

***Attalea*: Insights into the Diversity and Phylogeny of an Intriguing Genus**

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Ongoing phylogenetic studies are revealing surprising relationships among species, greatly challenging the classical interpretation of characters in *Attalea*, and forcing us to rethink completely the morphology of these palms.

Attalea has long been a subject of taxonomic debate (reviewed by Pintaud 2008), with a long-lasting disagreement among authors about generic concepts (either the recognition of a single, broad genus *Attalea*, or several,

smaller genera including *Attalea sensu stricto* along with *Orbignya*, *Scheelea*, *Maximiliana* and sometimes a few more monotypic ones), and also about species concepts, resulting in a wide range of species number estimates (29–67).

However, recent progress in taxonomy and phylogeny is giving clues to the understanding of this complex group of Neotropical palms.

First, phylogenetic studies by Meerow et al. (2009, 2014) firmly established the monophyly of a broad genus *Attalea*, supporting the last generic treatment (Dransfield et al. 2008). *Attalea* as now definitely circumscribed is very diverse, ranging from relatively small acaulescent species (Fig. 1) to gigantic arborescent ones (Front Cover), with a corresponding variability in organ size and complexity (Fig. 3). At the same time, the enlarged genus is well-defined by a single character: the asymmetrical tip of the pinna. This well-known characteristic is always accessible for identification, even in sterile and juvenile palms (Kahn 1990). More precisely, what corresponds normally to the pinna apex in palm leaves is in fact symmetrical, acute, but it is exceeded by a projection that develops above and on one side of it (Fig. 4A). This unilateral projection is further accentuated by a distinctive brown indument abaxially in several species (Fig. 4A & C). In some other species, the unilateral projection is glabrous or glabrescent, and it often breaks with leaf expansion or subsequent aging, leaving an

asymmetrically truncate, or more or less unequally bifid tip, with the formation of a sinus (Fig. 4B & D). Whatever the case, the pinna tip variability is most useful for species identification (Fig. 4C), even if there is some instability in some species (Fig. 4D).

Very interesting and totally unusual is also the gynoecium evolution in *Attalea*. Palms in general, as monocots, have flowers based on a trimerous structure, with each whorl of floral parts (sepals, petals, stamens, carpels) made of three elements. Particularly distinctive is the fundamentally tricarpellate-triovulate gynoecium of palms (Dransfield et al. 2008). This basic structure is altered in many ways to produce the great diversity of floral morphology found in the palm family. As far as the gynoecium and its post-anthesis development is concerned, there is a general trend of reduction of the number of ovules and/or seeds per flower/fruit from three to one. This reduction is achieved by various pre-anthesis or post-anthesis processes, depending on palm lineages. A remarkable pre-anthesis modification is pseudomonomy, in which a single carpel fully develops and carries the fertile ovule, the other two aborting early in development. This condition characterizes, for

1. *Attalea plowmanii* is a subacaulescent species from western Amazonia with small infructescences bearing a dozen fruits.

