

Finnish Museum of Natural History LUOMUS, Botany Unit
Faculty of Biological and Environmental Sciences
Doctoral Programme in Wildlife Biology LUOVA
University of Helsinki, Finland

BARKS AND FORMAL TAXONOMY IN THE FAMILY ANNONACEAE

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ACADEMIC DISSERTATION

To be presented for public discussion with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki, in Nylander Hall, Botany Unit of the Finnish Museum of Natural History,

on the 27th of March, 2020 at 12 o'clock

Helsinki 2020

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Cover illustration: Flower branch of *Oxandra saxicola* Maas & Junikka *sp. nov.*
(watercolour by Paula Vilkki)

Dissertationes Schola Doctoralis Scientiae Circumiectalis, Alimentariae, Biologicae

ISSN 2342-5423 (Print)
ISSN 2342-5431 (Online)

ISBN: 978-951-51-5896-3 (Print)
ISBN: 978-951-51-5897-0 (Online)
<http://ethesis.helsinki.fi>

Unigrafia
Helsinki 2020

Entre l'arbre et écorce il ne faut pas mettre le doigt.
(Médecin malgré lui, Molière 1666)

List of original publications

This PhD thesis is based on the following publications, which are referred to by their Roman numerals in text:

- I. **Junikka, L.** 1994: Survey of English macroscopic bark terminology. — IAWA Journal 15(1): 3-45. <https://doi-org.libproxy.helsinki.fi/10.1163/22941932-90001338>
- II **Junikka, L.** & Koek-Noorman, J. 2007: Anatomical structure of barks in Neotropical genera of Annonaceae. — Annales Botanici Fennici 44:79-132. <https://www.jstor.org/stable/23727695>
- III Lopes, J. C., **Junikka, L.** & Mello-Silva, R. 2013: *Oxandra unibracteata* (Annonaceae), a new species from the Atlantic Forest and a new synonym of *O. nitida*. — Phytotaxa 84(1): 25-30. <https://doi.org/10.11646/phytotaxa.84.1.2>.
- IV **Junikka, L.**, Maas, P.J.M., Maas-van de Kamer, H. & Westra, L.Y.Th.: 2016: Revision of the genus *Oxandra* (Annonaceae). — Blumea 61 (3): 215-266. <https://doi-org.libproxy.helsinki.fi/10.3767/000651916X694283>

Table of contributions

	I	II	III	IV
Original idea	LJ	JK-N, LJ	JL, LJ	PM, LJ
Study design	LJ	LJ, JK-N	JL, LJ, RM-S	LJ, PM
Data gathering/ preparation	LJ	LJ	JL, LJ	LJ, PM, HM-K, LW
Analysis	LJ	LJ, JK-N	JL, LJ	LJ, PM
Manuscript preparation	LJ	LJ, JK-N	JL, LJ, RM-S	LJ, PM, HM-K, LW

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Abstract

This dissertation deals with bark morphology and anatomy of the Neotropical members of the family Annonaceae, and formal taxonomy of the genus *Oxandra*. This mainly pantropical family comprises ca. 2440 species in 109 genera, which belong to the early divergent mangoliids. About one-third of these taxa occur in the Neotropics (few also in N-America), where they contribute a significant part of plant diversity, both in abundance of species and individuals. Members of the family are mainly trees, shrubs and lianas, which are growing predominantly in tropical and subtropical lowland rainforests. The family is monophyletic and can be recognised, in addition to its flowers and fruits, also by its wood and bark, which possess homogenous, distinctive features representative to the family.

The first study deals with the macroscopical patterns seen in the outer structures and in the slash (i.e. tangential cut) of the bark and with the terminology used in the bark descriptions. Morphological terminology of barks is critically surveyed in the forest floras and the expert papers and terms are listed for a comparison of bark features. Suggestions are given for a standardised usage of the terms to stimulate a practice of pertinent field notes and to facilitate understanding of the descriptions. The second study concentrates on the structural anatomy of barks in 32 Neotropical genera of Annonaceae. Selected character states at the family and genus levels are scrutinised for identification purposes. Taxonomical and phylogenetic relevances of bark characters are discussed in view of the tentative molecular phylograms. Although the value of the bark characters, in the present understanding, proved to be negligible, some features may help to delineate some genera and even tribes as such. The systematically most distinctive features in bark structure are the sclerification of the phellem cells, the shape of fibre groups and the occurrence of crystals in bark components.

A taxonomic revision based on morphological characters is presented for the Neotropical genus *Oxandra* (Annonaceae). Twenty-seven species are recognised in the genus, which has wide distribution in Central and South America. Two species occur in the Antilles, but the majority are growing in the lowland rainforests of the Amazonia and in the Atlantic rainforest. A few species are flourishing in drier habitats and in nutrient-poor soils. Altogether five species, i.e. *O. aberrans*, *O. bolivarensis*, *O. rheophytica*, *O. saxicola* and *O. unibracteata*, are described as new to the science. A special attempt is made to find supportive morphological characters in view of the possible division of the genus, because of the polyphyly uncovered by the earlier phylogenetic analyses (verified by plastid data) in the tribe Malmeeae, in which the genus belongs. Only few morphological characters, i.e. the midrib type of the leaves, the length of stipe of the apocarpous fruits and, less so, geographical distribution pattern of the species, corroborate the evidence of segregation of the genus in two clades found in various phylogenetic studies. However, last preliminary results of nuclear and mitochondrial sequence data show the genus to be monophyletic. More species and more resolutions are needed from plant genomic research to make definitive statements about the status of the genus.

Summary

1. Introduction

1.1. Tropical biodiversity

Climate change, overpopulation, and a loss of biodiversity threaten almost all ecosystems on Earth (IPCC 2019, IPBES 2019). These challenges are both shocking and closely intertwined. The main driver for species extinction is the growth of human population along with the increasing consumption per capita, which also promote climatic warming. It has been estimated that the current rates of extinction are 1000 times the background rate of extinction (Pimm et al. 2014). Tropical forest ecosystems play a vital role in curbing the rise in carbon dioxide levels, especially with the trees as the key structural components of these forests. Furthermore, tropical trees are sources of timber, non-timber products, and providers of other ecosystem services plus a home for millions of arthropod species and numerous birds and mammals (Stork 2018, Douglas et al. 2014, Terborgh et al. 2008).

Slik et al. (2015) estimated that there are between 40 000 - 53 000 species of tropical trees using fitted value of Fisher's alpha and an approximate pantropical stem total. The tropics are still quite uncharted, there still being vast regions that have not been thoroughly surveyed and therefore there are many undescribed taxa to be found. For example, many regions in tropical South America are very poorly known (Schulman et al. 2007). While tropical forests in western Amazonia are still very extensive, eastern and southern Amazonia have already undergone severe deforestation because of increasing human influence. New roads, animal husbandry, soya culture, illegal logging and mining are continuously claiming new areas of the virgin forest (Kirby et al. 2006). Hubbell et al. (2008) have estimated the number of tree species (diameter at breast height >10 cm) and their expected extinction rate in the Brazilian Amazonia. The population size of almost half of local species, i.e. over 5 000 species, was estimated to be less than 10 000 individual trees. Nearly half of the species were estimated to go extinct, if present deforestation rates will prevail. All this underlines the urgency of biodiversity surveys and the discovery of tree diversity hotspots, which should be protected for future generations.

Systematics plays a crucial role in plant diversity surveying. New taxa of tropical forest trees are often first identified from herbarium specimens, but only if high-quality specimens with both fertile and vegetative organs are available. The lack of reproductive structures in many herbarium specimens makes even the determination of previously known taxa very challenging. Many authors (e.g. Keller 1994, Hawthorne & Jongkind 2006) have effectively utilized vegetative characters including leaf morphology, vestiture, bark texture and colour (also seen in the slash, which is an oblique tangential section through the bark), scent, exudates, shape of buttresses, trunk and crown in tree species identification. Such features can be useful, but collecting such data, especially from large canopy trees in tropical rainforests, is often a challenging task. Furthermore, rainforest trees commonly have a varied rhythm in their flowering and fruiting. In a climate of well-marked annual dry seasons, the peaks of flowering tend to be more frequent than in ever-wet rainforests. Some species have annual synchronous mass flowering over hundreds of square kilometres (Wood 1956), others flower more rarely (Corner 1988), some only once in a decade or two (Holtum 1940), and there are also monocarpic species that flower only once and die after the fruit have ripened (Rodrigues 1962). Also, the duration of the flowering is very variable, from one day to several weeks, depending on species.

For all of the above-mentioned reasons the flowers or fruits cannot always be used to assist in the identification of tree species. Moreover, the richness of the tree flora, in which a one-hectare plot of the tropical forest may encompass between 50 and 300 species (diameter at breast height or dbh > 10 cm) in mature tropical forest, is tremendous (Philips & Gentry 1994) and field surveys in such forests take a lot of time.

In spite of these and many other practical difficulties, new herbarium specimens from tropical forests are continuously being collected, and forest inventories are successfully undertaken to map tree species diversity of limited regions (e.g. Flora da Reserva Ducke near Manaus). Moreover, large systematic research programs have been erected to combine the efforts of experts, who work on the same target groups, such as the family Solanaceae (<http://solanaceaesource.org/>) and Annonaceae (<http://annonaceae.myspecies.info/>).

