Satranala (Coryphoideae: Borasseae: Hyphaeninae), a new palm genus from Madagascar

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Summary. Satranala, a new Borassoid palm genus related to Bismarckia, Hyphaene and Medemia discovered in the rain forests of northeastern Madagascar is described as new, with a single species, S. decussilvae.

The Borassoid palms (tribe Borasseae of subfamily Coryphoideae) represent a well circumscribed apparently monophyletic group of dioecious palms with induplicately palmate-leaves, that are divisible into two discrete, morphologically rather uniform subtribes, Lataniinae and Hyphaeninae (Uhl & Dransfield 1987). Generic delimitation within the two subtribes is clear and for the most part not controversial. Lataniinae comprises four genera, Borassus, Borassodendron, Latania and Lodoicea, and Hyphaeninae three genera, Hyphaene, Bismarckia and Medemia. The genera are easily keyed out on reproductive features and these are correlated with striking morphological features that allow the genera to be separated when sterile. The differences between the genera are discussed in detail by Uhl & Dransfield (1987). In Lataniinae all the genera are familiar palms now widely cultivated throughout the tropics and subtropics. In Hyphaeninae two genera, Bismarckia (monotypic) and Hyphaene (with about ten species), are also familiar cultivated palms although the species of Hyphaene remain poorly circumscribed and difficult to name (see Dransfield 1986). The third genus, Medemia, with one or possibly two species, is known from a few herbarium specimens collected from southern Egypt and northern Sudan. Once familiar to the ancient Egyptians, it is now extremely rare if not already extinct. It was last reported in the field from southern Egypt in 1963 (Boulos 1965). Attempts to mount an expedition to refind it in 1992 were abandoned for lack of funds (Johnson, pers. comm.). Despite no living material being available for study, Medemia is well represented in herbaria and the palm is surprisingly well circumscribed and instantly identifiable because of the lack of petiolar spines, the lack of an adaxial hastula at the base of the lamina and the ruminate endosperm.

The only area of possible contention in the delimitation of genera in the Borasseae involves the genera of the Hyphaeninae. When the palm now known as Medemia argun was first described it was included by Martius (1845) in Hyphaene as Hyphaene argun. Bismarckia nobilis, endemic to Madagascar, was first described in that genus but was subsequently included by some authors in Medemia as M. nobilis. However, Bismarckia is now widely accepted as a monotypic genus, distinct

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from *Medemia* which is also regarded as distinct from *Hyphaene*. In *Borasseae* the genera are neatly and unambiguously circumscribed and of all palm tribes this seemed one of the best known and understood.

This was the widely accepted taxonomy of the Hyphaeninae in 1991 when one of us (HB), working in the forests of eastern Madagascar encountered a fan palm looking quite like Bismarckia nobilis but growing in humid rain forest in a deep valley instead of in western palm savanna (Battistini & Richard-Vindard, 1972), the normal habitat of Bismarckia. All the individuals were sterile but a careful search revealed fallen fruits under two of the trees, and these were very different from those of B. nobilis. A return visit by both of us in April 1992 resulted in the collection of staminate inflorescences as well as good vegetative material. Although pistillate inflorescences are still unknown, it is clear that the palm is both distinct and undescribed. As with many of the recent palm discoveries from Madagascar, this forest fan palm has called the accepted classification into question and has forced us to re-examine generic delimitation within Hyphaeninae. In some respects what we publish here must be regarded as a pragmatic solution. The new fan palm is still incompletely known and, as its only known locality is remote, more material is unlikely to be available in the near future. Furthermore, until someone can rediscover *Medemia argun*, that genus too will remain incompletely known. In the meantime, the new palm needs a name that will allow us to draw attention to the importance of the east coast forests of Madagascar, their fragility and their uncertain future.

Superficially the new palm has the appearance of Bismarckia nobilis. However, its fruit is remarkable. As in all members of Borasseae the seed is enclosed in a heavily sclerified endocarp but the endocarp in this new taxon is strongly winged, in marked contrast to endocarps of Hyphaene that have an even surface but with adherent fibres, Medemia that has a rather thin somewhat fibrous endocarp and Bismarckia where the endocarp is smooth but with faint ridges. Internally, the endocarp of the new palm is smooth, as in Hyphaene and Medemia, while in Bismarckia the endocarp is flanged internally, with the flanges penetrating the seed. Finally, as in Medemia the endosperm is ruminate; however, unlike hollowseeded Medemia the new palm has solid seeds. This unique combination of fruit and seed characters makes inclusion of the newly discovered palm in any described genus problematic without redefining the limits of genera. It could be argued that the new palm is intermediate between Bismarckia and Medemia and that the two genera should be included under Medemia. However, we believe that such a synonymy would hide the morphological variation that occurs within the subtribe. Is the forest fan palm a new species of Bismarckia? This was our first reaction, but after examining our material in more detail we have been drawn to the conclusion that there are too many differences between the two palms and that the unique combination of characters in the newly discovered palm is best reflected in the description of a new genus which we propose to call Satranala (Malagasy - "forest fan palm"). Preliminary cladistic studies of the genera of Borasseae lend support to the recognition of a separate genus, even though much information is missing. Molecular studies of the group are hampered by the lack of fresh material of the new palm and of Medemia. Pollen of S. decussilvae resembles

