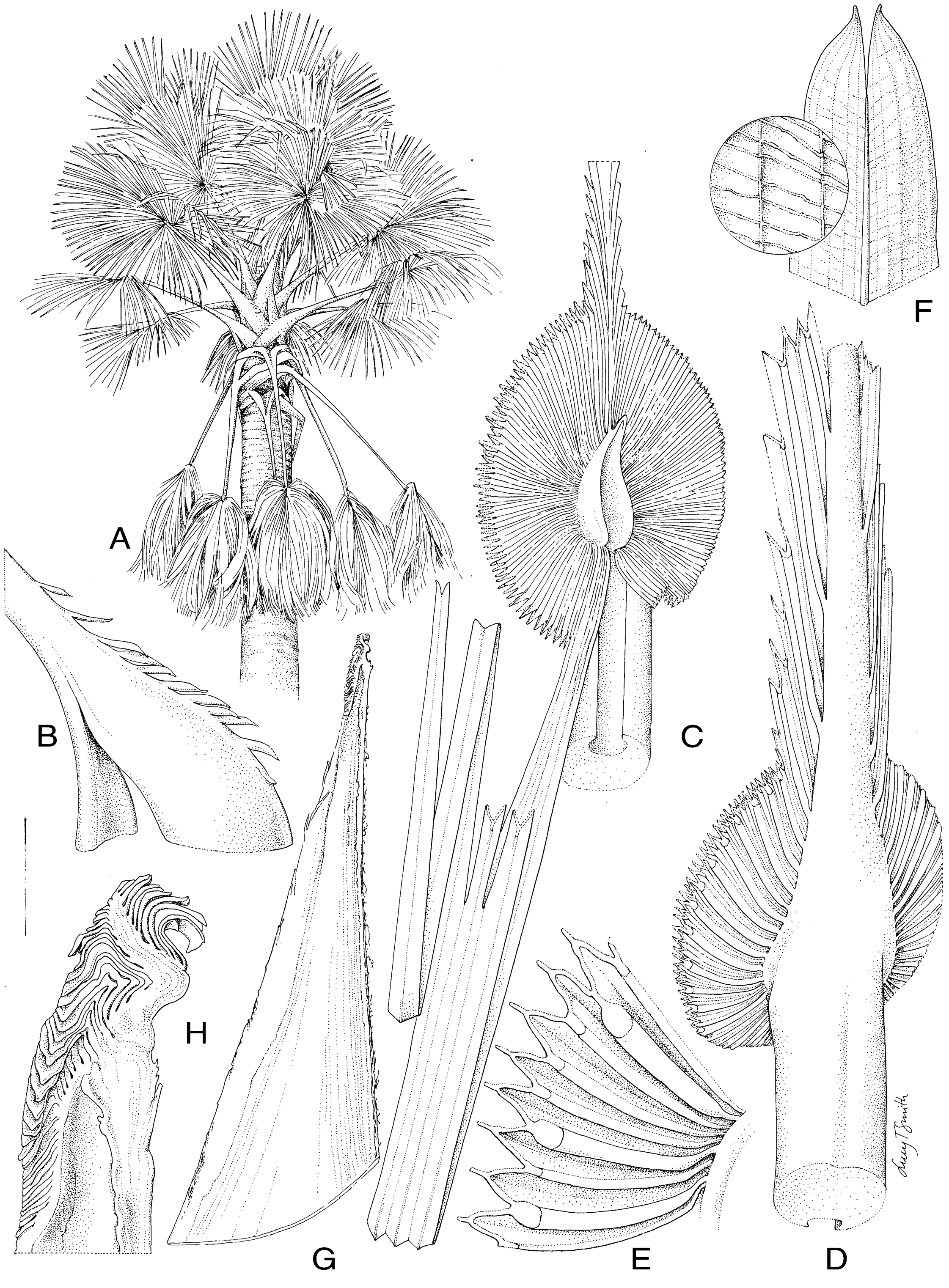

Figure 1. ***Tahina spectabilis***: A, habit; B, petiole base showing central cleft; C, base of lamina, adaxial view; D, base of lamina, abaxial view; E, detail of base of folds, showing hierarchy of different sizes and positions; F, detail of tip of mid-lamina segment with enlargement to show transverse veinlets; G, reduced leaf subtending an inflorescence branch; H, tip of reduced leaf, enlarged, showing aborted, contorted lamina. A, B, from photographs; C–H, from *Rakotoarinivo RMJ337* (K). Drawn by Lucy T. Smith. Scale bar: A, 4 m; B, 25 cm; C, D, G, 6 cm; E, F, 3 cm; H, 1.5 cm.

