TAXON 39(1): 16–32. FEBRUARY 1990

STUDIES IN ANNONACEAE. XIII. THE ROLE OF MORPHOLOGICAL CHARACTERS IN SUBSEQUENT CLASSIFICATIONS OF ANNONACEAE: A COMPARATIVE SURVEY

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Summary

A comparative survey of several historical classifications of Annonaceae down to the subtribal level is given. The role of various key characters is briefly discussed. The present paper at the same time may be considered as an introductory paper to forthcoming publications of general studies on flower and fruit characters now being conducted at Utrecht.

Introduction

The history of systematic work on Annonaceae roughly covers the last one-and-a-half century. For a long time, the best-known authority on this family was, without any doubt, R. E. Fries, whose activities included the first six decades of this century. In recent years interest in Annonaceae has been renewed. At present a multidisciplinary project on the systematics of Annonaceae is in progress at Utrecht.

The Annonaceae form a large, generally easily recognizable and apparently natural family. Delimitation of tribes and genera, however, has been the subject of repeated discussion.

Since Dunal (1817) made a first subdivision of the family (including nine genera), many authors have turned their attention to the subject. Some of them confined themselves to certain geographical areas (Hooker and Thomson, 1855; Jovet-Ast, 1942; Sinclair, 1955). Others produced classifications based on a limited number of characters only (Le Thomas, 1983; Walker, 1971; Christmann, 1987). These fall outside the scope of the present paper and will not be treated here.

Three early classifications, i.e., pre-dating that of Bentham (1862) but following Dunal's work, should be mentioned briefly here. In Reichenbach's (1837) key, the family is divided into three tribes, one of these again into three subtribes. This, apparently, was the first time that a subdivision into tribes was made. Shortly thereafter, Endlicher (1839) published his classification with three tribes including 16 genera, to which are added five genera of uncertain status, and the genus *Eupomatia* which is placed under the heading "Anonaceis affines," bringing the total number of genera to 22. Agardh's (1858) treatment recognized four families: Hornschuchieae, Annonaceae, Monodoraceae, and Eupomatiaceae (although the endings vary, it is clear from the format of the work that all of the groups are of equivalent rank).

Bentham's (1862) classification, derived to some extent from that of Hooker and Thomson (1855), may be regarded as the first truly large-scale classification of the whole family. This was followed by the ones of Baillon (1868), Prantl (1891), Engler and Diels (1900), Engler (1897, 1908, 1915), Hutchinson (1923, 1964), and R. E. Fries (1959). Table 1 gives a comparison of subfamilies and tribes which are distinguished in these seven systems.

Diels (1932) expounds how, apart from a number of characters of lesser importance, one may recognize three characters of crucial importance for the taxonomy of Annonaceae, viz., apocarpy versus syncarpy, the shape of the petals, and the number of ovules per carpel. It seems, however, that there is little correlation between states of these three characters. The resulting reticulate pattern, as it were, seriously impedes classification of the family.

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The great difficulties encountered in attempts at classification that go further than merely producing a scheme for identification purposes are also aptly mentioned by Fries (1959): "Die Schwierigkeiten liegen in der richtigen Beurteilung des systematischen Wertes der einzelnen Merkmale wie auch in der oft noch unvollständigen Kenntnis der Blütenmorphologie vieler Gattungen."

All classifications down to the (sub)tribal level, so far, have relied to a greater or lesser extent upon the following characters:

1) carpels free or connate; 2) aestivation of petals; 3) number of petals; 4) relative length of petals; 5) differentiation in shape of petals; 6) petals free or connate; 7) shape of apex of stamen (apical prolongation of connective); 8) placentation and the number of ovules per carpel; 9) inflorescence position; 10) phyllotaxis; and 11) indument.

These characters will be discussed in the ensuing sections. Please note that the following text should be read in connection with Tables 1 and 2. The list of genera in Table 2 in the seventh column (under "Fries") is that as used by Fries in his 1959 survey. For the sake of clarity, the table follows the nomenclature as used by Fries. Any nomenclatural changes that were made by later authors may be found among the footnotes accompanying Table 2. Newer taxa, published in the post-Friesian era, are not included (the reader interested may want to consult in due time an enumeration of Annonaceous genera with bibliography and indication of current status, now being prepared in Utrecht and to be published shortly).