1.2. Diversity and morphology of the family Annonaceae

The pantropical angiosperm family Annonaceae is currently estimated to include ca. 2440 species in 109 genera (Lopes et al. 2018). The Annonaceae Project is a multidisciplinary investigation program launched in 1983, targeting the systematics of the family and especially its Neotropical taxa (Maas 1983). The initial aim of the project was twofold. The first goal was to produce morphological character analyses of the family and the second goal was to compile updated revisions of the genera, based on as many morphological features as possible.

Already Walker (1971) had started studies on pollen morphology and phytogeography of the Annonaceae and made a phylogeny of the family placing genera in subfamilies and tribes. Van Heusden (1992) published a worldwide survey of flower morphology, in which she analysed petal/sepal phyllotaxis, hairiness, androecium and gynoecium structure. Fruit and seed morphology were treated on the genus level by van Setten & Koek-Noorman (1992). Fruit and seed characters were used in the first attempt to cluster taxa, in which 16 informal groups of taxa were identified, largely supporting the results of Walker (1971) and van Heusden (1992). These groupings did not always correspond with those of Fries (1959), who was the last to monograph the family based on morphology alone.

In the light of wood structure, the Annonaceae has been seen to represent a natural, highly homogenous group (e.g. ter Welle 1984 and 1998, Metcalfe 1987). Later Koek-Noorman and Westra (2012) compiled a macrophotographic wood atlas of the family, which demonstrated that few genera could be recognised on the strength of single character state or a combination of character states. In some species poor genera are very homogenous, but large ones, such as *Annona*, demonstrate a lot of variability in wood structure. Even within single species, or even within one individual, wood anatomy can vary markedly depending on the age, the organ being studied, environment, etc.

Few studies have dealt with the bark structure of trees in the family Annonaceae. Zahur (1959) described the bark anatomy of five species from three genera, i.e. *Annona* (3 spp.), *Cananga*, and *Mezettia*, all from the Hawaiian Islands. He focused on the secondary phloem, particularly the evolution and structure of sieve tube elements, companion cells and phloem fibres. Roth (1981) studied the bark of four genera, i.e., *Anaxagorea*, *Rollinia* (now included in *Annona*), *Unonopsis*, and *Xylopia* (2 spp.), all from Venezuela. Rollet (1982) published drawings of 14 transverse sections of barks of *Anaxagorea*, *Cleistopholis*, *Enantia* (= *Annickia*), *Monocarpia*, *Monodora*, *Platymitra*, *Rollinia* (now included in *Annona*), *Unonopsis*, and *Xylopia* (6 spp.). All of these sections show structures typical to Annonaceae bark: such as funnel formed dilatation tissue, reduced formation of rhytidome, and a strong scent of the exudation (Roth 1981).

Van Setten & Koek-Noorman (1986) investigated the leaf anatomy of Neotropical genera of the Annonaceae. The results did not reveal any clear principles which could be used to classify genera, with the exception of the special trichome types found in some genera (*Anaxagorea*, *Duguetia*, *Tetrameranthus*).

Doyle and Le Thomas (2012) summarised the results of a long-lasting study of pollen evolution in the Annonaceae. They also reviewed the systematic significance of pollen characteristics in the light of the most recent molecular evidence. Gottsberger (2012) reviewed the diversity of pollinators associated with different genera of Annonaceae. They also compared morphological adaptations in flower structures and highlighted the ecological significance of floral rhythm, flower size, petal thickness, stamen structure, and odour production. Goodrich (2012) studied the role of floral scents in pollination strategies and chemical composition of the volatiles.

The first phylogenetic analyses based on morphological characters were conducted by Koek-Noorman et al. (1988) on the genus *Tetrameranthus*. Later Doyle & Le Thomas (1994, 1996, 1997) studied phylogenetic relationships between genera based on morphological characters. Since then the focus has shifted to molecular phylogenetic relationships on the global scale (e.g. Richardson 2004, Pirie 2006, Chatrou et al. 2012, Guo et al. 2017), and associated character evolution, for instance in the African taxa (Couvreur et al. 2008) and in the Neotropical tribe Malmeeae (Lopes et al. 2018).

1.3. Neotropical Annonaceae with emphasis on the genus *Oxandra*

About one-third of the annonaceous taxa occur in the Neotropics: currently ca. 825 species in 34 genera are recognized (Chatrou et al. 2012, Westra & Maas 2012, Erkens et al. 2014, Maas et al. 2015, Junikka, et al. 2016, Erkens et al. 2017, Pirie et al. 2018 and Maas et al. 2019). In association with the Annonaceae Project several new revisionary studies were undertaken in the Neotropics, including those of Maas and Westra (1984, 1985) on the genus *Anaxagorea*, Maas and Westra (1992) on the genus *Rollinia* (now included in *Annona*), Chatrou (1998) on the Malmea alliance and Chatrou and He (1999) on the genus *Fusaea*. Since then, also taxonomic treatments of 11 genera have been published, and only five genera are still under ongoing research. Revisions of *Desmopsis*, *Ephedranthus* and *Sapranthus* are nearly completed, but the two species-rich genera *Annona* (162 spp.) and *Xylopia* (ca. 50 spp. in the Neotropics) are still in the making (Erkens et al. 2017, Chatrou et al. 2012). It has been indicated that not all previously revised genera (e.g. *Klarobelia*, *Oxandra*, *Stenannonia*) are monophyletic and need to be revisited in the light of molecular studies (Erkens et al. 2017).

The genus *Oxandra* was described in 1841 by A. Richard and included the species *O. virgata* (Sw.) A.Rich. (= *O. lanceolata* (Sw.) Baill.) and *O. laurifolia* (Sw.) A.Rich. Fries (1931) published the first monograph with descriptions of 17 species, of which 6 new to science. Later Fries (1959) summed up his work on Annonaceae in the second edition of 'Die Natürlichen Pflanzenfamilien' with descriptions of 22 species. New species have later been found from Central-America (1 - Miranda 1961; 3 - Lundell 1974a,b, but now put in the synonymy), from Surinam (1 - Jansen-Jacobs 1970), NE Brazil (1 - Maas, et al. 1986) and now 5 species described in the Articles **III** and **IV**.

Different authors have placed the genus *Oxandra* in different subgroups within the family. In the most recent and prevalent treatment of the family subgroups Annonaceae has been divided into four subfamilies (Chatrou et al. 2012) as follows: Anaxagoreoideae (1 genus), Ambavioideae (9 genera), Annonoideae (51 genera), and Malmeoideae (47 genera). The genus *Oxandra* has been placed in the subfamily Malmeoideae, and there into the tribe Malmeeae, which includes 13 Neotropical genera. Already Walker (1971) recognised the

tribe Malmeeae which is characterized by columellar-monosulcate pollen grains. Both delimitations of the tribe Malmeeae conform, except that Chatrou et al. (2012) placed the African genus *Annickia* in the tribe Piptostigmateae. Typical features of the tribe Malmeeae are: the hairs are simple, inflorescence rhipidiate, terminal or axillary, flowers bisexual or androdioecious, petal aestivation valvate or imbricate, carpels free in flower and fruit, placentation basal, rarely lateral, aril absent, ruminations in seed spiniform, in irregular pegs or lamelliform, endosperm glass-like or soft, and pollen monosulcate.

Fries (1959) regarded *Oxandra* as currently circumscribed natural, but this view has since been refuted and its polyphyly is strongly supported by phylogenetic analyses based on plastid data. Already Richardson et al. (2004) found, when investigating historical biogeography of the families Rhamnaceae and Annonaceae, that the genus *Oxandra* is polyphyletic. Pirie et al. (2006) analysed the South American centred (SAC) clade using chloroplast DNA sequences with markers from 96 accessions under maximum parsimony and Bayesian inference. The tribe Malmeeae was recovered as monophyletic involving 13 genera. Eleven species of *Oxandra* were included and two well-supported clades, consisting only *Oxandra*, emerged. One clade (called here oxandra euneura group or **euneura group**) included *O. asbeckii*, *O. euneura*, *O. polyantha*, *O. longipetala*, *O. espintana*, and *O. nitida* (now included in *O. espintana*) while the second clade (called here oxandra laurifolia group or **laurifolia group**) included *O. laurifolia*, *O. macrophylla*, *O. sphaerocarpa*, and *O. xylopioides*. *O. venezuelana* fell into isolated lineage and was found a sister to *Pseudomalmea diclina*.

Chatrou et al. (2012) used previously published and new sequence data of eight plastid loci (protein coding *rbcL*, *matK*, *ndhF* genes and intron, *trnL*, and spacer regions *trnT-L*, *trnL-F*, *trnS-G*, *atpB-rbcL* and *psbA-trnH*). The results of their phylogenetic analysis gave support to the previously described two clades and the polyphyly of *Oxandra*. In the mega-phylogeny of Annonaceae (Guo et al. 2017) in which a supermatrix with eight chloroplast markers was used to build a comprehensive tree of 705 species (29%) in 105 genera (98%) of the family Annonaceae. Two *Oxandra* species (*O. lanceolata* and *O. riedeliana* - both can be included in the euneura group) were included in the matrix. Phylogeny inference showed that *Klarobelia*, *Pseudephedranthus* and *Pseudomalmea* are deeply nested within the genus *Oxandra*, which itself is paraphyletic. Authors suggest that one solution is to merge the three above-mentioned genera into *Oxandra*. An alternative solution is to split the genus in two. Most nodes within this clade are poorly supported because of few DNA regions sequenced. *O. venezuelana* is sister to a group consisting of all other *Oxandra* species and *Klarobelia*, *Pseudephedranthus* and *Pseudomalmea* species.