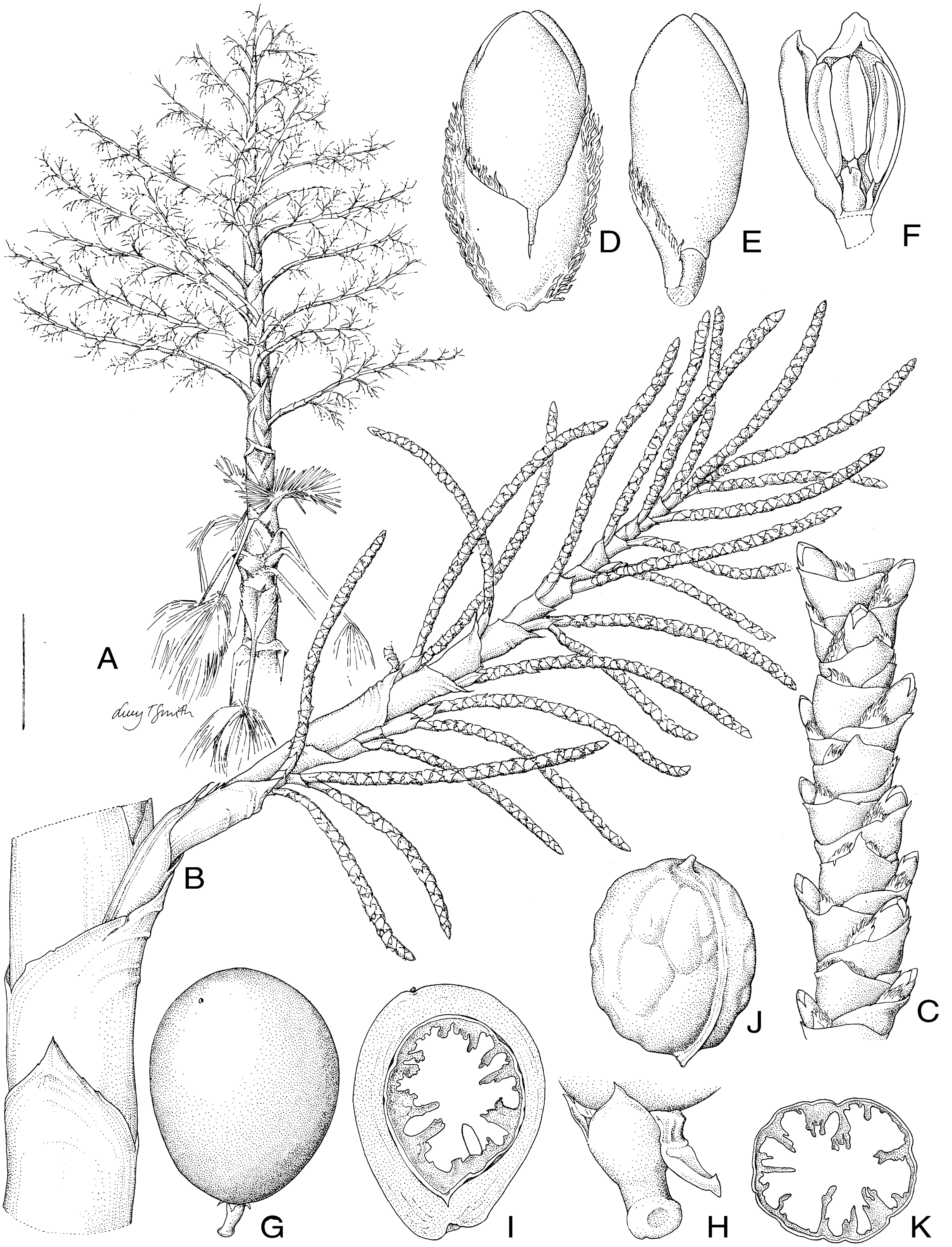

Figure 2. ***Tahina spectabilis***: A, flowering habit showing compound inflorescence composed of lateral inflorescences; B, part of lateral inflorescence; C, portion of rachilla; D, mummified flower bud enclosed with bracteole; E, mummified flower bud, bracteole mostly removed, showing calyx; F, flower, sepals and one petal removed; G, mature fruit, borne on stalk; H, detail of fruit base showing sepals and one remaining petal; I, fruit in section; J, endocarp; K, seed in cross-section. A, from photographs; B–K, from *Rakotoarinivo RMJ337* (K). Drawn by Lucy T. Smith. Scale bar: A, 1.5 m; B, 4 cm; C, 7 mm; D, E, F, 2.5 mm; G, H, J, K, 1.5 cm.

Typus: Tahina spectabilis J.Dransf. & Rakotoarinivo.

