APPENDIX A: VOUCHER MATERIALS AND GENERIC DESCRIPTIONS

***Brochoneura* Warb. (Figs. 2-8)**—Specimens examined: *B. acuminata* (Lam.) Warb., H. Sauquet 19 (pickled flowers; Madagascar: Toamasina: Fenoarivo-Atsiranana: Tampolo forest; 11 XII 1999; monoecious; MO, P!, TEF), Fig. 2; H. Sauquet 24 (pickled flowers; Madagascar: Tolañaro: Mandena forest; 17 XII 1999; monoecious; MO, P!, TEF), Figs. 3-4; *B. vouri* (Baill.) Warb., H. Sauquet 15 (pickled flowers; Madagascar: Toamasina: Fenoarivo-Atsiranana: Tampolo forest; 11 XII 1999; male; MO, P!, TEF), Figs. 5-8.

This genus consists of three species restricted to littoral rainforests along the eastern coast of Madagascar (Capuron, 1973; Schatz, 2001), two of which, *B. acuminata* and *B. vouri*, were investigated in this study. What best distinguishes *Brochoneura* from the two other Malagasy genera of Myristicaceae (*Haematodendron* and *Mauloutchia*) is its compact inflorescences, in which sessile flowers are clustered into terminal globose heads or hemiglobose heads appressed to the axes of the inflorescences (e.g., Figs. 2 and 5). Stamens are fused into a typical myristicaceous synandrium (Figs. 3-4), consisting of a column of sterile tissue and a collection of three (e.g., Figs. 3 and 6) to occasionally four (e.g., Fig. 2) sessile anthers attached to the upper part of this column. A peculiarity of the androecium of *Brochoneura* compared to other genera of Myristicaceae is the pattern of anther attachment to the column, which is unusually centered along the back of the anther (Fig. 7). In all the specimens dissected (including the third species, *B. madagascariensis*, and many specimens not listed in this paper), I observed no relevant variation in the androecium characters that could be used to distinguish among the three species of *Brochoneura*.

***Cephalosphaera* Warb. (Figs. 9-11)**—Specimen examined: *C. usambarensis* (Warb.) Warb., H.J. Schlieben 2861 (dry flowers; Tanzania: Tanganika: Morogoro: Uluguru mountains; 21 X 1932; male; P!, Z), Figs. 9-11.

This monotypic genus is endemic to a few submontane forests in Tanzania (Lovett and Friis, 1996) and is known from very few collections so far. As in *Brochoneura*, the inflorescences of *Cephalosphaera* are characterized by compact clusters of sessile flowers, shaped like more or less elongate terminal globose heads (not shown). The androecium architecture (Fig. 11) is also very much like that of *Brochoneura*, except for a mean anther number of four (Fig. 9) rather than three and the fact that the anther attachment region extends to the upper part of the adaxial side of the anther (Fig. 10).

***Doyleanthus* Sauquet (Figs. 12-17)**—Specimens examined: *D. arillata* Capuron ex Sauquet, R. Capuron 18904 SF (dry flowers; Madagascar: Sambirano: South of Ambanja: between Ankaramy and Ankingameloka; 7 XI 1958; male; P!, TEF), Figs. 15-17; R. Capuron 27198 SF (pickled flowers; Madagascar: Sambava: Antsirabe Ava.: Andrangana; 2-7 XII 1966; male; P(alc.fl.)!, TEF), Figs. 12-14.

This new monotypic genus is described at the end of this paper from specimens collected in northern rainforests of Madagascar. Although it is very similar to *Mauloutchia* in most characters, its synandrium structure (Figs. 12 and 16) closely resembles that of *Brochoneura* and *Cephalosphaera*, with 3-5 anthers. The exact pattern in which anthers are attached to the column remains unclear, although striking similarities with *Cephalosphaera* were observed when dissecting flowers of the two genera.

Knema Lour. (Figs. 18-21)—Specimen examined: *K.* sp., J. Munzinger & F. Engelmann 236 (FAA-preserved flowers; Laos: Champassak, Vat Phou; 30 XI 1998; male; P!), Figs. 18-21.

