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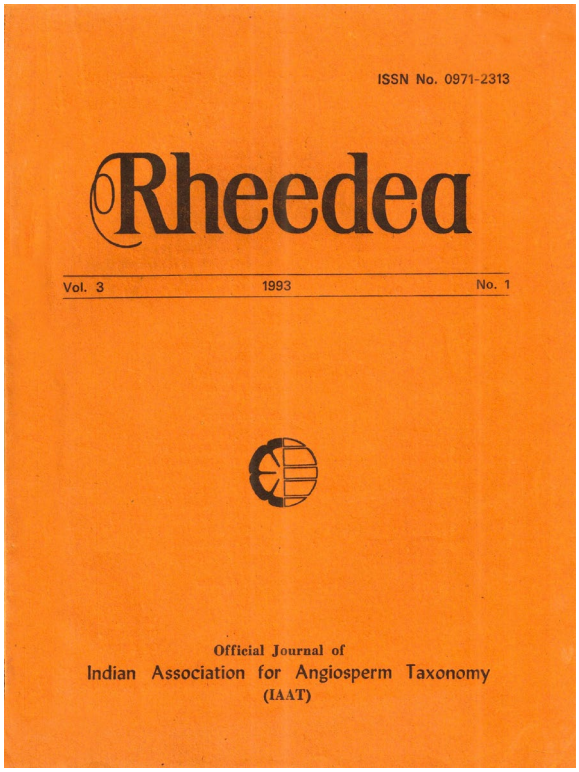

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Evolutionary history and classification of the Laurales, especially of the Monimiaceae: Deductions based on fossil records and on the Anthocorm Theory

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Abstract

The putative phylogeny and relationships of the Laurales, in particular of the Monimiaceae, are discussed in the light of fossil evidence and of interpretations based on the Anthocorm Theory. The conclusion is drawn that the group is a close-knit, ancient one at least as old or possibly even older than the Magnoliales, and that the recent representatives are terminal and did not give rise to other, more advanced forms. There are, therefore, reasons to raise this taxon to the rank of Lauranae.

The Calycanthaceae (the Idiospermaceae inclusive) are aberrant because they have holanths in contrast to the other lauralean families that bear anthoids. The twining and parasitic genus *Cassytha*, conventionally a member of the Lauraceae, is also aberrant and apparently represents an early offshoot from a lineage that led to the recent Lauraceae and related families, so that a point can be made for the recognition of a separate family Cassythaceae. The Trimeniaceae are also an early offshoot of a lineage leading to the Lauraceae-nexus and presumably also to *Cassytha*.

Some results and interpreations have been applied to other groups such as Chloranthaceae and Piperales, and a suggestion is made regarding the origin of other twining parasites such as the Convolvulaceae-Cuscuteae.

1. INTRODUCTION

Recent discoveries of fossilised reproductive structures of Laurales of the Cretaceous (*Prisca*, described by Retallack & Dilcher, 1981, and according to Drinan *et al*, 1990, in their paper on *Mauldinia*, of lauraceous affinity), in combination with the repeated finds of vegetative parts and cuticles attributed to early lauralean forms, suggest an early appearance of the order that canhardly be doubted and this is accepted here as factual. In phylogenetic terms this means that the Lauralean clade (which appears to be a rather homogeneous unit and, therefore, must be monophyletic) became separated soon from the early phases of the major clade also leading to Magnolianae and Ranunculanae, conceivably

already in the late Jurassic. It is, accordingly, quite inane to derive the lauralean assembly from a magnolealean one (the traditional viewpoint) also because the fossil evidence is at variance with this idea. *Prisca* is the most primitive, tangible protolauralean fossil known and in fact epitomises a female anthocorm (see Chapter 2). It is plausible that since *Prisca* must have been monoecious or dioecious, the other diclinous, primitive recent Laurales are descendants of diclinous forbears, but *Mauldinia* was monoclinous and this means that bisexual blossoms originated rather early in the lauralean clade. Another difference between *Prisca* and *Mauldinia* is that the first still has a primitive anthocorm and uncontracted gynoclads whereas *Mauldinia* already had discrete anthoids (and merandra), see Chapter 2.

In view of the situation in *Amborella* and in the Monimiaceae, one can visualise a male counterpart of *Prisca* in which the monogyna, to all intents already carpels but perhaps not quite closed yet at anthesis, are replaced by holandra (see Fig. 1). The predominance of monocliny in the Lauraceae and associated families demands that also ambisexual gonoclads occurred in early lauralean forms. These conclusions lead to a reconstruction of phylogenetic lineages as we shall see.

Unfortunately lauraceous pollen is so poor in sporopollenin in its exine that it decays quickly, with the result that fossil pollen of lauralean taxa is not likely to be found and certainly not as *sporae dispersae*. This may prevent any more or less reliable assessment of the frequency of occurrence of lauralean taxa in past eras but is not such a great hindrance. The pollen type of the recent lauralean families differs from the monosulcate type, so commonly found in Magnoliales and Monocotyledons (and Bennettitaleans), which means that Laurales presumably branched off from the early stages of the Magnoliid-Nymphaeoid-Ranunculoid-Caryophyllid-Monocot clade and evolved independently from at least the lower Cretaceous or possibly even earlier.