Description: Massive, solitary, unarmed, hapaxanthic, hermaphroditic, tree palms. STEM erect, closely ringed with leaf scars. LEAVES induplicate, costapalmate, marcescent in immature individuals, tending to abscise under their own weight in trunked individuals; sheath with a conspicuous triangular cleft below the petiole, the margins tending to erode into broad lobes; petiole massive, long, covered with white wax, adaxially deeply channelled, abaxially rounded, margins smooth, adaxial hastula well developed, abaxial hastula a hard low rather irregular crest at the base of the lamina; blade divided to *c*. one-half of its radius into multifold segments, these in turn more shallowly divided into single-fold segments, themselves shallowly divided along the abaxial folds, main abaxial ribs of blade very conspicuous, very crowded at the base of the blade, some much more robust than others, the less robust ribs tending to be inserted in a more adaxial position compared with the robust ribs; segments with prominent longitudinal veins, abundant regularly arranged transverse veinlets (Fig. 3D), glabrous, the undersurface of the blade with thin white wax. INFLORESCENCES above the leaves (Fig. 3B, E), subtended by reduced scale-leaves, forming a massive compound inflorescence-like structure, individual inflorescences branched to three orders, all branches ending as rachillae; prophyll of first-order branches two-keeled, empty; bracts of first-order branches conspicuous, tubular, with short triangular limbs, mostly entire but sometimes splitting and tattering, densely covered with thick white tomentum, each subtending a second-order branch; second-order branches crescentic in cross-section at the base, bearing a tubular, two-keeled prophyll some distance from the base, subsequent bracts strictly tubular, striate, with triangular sometimes tattering limbs, covered in caducous white tomentum, each subtending a branch of the third order; basal third-order branches bearing branches of the fourth order; rachillae straight, cylindrical, rather rigid, bearing very conspicuous distichously arranged, tubular, striate, overlapping, ± glabrous rachilla bracts, each enclosing a cincinnus of up to two flowers (?sometimes more); first bract on cincinnus tubular, two-keeled, two-lobed, the wings densely woolly hairy, subtending a stalked flower; second bract on the cincinnus similar, it too subtending a flower, in the distal part of the rachilla a second flower sometimes lacking, distal to the second flower a few empty tubular bracts. FLOWERS ?hermaphroditic, borne on short stalks; distal to this, the flower with a stalk formed by the base of the calyx and the receptacle; sepals 3, membranous, connate in the basal half, the lobes lanceolate with triangular tips; petals 3, basally connate and adnate to the receptacle to form a stalk-like base, the free lobes ± boat-shaped, basally imbricate, the margins usually inrolled, apically somewhat cucullate; stamens 6, filaments very short, tapering from a fleshy base; anthers elongate, basifixed, introrse; gynoecium tricarpellate, syncarpous, triovulate, ovary pyramidal, angled and grooved, style short, slightly three-grooved, stigma scarcely differentiated, ovule form unknown. POLLEN not studied. FRUIT (Fig. 3F) broadly ellipsoid to obovoid, borne on the stalk-like corolla base, single-seeded with apical stigmatic remains; epicarp smooth, glabrous, mesocarp moderately thick, spongy, with few longitudinal fibres, endocarp thin, crustaceous, with a pronounced longitudinal groove and a short apical beak, and irregularly anastomosing grooves. SEED globose, laterally attached with an elongate hilum, and with deep grooves corresponding to the rapheal bundles, endosperm strongly ruminate, without a central hollow; embryo subbasal. GERMINATION remote-ligular; eophyll palmate. CYTOLOGY unknown.

Etymology: Tahina – Malagasy for ‘blessed’ or ‘to be protected’; also one of the given names of Anne-Tahina Metz, the daughter of the discoverer of the palm.

TAHINA SPECTABILIS J.DRANSF. & RAKOTOARINIVO, **SP. NOV.** (FIGS 1–3)

Diagnosis: Palma solitaria grandis hapaxantha ad 10 m alta, tronco ad 50 diametro; inflorescentia terminalis composita ad 4 m alta; fructus ad 3.5 × 2.7 cm, endospermio ruminato.

Typus: Madagascar, Mahajanga, Analalava, Antsanifera, Antsingilava, *Rakotoarinivo et al. RMJ337* (Holotypus K; isotypi BH, MO, P, TAN).

Description: Solitary tree palm, 4–10 m tall. STEM bulbous at the base, diameter at breast height 50 cm, internodes 8–10 cm, nodes 1.5–3.5 cm. LEAVES marcescent in young individuals, costapalmate, 12–18 in the adult crown, leaf sheath 80–100 × 52–58 cm, fibrous in the margin, petiole 3.50–3.80 m long, abaxially deeply channelled, margin smooth, proximal part 10.5–12 cm in diameter, distal part 6–8.5 cm in diameter, costa *c*. 1.60 m long, lamina 3.80–4.10 m in diameter, divided to *c*. one-half the radius into 110–122 induplicate segments, thinly covered with white tomentum on the abaxial surface, segment apices bifid. INFLORESCENCE terminal, compound, 4 m long, each lateral unit branched to three orders, 21 first-order branches up to 2.50 m long, tubular bract 9–25 cm long, open at 6–9 cm in the distal part, covered with white caducous indumentum, rachillae 10–15 cm. FRUITS broadly ellipsoid to obovoid, 25–30 × 20–22 mm, borne on the stalk-like corolla

Figure 3. A, The '*tsingy*' at Antsingilava, Analalava, with crowns of ***Tahina spectabilis***. B, Individual of ***T. spectabilis*** just after anthesis. C, Abaxial surface of lamina base showing folds. D, Detail of transverse veinlets. E, Inflorescence. F, Infructescence. All photographs by Nathalie Metz.

base, 5–7 × 2 mm, perianth persistent, green yellowish at maturity, 3–3.5 cm long, 2.3–2.7 cm wide, stigmatic remaining apical, pericarp fleshy, endocarp 13–17 × 17–22 mm. SEED globose, 1.8–2.2 cm long, 1.4–1.8 cm wide, with anastomosing grooves, endosperm strongly ruminate.