This Asian genus, with about 95 species, is widely distributed from India to Nepal to Southeast Asia (de Wilde, 2000). Photographs of an undetermined species collected in Laos are presented here, showing all the characteristic features of the peculiar synandrium architecture of this genus. Often described as a peltate disc, the androecium of *Knema* typically has the shape of an inverted, more or less triangular cone, with a set of 3-25 small anthers (Figs. 18 and 21). Similarly shaped columns (with the upper part wider than the stalk) are found in the mainland African genus *Scyphocephalium* and in several species (traditionally referred to as section *Coniostele*) of the neotropical genus *Compsoneura*. The pattern of anther attachment seems to vary considerably within the genus, but the attachment zone in this particular species appears to cover the whole adaxial surface of the anther (Figs. 19-20), whether the connecting tissue is interpreted as a widened connective or an extension of the sterile tissue of the column.

Mauloutchia Warb. (Figs. 22-50)—With six described species, *Mauloutchia* is the largest genus of Myristicaceae in Madagascar. It is widely distributed in all lowland rainforests of the island (along the eastern and northern coasts), up to 500 m (Capuron, 1973; Schatz, 2001). The most common and best-known species are *M. chapelieri* and *M. humblotii*. The remaining species are known from only a small number of collections. Although this fact is poorly emphasized in the literature, there is a striking variation in androecium characters in *Mauloutchia*, which deserves a careful species-by-species examination.

Mauloutchia chapelieri (Baill.) Warb. (Figs. 22-29)—Specimens examined: R. Capuron 24900 SF (pickled flowers; Madagascar: Sambava: South of Antsirabe Ava.; 18 & 21 X 1966; monoecious; P!, TEF), Figs. 24-25; H. Sauquet 30 (pickled flowers; Madagascar: Toamasina: Maroantsetra: Masoala National Park: Ambanizana; 5 I 2000; monoecious; MO, P!, TEF), Figs. 22-23, 26-29; H. Sauquet 9 (pickled flowers; Madagascar: Toamasina: Réserve Naturelle Intégrale de Betampona; 8 XII 1999; monoecious; MO, P!, TEF): not shown.

This species is characterized by a great number of anthers (20-60; Capuron, 1973) irregularly arranged on an elongate column (Figs. 22 and 24-26), to which they all seem attached by filaments (Figs. 23 and 27-28). The presence of such filaments in *Mauloutchia* is unique in Myristicaceae. However, close examination of this species reveals that in some cases, two anthers may share a single filament (Fig. 29). This pattern calls into question the nature of the filaments in *Mauloutchia* and suggests that such structures in this genus may not be homologous with the typical filaments found in other angiosperms. The irregular insertion of the filament-like

structures on the column in this species (Figs. 23 and 26-27) also challenges the idea that the androecium column in Myristicaceae was simply derived from the fusion of filaments.

Mauloutchia coriacea Capuron (Figs. 30-31)—Specimen examined: R. Capuron 11789 SF (type) (dry flowers; Madagascar: Tolañaro: North of Mahatalaky: Bemangidy forest; 26 III 1955; male; P!), Figs. 30-31.

The androecium of *M. coriacea* is similar to that of *M. chapelieri* in architecture (Fig. 30), but has fewer (22-27) and longer anthers and shorter filaments (Fig. 31). In addition, anthers inserted towards the apex of the column seem shorter than those inserted below (Fig. 30), so that all anther apices reach approximately the same level at the top of the synandrium.

Mauloutchia heckelii Capuron (Figs. 32-34)—Specimen examined: H. Sauquet 6 (pickled flowers; Madagascar: Toamasina: Réserve Naturelle Intégrale de Betampona; 7 XII 1999; monoecious; MO, P!, TEF), Figs. 32-34.

In addition to the presence of a well-developed, deeply laciniate aril (rudimentary elsewhere in the genus) and peculiar leaves, *M. heckelii* stands apart from the other species of *Mauloutchia* in having compact inflorescences in which all flowers are sessile (Fig. 32). However, the androecium of this species is similar to that of *M. chapelieri* in architecture (Figs. 33-34), with fewer (12-20) anthers and shorter filaments (not shown).