2. MORPHOLOGICAL ASSESMENT OF THE FLORAL REGION

In recent compilations (Meeuse 1990, 1992) the floral evolution of the angiosperms was again discussed in the light of the Anthocorn Theory. Although the general idea is quite clear, whenever possible a more detailed analysis of a given taxonomic group in indicated. Such an approach must start from certain assumptions (which are often substantiated by fossil evidence: e. g. *Archaeanthus*, *Meeusella*, *Caloda* and *Prisca* provide tangible archetypes), *viz.*

(a) the diversification of the major clades of the angiosperms began before the Jurrasic-Cretaceous borderline;

(b) ancestral strobiloid structure (anthocorms) gave rise to two kinds of F(unctional) R(eproductive) U(nits)s: anthoids and holanths respectively, and

these two (together constituting the conventional 'flowers') occur in the recent angiosperms. Apart from this floral evolution, the transition from a mesocycadophytic (= advanced glossopteridalean) condition to a full-fledged angiospermous one was gradual and mainly characterised by such advancements as wood vessels, companion cells in the phloem, *Pollenkitt* and angioody ('angiospermy');

(c) the anthocorm is defined (Meeuse 1975a, 1981, 1992) as a structure consisting of a central axis bearing bracteated axes of a higher order (gonoclads); these gonoclads were originally all male *(androclads* bearing ebracteate holandra, the latter usually becoming schizandra = a perigone member with its associated merandra = anthers on intercalated filaments), or all female *gynoclads* bearing ebracteate monogyna = ovuliferous cupules by subsequent closure becoming carpels), but later partially male and partially female ones (usually in the form of androgynoclads) originated;

(d) as is evident from (c), the sex distribution is often predominant or almost universal in certain taxa, but there are several exceptions, also in more or less primitive taxa, *e. g.* Chloranthaceae, Cyperaceae and Laurales, in which di- and monoclinous taxa occur side by side;

(e) apart from rather frequent oligomerisations of the number of gonoclads per anthocorm and of the number of monogona (holandra/schizandra and monogyna) per gonoclad, the principal changes in the angiospermous floral region were a shortening and contraction (brachyblasty) of either the anthocorm axis (the anthocorm thus turning into a holanth), or of the gonoclad axes (the anthocorm thus becoming transformed into a number of coaxial anthoids).

Armed with this arsenal and using ancillary evidence from recent forms and some fossils one may attempt a reconstruction of the evolutionary history of the floral region of a given recent angiosperm taxon and hope to elucidate its phylogeneric origin.

3. SOME CHARACTERISTICS OF THE MONIMIACEAE AND OTHER LAURALES

The Laurales, the Amborellaceae and Monimiaceae-Monimiodeae in particular, have been rather neglected in disquistions concerning primitiveness in angiosperms. (The general taxonomy and evaluation of the characters follow in Chapters 4 and 7). The primary approach is a search for archaic and plesiomorphic features to build on.

The reasons why the Monimiaceae have not been extensively studied are partly because their floral morphology was rather baffling and one tended to accept a reduction and oligomerisation and a secondary dicliny of their FRUs in respect of a magnoliaceous archetype (and the erroneous conclusion that the Laurales are reduced and advanced descendants of a magnolialean ancestral stock

apparently still prevails see, *e.g.* Endress 1972, 1986), and partly, I think, because the scarcity of fresh or spirit material, especially of Monimiaceae growing in tropical forests in apparently often small populations, was prohibitive to extensive studies. The accessibility of tropical rain forests has increased in the last few decades owing to, among other things, the use of helicopters and the like and an increased interest in their botanical exploration before it is too late. The floral biology is also very poorly known, which is unfortunate because, as I hope to demonstrate, not only such archaic taxa as *Amborella* but also Monimiaceae may have retained ancient anthecological syndromes. The case histories must, of necessity, be established in the native region where the prospective pollinating animals occur, but this may be difficult in especially dense stands of forest in which only scattered individuals of the plant species concerned are found. Second best is to grow the species in botanical gardens in their native area (e. g., *Amborella* in New Caledonia, species of *Tambourissa* in Madagascar and the Mascarene Islands, etc.), which is also recommendable because many species, especially those with a rainforest habitat, are becoming threatened with extinction.

The vegetative anatomy of the Laurales is rather well known and amply treated in Metcalfe (1987). It appears that the Laurales constitute a close-knit group rather distinct from the Magnoliales (in e. g. the nodal anatomy) and more or less clearly standing apart.