Lopes et al. (2018) investigated phylogenomics reconstructed using Bayesian inference (BI), maximum parsimony (MP) and maximum likelihood (ML) of 32 taxa, using DNA sequences of 66 molecular markers of the chloroplast genome and evolution of the floral traits the tribe Malmeeae in 27 species (incl. nine *Oxandra* species with *O. guianensis* and *O. martiana* as new). The reconstruction of ancestral states was carried out for characters associated with sexual systems, floral morphology and midrib type of the leaves. The results most relevant concerning *Oxandra* for this study include the following. Androdioecy is found in Malmeeae in six genera, including *Oxandra* (*O. martiana*, *O. maya*, *O. mediocris* and *O. panamensis*), and it is most frequent in this tribe in the family. Hermaphroditism is plesiomorphic in Malmeeae (as in many other Annonaceae), in which androdioecy has evolved independently four times. The evolution of androdioecy deviates in tribe, because it is neither derived from dioecy nor an intermediate step to the evolution of dioecy, but rather derived from hermaphroditism. In Malmeeae dioecy has not been reported. Imbricate petals (versus valvate), presence of 1-2 flowers (versus 1-many) found in *Oxandra* and many other genera in Malmeeae represent an ancestral state. Furthermore, convex/concave

midrib in the leaves has a complex evolution with many reversals in the tribe. Species of the euneura group (incl. *Oxandra euneura*, *O. polyantha*, *O. asbeckii*, *O. longipetala*) have convex midribs, except *O. espintana* (slightly impressed to slightly raised). Species of the laurifolia group (incl. *O. laurifolia*, *O. guianensis*, *O. macrophylla*, *O. martiana*) possess impressed to flat midribs, which are regarded ancestral. Very characteristic to *Oxandra* (and some other members of the tribe) is the tongue-shaped connective, which also represents an ancestral state. Tribe Malmeeae is monophyletic, which is well supported in all three analyses, and again the genus *Oxandra* appears in rather divergent groups showing polyphyly. Also *O. venezuelana* has a different position in each analysis. For instance, in MP analysis, *O. venezuelana* together with *Ruizodendron ovale*, act as a sister group to the euneura group and to members of *Pseudomalmea*, *Klarobelia* and *Pseudephedranthus* genera (Lopes et al. 2018).

According to Lopes et al. (2018), the differences in seed ruminations present supportive evidence of the split in two of the genus *Oxandra*. Species of the laurifolia group have spiniform while species of the euneura group (except in *O. polyantha*) have peg-shaped rumination. However, the euneura group belongs to the same clade as *Pseudomalmea diclina*, *Pseudephedranthus fragrans*, *Klarobelia inundata*, *Ruizodendron ovale*, and *Oxandra venezuelana*, which all have a lamellar rumination which thus represents the ancestral state. All above phylogenetic studies based on chloroplastid data indisputably demonstrate that the genus *Oxandra*, as currently circumscribed, is polyphyletic.

Chatrou (2019) and his co-workers have created a sequence data set of 15 species of *Oxandra* and 13 species of other genera in the Malmeeae obtaining alignments of ca. 61 000 positions of plastid data, nearly 6 000 positions of nuclear ribosomal DNA, and ca. 50 000 positions of mitochondrial data. Phylogenetic analysis of the plastid data confirmed earlier findings of the polyphyly in *Oxandra*. Species were placed in two clades, which were not sister clades. According to Prof. L.W. Chatrou (pers. comm.), clade one includes the following taxa: *O. asbeckii*, *O. bolivarensis*, *O. espintana*, *O. euneura*, *O. kruckhoffii*, *O. longipetala*, *O. polyantha*, *O. riedeliana*, and *O. surinamensis* and clade two: *O. guianensis*, *O. laurifolia*, *O. macrophylla*, *O. martiana*, *O. panamensis*, and *O. sphaerocarpa*. As one can see, the clades are practically the same as euneura group (clade one) and laurifolia group (clade two), but four new species were added to the phylogenetic analysis. However, analysis of nuclear and mitochondrial data differed in containing the same two clades, but in this case, they were sister clades. In other words, *Oxandra* was rendered as monophyletic genus based on ribosomal and mitochondrial data. This result sheds new light to the discussions of feasible taxonomical changes in the genus.

The pollination biology of *Oxandra* is largely unknown, but some few observations have been made in the field. Rove beetles (Staphylinidae) and thrips (Thysanoptera) have been reported to pollinate flowers of *Oxandra euneura* (Webber & Gottsberger 1996). Thrips are notably more uncommon visitors in Annonaceae flowers than beetles, which are commonly seen in the flowers of other annonaceous genera. There is a maximum of three flowers in anthesis at the same time in each *O. euneura*-tree. Protogynous flowers open in the morning, when outer petals open completely, whereas inner petals remain in a semi-open position. In the first-day pistillate stage flowers emit a sweet scent, like perfume, reminiscent of Palmolive™ toilet soap. Pollen release takes place the next morning, initiating a staminate phase and inner petals spreading apart. Staphylinidae beetles typically exist in all flowers of *O. euneura*, but Thysanoptera are rarer visitors (Gottsberger 2012). Thrip-pollinated flowers can be recognised by a small pollination chamber (connective appendages curved over centre of the flower) with small apertures and small pollen grains. Typical features of beetle-pollinated flowers include pale colouration (white to yellow) and the pres-

ence of a pollination chamber (Saunders 2012). Many other *Oxandra* species seem also to share these characters.

Oxandra pollen has been studied by von Morawetz and Waha (1986), who found pollen grains to be single with widely extending sulcus. The exine is columellate, tectate and has a massive, hardly foliated basal layer. It has a coarsely alveolar and regularly distributed intine. The chromosome number is $2n=18$ as counted from the specimen now identified as *O. polyantha*.

Oxandra mediocris in Western Amazonia is reported to be a keystone species for fruit-eating animals, both based on high and consistent productivity during the season when other fruits are scarce, and their apparent popularity among many frugivores, including both primates and birds (Stevenson et al. 2015).

The only species of *Oxandra*, which has been recorded as a timber tree, is *O. lanceolata*, commonly known as Lancewood. The timber is hard, heavy, compact, fine-textured, straight-grained, tough, elastic, but not resistant to decay. Most of the timber has been extracted from Cuba and Jamaica. The pale-yellow sapwood has been used for example for fishing rods, billiard cues, archery bows, and articles of turnery (Record & Hess 1943).

1.4. Bark structure and its use in tree species identification

There are three principal vegetative parts of trees which are best observable already in the field: 1) habitus of a tree (form of roots, stem, branches and architecture of the tree crown), 2) morphology, vestiture and arrangement of leaves, and 3) characteristics of the bark. The morphology of all these can vary widely according to habitat and age.

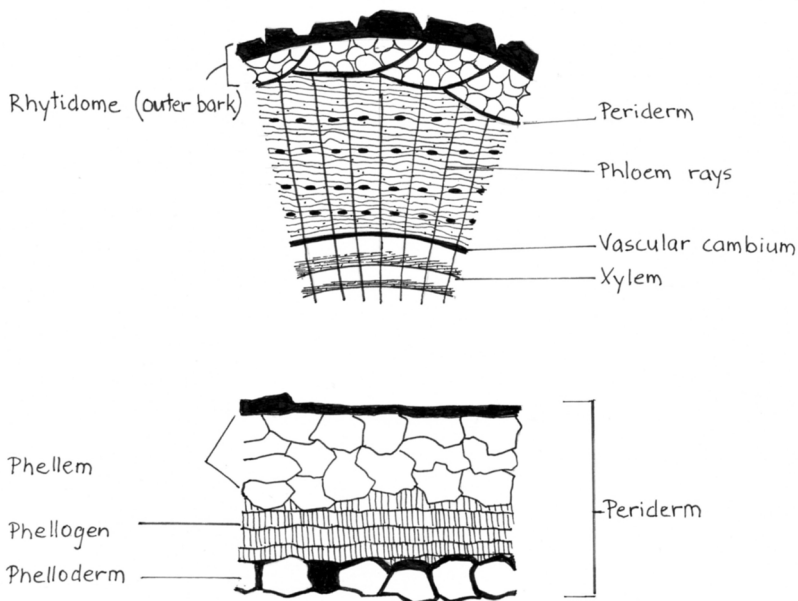


Figure 1. Schematic drawing of the general arrangement of mature bark tissues on woody stems. Close-up drawing of the tissue arrangement in the last-formed periderm. Redrawn from: Romero, C. 2014: Bark: Structure and Functional Ecology. — In: Cunningham, A.B., Campbell, B.M. & Luckert, M.K. (eds.), Bark: Use, Management and Commerce in Africa: 5-25. Advances in Economic Botany 17. New York Botanical Garden Press.