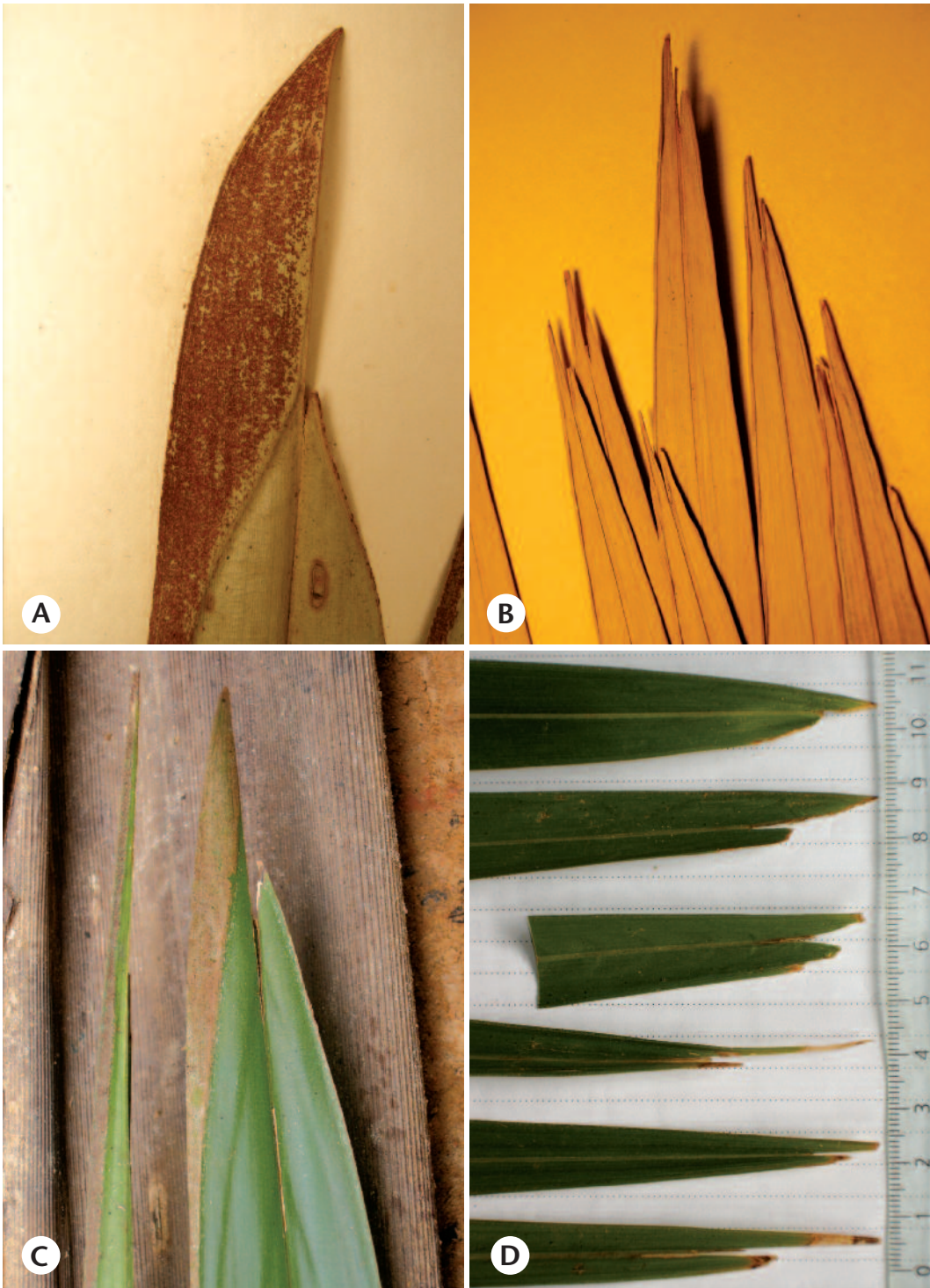




3. Variation in complexity of the morphology of *Attalea*. **A.** *Attalea eichleri*, a small acaulescent species of the southern Amazonian periphery, has a diminutive, almost spicate pistillate inflorescence with a fertile part just 10 cm long (P00118497, Weddel 2705, lectotype [P], from Brazil). **B.** *Attalea weberbaueri*, an arborescent species from the central-eastern inter-Andean valleys of Peru, has large, ramified inflorescences with over 400 rachillae and an infructescence weighting more than 30 kg.

example, the largest palm tribe, Areceae (Baker et al. 2011). Cocoseae, on the other hand, have a typical tricarpellate (syncarpous), triovulate gynoecium, forming in fruit the well-known woody endocarp with three opercula exemplified by the coconut. However, in most Cocoseae genera, a single seed develops and occupies all the space available inside the endocarp. The few not strictly one-seeded Cocoseae are *Butia* (1–3 seeds per fruit), *Barcella*, *Allagoptera* and *Parajubaea* (1 or 2 seeds) and *Attalea* (1–8 seeds). *Attalea* is therefore the only genus in Cocoseae in which there is a trend of increasing seed number, with commonly 3–6 seeds per fruit in many species (Fig. 5A) and up to 8 in some species, although others present the one-seeded fruit reduction, particularly *A. colenda* (Fig. 5B). In Cocoseae, the hard, woody endocarp is the disseminated unit or diaspore, so there is little evolutionary interest in producing multi-

seeded fruits because seedlings coming from the same fruit will compete for establishment, and at the best, a single one will develop correctly. So, why is there an increase in seed number in *Attalea* fruits? A possible explanation is co-evolution with bruchid beetles (Harms & Dalling 2000). These insects commonly reproduce on *Attalea* fruits, the developing larvae feeding on seeds (one larva per seed), and eventually the adult gets out of the endocarp leaving a characteristic circular hole (Fig. 5C & D). So, increasing seed number can be seen as a response of the palm to this parasitism to maintain diaspore efficiency (statistically, at least one seed in multi-seeded fruits remains free of parasites) while providing more reproductive sites for the insects, and conversely, bruchid parasitism can be seen as a necessary regulatory mechanism of germination, lowering seedlings mutual competition, so that an equilibrium with



4. Pinnae tip structure and shape are essential for characterization in the genus *Attalea*, and differ in each species. **A.** *Attalea allenii*, prominent falcate unilateral projection above symmetrical, acute apex, with a dark brown scaly indument continuing on pinnae side (Monsalve 1687 [CUVC], from Colombia). **B.** *Attalea exigua*, asymmetrically bifid, sinuate, glabrescent tip (P00118539, Glaziou 22267 [P], from Brazil). **C.** Comparison of pinnae tips in two sympatric species in Jenaro Herrera, Peruvian Amazon: left, *A. peruviana* with subulate projection, right *A. polysticha* with lanceolate projection. **D.** Variability of pinnae tips in a single leaf of *A. weberbaueri*.

shared benefits is achieved in that palm-insect relationship. However, in the *Attalea butyracea* complex, in which bruchid parasitism is high, one-seeded fruits are most common, with 2- or 3-seeded fruits representing 5–30% of the total within a given population. In fact, many factors, including bruchid mortality in infested fruits, and rodent predation and dispersal certainly interfere (Harms & Dalling 2000, Gálvez & Jansen 2007), so nothing is simple. The fascinating biology of *Attalea* includes many other intriguing adaptations such as neoteny in acaulescent species and functional dioecy.