This point towards an early separation of these taxa rather than to a close relationship and this does not warrant a derivation of the Laurales from some magnolian ancestral taxon. The idea still current among a majority of the 'leading' systematists is that all kinds of 'flowers' (FRUs) are derived from a type epitomised by the recent Magnoliaceae, but as I have pointed out (Meeuse 1992) there are workers who accept a so-called 'simple' flower as the most primitive one and some come very close to the last step, i. e., to recognise the incidence of two kinds of FRUs: their "simple" FRUs (my anthoids) and more intricate ones (my holanths). The presence of anthoids in all Laurales, the Calycanthaceae/ Idiospermaceae excepted, is, therefore, not a secondary development but simply one of the alternative pathways of 'flower-making'.

The relationships with a Magnoliales-nexus is clear from certain chemical features and from *e. g.*. the very frequent trimery of the anthoids. The Laurales are nevertheless rather isolated and clearly represent an ancient group that diverged early but retained its principal characters to this day and was rather successful: the family Lauraceae is a rather large one. The taxon has not evolved much beyond a stage in principle already attained in the Cretaceous *Mauldinia* and apparently did not give rise to other lineages.

Among the more archaic features one may count the homoxyly in *Amborella* and the predominance of holandra in this and in several other taxa

(*e. g.* in Monimioideae), but the Lauraceae and related families have a rather advanced wood anatomy. As was posed by several workers, early angiosperms and their immediate precursors were most probably of modest stature and at best shrubby but in the Lauraceae group lofty trees often with clean boles originated secondarily. This is a general trend in most dicotyledonous clades and among the recent representatives. The more primitive members retain the more modest habit while the more advanced tend to become large trees (compare the similar trend in Amentiferae and other hamamelidid groups, and in the Dipterocarpaceae in the dilleniid clade). A secondary decrease in size, as is manifest in most of the (advanced) sympetalous dicots (Scrophulariales/Lamiales, Gentianales, Asterales etc.), i. e. a 'return' to a suffruticose, to ultimately herbaceous forms did not occur in the Laurales if *Cassytha* is disregarded (but *Cassytha* is a sepcial case to be discussed later). A consistent feature in the Laurales is the simple leaf. In contrast to the situation in some other clades the ancient prevalence of compound or at least dissected leaves completely disappeared or perhaps almost so. *Sassafras* with lobed leaf-blades may be an atavistic exception but it is lauraceous and advanced in respect of *Amborella* and Monimiaceae that always have simple leaves as far as I can ascertain, so that its leaf shape may be a secondary development. However, *Sassafras*-like leaves have been reported from Cretaceous rocks and recent *Sassafras* may have retained a plesiomorphic leaf shape that has disappeared in other taxa.

4. FLORAL EVOLUTION IN THE LAURALES

The basic structure of the floral region is a unisexual anthocorm as found in *Prisca*. There must have been at least one other kind with ambisexual gonoclads (as in the early *Mauldinia*). The equivalence of a monogynon and a holandron requires a male counterpart of *Prisca* (see Fig. 1): androclads bearing holandra-holandra because they preceded schizandra and also because several more primitive lauralean groups retained their holandra. Similarly, the monocliny of *Mauldinia* requires an early advent of androgynoclads. In the majority of the cases the gonoclads turned into anthoids, primitively unsexual in *Amborella* and the Monimioideae, (A glance at representatives of these taxa reveals, as may be expected, that the anthoids appear as in the examples shown with primitive holandra each bearing up to rather appeciable numbers of anthers). Apparently soon a trend developed to change holandra into schizandra in the groups centred around the Lauraceae. This trend was concomitant with the advent of usually nectariferous glands towards the base of the filament and of the valves by which the anthers dehisce. In the Trimeniaceae and Calycanthaceae the holandra became bithecate and of the kind conventionally described as 'stamens with a produced connective' (see Meeuse 1992, p. 62 and fig. 3 d, e, f). The proximal holandra became tepaloid by the loss of the anthers (transitional stages are sometimes present).

The evolutionary trends in the androecial members is thus evident if the situation in the *Amborella-Hedycarya* type is accepted as original (see Fig. 1).