Mauloutchia humblotii (H. Perrier) Capuron (Figs. 41-44)—Specimens examined: H. Sauquet 11 (pickled flowers; Madagascar: Toamasina: Réserve Naturelle Intégrale de Betampona; 8 XII 1999; male; MO, P!, TEF), Figs. 41-42; H. Sauquet 5 (pickled flowers; Madagascar: Toamasina: Réserve Naturelle Intégrale de Betampona; 7 XII 1999; male; MO, P!, TEF), Figs. 43-44.

The androecium of *M. humblotii* is similar to that of *M. coriacea* in architecture and anther length (Fig. 41), but has many fewer anthers (5-10; the lowest number in the genus). It also resembles *M. coriacea* in the almost equal level of all anther apices at the top of the synandrium (Figs. 41-42). However, it differs from all androecia described so far in this genus in the very short length of the column (Figs. 41 and 43) and of the filaments (Figs. 43-44), if any are present. Another new character revealed by this species is the possibility that anther phyllotaxy in *Mauloutchia* may be spiral or two-whorled (Fig. 42) rather than irregular, which may be more difficult to observe in species with many more anthers, such as *M. chapelieri* (Figs. 22-23 and 26-27).

Mauloutchia parvifolia Capuron (Figs. 35-37)—Specimen examined: 10159 SF (dry flowers; Madagascar: Farafangana: Morarano; 9 X 1953; male; P!), Figs. 35-37.

The androecium of *M. parvifolia* is very similar to that of *M. heckelii* in architecture, anther number (6-22), and filament length (Figs. 35-37).

Mauloutchia rarabe (H. Perrier) Capuron (Figs. 38-40)—Specimens examined: 4861 SF (dry flowers; Madagascar: Farafangana: Ihorombe: Matsinjoriaka; 28 XI 1951; male; P!), not shown; R. Capuron 28149 SF (pickled flowers; Madagascar: Toamasina: Moramanga: Beforona: East of Marozevo; 23 I 1968; monoecious; P!, TEF), Figs. 38-40.

The androecium of *M. rarabe* is very similar to that of *M. coriacea* in architecture, column length, anther length, almost equal level of all anther apices, and filament length, but has fewer anthers (7-23).

Mauloutchia sp. nov. 1 (Figs. 45-48)—Specimen examined: R. Capuron 23961 SF (type) (dry flowers; Madagascar: Farafangana: Amporoforo forest; 9 XII 1964; monoecious; P!, TEF), Figs. 45-48.

Based on a very distinct leaf size and shape, this new species of *Mauloutchia* (described in a separate paper) is known from very few collections in central-eastern Malagasy rainforests. Its androecium is very similar to that of *M. humblotii* in architecture (Figs. 46 and 48), short column length (though slightly longer; Fig. 46), anther length, and very short or possibly nonexistent filaments (Fig. 47), with slightly more anthers (on average; 8 to 12).

Mauloutchia sp. nov. 2 (Figs. 49-50)—Specimen examined: R. Capuron 28666 SF (dry flowers; Madagascar: Tolañaro: North of Mahatalaky: Bemangidy forest; 14 II 1968; male; P!, TEF), Figs. 49-50.

Based on very distinct fruit and pollen sculpturing, this new species of *Mauloutchia* (also described in a separate paper) is known from very few collections in southeastern Malagasy rainforests. Its androecium is very similar to that of *M. heckelii* and *M. parvifolia* in all characters, except for an apparently longer column stalk and fewer anthers (8-12).

Staudtia Warb. (Figs. 51-52)—Specimen examined: *S. kamerunensis* Warb., A. Hladik 1842 (dry flowers; Gabon: Makokou: Plateau d'Ifossa; 30 XI 1971; monoecious; P!), Figs. 51-52.