Types: MADAGASCAR. Mahajanga, Analalava, Antsanifera, Antsingilava, 14°45′01″S, 47°25′53″E, altitude 9 m, 19.i.2007. *Rakotoarinivo et al. RMJ337* (holotype K, isotypes BH, MO, P, TAN).

Distribution: Tahina spectabilis is known only from one locality in Analalava district, in the north-west of Madagascar. In the gently rolling hills and flatlands of the region, now dominated by anthropogenic grasslands, there is a small outcrop of '*tsingy*', karst Tertiary limestone, running approximately

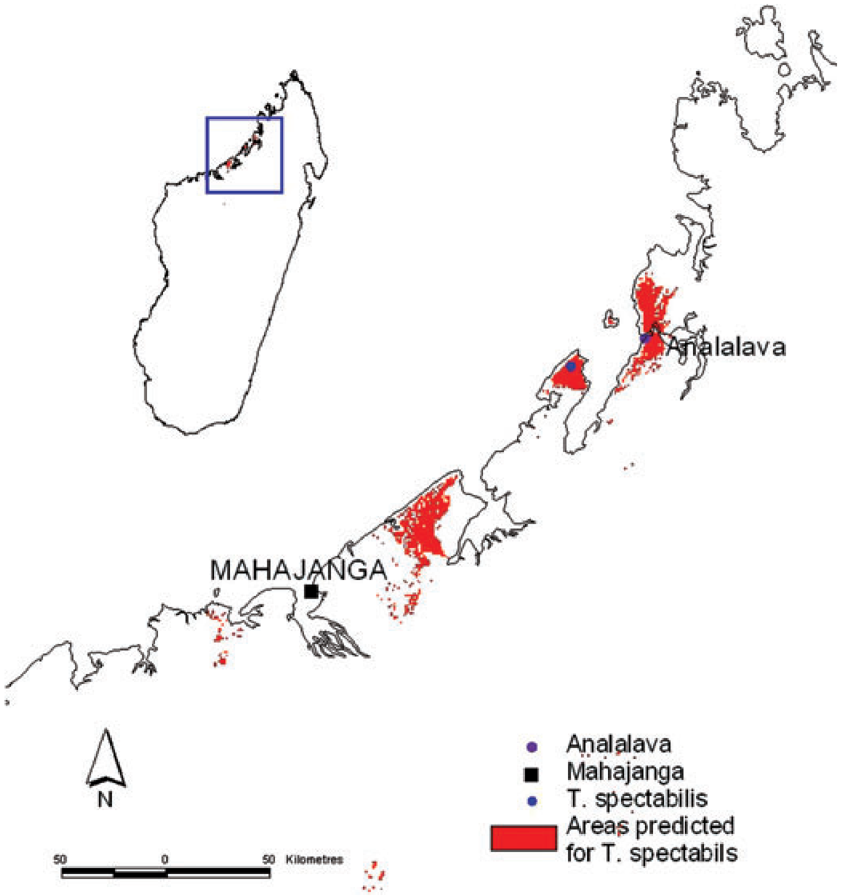

Figure 4. Actual and predicted occurrences of ***Tahina spectabilis***.

north–south and about 250 m long, carrying a seminatural vegetation (Fig. 3A). The outcrop is visible in satellite imagery at Google Earth and the grey crowns of the palm are even visible, although blurred.

Ecology: Although the annual precipitation is estimated to be about 1600 mm, the climate of this locality is classed as dry and warm. Drought is manifest because of the eight dry months, the mean annual temperature around 27 °C, and the very strong insolation throughout the year (source: Bioclim, 2006; http://www.bioclim.org). Moreover, the high permeability of the limestone may also decrease the moisture rate during the warmest period of the day. At the same time, edaphic conditions in the *tsingy* are harsh; soil scarcely exists in many places, and leaf litter is always thin and poorly decomposed. The vegetation is a low woodland dominated by xerophytes and succulents, such as species of *Euphorbia, Aloe*, and *Kalanchoe*. About 90 individuals were seen, most of them growing on the sandstone plain at the edge of the *tsingy*, and a single, short individual was also found near the village of Antsanifera. The sandstone plain is covered by herbaceous savannah with abundant individuals of the palm *Hyphaene coriacea*, and environmental conditions are totally different. The humidity rate is much higher as water stagnates during the humid season. Individuals of *T. spectabilis* on these flats are robust and often occur in groups of two to five trunks. The individual sampled was on this plain.

Analysis of the potential distribution of *T. spectabilis* using Maxent 2.2 identified only the coastal region of the north-west, between Analalava and Mitsinjo (Fig. 4), as a suitable habitat. This small predicted area can primarily be explained by the high sensibility of this palm to temperature variations during the coldest and driest season (June–September) as well as the geology type (Fig. 4; training gain, 2.7–3.2). The coastal region in which the palm is found is always much warmer than the adjacent inland area. Temperatures between June and September in the coastal region do not fall below a mean of 25 °C and a minimum of 19 °C, whereas those inland may decrease to 22 and 16 °C, respectively. These temperature differences over a small distance seem to be critical, and may inhibit the colonization of new areas.