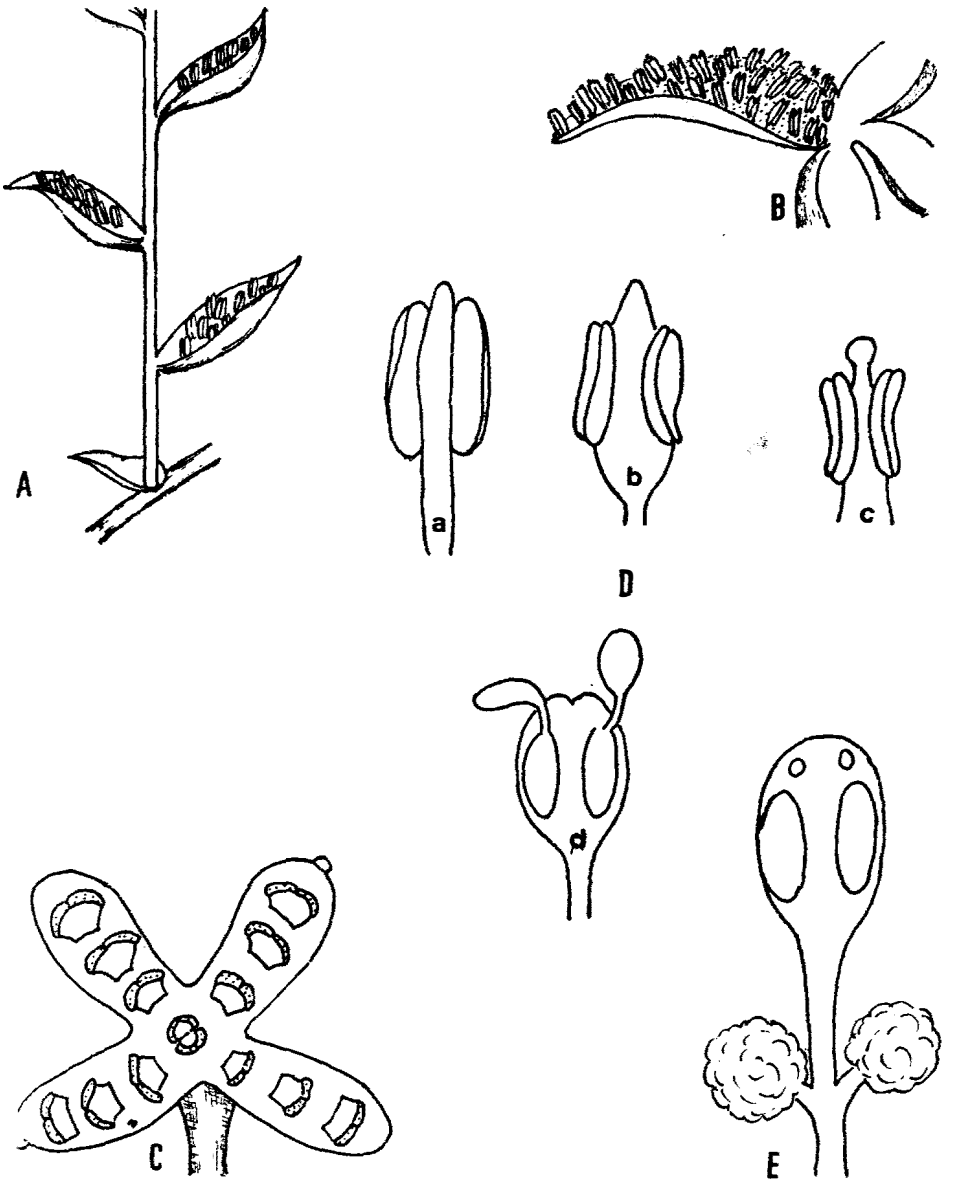

Fig. 1. Polliniferous organs of Lauranae. A. Theoretical male counterpart of *Prisca*: coaxial holandra of an anthoid (only a part shown). B. *Amborella*- *Hedycarya* type, one holandron (with numerous erect, sessile anthers) of a male anthoid shown, developed from A by brachyblasty and oligomerisation of the holandra. C. Anthoid of *Ephippiandra*, number of anthers of each holandron reduced to one longitudinal row and all adnate to supporting sterile part. D. Alternative specialisation of holandron: Number of anthers per holandron reduced to two and adnate. E. Merandron type of Lauraceae; often two large and two small valves (valves not drawn) basal glands present.

The trends in the gynoecial morphology are also quite clear of the sequence in Fig. 2 is accepted. The most primitive type is *Prisca*, in which each gynoclad bears numerous sessile monogyna. A reduction in their number leads to a situation as found in *Amborella* (in which the oligomerisation of number of carpels has far more advanced than in other genera such as e. g. *Hedycarya*, *Ephippiandra* and *Tambourissa*). *Amborella* retained the gynanthocorm build-up but the monogyna are stalked (not so in other than lauralean taxa). Aggregation is common and the brachyblasty of the anthoid is often concomitant with pachyblasty resulting in a broad receptacle-like structure (as in *Ephippiandra*) that became saucer-shaped (as in *Hedycarya*) to urceolate (as in *Kibara* and *Tambourissa*). A marked oligomerisation to a few or a single carpel occured in the Trimeniaceae, Cassythaceae and Lauraceae.