This monotypic genus is widely distributed throughout western and central tropical Africa. As in *Brochoneura* and *Cephalosphaera*, the inflorescences of *Staudtia* consist of compact, spherical terminal clusters of sessile flowers (not shown). The androecium architecture (Figs. 51-52) is also very much like that of these two genera, with three (to four) anthers, which seem to be attached to the column along the whole length of their adaxial side, although the poor quality of the material sampled for this species makes it difficult to assess this character accurately.

APPENDIX B: DISCUSSION OF CHARACTER EVOLUTION

Character evolution in Myristicaceae in the context of phylogenetics—Although the origin of the synandrium remains unresolved, some conclusions can be drawn about what the most recent common ancestor of extant Myristicaceae looked like and how it may have evolved

into the various forms observed in the family. With all its limitations, cladistic scoring of morphological characters has proven a powerful tool for comparative studies and reconstruction of morphological evolution (e.g., Doyle and Endress, 2000). I will therefore use the characters scored in Sauquet et al. (2003) and map them onto the estimated phylogenetic trees as a basis for discussing androecium evolution in Myristicaceae.

However, one great difficulty inherent in this approach is the lack of any well resolved, strongly supported hypothesis for phylogenetic relationships among genera, despite an extensive sampling of morphological and molecular data. This was mainly a consequence of a very low level of molecular variation in Myristicaceae and the comparatively long stem branch leading to the extant family. Despite these uncertainties, concurrent evidence from molecular and morphological data unambiguously placed *Mauloutchia* in a derived phylogenetic position, well nested within what we called the mauloutchioid clade (Fig. 1), and this result has fundamental implications for androecium evolution in the family.

Before discussion of particular androecial characters, a few comments on the evolution of general floral morphology in Myristicaceae seems important. All character numbers in the next paragraphs refer to the morphological matrix of Sauquet et al. (2003).

General floral morphology (characters 41-48)—*Character 41. Sex distribution: (0) bisexual; (1) unisexual monoecious; (2) unisexual dioecious*—Within Magnoliales, unisexuality represents an unambiguous synapomorphy of Myristicaceae, but evolved twice independently in Laurales (once in Siparunaceae, and once in Monimiaceae), the putative sister order of Magnoliales (see Sauquet et al., 2003). Most Myristicaceae are dioecious. Exceptions are all genera in the mauloutchioid clade except *Cephalosphaera*, and, outside mauloutchioids, *Endocomia*, part of *Iryanthera*, and part of *Pycnanthus*, all of which are monoecious with various degrees of monoecy depending on how close together male and female flowers are found on the same tree (see de Wilde, 1991). Our phylogenetic results imply that dioecy was ancestral in Myristicaceae and that a shift to monoecy occurred later at least four times in the family.

Character 44. Perianth whorls (series when phyllotaxy is spiral): (0) more than two; (1) two; (2) one; (3) absent—The fact that Myristicaceae only have one perianth whorl represents another synapomorphy of the family, which was derived from more than two perianth whorls. One whorl also evolved independently in *Eupomatia* and *Galbulimima*, probably from a bract on the pedicel (Endress, 1977).

Character 45. Perianth merosity: (0) irregular; (1) in threes; (2) in twos—Conversely, perianth trimery in Myristicaceae is an ancestral feature for Magnoliales and possibly for a much larger clade of angiosperms (Doyle and Endress, 2000). Variations around the basic number of three tepals are quite common in Myristicaceae (usually ranging from two to five tepals), but seem to have been fixed only in species of *Horsfieldia*, most of which belong to section *Irya* (de Wilde, 2000).

Character 48. Inner staminodes: (0) absent; (1) present—Inner staminodes are common in basal angiosperms (Endress, 1984, 2001), including Laurales and Magnoliales. In the phylogenetic analysis of Sauquet et al. (2003), their ancestral status in Magnoliales is equivocal, because this character was considered not applicable in Myristicaceae (which were thus scored as unknown), on the grounds that the absence of inner staminodes in the family may simply be a consequence of its shift to unisexuality and stamen fusion. However, unisexuality does not necessarily imply loss of inner staminodes, as illustrated by Monimiaceae. Assuming inner staminodes were absent in the ancestors of Myristicaceae, they would be a synapomorphy of the clade consisting of *Degeneria*, *Galbulimima*, *Eupomatia*, and Annonaceae and would be derived independently in Laurales. However, assuming they were present in the ancestors of Myristicaceae, they would be a synapomorphy of Laurales plus Magnoliales.