Barks can be defined as all tissues outside the vascular cambium. Bark in mature trees, shrubs and lianas can be divided into phloem or inner bark, which develops from the vascular cambium, and outer bark or rhytidome, which develops from the cork cambium. The rhytidome comprises the innermost periderm and subsequent periderms with tissues isolated by them. The outer layers of the rhytidome can shed as scales, when trunks and branches mature and age (see Fig. 1) (modified from Angyalossy et al. 2016, see more the bark terminology in the Article I).

Bark functions as a conducting tissue, a biomechanical support, and as a protective covering of the trunk against mechanical damage, herbivory and fire. It is also an important storage for carbohydrates, nitrogen, water and a site for carbon fixation (Romero 2014). The external appearance of the bark can be used in many cases as a taxonomic character, when bark variation is understood properly. Inherited differences in surface structure result from: 1) the position of the first periderm in the stem, 2) the arrangement of subsequent periderms, and 3) the arrangement of different cell types in the phloem. In addition to inherited features, environmental factors may strongly affect early periderm development and probably also subsequent periderms, and this in turn has an impact on the appearance of the bark surface. Already during periderm initiation environmental factors such as light intensity, photoperiod, temperature, soil moisture and relative humidity, are reported to induce changes (see more in Borger 1973). Furthermore, in growing and mature trees, weathering, such as the exposure of the bark to sun and prevailing winds, can change the appearance of the outer bark. The key factor in the external appearance of the bark and protection of the inner bark from weathering effects is periderm.

Close correlation has been demonstrated between certain bark characters (i.e. firm bark with fibrous plates in the inner bark) and certain plant families, e.g. in Annonaceae, Lecythidaceae, Bignoniaceae, Boraginaceae (Roth 1974). Still, some large families like Fabaceae and Sapotaceae seem to be very heterogenous in their bark characters and other morphological features (Rejmánek & Brewer 2001). This may help a plant collector to identify trees to a single genus and even species but may be quite confusing at the family level.

Bark features are potentially very important for the identification of rainforest trees, as the trunk may often represent the only part of the tree that can easily be accessed. On the other hand, the bark of many tropical trees is very hard and thus difficult to slash with a machete or even with a saw. Many researchers have thus preferred to collect material from thick branches, but their bark is usually not well developed and does not provide prime specimens, except for anatomical studies. Another commonly used method is to only write down descriptions of bark patterns visible on the trunk. Such field notes often turn out to be difficult to interpret because of the lack of common terminology both well-established and well-known. One useful option is to use a camera (and tripod) and take several photos of the different sides of the trunk, also of the slash, which may well “tell more than a thousand words” especially if examined by an expert. Experts can often identify the family, genus or, in some cases, even the tree species solely based on bark characters (e.g. Schulman et al. 1998, Hawthorne & Jongkind 2006).

Many foresters and botanists (e.g. de Rosayro 1953, Wyatt-Smith 1954, Rollet 1980, 1982, Torres et al. 1994) have used bark characters in forest inventories and compiled an often rather simplified terminology for classifying the frequently extensive range of variation they have observed in the field. These attempts, although very useful in practical field work, have not necessarily used the same terms, or the terms have had diffuse and partly overlapping meanings. This is a major problem as scientific terms should be unambiguous, simple and well-defined in order to be universally acceptable and easy to use.

Sound terminology is a necessity before easily understandable and reliable descriptions of tree taxa can be compiled.

Even scientific floras of tropical regions have usually largely neglected bark characters and typically only include the most conspicuous bark features, if even them. The main reason may be a lack of time and inadequate data collection in the field, which leads to short and poor description on labels of herbarium specimens – and eventually leading to the lack of relevant information in finalized floras.

Even field guides that use only bark characteristics and other vegetative features for identifying tropical tree species, are relatively rare. However, there are exceptions, including Symington (1943), Pennington & Sarukhán (1968), Hawthorne (1990), Polak (1992), and LaFrankie (2010). Some of the publications even provide keys based on bark features (e.g. Schulman et al. 1998, Hawthorne & Jongkind 2006). Ribeiro et al. (1999) (Flora da Reserva Ducke) relied on colour photographs of both bark and leaves, including high-quality close-up pictures of slashed bark. The team benefited from the contribution of several international experts of various plant families, who provided taxonomic treatments, later published in *Rodriguesia* (e.g. Maas et al. 2007a). These examples serve as models for how we could and should use bark as an identification tool for the benefit of not only professional botanists and foresters but also the general public.

How reliable are bark characters in the identification of tropical tree taxa? Every trained botanist will agree that they do not offer an easy shortcut for recognizing trees in the field. The successful use of bark and other vegetative characters requires considerable insight and training, possibly even more so than the use of reproductive characters. Sometimes identification to species level is not possible without associated references to fertile material (Rejmanek & Brewer 2001). Still, in field guides and floras compiled for the restricted areas, the results of positive identification can be relatively good, for example in Ugandan trees ca. 70% (Hawthorne 1990, cited in Rejmánek & Brewer 2001). Quite similar results were obtained in the East Usambaran Mountains, Tanzania, where ca. 50% of all tree taxa were treated for the book (Schulman et al. 1998). However, one must admit that the descriptive terminology that relates to bark is often poorly mastered even by the most experienced plant collectors.

Extensive anatomical surveys of barks are still very rare compared to wood anatomical surveys, especially in the tropics. However, some outstanding systematic bark studies must be mentioned, including those by Chattaway (1953, 1955a,b, 1959) of the genus *Eucalyptus*, Whitmore (1962a, b, c) of the family Dipterocarpaceae, van Wyk (1985) of the African members of the genus *Eugenia* and Richter (1981, 1985, 1990) of the family Lauraceae. Recent systematic bark research is represented by Kotina & Oskolski (2010), who found differences in the inner bark in family level between Araliaceae (17 genera), Myodocarpaceae (2 genera) and Apiaceae families (2 genera). In addition, distinguishing characters were detected in *Polyscias*, and corroboration of the polyphyly in the genus *Schefflera* (sect. *Schefflera*) on subgeneric level.

1.5. Aims of the thesis

The aim of this thesis was to produce new information on the bark anatomy of tropical trees with special emphasis on Neotropical Annonaceae and to revise the genus *Oxandra*.

The first goal (Article I) was to revise the terminology used in scientific descriptions of bark structure of tropical trees.

The second goal (Article II) was to investigate bark anatomy of Neotropical genera of the family Annonaceae and to use the newly revised terminology in practice.

The third goal (Articles **III** and **IV**) was to revise the genus *Oxandra* based on herbarium material and to identify morphological characters that can be used together with DNA sequence data for future analyses aiming at re-circumscribing the genus.

2. Materials and methods

2.1. Construction of proper macroscopical terminology

The research dealing with bark morphology, the bark terminology papers, and more recent local forest guides/floras were carefully perused, and the terms used were gathered together (**I**). Altogether 64 literature references were studied. Descriptive bark terms were listed, and definitions copied. Terms were grouped under titles: 1. bark and its component tissues; 2. bark texture i.e. consistency; 3. a) bark patterns in cross and tangential section; b) fissuring; c) scaling; d) external markings; 4. exudation, i.e. quality and type of liquid flow; 5. bark cutting - technical definition of slash. Terms were selected, if possible, so that they describe a character as simply as possible, preferably not complex entities, which, in fact, include many separable characters. Care was also taken to ensure that the understanding and the using of the term would be consistent. All definitions of the terms found in the literature were compared and placed in the order of preference. Quite frequently definitions were polished, improved or renewed entirely. Moreover, a list of the rejected terms was compiled, and reference was made to the accepted term.

2.2. Collection of bark samples in the field

Bark slashes have been cut and samples collected (14 genera/44 species) from Reserva Florestal Adolpho Ducke or the Ducke Reserve, Manaus, Brazil, which has a good selection of Annonaceae trees (16 genera/60 species) within the reserve (see Maas et al. 2007a). This offered an opportunity to produce comparison data on the variation of morphological bark features in restricted area and taxa of the family Annonaceae. Also, the usefulness of the defined terms (**I**) was tested in the field.

The Ducke Reserve has been protected for decades and the trees were growing mostly in half or deep shade in the forest, which enabled direct comparison, because environmental factors affecting bark were relatively similar. Trees were already marked and mapped thanks to the international Flora da Reserva Ducke -project (Ribeiro et al. 1999). Barks were collected, when possible, from trees more than 10 cm dbh. Many taxa are small trees and thickness growth is modest and therefore dbh was smaller in some samples. The tools used in the field were saw, machete and knife. Sometimes bark, and especially wood, was very hard and the sample was detached with a saw, and the cut surface or slash on the trunk was tidied up with a chisel, so that the inner and the outer bark with all their components were as clear as possible. It is important that the slash illustrates the tangential and cross section of the bark. A piece of bark attached with sapwood was put in a paper bag with the relevant collection number, the number of the tree in the reserve and the possible collection number of the herbarium voucher specimen.