The various types of anthoidal FRUs persisted to this day, only the Calycanthaceae having formed holanths. What happened in this family is that a dense whorl of androgynoclads around the tip of the pachy- and brachy-blastic anthocorm axis bent inwards to become adnate to the broadened anthocorm top. The androgynoclads bore their monogyna on the abaxial side. The vascular anatomy clearly indicates that the androgynoclads bent inwards, as shown by Tiagi (1963 p. 226, fig. 1, reproduced in Meeuse 1972). This kind of holanth, incidentally, also originated in *Eupomatia* and *Nelumbo*, in contrast to the typical Magnoliaceae in which the more or less clearly thickened anthocorm axis remained somewhat elongate so that the androgynoclads became adnate in a vertical position. As regards the formal floral morphology, taxonomic treatments of genera or families were (perhaps less frequently so nowadays) accompanied by floral diagrams and/or floral formulae as an aid to obtain a quick overview of the situation in the taxon concerned and also to enable comparisons between different taxa. Both formal methods are based on (usually tacit) tenet regarding the sequence and the mutual spatial relations of floral parts. A conventional 'flower' was supposed to bear appendages, either in the form of a continuous helix (or several intermingled helices), or in the form of whorls of similar elements. It is clear that the incidence of holanths next to anthoids, and of holandra next to schizandra renders a single yardstick unapplicable to all kinds of FRUs, but even within the category of the anthoids with schizandra the methodology leads to spurious results. The Lauraceae serve as an illustrative example (another one is found in the Cyperaceae: Meeuse 1975b). Conventionally the usually trimerous Lauraceae have basically three consecutive whorls of sepals or petals/tepals and three whorls of androecial members (the constantly monomerous gynoecium can be disregarded). In formula: TEP 3+3+3 (perianth members free or basally fused), ANDR ('stamens') 3n+3n+3n (n is = 0-3 or sometime more, usually 0 or 1 in the outer two whorls and often 3 in the innermost one). The actual situation is that each perianth member has (0-)1 to several opposed merandra ('stamens', *i. e.*, there are three whorls of perianth members with their associated androecial elements (A): TEP $3\times (1+nA)+3\times(1+nA)3\times(1+nA)$. In a floral diagram one