Phylogeny

The molecular phylogeny of *Attalea* has been addressed partially by Meerow et al. (2009, 2014). These studies were based on a set of nuclear DNA markers belonging to the WRKY gene family. For our part, we generated a phylogeny for a sampling of species largely matching that of Meerow et al., using three new chloroplast DNA markers developed by Scarcelli et al. (2011), namely *psbK-trnS*, *rps15-ycf1* and *rrn4.5-trnN*, along with the nuclear markers PRK, PhyB and CISP4 recently used by Roncal et al. (2013) in a phylogeny of the genus *Astrocaryum*. The newly generated sequences were deposited in Genbank under accessions KP307929–307942 (PRK), KR559512–559524 (PhyB), KR559525–559540 (CISP4), KT321478–321492 (*rrn4.5-trnN*), KT321493–321508 (*psbK-trnS* and *rps15-ycf1*). Interestingly, the phylogenies of Meerow et al. and ours are highly congruent, indicating a strong signal in the phylogenetic structure of *Attalea* (Fig. 6). In both studies, *Attalea* in its broad sense is primarily divided in two well-defined clades: one corresponding to species from central and eastern Brazil belonging to the former genus *Attalea sensu stricto*, and one incorporating all other species sampled in *Attalea sensu lato*. In the later clade, the Haitian *Attalea crassispatha* is sister to all other species formerly incorporated in the genera *Orbignya* and *Scheelea*. This is interesting because while *Attalea sensu lato* is very common in both South and Central America, it is almost absent from the Caribbean islands (except from Trinidad, the flora of which is an extension of that of Venezuela). *Attalea crassispatha* is therefore very isolated both geographically and phylogenetically. Moreover, there is a consistent signal of dispersion of Cocoseae from northern South America to the Antilles in Mio-Pliocene, with the age of the separation of *Acrocomia crispa* in Cuba from South

American species estimated at 16 MYBP, the age of the divergence of *A. crassispatha* with continental species at 9 MYBP, the age of the split between *Syagrus amara* and the *S. orinocensis/stenopetala* clade at 5 MYBP, and the age of divergence of *Aiphanes minima* from *A. horrida* at 3 MYBP (Meerow et al. 2014).

In the group of species sister to *A. crassispatha*, two entities are distinct: a “babaçu” subclade including the species *A. speciosa* and its close relatives, formerly included in the genus *Orbignya*, and a subclade including all species previously belonging to the genus *Scheelea*, consistently associated with *A. cohune* and *A. guacuyule*, two closely related (and sometimes treated as synonyms) species formerly included in *Orbignya*. Adding to this the fact that Glassman (1999) treated *A. crassispatha* in the genus *Orbignya*, we can see that this former genus is indeed paraphyletic with respect to the other species sampled in this subclade. Moreover, the addition in our study of *A. tessmannii* and *A. amygdalina*, which have always been treated as part of *Attalea sensu stricto* makes this former concept of the genus polyphyletic, because these two species from the western Amazon and the Colombian Inter-Andean valleys, respectively, cluster with the *Scheelea* group and not with the Eastern-Central Brazilian *Attalea sensu stricto* clade. This phylogenetic structure indicates that the major division in the genus is geographic, beginning with the middle Miocene (20–10 MA) split between the Amazonian and Cerrado-Mata Atlantica palm floras, a signal found in several genera including *Attalea*, *Syagrus* and *Astrocaryum* (Meerow et al. 2009, 2014, Roncal et al. 2013).

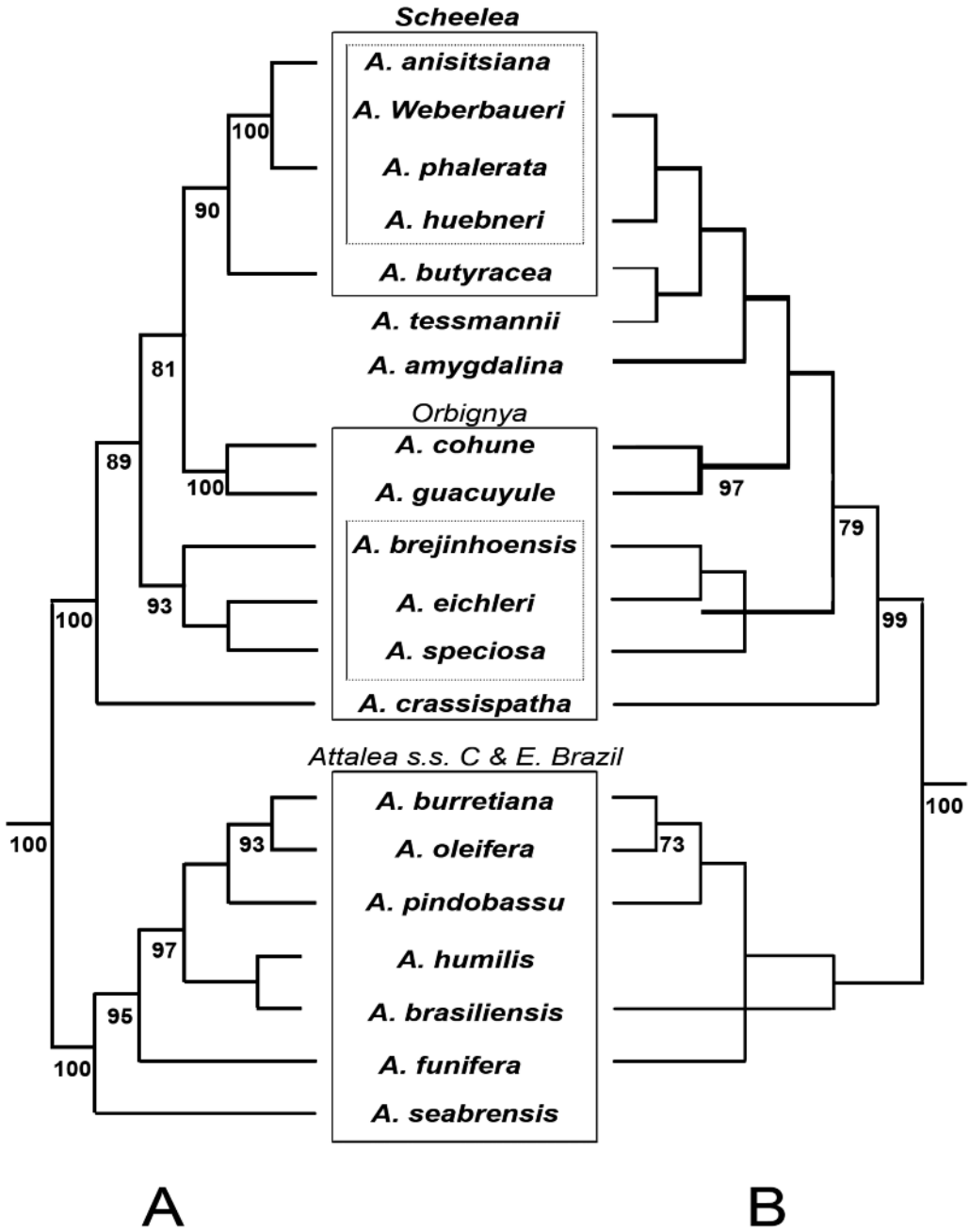
Although we now have a clearer view of the phylogenetic structure of the broad genus *Attalea*, the addition of more species in the analysis, especially the unsampled former genus *Maximiliana* is still necessary to get a complete picture of the evolutionary relationships within *Attalea*. This more complete analysis is now approaching completion (Freitas et al. in prep.).