All characters on the slash visible to the naked eye were noted with the help of the protocol, which included entries of fresh characters, such as colour, scent, exudation (the type, consistency, readiness to flow, etc.) and environmental factors, such as the exposure of the bark surface or shadiness of the collection site and the diameter of the bole at breast height (dbh). Simple, descriptive bark terms were used in the protocol.

Photographs were taken from the fresh slash as soon as possible, because the slashed surface has a tendency to fairly immediate discolouration. After slashing, discolouration (oxidation) may happen promptly, and this possible darkening of the slash was also recorded. The surface of the trunk was also photographed from different sides in order to see its variation due to possible exposure to sunshine. A ruler or a scale was set in the

photograph and all photographs were taken in the same manner. Barks were photographed using a flash when the trunk was shaded by thick tree canopy. Without a flash, the photos tended to turn out green-tinted. Also, the use of a tripod often proved to be beneficial.

2.3. Making anatomical sections

Bark samples used in the anatomical sections (II) were obtained from the above-mentioned Ducke Reserve (RFD - 21 samples) and from the xylarium of the former Utrecht herbarium (Uw, now included at the herbarium of the Leiden University), except for one sample, which was made available by the Institute for Wood Biology and Wood Protection, Federal Research Centre of Forestry and Forest Products, Hamburg (RBHw).

Voucher specimens were determined by Prof. Paul Maas and his co-workers. Small bark samples were impregnated in polyethylene glycol (PEG) and sectioned with a sliding microtome at the Wood laboratory of the Utrecht University. Pieces of bark (usually including xylem) of 10x10x5 mm were placed in small glass tubes with perforated plastic caps and cooked for ca. two hours to soften the tissues, after which the tubes were filled with polyethylene glycol (PEG 1500) and water in a 1:4 ratio. For harder bark tissues (with sclereids) PEG 2000 was used. These tubes were then kept in an oven at a temperature of 60 °C for three days, after which the PEG/water mixture was replaced with pure PEG and the tubes were retained in the oven for one more day. The PEG-impregnated bark samples were then sectioned. Transverse, radial and tangential sections were cut on a sliding microtome (Reichert), held together by adhesive tape to prevent fragmentation of the fragile tissues. The taped sections were rinsed with water to remove PEG and then double-stained in 1% aqueous solution of Astrablue and Acridin red-crysoidin for three to five minutes. After staining, the taped sections were transferred as such or the tape was removed using xylene and the sections were then shifted to slides. Sections were embedded in Canada balsam.

2.4. Study of the genus *Oxandra*

Because of the size of the genus, only morphology- based treatment of the genus without phylogenetic reconstructions was carried out in the scope of the thesis (III, IV). A lot of new collected material was available since the last revision of Fries (1959) and the new treatment of the genus was necessary. After initiation of revision, when polyphyly was observed in the genus (Sauquet et al. 2003, Chatrou et al. 2003), more focus was put to find any morphological traits which would support phylogenies produced by DNA sequence data. Also, a close look was made to the earlier bark anatomical studies of the genus, to find out if bark anatomy gives any systematic support to differences found within the genus, which could clarify the taxonomy of the genus.

Over 1900 herbarium sheets were studied and identified. All notes from the herbarium labels were entered in the database. Collection localities were carefully checked and latitude/longitude data were retrieved when it was possible to locate the collection site reliably. Distribution maps (IV) were created for all *Oxandra* species using DMAP for Windows software (programmed by Dr. Alan Morton). Vernacular names were gathered and listed in alphabetical order in reference to scientific name. Identification lists of the specimens arranged according to the first collector were compiled. Identification labels were attached to the herbarium specimens determined. Descriptive biological terminology of Systematics Association Committee for descriptive biological terminology (1962), Hickey (1979), Radford et al. (1974) and Stearn (1992) were used throughout.

2.5. Studied herbarium material

Revision of the genus (**III, IV**) was started by ordering *Oxandra* specimens from main herbaria in Europe, the United States and South America. Material for the study was sent from the following 55 herbaria: AAU, ALCB, B, BP, BR, C, CEPEC, COAH, COL, CUVV, CVRD, DUKE, E, F, FHO, G, GB, GOET, GUA, H, HBG, HRB, HUA, IAN, INPA, K, L, LE, LIL, LPB, MBML, MEXU, MG, MICH, MO, NA, NY, O, P, PR, R, RB, RUSU, S, SP, SPF, U, UC, ULM, US, VEN, VIES, WIS, WU, Z (Thiers 2016). Measurements were done on representative herbarium specimens. Specimens were studied at the Botany Unit, Finnish Museum of Natural History, at the herbarium of the Leiden University and various herbaria in South America and Europe.

3. Results and discussion

3.1. Bark as an aid in the identification

The family Annonaceae is well-known for its homogenous barks (on outer appearance and slash), in which funnel-formed dilatation tissue is clearly visible by naked eye in the cross section of the bark. In addition, fibre groups, which are often aligned and alternate with parenchyma cells and sclereid groups, are frequent in the cross section. Fibres make the inner and the outer bark quite firm and hard (= 'carahuasca' in Peru and 'envira' in Brazil), especially in the younger age (Roth 1974).

The author studied 44 species of the 14 genera of the family Annonaceae, all of them trees except *Annona haematantha* - a liana, in 1996 in the Ducke Reserve (see Maas et al. 2007a for the bark descriptions, which are not included in this thesis). The above-mentioned general distinguishing features together with the black phelloderm seen in the slash were found to be very representative in the family level. Furthermore, non-regular dilatation tissue was revealed as flame marks and sclerenchymatic elements (fibres and sclereids) as streaks, which were clearly distinct as darker coloured structures. Discolouration was frequent and darkening followed in a few minutes. Only sap flow was noticed, and its smell was usually recorded as aromatic.

In the family level, the above-mentioned features give a useful hint to which family the tree belongs. However, the identification of the family members becomes more difficult when genera were taken under scrutiny. External markings, like eye-marks/hoops were present in 25 species, in various-sized trunks. Dimpled barks and pockmarks were encountered, but the markings were not always distinctive. Lenticels can be good characters in young and mature trees, which have smooth, i.e. non-scaling and non-fissuring appearance. Lenticels occurred in all taxa with smooth barks, except in *Xylopia neglecta*. Lenticels may be found also in species that have scales or are sloughed, but usually they were not related to the thickness of the trunk. Lenticels were clearly visible and aligned vertically or horizontally in 12 species.

Many annonaceous species were variously scaled and/or fissured, except in 12 species (with lenticels), which were predominantly smooth. The fissures were usually shallow, V- and boat-shaped. The ridges were mostly flattened. The scaling and fissuring types were very variable due to the age of the bark and its exposure, so one has to point out that these features are not very reliable features in the field, and surveyors of the trees may interpret these characters in various ways. The outer texture is commonly homogenous and hard, but some barks have a corky touch, which is easy to discern.

A valid feature and easy to distinguish is the corrugations visible in the sapwood. In the material in question, four taxa possessed corrugations. The colour of the slash and subsequent discolouration were very variable and determining the hue of the slash was often too vague to be used as a reliable field character. In my material, however, some taxa such as *Anaxagorea manausensis*, *Cymbopetalum euneurum*, and *Ephedranthus amazonicus* showed very light brown or cream-coloured inner bark surface in the slash. Usually the slash was dry, but *Unonopsis* spp. seemed to ooze translucent liquid, probably gum. Although all Annonaceae in the Ducke Reserve were studied in April, they did not show copious exudation after slashing the bark. However, *Annona paludosa*, studied in French Guiana in September, had a profuse leakage of reddish liquid, probably gum. Furthermore, at least several *Unonopsis* species and the genus *Onychopetalum* have shown a flow of red exudation in their bark (Maas et al. 2007b). If this is a seasonal phenomenon, it should be studied further.

It is often mentioned that Annonaceae family owns an aromatic or “Ranalean” odour. The smell of the bark in this material was slightly variable, not always strong, but sometimes pungent, sweetish or even with a fetid nuance. The well-known yalang-yalang oil used in perfumery is steam-distilled from the flowers of *Cananga odorata* and *C. latifolia* (Groom 1992), belonging to the same family. Very often the exact smell is difficult to describe universally. Smells are a part of our cultural knowledge, and therefore smells may be interpreted in various ways among the researchers from other countries. Furthermore, some smells may be hard to recognise even among the members of the same cultural background, if smells resemble one another too much.