Androecium morphology (characters 49-65)—*Character 49. Androecium phyllotaxy: (0) spiral; (1) whorled; (2) irregular*—Spiral stamen phyllotaxy appears to be a synapomorphy of Magnoliineae (with a later shift to irregular phyllotaxy in Annonaceae), whereas stamen phyllotaxy was ancestrally whorled in Magnoliales and Myristicaceae. However, further evolution of stamen phyllotaxy occurred in *Mauloutchia*. Although in some species of the genus anthers may appear to be arranged in two whorls (either one above the other, e.g., *M. heckelii* [Fig. 34] or concentrically, e.g., *M. humblotii* [Fig. 42]), patterns observed throughout *Mauloutchia* lead rather to an interpretation of all species of the genus as having either an irregular or spiral phyllotaxy. Whichever is true, all species of *Mauloutchia* differ fundamentally from the rest of the family in not having just a single whorl of anthers (see Fig. 53). In the present phylogenetic context, this difference represents an unambiguous synapomorphy of the genus (Fig. 55).

Character 50. Anther apices: (0) all at (almost) same level; (1) at various levels—This character was introduced only to account for potentially informative differences within *Mauloutchia* and was scored as missing data ("?") in all taxa outside Myristicaceae because its significance and primary homology in taxa with entirely free stamens are questionable. Although this character may appear to be artificial, it proved very useful in describing and distinguishing among the various patterns observed in *Mauloutchia* and does not show any homoplasy on the phylogenetic tree we obtained for the genus (Fig. 55). The shift to anther apices at various levels may be a simple consequence of reduction in anther length (since anther insertion was already at various levels at this stage in the history of *Mauloutchia*), but I have not yet found a satisfactory way to quantify anther length.

Character 52. Number of anthers: (0) 2-4-(5); (1) 5-~12; (2) ~12-~20; (3) over 20; ordered character—Anther number is a highly variable character among genera and within the largest genera (Fig. 53). Numbers are based on literature data (Hutchinson, 1964; Capuron, 1972, 1973; de Wilde, 1991, 2000) and personal observations (especially in the mauloutchioid genera). Particular caution was taken with old literature data on this issue, as observations have long been obscured by different interpretations of what an anther corresponds to in synandria with all anthers fused directly through their connectives.

Although such quantitative characters are often criticized as cladistic characters, identification of ranges of numbers that minimize overlap, based on actual observations, usually allows scoring of discrete classes of variation as character states. This approach led to definition of the four classes above. Taxa outside the family were all scored as missing data ("?"), as it is unclear whether variations in anther number in the fused androecium of Myristicaceae can be compared with those in taxa with free stamens, in which numbers appear to vary continuously or in multiples of three. Based on the assumption that the evolution of anther number probably occurred by addition or loss of small numbers of anthers, we have ordered this character. Although the taxonomic representation used did not allow intrageneric variation to be taken adequately into account and led to the largest genera being scored as polymorphic (e.g., *Knema* scored 0/1/2/3), most terminal taxa fell into one or two adjacent classes of anther number (Fig. 54), allowing a few conclusions regarding the evolution of anther number in Myristicaceae.

On strict parsimony grounds, the optimization of this character at the base of Myristicaceae is equivocal, with a range of two to 12 anthers (Fig. 54). However, the high concentration of taxa with only 2-4 anthers in the mauloutchioids and the clade consisting of *Otoba*, *Coelocaryon*, and *Pycnanthus* suggests an interesting basic number of three anthers. Several independent increases occurred within the family. Within *Mauloutchia*, there was a gradual increase to 60 anthers in *M. chapelieri*, nested among species with lower anther numbers. Another marked trend in anther multiplication led to the great numbers observed in *Horsfieldia*, *Knema*, and *Myristica*. However, the polarity of change in these individual genera remains unclear, depending on their relationships, which are not yet resolved.