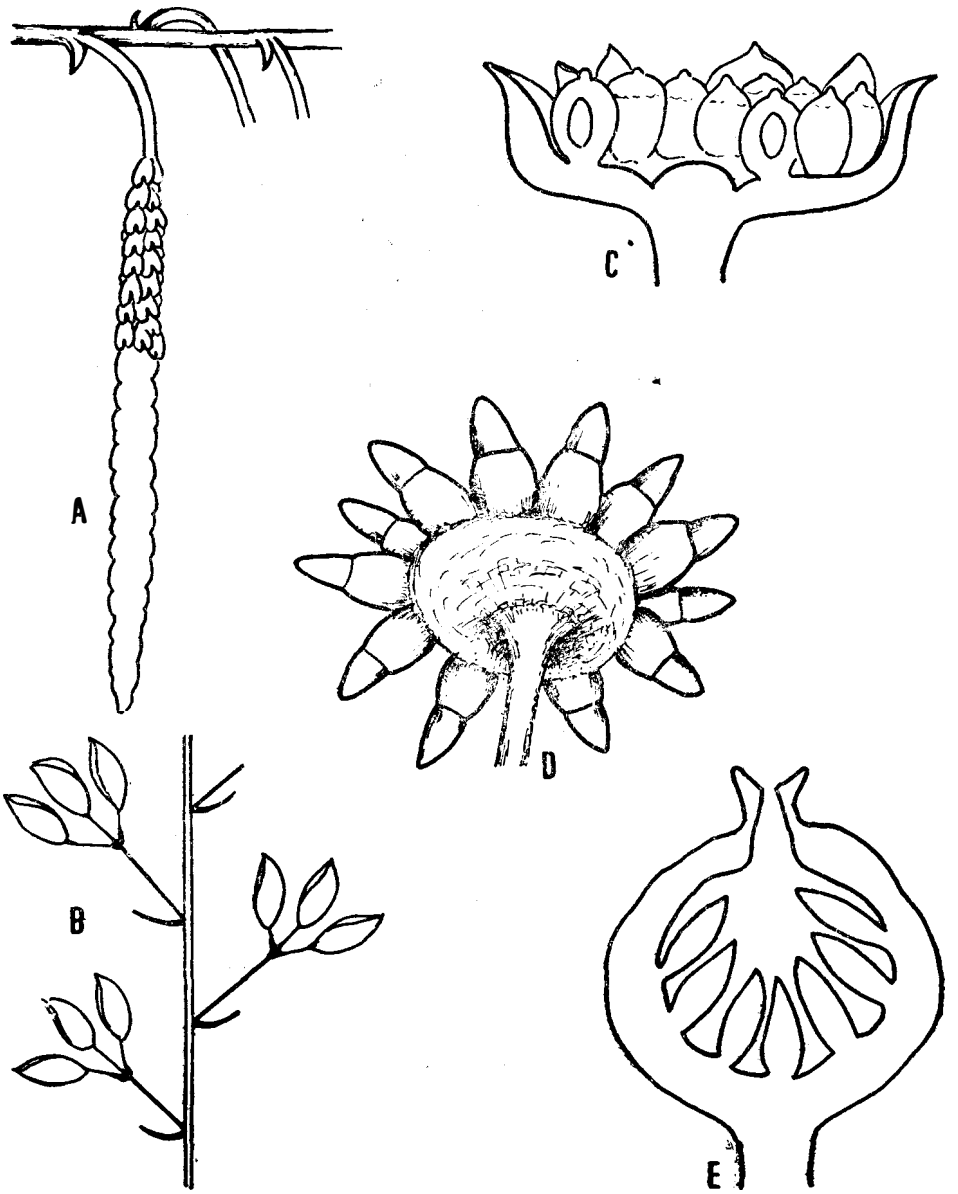

Fig. 2. Ovuliferous organs of Lauranae. A. Most primitive type known: part of anthocorm of *Prisca* consisting of main axis and bracteated lateral axes (gynoclads) each bearing numerous sessile monogyna (pre-carpels). B. Part of anthocorm of *Amborella*. The bracteate gynoclads usually bear only three stalked monogyna. C. Anthoid of the *Hedycarya* type: brachy-and pachyblasty of the gynoclad axis resulted in a receptacle-like, saucer-shaped structure bearing numerous erect ovules (median section). D. Anthoid of *Ephippiandra*, very similar to *Hedycarya* but receptacle-like structure very shallow, more disc-shaped. E. Anthoid of the *Kibra-Tambourissa* type: the receptacle-like structure has become urn-shaped with a narrow aperture and surrounds the monogyna which in *Tambourissa* are almost completely sunken into what becomes the friut wall.

cannot draw three outer whorls of perianth members centripetally followed by three or more whorls of androecial elements: *the whorls alternate.* Significantly, the innermost petaloid elements of the anthoids of the ancient *Mauldinia* often became detached with their associated merandra as a unit and became fossilised as such (Drinan *et. al.* 1990, figs 4a, 4b on p. 376).

5. THE CASE OF *CASSYTHA*

Cassytha is a case apart in that it differs from all other Laurales in its parasitic habit. The genus differs from the Lauraceae to which it is almost unanimously referred, by its twining habit and by the abundance of endosperm (and a relatively small embryo). Twining taxa occur in some more primitive lauralean families and, in addition to the embryological features, this indicates a greater ancientry of *Cassytha* than the current classification suggests. The ancestors of *Cassytha* must have been lianas and this have something to do with the parasitic habit and the host spectrum, as will be explained in a forthcoming paper also dealing with the genus *Cuscuta* (which provides a beautiful example of convergent evolution).

A progressive transfer of the storage tissues from the endosperm to the embryo seems to have been the general trend in the evolution of the Laurales (Dahlgren 1983) and a copious endosperm and small embryo are almost certainly plesiomorphic. Since this condition has been reported in *Mauldinia* it is inconceivable that *Cassytha* is derived and, therefore, not likely to have originated from large trees and, as all other Lauraceae are non-climbing shrubs to lofty trees, it must have had a climbing ancestor and in this feature it comes closer to the Trimeniaceae, *i. e.,* to a greater ancientry than that of the other Lauraceae. Another relevant point is that Corner (1992) recently defended his contention that on the whole (and more so in primitive angiosperms) pachychalazy is advanced and he specifically mentioned Lauraceae (*Cassytha* excepted!) as an example. Most probably *Cassytha* has a more plesiomorphic seed anatomy and in this respect also differs from the Lauraceae proper. As an early offshoot (see the diagram in Fig. 3) one may well consider *Cassytha* worth family ranking.

Another possible indication of the ancientry of *Cassytha* is the geographical distribution of the genus. If that of the rather wide-spread *C. filiformis* (whose fruits are presumably dispersed by sea-currents) is disregarded, the representatives are Australian (see Weber, 1981) the other African species are, in my opinion, not more than varieties of *C. filiformis*) and restricted in their occurrence in the area where also a large number of primitive Laurales (*Amborella,* Trimeniaceae, several Monimiaceae) occur. The other Lauraceae certainly do not have a distributional centre in the Australian region and may well be more modern: in other words, *Cassytha* is more likely to be an ancient offshoot than a more recent one. The case of *Cassytha* matches that of *Casuarina* of which one hydrochorous

coastal species (*Casuarina equisetifolia*) is wide-spread and the other ones occur in or near the Australian region.

6. THE POSITION OF THE TRIMENIACEAE

The Trimeniaceae have long been recognised as related to the Monimiaceae or have even been incorporated in them. The present trend is to place them, as a family, somewhere near or between the Amborellaceae and Monimiaceae (for a discussion, see Endress & Sampson 1983). The Trimeniaceae are apparently rather primitive in some respects and, I believe, represent an early offshoot of a lineage also leading to the Monimiaceae and the Lauraceae nexus. The climbing habit of the species segregated as *Piptocalyx* (which in my opinion should be merged with the non-scandent *Trimenia*) is a primitive feature, but the early tendency towards a reduction of the gynoecium to one or rarely two monogyna per anthoid is an advancement also found in especially the Lauraceae group. The monocliny is not necessarily an advanced feature but must have originated early because monocliny (or the incidence of bisexual and male anthoids on the same invidual) is found in some Monimiaceae (e. g. *Hedycarya*. Sampson 1969) and in Lauraceae (and monocliny also occurred early in the Cretaceous *Mauldinia*).