Gynoecium Structure

1. Placement of Monodora *and* Isolona.—*Monodora* Dunal has nearly always been placed in Annonaceae, though mostly in an isolated position. Both Dunal (1817) and de Candolle (1824) placed *Monodora* apart because of "one single carpel with numerous ovules" vs. "many carpels, free or connate." Only Agardh (1858) placed it in a separate family.

Although later authors consider the gynoecium of *Monodora* as a cyclic arrangement of connate carpels, they all agree that *Monodora,* together with the genus *Isolona* described later and regarded as closely related, has to be placed in a separate tribe or subfamily. The only exception is Bentham (1862) who includes *Monodora* in Mitrephoreae. (Delimitation of Mitrephoreae, in the course of time, has been the subject of much discussion; see *Shape of Petals,* part 1.)

*2. Delineation of Annonineae/*Annona*-group.*—Apart from the case of *Monodora* and *Isolona,* all Annonaceae carry carpels in spiral(s). These carpels are mostly free. In a number of genera they become fused. Fusion of carpels may be partial or complete. Syncarpy thus resulting is an important taxonomic character, though it not necessarily always indicates close relationship. The group where syncarpy dominates heavily is centered around the core of the large genera *Annona* and *Rollinia,* and the small genus *Raimondia.* These three genera are considered by nearly all authors to be very closely akin. Syncarpy here is complete in the bulk of species (only in *Rollinia* there are a few exceptions).

Rolliniopsis much resembles *Rollinia,* and is included in the *Annona*-group by Fries. It is distinct however by apocarpous fruits, for which reason it was placed in Xylopineae-Hexapetalae by Hutchinson.

Anonidium is also included in the *Annona*-group by Fries on the basis of carpels coalescing and immersed in the torus.

Ararocarpus, placed in Annonineae by Hutchinson, is referred to the *Xylopia*-group by Fries notwithstanding the fact that carpels, partly connate ("etwas vereinigt") at first, coalesce into a syncarpium. Sinclair (1958) came with a radically different approach to this genus in considering it as a freak of Nature: in fact it is a species of *Meiogyne,* distinct only in having an extremely high number of carpels. The resulting lack of space prevents a normal development of individual carpels; instead, a fusion occurs leading to the "abnormal" fruit. *Anonidium,* on the other hand, caused a problem here (see also *Aestivation of Petals*). Because of its imbricate inner petals, *Anonidium* is placed in Uvarieae by Engler

and Diels and Hutchinson. Fries rather lays emphasis on the valvate outer petals and finds sufficient reason to put the genus in Unoneae (*Annona*-group).

3. The position of Fusaea.—The only genus with wholly syncarpous fruits that has not been referred to the *Annona*-group at one time or another is *Fusaea.* It is in fact closely related to *Duguetia,* and it has even been treated as a section of that genus (e.g., Baillon, 1868: 336). *Duguetia* has always been classified in Uvarieae notably because of the imbricate petals. Fries distinguished a *Duguetia*-group, with *Duguetia* and *Fusaea,* and four more recently described genera, characterized by leaf-opposed flowers (inflorescences) with one basal ovule in each carpel. Carpels in the *Duguetia*-group are mostly sessile, and more or less connate at the base. The heterogeneous element here is *Malmea* with stipitate monocarps, which illustrates once more the relativity of syncarpy. It is worth mentioning that Sinclair (1955) regards *Anonidium, Fusaea,* and *Pachypodanthium* as a distinct, and the most advanced, group within Uvarieae.

Aestivation of Petals

Authors almost unanimously regard the difference between valvate and imbricate petals as one of the most important differentiating characters.