Morphological evolution and taxonomy

The fact that the new phylogenetic data contradict the classical morphological boundaries within this group of palms implies that a new interpretation of characters, and a revised homology assessment of them, is needed. For example, the former genera *Orbignya*, *Scheelea*, *Maximiliana* and *Attalea sensu stricto* look reasonably well defined



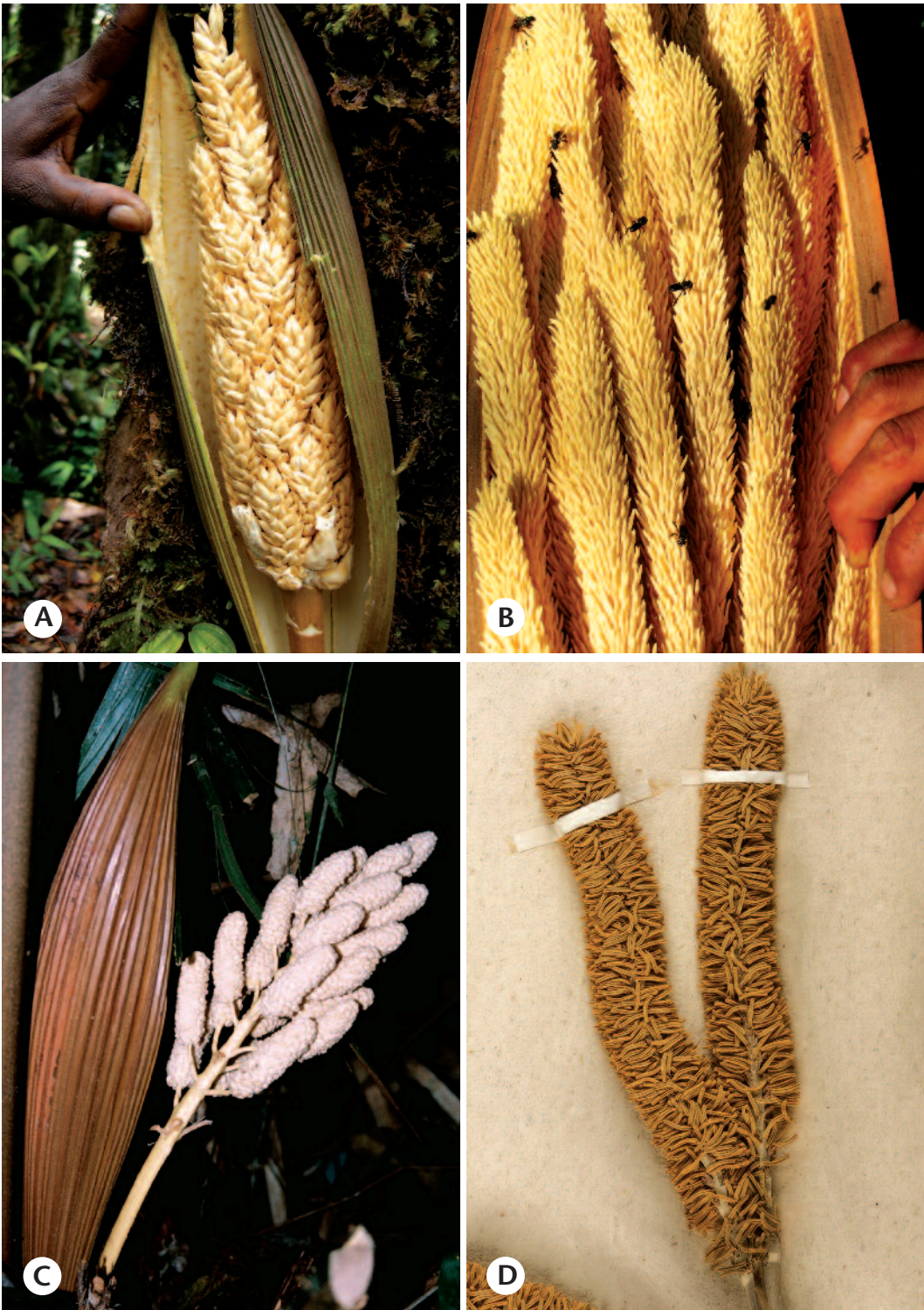
5. Seed evolution and ecology in *Attalea*. **A.** Fruits of *Attalea huebneri* laying on the ground, with a cross-section of a 5-locular, 6-seeded endocarp. **B.** Cross-section of the one-seeded fruit of *Attalea colenda*, a species showing a unique endocarp and seed structure, more reminiscent of *Cocos* or *Astrocaryum* than of other *Attalea* species, and which has been once classified in a distinct genus, *Ynesa*. **C.** Old fruits of *Attalea weberbaueri* on the ground, with an endocarp showing exit hole left by a bruchid beetle. **D.** Longitudinal section of endocarp of a heavily parasitized fruit of *A. weberbaueri*, showing bruchid beetle larva in a seed cavity.