There is one special trend that characterises the Trimeniaceae and warrants a separate status at the family level. As far as I can ascertain it is the only lauralean taxon in which the proximal holandra became sterile but retained the more laminiform primitive shape to become tepals presumably also acting as semaphylls. Transitions between the tepals and the fertile holandra are not rare (see Endress & Sampson 1983: Fig. 12). A similar formation of the perianth members from holandra is known from several Magnoliales and large-flowered Nymphaeaceae (in which also transitions between them are sometimes or regularly found).

7. PHYLOGENETIC EVALUATION

Among the characteristic features of the Laurales the two consistent, outstanding ones are the pollen type and the hardly decay-resistant exine; others are *e. g.* the almost invariably simple leaf blades, the nodal anatomy (in which they differ from most if not all other Magnoliales) and, in groups with schizandra, the presence of a pair of subbasal glands on the filaments and the valvular dehiscence of the anthers. As stated before, the occurrence of lauralean taxa with holandra, often bearing rather numerous erect anthers, is a very primitive (plesiomorphic) feature not encountered in the Magnoliales proper. The holandra of *Chloranthus*, if the Chloranthaceae are included in this assembly, have three anthers, in all other Magnoliales the holandra have only two longitudinally adnate anthers and are more advanced.

On the other hand, phytochemical indications, ethereal oil cells and the rather consistent floral trimery in most of the Laurales, show that the Laurales

belong to the major Magnolioid-Nymphaeoid-Ranunculid-Caryophylloid-Monocot clade, but since these features are plesiomorphic in that clade they have no bearing upon the question of the interrelations among the various subordinate lineages within that major clade. In view of the ancientry of the Laurales as a distinct taxonomic group—they may be as old as, or presumbly even older than the Magnoliales—there is every reason to raise the rank of the Laurales to that of a superorder Lauranae, but I shall refrain from proposing this formally at this stage because the status of other members of the Magnolianae also ought to be considered.

The subdivision of the Laurales/Lauranae must primarily be based on the following consideration (and the pertaining features or character states):

(1) homoxyly versus heteroxyly—this separates the homoxylous *Amborella* from all other taxa and in view of the lack of other (e. g. phytochemical) characteristics indicates a rather isolated position of the genus, but in several respects it does not differ appreciably from the Monimiaceae-Monimieae and a family rank for the genus seems to fit the evidence best;

(2) holanths versus anthoids—these two alternative characters separate the Calycanthaceae s. l. (with holanths) from all other taxa (that have anthoids);

(3) holandra versus schizanda—holandra are plesiomorphic in respect of schizandra and this provides indications regarding the rate of evolutionary advancement of a lauralean taxon: holandra are found in the Amborellaceae, Monimiaceae—Monimieae, Trimeniaceae and Calycanthaceae and these taxa are more primitive in respect of the taxa with schizandra;

(4) small embryos (and an abundant endosperm) versus large embryos (and a small quantity of endosperm)—the first combination is apparently plesiomorphic and indicates a more primitive status in respect of the other situation.

It follows that *Amborella* is the most primitive taxon and that the Amborellaceae represent an early offshoot of the lauralean clade; significantly the female reproductive organs are very primitive and still in the anthocorm phase. The Calycanthaceae s.l. must also represent an early offshoot because the embryological features are plesiomorphic and in several respects the family is somewhat isolated from the remainder (which also indicates an independent evolution of some duration). The Monimiaceae and the Trimeniaceae (with holandra) are the next most primitive ones in respect of the remaining taxa. The incidence of scandent forms in these two taxa is, to my mind, an original condition because the whole magnoliid nexus contains several primitive families with scandent representatives (lianas); this point is relevant as regards the taxonomic position of *Cassytha*.

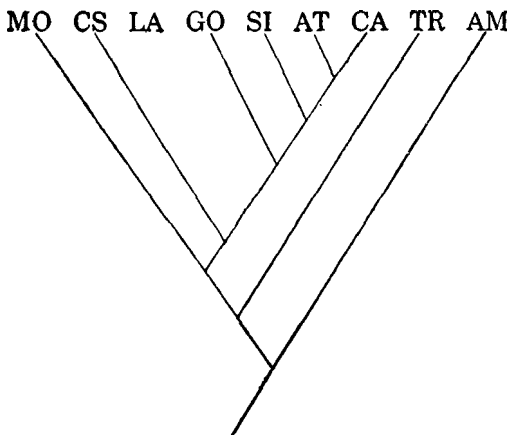

Fig. 3 Tentative cladogram of the Lauranae MO=Monimiaceae, CS=Cassythaceae, LA=Lauraceae, GO=Gomortegaceae, SI=Siparunaceae, AT=Atherosperma(ta)ceae, CA=Calycanthaceae, TR=Trimeniaceae, AM=Amborellaceae.

The Antherospermeae, Siparuneae, Lauraceae (without *Cassytha*), Gomortegaceae (and Hernandiaceae if one separates it as a family) are the most advanced, more or less in that order. *Cassytha* has some plesiomorphic features and is clearly derived from woody climbers (which, I believe, also indicates a certain degree of ancientry), which means that this parasitic genus is older than one would expect from the current classification as a subfamily or tribe of the Lauraceae and that *Cassytha* is an offshoot of a lineage that (also) led to the recent Lauraceae. In view of its plesiomorphies and specialisation I am of the opinion that the family Cassythaceae, proposed by Lindley (1853), should be reinstated.