Character 53. Stamen fusion: (0) free to base; (1) partially or completely fused—All stamens of Myristicaceae were considered to be at least partially fused, because of the shared central column found in all genera (including *Mauloutchia*), although this assumption may be criticized depending on the interpretation of the column (discussed below). Stamen fusion thus appears to be a synapomorphy of Myristicaceae and was unambiguously derived independently in Canellaceae and *Eupomatia*.

Character 54. Filament (free sterile portion below anther): (0) present; (1) absent (whether by reduction or fusion among filaments)—Whether due to loss or to fusion, free filaments are absent in all Myristicaceae except *Mauloutchia*. However, this genus was nested among taxa with strictly sessile anthers in all analyses. The absence of free filaments therefore represents a synapomorphy of the family, with a reversal in *Mauloutchia*. Along with stamen fusion, Canellaceae also lost free filaments—another convergence with Myristicaceae.

Character 56. Connectives: (0) free (basifixed anthers); (1) fused for part or all of the length of the anthers (to a central mass), or centrifixed sessile anthers—In most genera, the connectives seem to be completely fused to the column and cannot be distinguished from it, which explains why it is very often hard to tell which theca goes with which. However, notable exceptions are those genera or species in which anthers are fixed to the column by their base only (referred to as basifixed anthers): some species of *Compsoneura* (traditionally referred to as section *Compsoneura*), all of *Mauloutchia*, and all of *Otoba*. It is unclear whether *Knema* has

basifixed anthers or not (which may depend on the species), because of the continuity between the connective tissue and the peltate disc around which anthers are inserted (Figs. 19-20). The centrifixed anthers of *Brochoneura* (see Fig. 7) represent yet another exception, which was not observed in any other genus (although this condition may be difficult to distinguish from completely fused connectives without SEM study). Although these exceptions are often referred to as free anthers, I prefer to use the term free connectives instead, to avoid confusion between this character and the filament character. Finally, in genera such as *Horsfieldia* or *Paramyristica* (Fig. 53; see also de Wilde, 2000), deep hollowing out of the column at the top may give the wrong impression that the anthers are basifixed, but close examination quickly rules out this possibility, as all anthers remain linked to each other by a thin connecting cup of sterile tissue.

Basifixed anthers appear to be independently derived in *Compsoneura* sect. *Compsoneura*, *Mauloutchia*, and *Otoba*, and it is unambiguous that connectives were fused in the ancestor of the family. Like stamen fusion and loss of filaments, connective fusion evolved independently in Canellaceae.

Character 57. Upper part of column (sterile tissue bearing anthers, = sterile part of synandrium sensu de Wilde, 2000): (0) truncate to deeply hollowed; (1) shortly and narrowly elongated (i.e., with a sterile apex); (2) greatly widened (including peltate disc)—The shape of the apex of the sterile column also shows some interesting variation among genera. It is narrow and truncate in most genera; slightly to deeply hollowed in *Gymnacranthera*, most species of *Horsfieldia*, and *Paramyristica*; shortly and narrowly elongate in *Myristica* and *Osteophloeum*; and greatly widened in some species of *Compsoneura* (traditionally referred to as section *Coniostele*), all of *Knema*, and *Scyphocephalium*.

Whereas the greatly widened apex of *Compsoneura* sect. *Coniostele* is an unambiguous convergence with *Knema* and *Scyphocephalium*, the possibility that it represents a synapomorphy of the latter two is not excluded. However, such a transoceanic disjunction (*Knema* is Asian, *Scyphocephalium* is West African) requires further phylogenetic testing (no molecular data are available so far for *Scyphocephalium*). The short sterile column apex of *Myristica* and *Osteophloeum* also appears to be a convergence, although it should be noted that the two genera also share strikingly similar pollen, which is unusual in having free bacula in the lumina of the reticulum. Finally, ancestral Myristicaceae most likely had a truncate column apex.

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