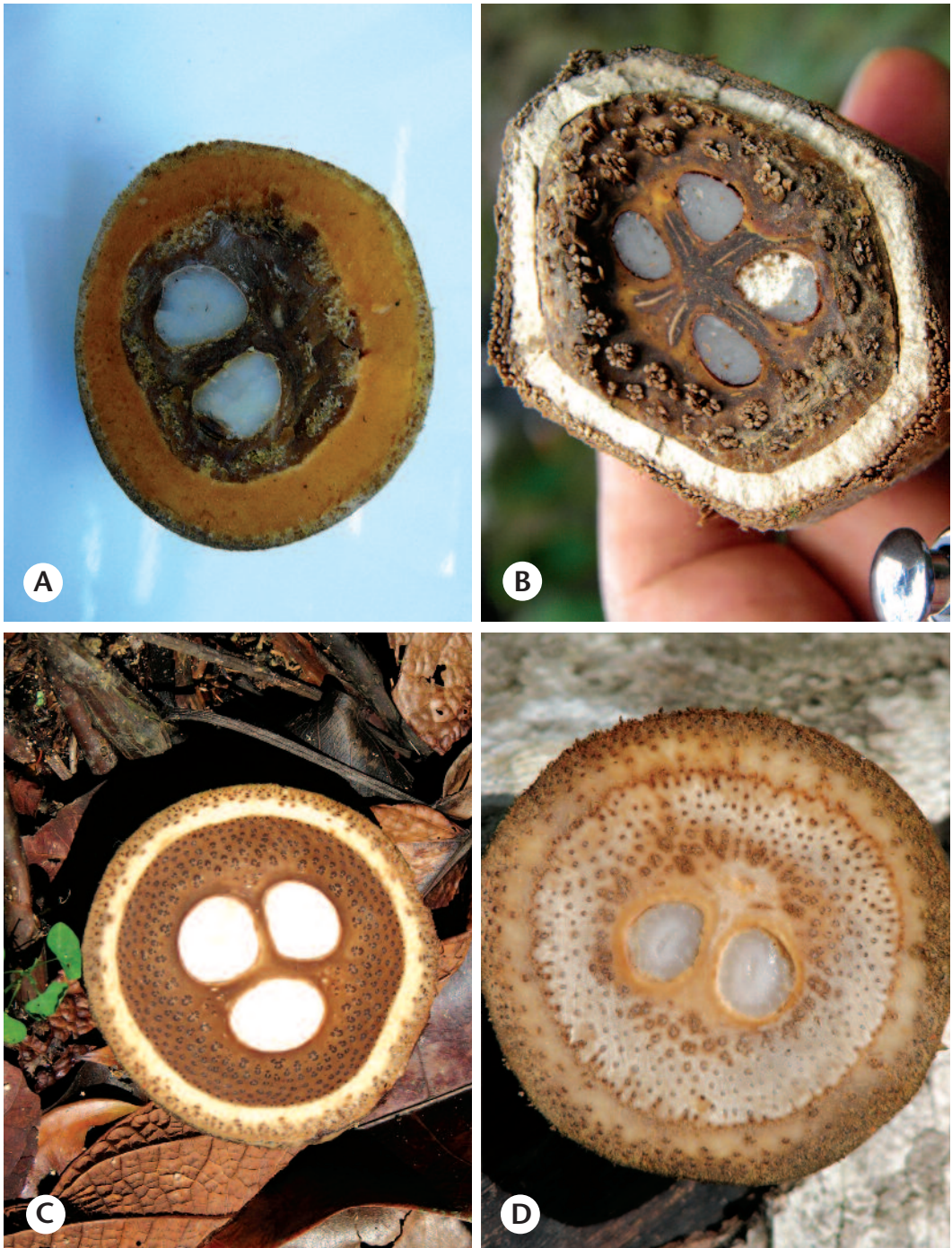
6. Phylogenetic relationships within the genus *Attalea*, comparing the topologies obtained by Maximum Likelihood analysis of nuclear WRKY genes by Meerow et al. 2009 (A), and combined chloroplast and nuclear genes in the present study (B). Figures below branches represent ML bootstrap values. Solid rectangles identify from bottom to top: the central-eastern Brazilian species previously included in *Attalea (sensu stricto)*; the species included in *Orbignya* (with the “Babaçu” clade in dot line); and those included in *Scheelea* (with the *A. phalerata* clade in dot line).