that of both Bismarckia and Medemia, but is some 6% larger.

The adaptive significance of the unusual fruit morphology has been the subject of speculative discussion between us as we prepared this account. It seems that there have been selective pressures favouring the penetration of the endosperm in the seeds of Bismarckia and Satranala by non-endospermic tissue. In Satranala the seed is ruminate in the usually accepted meaning of the term - i.e. it is penetrated by seed coat tissue. In the case of Bismarckia the seed is penetrated by flanges and ridges of endocarp tissue, with a particularly prominent intrusion at the base. Do these intrusions provide some form of protection against seed predation? If so then such protection is produced by two entirely different ways in the two palms. What is the significance of the large flanges on the endocarp of Satranala? Could this form some sort of mechanical protection against the endocarp being ground down in a large bird's gizzard? Another unusual feature of the endocarp of Satranala is that there is no germination pore opposite the embryo. In other members of the tribe there is a thin area of endocarp above the apical embryo through which the germinating embryo emerges. In Satranala the embryo lies in the typical apical position but opposite to the main woody wing of the endocarp.

The most striking differences between Bismarckia and Satranala are the fruit characters described above. There is one other apparently major difference, the symmetry of the lamina. The lamina in Satranala is dorsiventral while that of Bismarckia is isolateral; furthermore transverse veinlets are conspicuous in Satranala while being obscure or absent in Bismarckia. Within tribe Borasseae dorsiventral laminae have been recorded in Lodoicea and Borassodendron (not as cited in Uhl & Dransfield 1987), while in all other genera the laminae are isolateral. The significance of this difference is not fully understood but in this tribe it may be correlated with habitat, dorsiventral laminae being found in rain forest palms and isolateral laminae being found in palms of drier more open habitats.

Satranala J. Dransf. & Beentje, gen. nov. Palma insignis ad tribum Borasseas (subtribum Hyphaeninas) pertinens, a ceteris generibus subtribus lamina foliae dorsiventrale venulis transversalibus conspicuis, fructu endocarpio extus cristas latas anastamosantes ferenti, intus laeve, poro embryone opposito carenti, endospermio valde ruminato differt. Typus: Satranala decussilvae Beentje & J. Dransf.

Robust solitary pleonanthic tree palm. Stem erect, irregularly ringed with leaf scars, somewhat swollen at the base. Leaves induplicately costapalmate, neatly abscissing under their own weight in mature individuals; sheath lacking auricles, with a conspicuous triangular cleft below the petiole; petiole adaxially channelled near the base, distally \pm flattened, abaxially rounded, the margins sharp, bearing minute irregular teeth distally, surfaces covered in patchy hairs, scales and white wax; adaxial hastula present, abaxial hastula absent; blade divided to c. ¼ to ½ its radius along adaxial folds into induplicate segments, further divided by short splits along abaxial folds, interfold filaments caducous, lamina covered with thin white wax, transverse veinlets conspicuous, close, somewhat sinuous; lamina anatomy dorsiventral. Inflorescence interfoliar, only the staminate known, solitary, shorter than the leaves, branching to 2 orders; peduncle \pm rounded in transverse section; prophyll short, 2-keeled, included in the subtending leaf-sheath; peduncular