Relationships: The induplicate fan leaf clearly places *Tahina* in subfamily Coryphoideae. Within Coryphoideae, the syncarpous gynoecium is found in the clade that includes Chuniophoeniceae, Caryoteae, Corypheae, Sabaleae, and Borasseae (here termed the syncarpous clade, see Fig. 6). The Caryoteae have pinnate or doubly pinnate leaves and unisexual flowers arranged in triads. The Borasseae are all dioecious and have fruits with hard, sometimes ornamented, endocarps that usually have apical pores, and seeds with apical embryos. The Corypheae have hermaphroditic flowers arranged in cincinni subtended by minute incomplete rachilla bracts, and seeds with apical embryos. The strictly tubular imbricate rachilla bracts and pedicelliform corolla bases of the new palm are found only in tribe Chuniophoeniceae (Dransfield *et al*., 2005), a small well-supported tribe comprising three genera: *Nannorrhops* in Arabia, Iran, Afghanistan, and Pakistan; *Kerriodoxa* in southern Thailand; and *Chuniophoenix* in Vietnam, southern China, and Hainan. The three genera display unusual morphological diversity, particularly in vegetative characters, yet molecular evidence strongly supports their sister relationships. *Nannorrhops* (monotypic) is a shrubby clustering and dichotomously branching hapaxanthic palm of desert regions, with a leaf lacking a hastula; the large compound inflorescence is suprafoliar. *Kerriodoxa* (monotypic) is a relatively large, single-stemmed pleonanthic palm of the forest undergrowth with a single stem; it has a well-developed hastula and inflorescences are interfoliar. The two or three species of *Chuniophoenix* are either slender reed-like or moderate shrubby pleonanthic palms of forest undergrowth with clustering stems, leaves lacking hastulae, and interfoliar inflorescences. Table 1 displays the differences between these three genera and *Tahina*.

LEAF ANATOMY

General: Dorsiventral symmetry (Fig. 5A, B).

Epidermis: Trichomes exclusively abaxial, frequent, scattered; persistent bases elliptical in surface view, depressed in pits; four to eight cells in diameter (Fig. 5D). Hypodermis immediately adjacent to trichome bases with an extra layer (two-layered); these layers locally suberoliginified (Fig. 5E). Adaxial epidermal cells with regularly sinuous anticlinal walls; rectangular, proximodistally elongate (0.5)1–4(5) times as long as wide; not differentiated when positioned over costae (Fig. 5I). Abaxial epidermal cells like those adaxially; somewhat proportionately shorter (Fig. 5D).

Stomata: Scarcely sunken. Occasional adaxially where scattered intercostally; abundant abaxially, in irregular proximodistal rows without reference to costae (Fig. 5D, I). Cuticular ledges of guard cells are approximately equivalent in size and discrete. Terminal subsidiary cells are circular to somewhat elliptically mediolaterally extended in surface view, partly overarching the guard cells. Lateral subsidiary cells with additional inner and outer cuticular ledges paralleling those of the guard cells.

Hypodermis: Adaxially two- to three-layered (Fig. 5A–C), thick-walled but unlignified. Adaxial-most layer with cells strongly mediolaterally extended, appearing narrowly rectangular in surface view, organized into distinct proximodistal files; other layers with cells broadly mediolaterally rectangular to nearly circular in surface view, approximately isodiametric. Abaxially one-layered (Fig. 5A, B); cells commonly rectangular, mediolaterally extended in surface view. Substomatal chamber formed by two, proximodistally extended, C-shaped cells.

Mesophyll: Adaxial palisade well-differentiated, mostly four-layered, cells ad-/abaxially elongate. Abaxial spongy mesophyll five- to eight-layered (Fig. 5A, B).

Vascular bundles and venation: Largest (and very rare) proximodistal vascular bundle with one large metaxylem vessel and one phloem strand; bundles without wide metaxylem vessels predominate; not separable into discrete size classes (Fig. 5A–C). Proximodistal vascular bundle always bridged to (only) adaxial surface layer by extra layer of relatively inflated hypodermal cells (Fig. 5B). Bundle sheath with an adaxial buttress of thick-walled, lignified fibres 3–6(7) layers deep. Laterally, a uniseriate layer of radiate, thick-walled (but unlignified), inflated parenchyma cells abruptly substitutes fibres in the outer bundle sheath, and completes it abaxially (Fig. 5A, B). Transverse commissures are most commonly two to three times wider – hence more prominent – than the proximodistal vascular bundles (Fig. 5K). All commissural veins are positioned abaxial to the proximodistal vascular bundles and adaxial to the solitary, abaxial fibres (Fig. 5C). Commissures are each circular to depressed elliptical in cross-section, with a thick, strongly lignified fibre sheath of (3)4–6(7) layers, and a depauperate central xylem strand surrounded completely or principally adaxially by two to six phloem strands (Fig. 5C). Largest transverse commissures extend from the midrib to the segment margin (Fig. 5J); they diverge from the midrib at an approximately 90° angle, with a slightly sinuous course. Branching uncommon (Fig. 5K); reticulation rare and only in the vicinity of the midrib.