morphologically, especially in inflorescence and floral structure (Fig. 7). Particularly intriguing is *Orbignya*, so distinctive with its characteristic coiled and enrolled anthers, and staminate flowers often tightly packed on

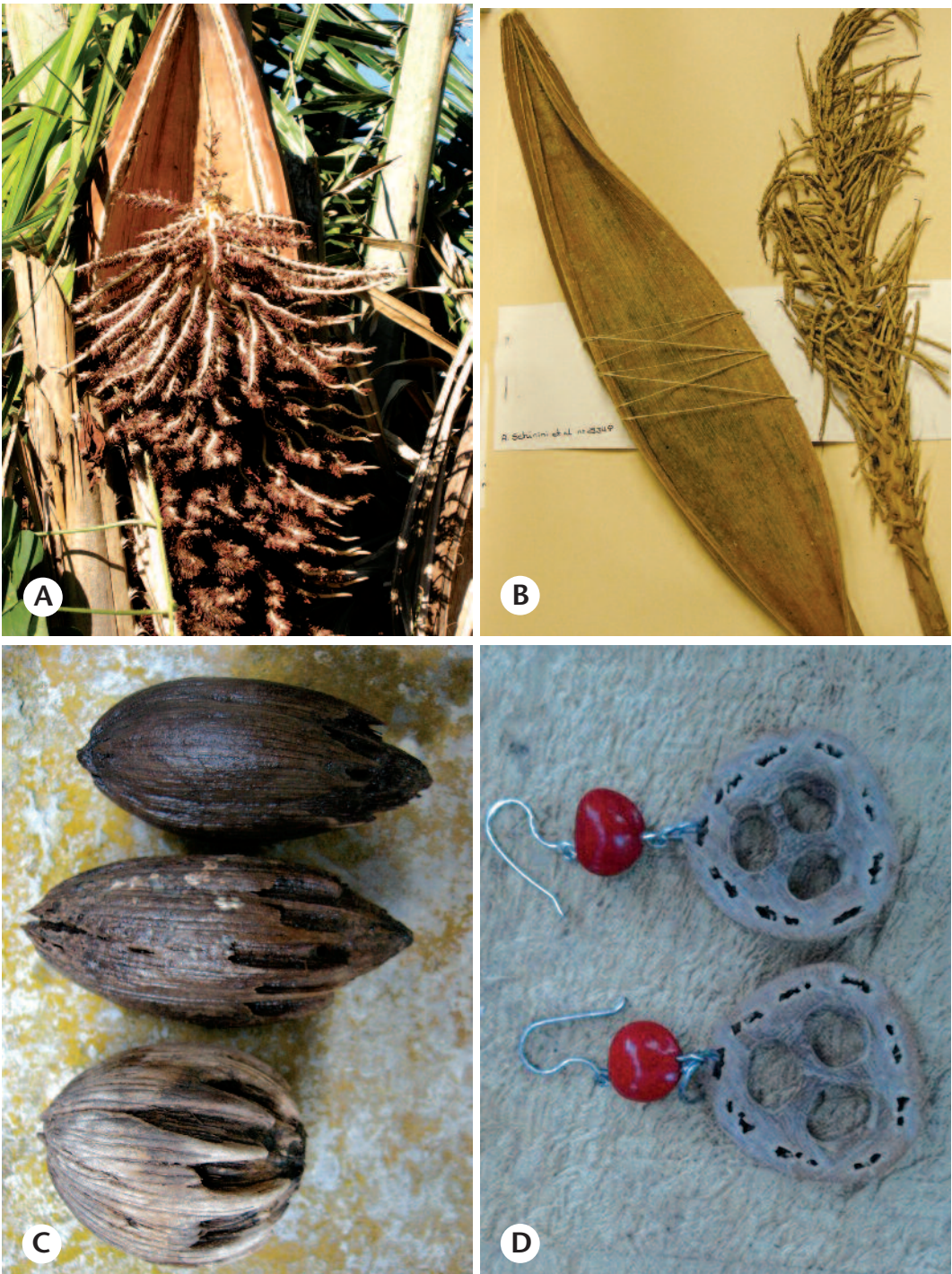
staminate rachillae (Fig. 7C), and pistillate rachillae contorted around pistillate flowers (Fig. 3A). However, since this taxon does not form a well-defined phylogenetic entity, with some species having affinities outside this