How well can the family members be identified based on the material found in the Ducke Reserve? Ribeiro et al. (1999) divide its 16 annonaceous genera and 60 species in 7 groups, of which the first group covers taxa (*Xylopia* spp.) with buttresses and stilt roots, which are valuable features, but are not included in this study. The second group comprises taxa with fissured barks and the third group involves taxa that possess lenticels aligned vertically. Identification of the other groups is based on the vegetative characters other than barks. Fissured barks are distinctive in some species of *Bocageopsis*, *Fusaea*, *Duguetia*, *Ephedranthus*, *Guatteria* and *Unonopsis*. The findings of the author (Maas et al. 2007a) are roughly similar in all genera with Ribeiro et al. (1999). However, there were some small discrepancies which are quite natural, i.e. obscurity of the character or the missing of the single individual in the forest (although they were mapped and numbered). *Guatteria* species with fissured barks in Ribeiro et al. (1999) were not encountered by the author in the reserve. The author detected lenticels in vertical lines in five *Annona* species, but also in some other taxa. However, Ribeiro et al. (1999) list the lenticels only in seven *Annona* species. Moreover, differences were found in the classification of fissured barks; how broad and deep the fissures are, etc. In both studies the bark samples were collected within the same year and in all probability the trees were the same ones. All of this shows that bark characters can be interpreted in different ways, even though the authors spent a couple of weeks together in the Ducke Reserve analysing the bark structures. To sum up the results: the lenticels of *Annona*, the abundant exudation *Unonopsis*, and the fissuration of *Bocageopsis* and some other above-mentioned genera seem to be valid characters which may be helpful in the field. In order to form a more comprehensive and reliable picture, more material from different habitats and from young as well as aged trees should be gathered and carefully analysed. To say the least, the results will probably be meagre, due to the very homogenous nature of the family. Bark maturing and the impact of the environment still blur the picture when seeking constant, distinctive bark characters. However, some genera and even species in the family may be identifiable because of possible exudation (such as above-mentioned *Annona paludosa* and *Unonopsis*), the colour of the slash (such as the bright yellow slash of the African species *Annickia kummeriae* in Schulman et al. 1998) or some other single character.

3.2. Terminology

When testing the terminology (I) in the practise of the field conditions (the Ducke Reserve and in other projects), the terms worked well in general. However, certain terms proved to be superfluous or should anatomically be on more solid grounds. Some terms should be considered more carefully, for instance: ‘Flakes’ or ‘flaky bark’ should be discarded, because the scales/flakes rarely completely fall in the measurements of these terms. ‘Rugose’ bark is also too interpretative, so smooth vs. rough are easier to apply. Moreover, the structures behind the term ‘streaks’, ‘ripple marks’/‘lamine texture’, ‘mottled phloem’ should be clarified anatomically, because macroscopical features of bark and their anatomical

counterparts should go hand in hand. Thus far, the knowledge is too scarce and only a small amount of investigation has been undertaken regarding the relation of bark anatomy and the maturing process of the bark. Ultimately, the external bark appearance is due to the microscopic patterns and processes, which are visible in the anatomy of the tree barks.

As far as the terminology is concerned, simple, unambiguous terms are the most useful. In contrast, terms which include character combinations can easily be misleading, such as ‘tesselated bark’, or ‘mussel-shell markings’. Based on the author’s own observations, there seemed to be uncertainty that the term was understood unambiguously and a surveyor used it correctly in the description of the field sample. Some colleagues, not professional field botanists (but anatomists), interpreted the terms very differently from what was meant in the bark terminology.

Macroscopic bark features, like microscopic ones, are highly diverse among tree taxa, but also vary strongly within individual woody plants according to the age of the trunk and the exposure of the bark. Macroscopic patterns, even more strongly than microscopic ones, present themselves as continuous and overlapping variables, making it difficult to define distinct character states. Moreover, concepts like bark texture and patterns seen in the slash vary interdependently, and even different types of fissured or scaly bark may exist in the same tree close to each other.

Although the terms fulfil the demand of lucidness, complex patterns are best understood by comparing the tree with proper bark photographs. However, photographs good enough to illustrate certain more rarely seen field characters of the bark, are badly needed to develop the terminology even further. The terminology should be improved in the future, on the basis of this synthesis, by critically evaluating characters, their applicability and understandability to professional botanists and foresters but also to educated laymen.

3.3. Bark anatomy in the use of formal taxonomy

Since the publication of the study of the anatomical structure of the barks in Neotropical genera of Annonaceae (II), more phylogenetic investigations have been carried out and new subfamilies and tribes have been erected to characterise more natural relationships between annonaceous genera and tribes. In this bark structure study phenetic similarities were compared with groupings constructed from the flower and fruit morphology studies of Neotropical Annonaceae taxa (Koek-Noorman et al. 1997). Some genera were regarded as isolated (*Anaxagorea* and *Xylophia*) or as intermediate positions (*Asimina* and *Diclinanona*). Already shown in the phylogeny (Sauquet et al. 2003) and in the most recent classification of subfamilies and tribes (Chatrou et al. 2012) *Anaxagorea* has a sister group relationship with the rest of the Annonaceae. Monophyly of the family is maximally supported. *Anaxagorea* is assigned as a sole member of the rank of the subfamily Anaxagoreoideae. *Xylophia* and *Artabotrys* are linked in the clade I, but clear synapomorphies still need to be investigated and evaluated. *Asimina* fell in the well-supported clade M together with *Annona* and other genera. There has been uncertainty of the position of *Diclinanona*, but later analysis results (Erkens et al. 2014) confirm findings of the Richardson et al. (2004), that the genus is a member of Annonoideae. There are a few other genera that have moved their position, e.g. *Crematosperma* group has merged into the tribe Malmeeae and *Cardiopetalum* group is now linked to Bocageaeae tribe together with *Porcelia* from Alphonsea group. The rest of the Alphonsea group, i.e. *Sapranthus* and *Tridimeris*, belong to the tribe Miliuseae together with *Desmopsis* (Ancana group)(Table 1, and Table 6 in II).

In the light of the latest phylogenies of the tribe Malmeeae (e.g. Guo et al. 2017 and Lopes et al. 2018) some genera (*Klarobelia*, *Oxandra*) show clear polyphyly, which are not yet taxonomically solved and need more research and evidence to establish generic limits.

The results obtained from bark analysis were discussed in the original paper, but Neotropical genera (Table 1) studied here are arranged anew according to the phylogeny of Guo et al. (2017) (Table 2), which is quite similar to the phylogram represented in Fig. 19 (in II and Chatrou et al. 2003). This study treats only those combinations which differ from the original analysis and should perhaps be noted in the light of the more recent phylogeny. Note that the specimen (Maas et al. 8297, Uw 30259) is now reidentified as *Pseudoxandra polyphleba*.

The tribes Duguetieae and Xylopieae seem to share features together with *Cardiopetalum*, *Hornschuchia* and *Anaxagorea*, in which crystals are only present in parenchyma. A constant feature in Malmeeae tribe is U-shaped cell walls in phellem cells, which differ only in *Pseudoxandra* and *Unonopsis*. *Ruizodendron* has sclereids, but there is no certainty (poor sample), if this is only some sort of cell wall thickening in phellem cells. The same phellem feature is shared by the tribe Miliuseae and *Xylopieae*. Furthermore, in the Miliuseae crystals occur only in sclereids in all bark components except in phellem. This feature is encountered also in *Oxandra* and some other genera of the tribe Malmeeae.

Subfamily and tribes	Genera (studied species/number of species in the genus from Chatrou et al. 2012, Maas et al. 2015, Erkens et al. 2017, Pirie et al. 2018 and IV)
Anaxagoreoideae	<i>Anaxagorea</i> (3/30)
Ambavioideae	<i>Tetrameranthus</i> (1/6)
Annonoideae (Bocageae)	<i>Cardiopetalum</i> (1/3), <i>Cymbopetalum</i> (2/27), <i>Hornschuchia</i> (1/10), <i>Porcelia</i> (1/7), <i>Trigynaea</i> (2/12)
Annonoideae (Guatterieae)	<i>Guatteria</i> (9/177) (incl. <i>Guatteropsis</i> , <i>Heteropetalum</i>)
Annonoideae (Duguetieae)	<i>Duguetia</i> (28/93), <i>Fusaea</i> (1/2)
Annonoideae (Xylopieae)	<i>Xylopiea</i> (4/157)
Annonoideae (Annoneae)	<i>Annona</i> (6/162) (incl. <i>Rollinia</i>), <i>Asimina</i> (1/7), <i>Diclinanona</i> (2/3)
Malmeoideae (Malmeeae)	<i>Bocageopsis</i> (2/4), <i>Crematosperma</i> (2/34), <i>Ephedranthus</i> (2/6), <i>Klarobelia</i> (5/12), <i>Malmea</i> (2/6), <i>Mosannonna</i> (3/14), <i>Onychopetalum</i> (1/2), <i>Oxandra</i> (7/27), <i>Pseudomalmea</i> (2/4), <i>Pseudoxandra</i> (3/23), <i>Ruizodendron</i> (1/1), <i>Unonopsis</i> (3/48)
Malmeoideae (Miliuseae)	<i>Desmopsis</i> (1/14), <i>Sapranthus</i> (1/6), <i>Tridimeris</i> (2/1)

Table 1. List of Neotropical genera of Annonaceae and their subfamilies and tribes according Chatrou et al. (2012). Note that representatives of the Monodoreae and Uvarieae tribes in Annonoideae subfamily and Piptostigmataeae, Maasieae, Fenerivieae, Dendrokingstonieae, Monocarpieae are not included in this anatomical bark study.