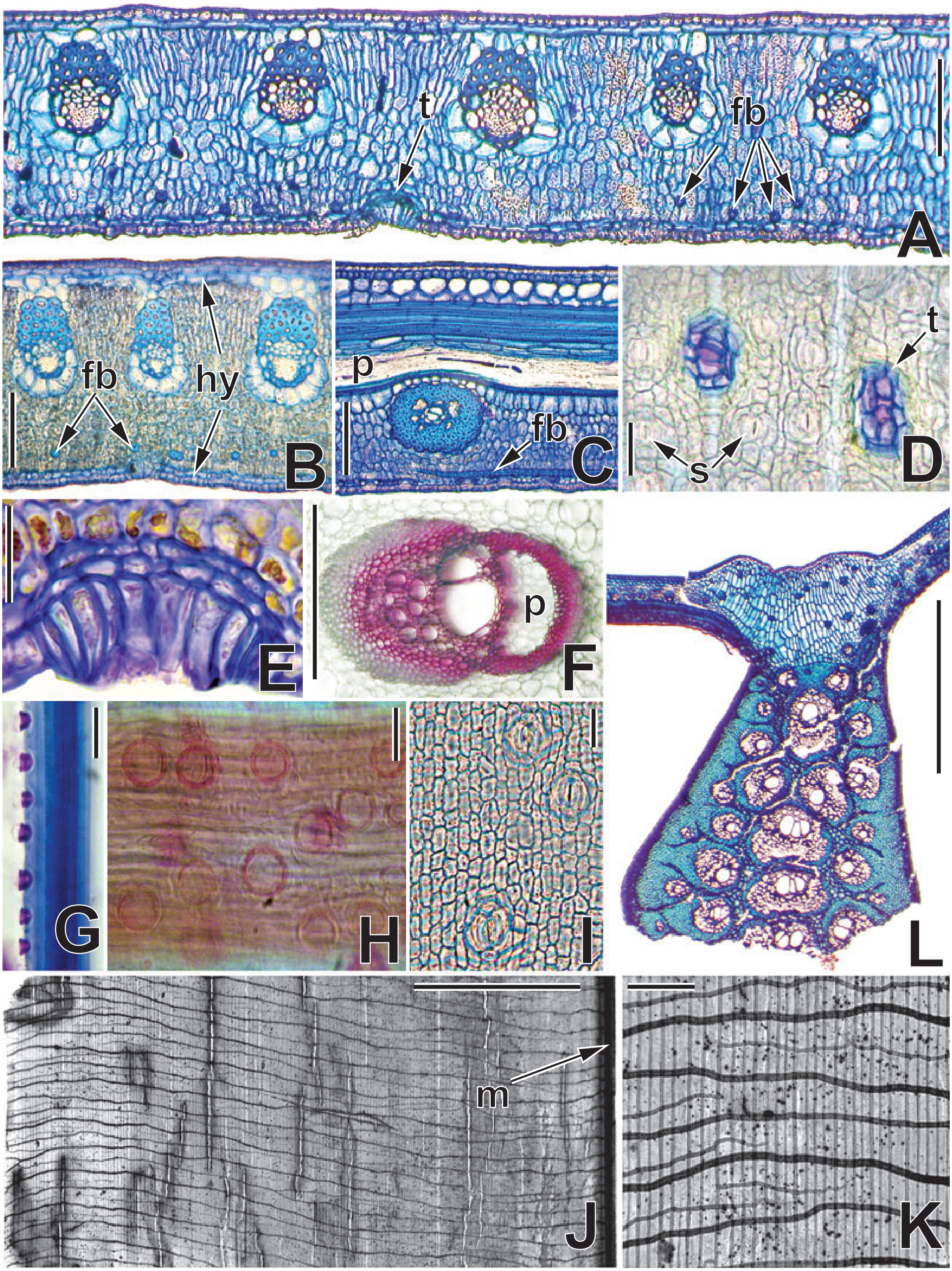
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Figure 5. A–K, Leaf lamina of ***Tahina spectabilis***; sections of lamina with adaxial surface towards top of figure. A, B, Transverse sections of lamina from thick and thin parts of same leaf; only proximodistal veins present. C, Longitudinal section of lamina; proximodistal vein in longitudinal view and transverse commissure in transverse view. D, Abaxial epidermis in surface view; cells of persistent trichome bases stained deep violet. E, Longitudinal section of trichome base with adjacent double hypodermis. F, Vascular bundle of petiole stained with phloroglucinol. G, Stegmata along proximodistal fibre bundle in side view; wall of individual silica cells unlignified and stained red with toluidine blue; silica body barely visible. H, Stegmata along transverse commissural fibre bundle in surface view; wall of individual silica cells lignified and stained red with safranin; silica body is central clear region. I, Adaxial epidermis in surface view. J, K, Cleared lamina. J, Half of a leaf segment, abaxial rib (midrib) removed at its insertion with the lamina (left side). Margin (m) at far right with marginal veins intensely stained. Note many large transverse commissures with uninterrupted course from midrib to segment margin. K, Detail of clearing showing relative sizes of proximodistal and transverse vasculature. L, Abaxial rib in transverse section; part of external rib lost in processing. Note peripheral fibre sheath. Scale bars: 100 μm in A–C; 25 μm in D, E, G–I; 500 μm in F; 1 mm in K, L; 10 mm in J. Abbreviations: fb, solitary fibre; hy, hypodermis; m, margin of segment; p, phloem region; s, stomata; t, trichome base.