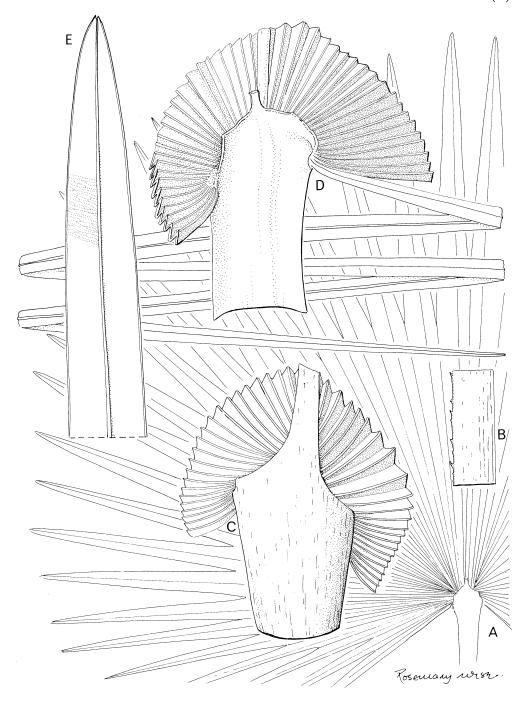


Fig. 1. Satranala decussilvae. A leaf, adaxial view \times 1/10; **B** petiole margin \times $\frac{1}{2}$; **C** petiole/leaf blade interface, abaxial view \times $\frac{1}{2}$; **D** idem, adaxial view \times $\frac{1}{2}$; **E** leaf segment apex \times $\frac{1}{2}$. All from Beentje et al. 4628. Drawn by Rosemary Wisc.

bracts several; rachis longer than the peduncle; rachis bracts decreasing in size distally, tubular, rather loosely sheathing, with a broad, split, triangular limb, sometimes strongly keeled, densely covered in rusty tomentum; first-order branches crescent-shaped in cross-section, longer than the subtending bract, not bearing a prophyll, branching at the tip to produce a group of 3-9 radiating, catkin-like rachillae, rarely at the inflorescence tip the group reduced to a single branch; rachillae slightly sinuous, bearing a tight spiral of rounded, densely hairy, striate bracts, connate laterally and partially adnate to the axis to produce pits, densely filled with hairs. Staminate flowers unknown; pollen (found remaining among inflorescence bracts) ellipsoid in apertural or non-apertural view; monosulcate; tectum coarsely rugulate-fossulate, but smoother around the tectum. Fruit developing from a single carpel, globose, stigmatic remains basal; epicarp smooth, mesocarp not known, endocarp hard, woody, externally with broad anastomosing flanges, one principal flange forming a crest along the vertical axis of the endocarp, internally the endocarp smooth, lacking a basal intrusion and lacking a germination pore opposite the embryo. Seed globose, basally attached; endosperm ruminate, deeply and irregularly penetrated by integumental tissue, solid, embryo apical. Germination and eophyll unknown.

DISTRIBUTION. Madagascar, one species in east coast rain forest.

Satranala decussilvae Beentje & J. Dransf. sp. nov., palma insignis ad 15 m alta, foliis costapalmatis ad 2·6 m latis, fructu globoso endocarpio cristato ad 48 × 45 mm diametro, endospermio ruminato. Typus: Madagascar, Mananara Avaratra, April 1992, Beentje, J. Dransfield & Andriampaniry 4628 (holotypus K; isotypi BH, MO, P, TAN, WAG).

Solitary tree palm, trunk 8-15 m tall, d.b.h. 15-18 cm, hard, smooth, ± straight, obscurely ringed with scars, sometimes with aerial roots above the base of the trunk; internodes 8-10 cm, nodal scars 1.5 cm wide. Leaves (9 in young plants) 20-24 in the crown, porrect, rather stiff, with up to 6 marcescent old leaves; sheath 46-60 cm long, 35 cm diam., at the very base 70 cm wide, split from 14-44 cm, abaxially chestnut brown near the base, more distally pale brown with scattered scales, adaxially chestnut brown, glabrous; petiole 140-150 cm (190-270 cm in young plants), proximally $7-10 \times 5-6 \text{ cm}$, distally $5 \times 1.5 \text{ cm}$, abaxially with thin white tomentum and wax, adaxially brown near the base, distally green with elongate scales, shallowly channelled, the margins proximally with spines to 3 mm, distally with minute spines; adaxial hastula forming a flange 3-8 mm high, with a central lobe to 15 mm long; blade costapalmate, 110-180 cm from hastula to apex, 240-260 cm wide, with 54-57 segments, costa to 33 cm. abaxially c. 2 cm wide at the base; segments almost flat, apically bifid for 1-10 cm, with three main veins and numerous close sinuous transverse veinlets, abaxially with conspicuous white wax, both surfaces with many large laciniate scales near the base, distally with few small brown scales; outer folds $88-102 \times$ 1·3-3·2 cm, unsplit in the basal 8-9 (outermost)-20 cm, intermediate folds $104-130 \times 4\cdot 4-5\cdot 5$ cm, unsplit in basal 50-52 cm, central folds $114-181 \times 100$ $4 \cdot 1 - 6$ cm, unsplit in basal 80 - 100(-137) in young plants) cm; for segment hang