Bark structure does not offer very much supportive evidence in the taxonomical problems of the family or tribe level. In the genus *Oxandra* the crystals are in long vertical chains (except *O. lanceolata*) on the abaxial side of the fibre groups, which is a unique feature in this material. However, bark anatomy does not support any distinction between *oxandra laurifolia* or *euneura* groups or merging *Klarobelia*, *Pseudomalmea* into *Oxandra*. On the other hand, some genera can be distinguished by their unique features, i.e. druses only in *Anaxagorea*, patterns of crystals in, the adaxial side (*Bocageopsis*, *Sapranthus*), in lateral side (*Guatteria* (incl. *Guatterioopsis*), *Hornschuchia*), and between fibre groups (*Cymbopetalum* and *Trigynaea*). In the present understanding, bark anatomy has not provided supportive evidence to the already published phylogenies, although it may help to delimit genera and even tribes as such.

Genera/ Character	1: Arc-shaped fibre groups: 0=absent; 1=partly; 2=present	3: Sclereids in wide fibre groups: 0=absent; 1=sporadic; 2=present; 3=frequent	6: Type of sclerification of phellem cells: 0=absent; 1=U-shaped; 2=reversely U-shaped; 3=thickened	5: Secretory cells in phellem: 0=absent; 1=few; 2=abundant; 3=bulk; 4=full	7: Parenchymatic phellem cells: 0=absent; 1=partly present; 2=exclusively present	8: Presence of crystals: 0=absent; 1=in parenchyma only; 2=in parenchyma and sclereids; 3=in sclereids only	2: Crystals in rays only present in parenchyma cells: 0=no; 1=often; 2=always	4: Location of crystals in relation to fibre groups: 0=absent; 1=around; 2=abaxial; 3=adaxial; 4=lateral.	9: Crystals lacking in rays
Desmopsis	0	1	1	0	0	3	0	0	
Sapranthus	0	3	1	4	1	3	0	3	
Tridimeris	0	0	1	4	1	3	0	0	
Mosanona	0	0	1	2-4	1	2	0	1	
Ruizodendron	0	0	3	0	0	2	0	0	
Ephedranthus	0	2	1	0-3	1	2	0	1	
Klarobelia	0	0	1	0-3	1	2	0	1	
Pseudomalmea	0	1	1	4	1	2	0	1	
Oxandra euneura group	0	3	1	4	0	3	0	2	
Oxandra laurifolia group	0	3	1	3-4	0	3	0	2	
Crematosperma	0	1	1	3	1	2	1	0	
Pseudoxandra	0	1	2	3	0	3	0	0	
Malmea	0	3	1	0-4	1	2	0	1	
Unonopsis	0	3	2	3-4	1	3	0	0	
Bocageopsis	0	1	1	4	0	3	0	3	x
Onychopetalum	0	3	1	4	0	3	0	0	
Annona	0	0	1-2	1-3	1	2	0	1	
Rollinia	0	1	0	0-2	2	2	0	0	
Asimina	0	1	0	0	2	2	0	0	
Diclinanona	2	0	1-2	1-2	1	0	n	n	
Xylopia	0	0	1	3-4	2	1	2	0	
Duguetia	1	1	1(0-2)	0-3	1	1	2	0	
Fusaea	1	0	0-1	0-3	1	1	2	0	
Guatteria	2	1	0-1	4	1	(3)	0	4	x
Guatterioopsis	0	0	0	4	2	(3)	0	4	x
Heteropetalum	0	0	0	4	2	0	n	n	n
Cymbopetalum	0	0	0	0-1	2	2	0	1	
Porcelia	0	0	0	0	2	2	0	1	
Cardiopetalum	0	0	0	0	2	1	2	0	
Trigynaea	0	0	3	0-1	1	2	0	0	
Hornschuchia	0	0	0	4	2	1	2	4	
Tetrameranthus	0	0	2	4	1	2	0	1	
Anaxagorea	0	1	2	0-4	1	1	2	0	

Table 2. Relative position of Neotropical genera deduced from the phylogeny published by Guo et al. (2017). Differences in branch length are neglected. The bark data has been extracted from Appendices 2 A-G, except in the character 5, in which data are estimated according to averages per genus (see II). Character explanations are in the title cells of the corresponding column. *Guatterioopsis* and *Heteropetalum* are now merged to *Guatteria* and *Rollinia* to *Annona*.

Bark anatomical data is still insufficient, because samples are disproportionate due to the incidental availability of the material. If bark samples were present in the xylarium, many samples were poor, or from either branches or young trees. It is also notable that cuttings fragmented easily in the lab procedures, especially those with sclereid tissue. In the future, bark anatomical studies of the family should be extended to taxa of other continents and taxa that were not treated in this study. Finally, more bark samples are needed from anatomically unknown annonaceous genera.

3.4. Distribution and ecology of the genus *Oxandra*

Based on the herbarium material, five new species were described, of which *Oxandra unibracteata* was published in Article III, and *O. aberrans*, *O. bolivarensis*, *O. rheophytica*, *O. saxicola* in Article IV. Currently the genus *Oxandra* consists of 27 species, which are distributed from the Mexican states Nayarit and Veracruz to Brazilian states Rio de Janeiro and Minas Gerais. Two species occur in the Antilles.

Although the genus is widespread, there are typical distribution patterns of the species that can be delineated from the material studied. Nine species are broadly speaking widespread in the catchment basin of Amazon and some reach also more distant areas. Two species are encountered only in the Guinean shield and eight species from the northern part of the Columbia to southern Mexico. NE Brazil houses two species and Coastal Atlantic rainforest three species. The new taxa are probably quite rare and need protective measures, i.e. *O. aberrans*, locus typicus is in Chiapas (Mexico), *O. bolivarensis* and *O. rheophytica* (both in two locations) in the river basin of Magdalena, but more widespread is *O. saxicola* in the dry habitats in Bolivia and Brazil (Bahia, Goiás, Tocantins, Mato Grosso do Sul).

Oxandra species are trees up to 50 m tall, but most of them reach less than 20 m. Few species remain shrubs less than 3 m tall. Most of the taxa flourish in, by and large, humid terra firme rainforests. Some species may grow in igapó flooded forests of black and clear waters, and/or in várzea, i.e., in flooded forests of muddy waters, or are settled in drier vegetation types, such as cerrado (savanna woodland), caatinga (deciduous xerophytic vegetation), campinarana (vegetation on pure leached white sand in the Amazon biome) and calcareous soils. This widespread genus also grows at elevations of sea level up to 1700 m, although most of the members of the genus are lowland inhabitants.

Most of the *Oxandra* species blossom, with smallish (usually 10-20 mm in diameter) green, white to yellow flowers, either from February to April or from August to December, only *O. euneura* seem to flower all year through. Apocarpus fruits consist of 1-25 indehiscent monocarps. Each monocarp is 1-seeded and has green, purplish, orange red to black colour. Fruiting season follows 1-2 month later, although some species are mentioned to produce fruit all year through.

3.5. Splitting or lumping - current issue in the taxonomy of *Oxandra*

Phylogenies of Richardson et al. (2004), Pirie et al. (2006), Couvreur et al. (2009, 2011), Chatrou et al. (2012), Guo et al. (2017) and Lopes et al. (2018) have uncovered the polyphyly in the genus *Oxandra*. Furthermore, the genus has been split up in two groups according to the shape of the midrib and seed ruminations, which have been called oxandra laurifolia group and oxandra euneura group (Lopes et al. 2018). In the above-mentioned phylogenies DNA sequences of various *Oxandra* species have been exploited. It appears that according to results obtained in the phylogenies the following *Oxandra* species can be classified under oxandra laurifolia group or laurifolia group: *O. laurifolia*, *O. macrophylla*,

O. sphaerocarpa, *O. xylopioides* (Pirie et al. 2006), and *O. guianensis*, *O. martiana* (Lopes et al. 2018), and accordingly oxandra euneura group or euneura group consists *O. asbeckii*, *O. euneura*, *O. polyantha*, *O. longipetala*, *O. espintana*, *O. nitida* (now merged to *O. espintana*) (Pirie et al. 2006), *O. lanceolata* and *O. riedeliana* (Guo et al. 2017).

Oxandra characters	Midrib type	Seed ruminations	Stipe length	Geography
LAURIFOLIA GR				
<i>O. guianensis</i>	impressed	spiniform	3-7 mm	Br. Guyana
<i>O. laurifolia</i>	flat	spiniform	3-8 mm	Antilles
<i>O. macrophylla</i>	impressed	spiniform/peg-shaped	3-6,5 mm	Andes
<i>O. martiana</i>	impressed/flat	spiniform	2-3(-7) mm	Atlantic rainforest
<i>O. sphaerocarpa</i>	impressed/flat	spiniform	6-16 mm	Andes + 1 Amazon
<i>O. xylopioides</i>	impressed	spiniform	1-4 mm	Amazonia
EUNEURA GR				
<i>O. asbeckii</i>	raised	spiniform/peg-shaped	1-2 mm	Amazonia, Guyanas
<i>O. espintana</i>	raised/flat	spiniform (flattened pegs)/lamellate	1-1,5 mm	Amazonia
<i>O. euneura</i>	raised	spiniform/peg-shaped	1 mm	Amazonia
<i>O. lanceolata</i>	raised	peg-shaped	1-2 mm	Antilles & Mexico
<i>O. longipetala</i>	raised	spiniform	1-2 mm	Panama + Brasil (Pará), Peru (Puno)
<i>O. polyantha</i>	raised	spiniform/peg-shaped	1-2 mm	Amazonia
<i>O. riedeliana</i>	raised	spiniform	1-2 mm	Amazonia
ISOLATED				
<i>O. venezuelana</i>	impressed	lamellate	3-10 mm	Mostly Panama + Venezuela

Table 3. Distribution of the selected morphological characters in two segregated taxonomic groups according to the DNA based phylogenies of Richardson et al. (2004), Pirie et al. (2006), Chatrou et al. (2012), Guo et al. (2017) and Lopes et al. (2018).