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Non-vascular fibres: Always absent from the adaxial half of the lamina. Abaxially present, and here usually of solitary fibres free in the mesophyll; thick-walled, lignified (Fig. 5A–C).

Stegmata: Silica bodies always spherical and minutely spinulose. Present in single files along fibres of the adaxial buttresses of the proximodistal vascular bundles. Basal cells cupulate, unlignified (Fig. 5G). Also associated with the transverse commissures, where common and scattered without apparent organization; cells spherical, very thick-walled, lignified; much wider than the associated fibre cells (Fig. 5H). Silica bodies here are generally larger than those of the adaxial fibre buttresses (Fig. 5G, H). Absent from solitary, abaxial fibres.

Abaxial rib: Almost wholly occupied by numerous (*c*. 30) moderate to very large vascular bundles which are nearly confluent with one another on account of the extreme thickness of their fibre sheaths. Ground parenchyma is scanty; thick-walled and lignified. Fibre sheaths of the most peripheral vascular bundles are completely confluent and form a complete, abaxial fibre sheath, 12–20 cells thick, around the perimeter of the midrib to the level of the expansion tissue (Fig. 5L).

Petiole anatomy: Vascular bundles with one or two large metaxylem vessel(s) and always one phloem strand (Fig. 5F).

Significance of anatomy: Although containing only four genera and five species, Chuniophoeniceae arguably displays as great a range of anatomical diversity as any clade within Arecaceae recognized at tribal rank. Detailed documentation and interpretation of the comparative anatomy of Chuniophoeniceae are forthcoming in a separate study. Each genus possesses clear, diagnostic autapomorphies. *Tahina* is at once distinguishable from all other coryphoid palms in having non-vascular fibres mostly solitary, always free in the mesophyll, and confined to the abaxial half of the lamina. Within Chuniophoeniceae, it is unique in having stegmata associated with the transverse commissures, and in that the abaxial hypodermis is both suberoliginified and has an extra layer adjacent to trichome bases (i.e. it is locally two-layered).

Leaf anatomical evolution is evidently homoplasious within Chuniophoeniceae. Paralleling the unique and distinctive distribution of character states observed in its morphology, *Tahina* possesses a mosaic of leaf anatomical character states variously shared by other Chuniophoeniceae. Although there are no obvious synapomorphic character states for the tribe, the abaxial ribs of *Chuniophoenix*, *Kerriodoxa*, and *Tahina* have a peripheral sclerotic sheath – an uncommon character state in Coryphoideae, found elsewhere only in the closely related Caryoteae (Tomlinson, 1961), and *Cryosophila* and related genera in Cryosophileae (Uhl, 1972; Evans, 1995). In addition to its uniformly single-layered abaxial hypodermis, *Chuniophoenix* shares with *Tahina* identical trichome base structure. *Nannorrhops* and *Tahina* both possess a multilayered adaxial hypodermis, distinguishing them from the other two genera of the tribe, which both have a one-layered adaxial hypodermis. The only anatomical character state that can be suggested as a synapomorphy for the grouping of *Tahina* and *Kerriodoxa* is that both share transverse commissures that frequently extend from the midrib to the segment margin, each with a thick, multilayered sheath of fibres. Such venation is unusual in palms as a whole; transverse commissures in palms are most often relatively short and include a narrow sheath of thin-walled cells. Transverse commissures like those of *Tahina* are, however, frequent in other members of the syncarpous clade exclusive of Chuniophoeniceae, and characterize *Corypha* and most dorsiventral taxa of Borasseae.