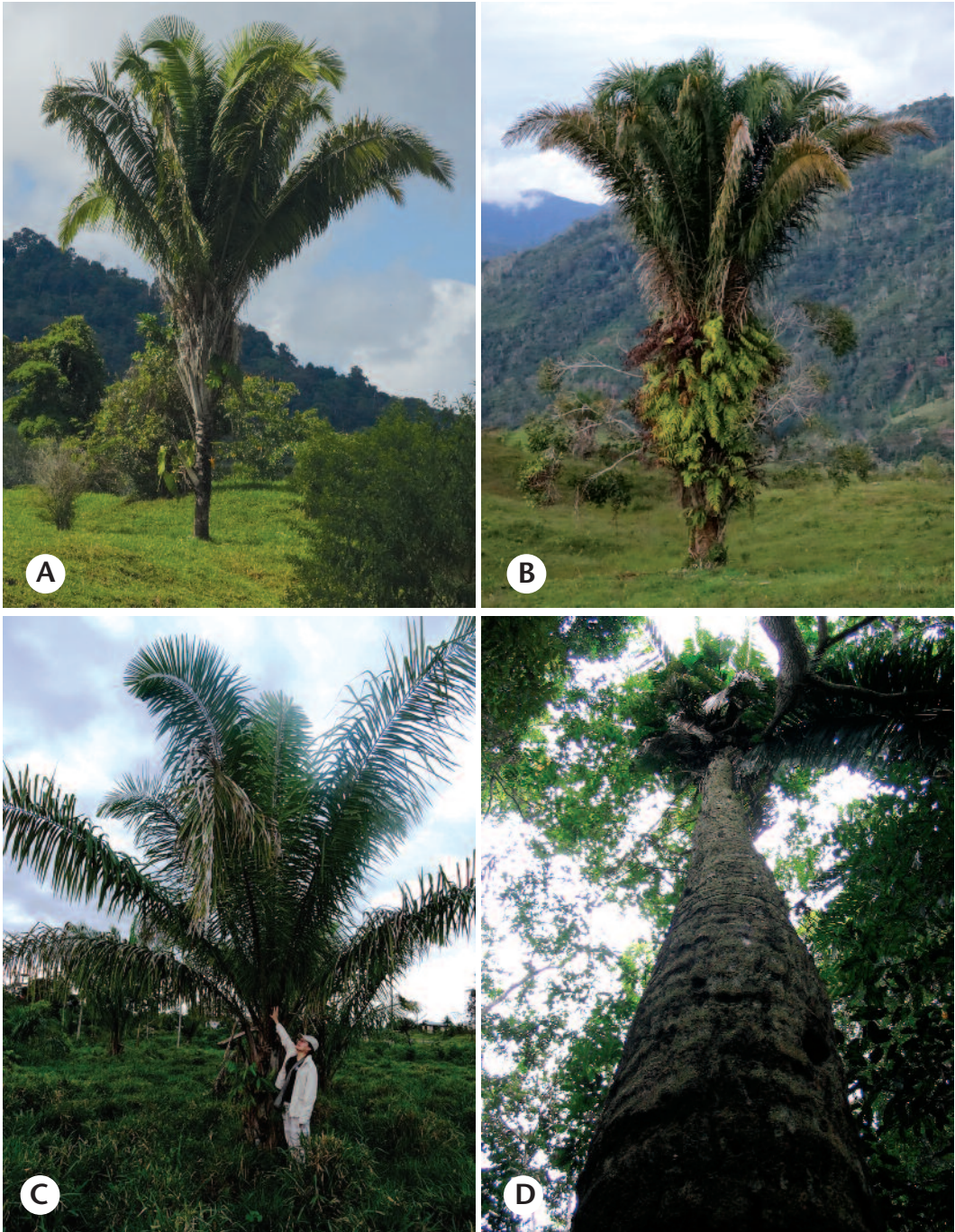
7. Diversity of inflorescences in *Attalea*. **A.** *Attalea*-type androgynous inflorescence, with a few basal, irregularly shaped pistillate flowers and numerous staminate flowers with triangular, flat petals (*A. allenii*, Quibdó, Chocó, Colombia). **B.** *Scheelea*-type staminate inflorescence with terete, fleshy petals (*A. bassleriana*, Pantoja, Loreto, Peru). **C.** *Orbignya*-type staminate inflorescence with densely packed flowers on rachillae (*A. polysticha*, Jenaro Herrera, Loreto, Peru). **D.** *Maximiliana*-type staminate rachillae with flowers having a reduced perianth and long, linear anthers (*Maximiliana maripa*, P01886492, *J. Triana* 734 [P], from Colombia).



8. Cross sections of fruits reveal a great morphological diversity and provide essential characters for species identification and delimitation of groups of allied species. *Attalea phalerata* complex: A. *Attalea huebneri* showing extremely thick, fleshy and juicy orange mesocarp at maturity, endocarp with large fiber clusters forming one peripheral circle, locular septa not marked; B. *Attalea moorei*, showing dry, white mesocarp and prominent fiber clusters forming 2 or 3 internal circles in the endocarp, locular septa marked; seed cavities widely separated with margin not thickened in both species. *Attalea butyracea* complex: C. *Attalea bassleriana* showing concentric small fibrous bundles of increasing size centripetally in the endocarp, and closely arranged seed cavities with thickened margin; D. *Attalea plowmanii* with the same structural characteristics as the anterior but with paler and superficially grooved endocarp (margin irregular in cross section). All species have a prominent fibrous exocarp.



9. Some characteristics of the *Attalea phalerata* complex. **A.** Staminate flowers are generally unilaterally arranged abaxially on staminate rachillae (except in *A. princeps* with a mostly spiral arrangement), and inflorescences have generally a thick peduncular bract, here in *Attalea moorei* in Peru. **B.** *Attalea anisitsiana* however has an unusually thin peduncular bract although it has the other distinctive characters of the *Attalea phalerata* complex (Schinini 29348 [G], from Paraguay). **C.** Endocarps can be variously shaped depending on fruit compression during development in infructescence, but are always prominently sculptured proximally and striate by the imprints of closely adherent internal mesocarp fibers, here in *Attalea huebneri* in Peru. **D.** Endocarps with large fibrous clusters forming one or few circles, and widely spaced seed cavities create aesthetic patterns used for fine handicrafts, here from *Attalea princeps* in Bolivia.