Oxandra venezuelana is isolated and is often found as a sister group to the rest of the *Oxandra* species and to other genera, such as *Pseudomalmea*, *Klarobelia* or *Pseudephedranthus fragrans*. Pirie et al. (2006) showed that a clade includes all accessions of *Oxandra* (plus accessions of *Pseudomalmea*, *Klarobelia*, *Pseudephedranthus*, *Ruizodendron* and *Ephedranthus*) received 97% BS. Further clades supported the euneura group alone by 100% BS, but only by <50% BS the clade of the laurifolia group together with other five above-mentioned genera. Furthermore, in the phylogeny of Chatrou et al. (2012) the polyphyly is clear, dividing the genus similarly in two groups and *Pseudomalmea*, *Klarobelia* and *Pseudephedranthus* were nested within *Oxandra*. Guo et al. (2017) in their large-scaled phylogeny display *Klarobelia*- *Pseudephedranthus* clade together with *Pseudomalmea* deeply nested within *Oxandra*. *Oxandra* is itself paraphyletic. All four gen-

era are close relatives and *Klarobelia* and *Pseudomalmea* can be distinguished from *Oxandra* in a number of bracts per pedicel with less bracts, petal shape possessing petals much longer, and stipe length being longer than 10 mm. *Pseudephedranthus* has longer petals vs. *Oxandra* and discoid stamens apices vs. apical prolongation in *Oxandra*. *Pseudomalmea* represents outwardly spreading petals vs. concave petals in *Klarobelia*.

All in all, these differences may be regarded negligible enough to establish a genus with the broad generic delimitation, in which *Klarobelia*, *Pseudomalmea* and *Pseudephedranthus* are merged into *Oxandra*. On the other hand, *Oxandra* could be split up and resulting in two genera, in which case euneura group together with the genera in the same clade would inherit *Oxandra* name, because *Oxandra* is the oldest genus name in the tribe and *O. lanceolata* is the type species of the genus. The laurifolia group would be treated as such a new genus. Most nodes of the clade are poorly supported and before the decision can be made, more DNA regions should be sequenced.

These two groups of *Oxandra* can be morphologically distinguished by the midrib of the leaf, which is in the euneura group raised except in *O. espintana*, in which it is slightly impressed to slightly raised. The midrib of the laurifolia group is impressed or flat (Table 3) (Lopes et al. 2018).

Lopes et al. (2018) also mention seed ruminations as an evidence of the split in two groups, but observations do not clearly underpin this hypothesis. Spiniform ruminations exist in the laurifolia group, except in *O. macrophylla*, which has also peg-shaped type. The euneura group inholds also simply spiniform ruminations in *O. longipetala* and *O. riedeliana*, peg-shaped in *O. lanceolata* and rest of the group is spiniform/peg-shaped type or spiniform (composed of flattened pegs)/lamellate. Although the phylogeny of Lopes et al. (2018) do not encompass *O. lanceolata* and *O. riedeliana*, but nevertheless, there is no congruity within groups. However, there are other characters that corroborate the disparity between the two groups. When the stipe lengths of the apocarpous fruits are measured, all stipes of the euneura group are short, up to 2 mm long, which diverge from the 2-16 mm long stipes of the laurifolia group. The only exception is *O. xylopioides* with 1-4 mm long stipes. Furthermore, geographical distribution of the euneura group is more obvious in Amazonia rainforest except *O. lanceolata*, which occurs in the Antilles and Mexico. In the laurifolia group only *O. xylopioides* has spread out widely in Amazonia as well (Table 3). See more discussion in Lopes et al. (2018) about the sexual systems of the flower morphology in the tribe Malmeeae.

The latest results of the phylogenetic analysis of Chatrou in conference abstract (2019) also confirmed polyphyly, when chloroplast DNA was analysed, but new data on nuclear and mitochondrial DNA disclosed both as sister clades. This strongly suggests that there is an old introgression of chloroplasts producing this pattern, giving a new insight to the taxonomy of the genus. So far, the research article has not yet been published so it is better to refrain from further deliberations of the possible mechanisms of this incongruence, such as an ancient chloroplast capture.

4. Conclusions

Synthesis of the terminology for bark morphology (**I**) fulfilled the need of standardisation of the terms used in the bark descriptions. The terminology has been tested in the field in describing homogenous barks of Annonaceae and found to be working well. Exact terms have helped to make better descriptions and to analyse more thoroughly the complicated or delicate morphological structures. This work has resulted in the improved determination of forest trees in the field. Yet a new user of the terminology needs training, and more feedback from other forest surveyors is needed in order to adjust and polish the terminology to advance understandability.

Bark anatomy has provided a few distinguishing characters but does not alone permit conclusions about the phylogeny of the family (**II**). Phylogenetically relevant characters can probably be listed as: the shape of phellem cells, the presence of crystals and the shape of fibre groups. Unfortunately, systematic studies in bark anatomy are currently meagre, because anatomical data is still insufficient, samples are disproportionate due to incidental availability and are often in immature state, i.e. are mostly samples from branches and young trees.

In addition to new species and new combinations (**III, IV**), only few separating morphological characters between laurifolia and euneura groups were observed in the material (**IV**). The convex vs. concave midribs, the stipe length of the apocarpous fruits and perhaps also the geography of the species support evidence found in various phylogenetic studies that the genus may potentially be treated in narrower sense. However, some closely related genera are deeply nested in the present *Oxandra* taxa, so the taxonomical decisions still have to wait for more extended DNA sequence data, i.e. from nuclear and mitochondrial sequences and more thorough phylogenies, to solve the problem.

Acknowledgements

I feel deep gratitude to Dr. Jifke Koek-Noorman (the Utrecht University), who supervised the bark morphological and anatomical research and Prof. Paul Maas (the Utrecht University and the Leiden University), who guided and participated in the revision of the genus *Oxandra*. They also kindly opened always their home for me during my stay in Utrecht.

Valuable was also the help and enthusiastic companionship of many experts, like Prof. Lars Chatrou, Ms. Hiltje van Kamer-Maas, Dr. Lubbert Westra, Dr. Roy Erkens, Prof. Michael Pirie, Dr. Marion Jansen-Jacobs and many others in the Annonaceae -project. In the wood laboratory of the Herbarium of the Utrecht University I was in many ways helped by Mr. Dewanand Makhan. At the Institute for Wood Biology and Wood Protection, in Hamburg, Dr. Hans Georg Richter and Dr. Michael Trockenbrodt gave me valuable assistance by teaching me to cut bark samples. Many local botanists were accompanying me in the field in Rio de Janeiro (RJ), in Santa Teresa (ES), in Ilhéus (BA) and in Manaus (Reserva Florestal Adolpho Ducke, AM) and helped me in collecting the bark samples and the herbarium vouchers. I would like cordially thank Dr. Mike Hopkins and Dr. Andre Carvalho for accommodating me for several weeks, when I was doing my field work in Manaus and in Ilhéus districts. I am indebted to the curators of various herbaria in South America and Europe, who guided me and sent me herbarium material for the revision.

In Helsinki, Prof. emer. Timo Koponen first suggested to me the subject of tropical tree barks for my master thesis and later provided me with a travel grant to meet researchers of the Annonaceae Project in the Utrecht University. Dr. Tuuli Timonen and Ms. Eija Rinne were always willing to discuss problems in interpreting anatomical samples. Mr. Pertti Rantiala patiently checked collection localities and found coordinates for mapping the specimens. Curator Raino Lampinen helped me in problems of map programming. Distribution maps (IV) were generated by the DMAP for Windows software written by Alan Morton, who also provided me with an appropriate base map for South and Central America.

Prof. Leif Schulman, Prof. Jouko Rikkinen, Dr. Henry Väre and Dr. Johannes Enroth (Thesis advisory committee) gave me valuable advice and constructive criticism in the final phase of the work. My sincere thanks to them all.

I also thank the pre-examiners, Prof. emer. Abraham E. van Wyk (Pretoria, South Africa) and Prof. Laura Yáñez Espinosa (San Luis Potosi, México), who kindly read my thesis. Financial support was given by Societas Biologica Fennica Vanamo (I) and the Finnish Cultural Foundation (I, II, and IV), and travel grants were provided by the Finnish Museum of Natural History (IV).

Permission to republish articles were given by Brill (I), Finnish Zoological and Botanical Publishing Board (II), Magnolia Press (III), and Naturalis Biodiversity Center (IV), which is greatly appreciated.

Last, but not least, I want to thank my dear wife, Mrs. Paula Vilkki, who encouraged me to finally finish off the thesis and who made an illustration of the new species, *Oxandra saxicola*, to the cover page of my thesis and redrew the figure 1 in the summary.

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