MOLECULAR ANALYSIS

The DNA sequences were added to the existing alignment of Asmussen *et al*. (2006) without affecting its total length of 7102 characters. The subset of this

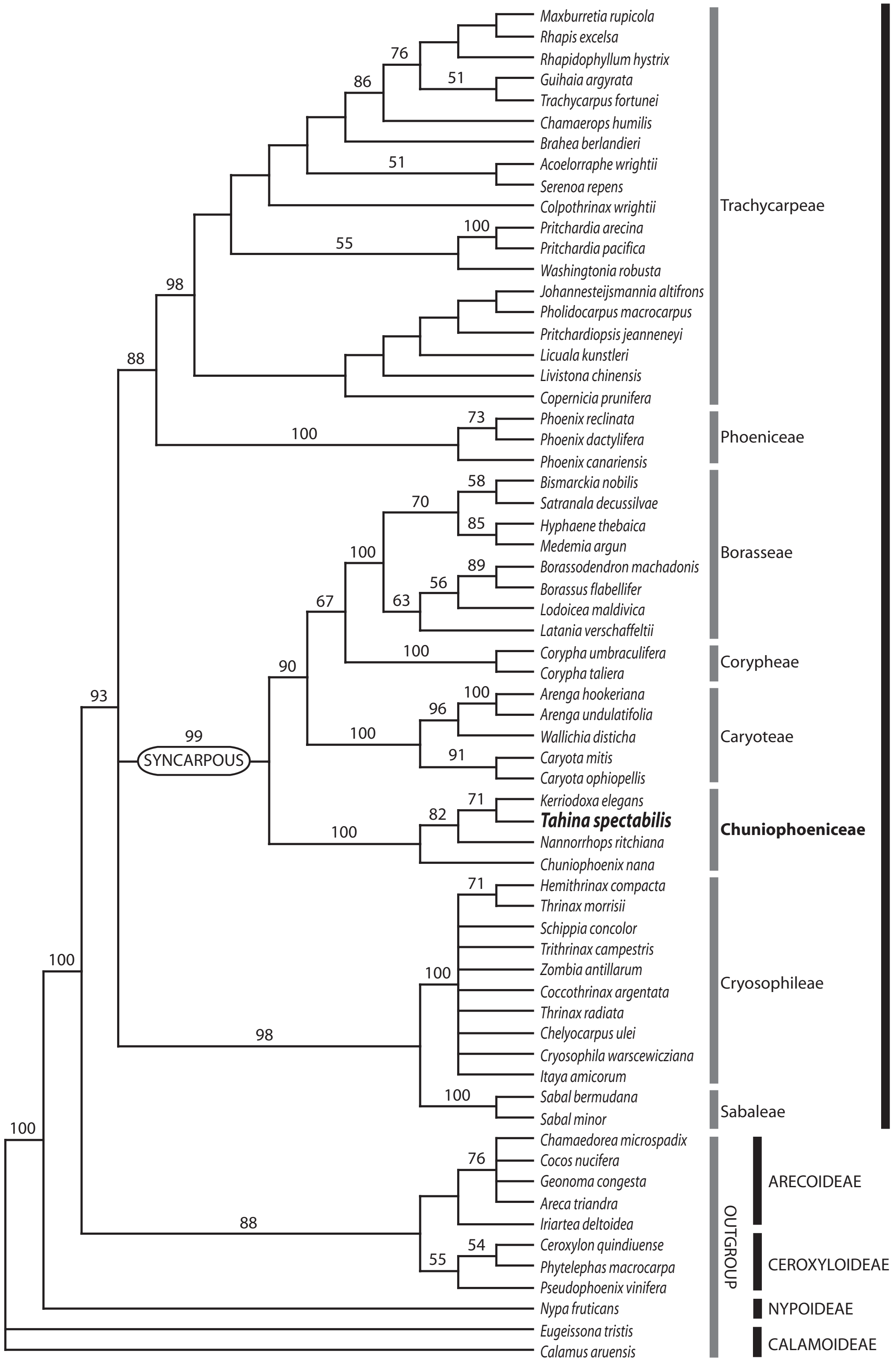

Figure 6. Plastid phylogeny of subfamily Coryphoideae with the position of *Tahina* within the syncarpous clade highlighted. The classification is that of Dransfield *et al*. (2005). The tree presented is a strict consensus of 282 trees (tree length, 1171 steps; consistency index, 0.73; retention index, 0.82) with bootstrap percentages given above the branches.

alignment analysed in this study comprised a total of 64 taxa, including 53 Coryphoideae representing all accepted genera in the subfamily (Dransfield *et al*., 2005; Govaerts & Dransfield, 2005) and 11 outgroups, and contained 350 parsimony-informative characters. The analysis yielded 282 trees of length 1171 steps (Fig. 6; consistency index, 0.73; retention index, 0.82).

A near-identical topology for Coryphoideae to that presented by Asmussen *et al*. (2006) was recovered, with the exception of a sister group relationship between the Chuniophoeniceae (Caryoteae (Corypheae, Borasseae)) clade (the syncarpous clade) and the Phoeniceae + Trachycarpeae clade, which was not resolved here. The syncarpous clade is highly supported [bootstrap percentage (BP), 99], as is tribe Chuniophoeniceae (BP, 100), within which *Tahina* is moderately supported as sister to *Kerriodoxa* (BP, 71). *Nannorrhops* is sister to this group (BP, 82).

CONCLUSIONS

Tahina is an astonishing new palm genus, clearly distinct in its morphology from any other coryphoid palm. Morphological, anatomical, and molecular evidence support its inclusion in the tribe Chuniophoeniceae. The geography of this well-supported group is highly paradoxical and, as yet, there is no obvious explanatory narrative for the distribution of the constituent four genera.

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