10. Some distinctive species in the *Attalea phalerata* complex. **A.** *Attalea moorei*, widely distributed in eastern Peru and adjacent Brazil and Bolivia, is unusual in having sessile leaves with perfectly regularly arranged pinnae all along rachis. **B.** *Attalea weberbaueri*, endemic in the inter-Andean valleys of central-eastern Peru, has the more common condition of sessile leaves with pinnae clustered in the proximal 2/3 of rachis. **C.** *Attalea princeps*, of the south-western Amazon and adjacent Andean foothills, is unusual in having distinctly petiolate leaves but, like the two former species, it is relatively short-trunked and likes semi-open vegetation under seasonally dry climates. **D.** *Attalea huebneri* is remarkable for its very tall habit. This extremely old specimen from Jenaro Herrera, Peru, is about 45 m tall. Although the crown looks small from ground level, each leaf is 12 m long. *Attalea huebneri* is also unique in distribution and ecology in the *Attalea phalerata* complex, occupying the wettest parts of the western Amazon in Brazil, Peru and Colombia, where it grows in *igapo* and *varzea* forests, often in association with *A. bassleriana*.



11. *Attalea moorei* × *phalerata*, here in Madre de Dios, Peru, probably occurs rather commonly in the vast area of sympatry of the two parent species in south-eastern Peru, Acre in Brazil and Pando in Bolivia.

group, these characters cannot be used as an evidence of exclusive common ancestry (synapomorphies). Moreover, with its peculiar and distinctive inflorescence and floral

morphology, *Orbignya* looks like a derived entity, while its species tend to be basal in the subclades of the phylogeny. Even more disturbing is the consistent association, with



12. *Attalea moorei* × *weberbaueri*, is a rare hybrid occurring in a narrow fringe of sympatry of the parent species in the central-eastern Andean foothills of Peru.

different phylogenetic markers, of *A. butyracea* and *A. tessmannii*, two species that hardly share any obvious common character. However, *A. tessmannii* has been regarded as an outlier in the former *Attalea sensu stricto* concept, because it has spirally arranged staminate flowers on

rachillae, a condition unusual in this entity essentially characterized by the unilateral arrangement of these flowers. On the contrary, the spiral arrangement of staminate flowers is shared with *A. butyracea* (formerly *Scheelea*), which is phylogenetically consistent.



A



B



C



D

13. Some species in the *Attalea butyracea* clade. **A.** *Attalea peruviana*, distinctive among similar species by the elongate petioles (western Amazonia). **B.** *Attalea bassleriana* with sessile leaves and pinnae waxy-glaucous abaxially (western Amazonia). **C.** *Attalea tessmannii*, showing long-petiolate leaves with clustered pinnae (western Amazonia). **D.** *Attalea macrocarpa* with a roof-like regular arrangement of pinnae in proximal part of rachis (north-eastern coast of Venezuela).

In order to re-evaluate in detail the morphology of *Attalea* and its significance, we have established a list of morphological descriptors with 700 items, each one composed of one or few related characters (more than a thousand in total), that we are currently using to describe fully many species directly in the field and to compare with the partial herbarium material. This arduous task is beginning to give good rewards, in particular in the *Attalea phalerata* complex, which spans most of the South American continent and appears to be very well defined as a group, both phylogenetically (Fig. 6) and morphologically (Figs. 8 & 9). At the same time there are clear-cut morphological differences, along with distinctions in ecology and distribution among included species, i.e., *A. phalerata sensu stricto*, *A. anisitsiana*, *A. weberbaueri*, *A. moorei*, *A. princeps*, *A. huebneri* among others (Fig. 10). Recognizing these different species provides much more biological information than considering all of them as variations within a single, broad *A. phalerata* species (Henderson et al. 1995), a lumping view that is, however, valid because all these entities form a monophyletic group and are inter-fertile when occurring sympatrically (Figs. 11 & 12). More studies are still needed to provide a complete systematic treatment of the *Attalea phalerata* complex with the alternative, splitting view, but it can be estimated that it is a group of about 10 distinct species.

A similar approach can be applied to the *Attalea butyracea* clade, but it is a still more complex group that includes morphologically similar species like *A. rostrata*, *A. osmantha*, *A. macrocarpa*, *A. peruviana*, which resemble closely *A. butyracea sensu stricto*, but also species which have been regarded sometimes as synonyms of *A. butyracea* despite having a clearly different morphology (*A. bassleriana*, *A. plowmanii*), and species that had never been suspected to have a link with *A. butyracea* but that appear closely allied to it in phylogenetic analyses like *A. tessmannii* (Fig. 13) and *A. insignis* (Cintia de Freitas, pers. comm.). *Attalea huebneri* has been considered as a synonym of *A. butyracea* by Henderson et al. (1995) but our work showed that it is in fact allied to *A. phalerata*.

Altogether, the information unravelled by recent work rises more questions than it provides answers to, and makes research on this intriguing genus that was described two hundred years ago (Kunth in Humboldt et al.

1816), and is still little understood, even more exciting.

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While preparing this manuscript J.C. Pintaud died; *Attalea* was the group to which he devoted greatest efforts in recent years, and this manuscript is a tribute to his excellent career.

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