The keys and descriptions in recent text books and manuals are adequate to identify the various taxa constituting the Laurales (or Lauranae). I differ in assessing *Cassytha* as a family and in positing that the Calyanthaceae s.l. are not the most primitive representatives (as is assumed by some workers on account of their polymerous holanths), but originated as an early offshoot by divergent floral evolution resulting in holanths and anthoids. The Antherospermeae and Siparuneae of the monographers and our contemporary systematists are characterised by having schizandra (and, therefore, a perianth). In this respect they are advanced and stand closer to the Lauraceae nexus and I accept a family rank for these taxa as was earlier proposed already. The diagram (Fig. 3) is a tentative cladogram.

If one desires a subdivion into ordines one may consider a grouping of:

—Amborellaceae

—Trimeniaceae

—-Monimiaceae, Atherosperma(ta)ceae, Siparunaceae and Gomortegaceae

—Calycanthaceae and Lauraceae
as separate entities, as suggested by some characteristic plesio-or apomorphic features.

8. FLORAL BIOLOGY

The primitive status of several members of the Laurales may well provide a clue to the advent of anthecological syndromes if the plausible assumption is made that primitive pollination mechanisms survived in this group. A simple comparative analysis of the more advanced and predominantly monoclinous forms, especially of the Lauraceae nexus, strongly suggests entomophily by presumably not very specialised insects but the data are scarce (Grant 1950 on Calycanthaceae; Lorence 1985; Niesenbaum 1992). The incidence of anemophily in especially diclinous taxa must not be ruled out, but as far as I can ascertain there are no record of the presence of any appreciable amounts of lauralean pollen types in (recent) pollen rains.

The colour of the semaphyllous parts of the FRUs is predominantly white to cream or (pale) yellow but purplish and brownish to reddish colours have been recorded in *Tambourissa* (Endress & Lorence 1983). It is interesting to find out what pigments are involved because the rich blues, purples and reds of anthocyanidins and the deep yellows of anthochlors are apparently lacking, which implies that advanced flavonoid synthesis has not developed in the Lauranae. The question arises whether the yellowish floral pigments in the Lauranae may have a a different function e. g. one associated with the absorption or reflection of infra-red or UV radiation: the insects recorded as visitors by Lorence and Nisenbaum may not have colour perception (the syrphids perhaps excepted). Another primary attractant, a floral scent, may be operative, but in spite of the abundance of ethereal oils in the leaves there are no indications of scent production in the floral region, but there may be odours not perceived by humans but acting as signals on insects.

As regards the visitors recorded, Niesenbaum does not specify any taxa, but Lorence (1985) reports Diptera belonging to the Drosophilidae, Lauxaniidae and Syrphidae and Coleoptera belonging to the Hydrophilidae, Nitidulidae, Rhizophagidae and Staphylinidae (apart from *Apis* as) visitors of *Tambourissa* but this does not mean that the oldest visitors of the Lauranae were beetles. More pertinent studies of pollen loads and of the visiting of both the male and the female anthoids of the same species by insects are lacking. Grant recorded small beetles in *Calycanthus* and Gottsberger (1977) made some observation, on *Mollinedia* and observed Thysanoptera which he believes to be pollinators. Endress (1980) reports larvae in floral parts and conceivably the (apparently unknown) insects whose larval stages develop inside the blossoms also acts as pollinators when they crawl around during mating and oviposition.

Recently, Feil (1992) reported gall midge pollination in *Siparuna*, a syndrome remniscent of the *Ficus*- Agaonidae relation: parasitic insects that pollinate during oviposition. The occurence of larvae in the floral parts of Monimiaceae, reported by Endress (1980b) may relate to such a mutualism between a parasite and a monimiaceous taxon.

Since neither all beetles nor all flies are primitive and the position of the basically carnivorous Staphylinidae is doubtful, beetle pollination need not be primitive in the Lauranae.

Endress (1979) and Endress & Lorence (1983), in my opinion, overrate the significance of the mucilaginous plug in the orifice of female anthoids of *Tambourissa* species. As I pointed out (Meeuse 1990, p. 45-54), stigmatic exudates played a role in the evolution of pollination syndromes and when in several monimiaceous genera *e. g. Kibara*, *Hennecartia* and *Wilkiea* the receptacle-like broadened axis of the female (and sometimes also the male) anthoids became hollow, in *Tambourissa* the stigmatic exudates of each separate carpel somehow fused into one plug of mucilage. This is, of course, an advancement (specialisation) of a sort but does not mean that *Tambourissa* and related genera are very derived.

The outcome of anthecological studies of the Laurales is decidedly meagre and more extensive and more convincing studies ought to be made to establish the transfer of pollen by taxonomically identified insect visitors beyond reasonable doubt.

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