An exception are Engler and Diels, who do not recognize such an absolute difference between both aestivation types. Their first subdivision of Uvarioideae (Annonoideae of other authors) in four tribes (Table 1) is based rather on petal shape. This is further discussed in *Shape of the Petals.*

It may be useful to point out that the term "imbricate" has not always been used in exactly the same sense. As for Annonaceae, imbrication refers to overlapping of lateral margins in bud. Often, however, only the upper margins are seen to overlap. This can lead to problems of interpretation, which explains the case of, e.g., *Sphaerothalamus,* see hereafter.

1. Delimitation of Uvarieae.—Though not always on the same taxonomic rank, in all classifications there appears a group that is mainly characterized by imbricate petals (Uvarieae, Uvariinae). There is, however, no common opinion on the delimitation of this group.

When we look at the genera already known to Bentham (1862), we note that only two genera placed in Uvarieae by Bentham (and later authors) were removed by Fries: *Sphaerothalamus* and *Porcelia.*

Sphaerothalamus, according to older authors, has petals imbricate at the apex only, but it is included by Airy Shaw (1939: 279) and by Fries (1959) in *Polyalthia,* and thus it is classified in Unoneae by Fries.

Porcelia, in spite of imbricate petals, nevertheless is admitted by Fries as the only exception in Unoneae (*Trigynaea*-group) because of its obvious overall similarity with the other members of this group.

It is curious that Fries fails to mention *Cardiopetalum* and *Froesiodendron,* two other members of the *Trigynaea*-group, in this respect. These genera, with petals described as imbricate ("dachig"), mismatch in the same character as *Porcelia.* The genus *Dasoclema* is regarded by Fries as closely related to *Monocarpia* even to such an extent that both genera are placed in the *Desmos*-group of the Unoneae. However, petals in the former are described as "warscheinlich dachig," and in the latter as "klappig."

The genera *Anonidium* and *Dendrokingstonia* (*Kingstonia*) have created a problem for taxonomists due to a different aestivation of the two whorls of petals. Fries, for reason of valvate outer petals, removed the two genera from Uvarieae, where they had been placed because of imbricate inner petals. It may be noted that in *Annona,* as is also seen in Fries's key to the sections, species with imbricate inner petals occur as well. This is the case, among others, with the widely cultivated *A. muricata.*

Genera placed by later authors in Uvarieae, but not by Bentham, generally may be said to have had a troubled taxonomic history. The clearest example is *Hexalobus*: Bentham

up to and including Hutchinson attribute a valvate aestivation to this genus. Engler and Diels create a separate group, Hexalobeae, based on plicate petals. Fries is the first to observe imbricate petals in *Hexalobus* and, accordingly, brings it in one group with *Cleistochlamys*, the other members being *Asteranthe, Lettowianthus,* and *Ophrypetalum.*

In a similar way Fries disagrees with earlier authors with regard to aestivation in *Tridimeris* and *Anomianthus,* and his taxonomy differs accordingly.

Heteropetalum, together with the genera *Guatteriella* and *Guatteriopsis* described later, is obviously so close to *Guatteria* that it naturally has to be placed together with it (Fries, 1942: 19), notwithstanding the valvate petals.

Finally, it may be worth noting that since the turn of the century the number of genera described has increased considerably. Uvarieae are subdivided by Fries in five groups, based on inflorescence position, aestivation of sepals, and placentation.

Number of Petals

The reader familiar with Annonaceae will know that the most common number of petals is six, in two whorls of three. Incidental occurrence of tetramerous flowers is regularly mentioned for species that normally have trimerous flowers. In *Asimina tetramera* Small the number of tetramerous flowers may even be roughly equal to the number of trimerous flowers in one population (Kral, 1960).

The aberrant genus *Tetrameranthus,* placed in a tribe of its own, among others, because of a phyllotaxis very different from that normally found in Annonaceae (see *Phyllotaxis*), has almost exclusively tetramerous flowers.

Hutchinson goes so far as to distinguish three subgroups within Xylopiineae solely based on the number of petals, viz., Hexapetalae, Tetrapetalae, and Tripetalae, later on (1964) referred to by him as Group A, Group B, and Group C, respectively. It should be added, though, that Engler and Diels had already recognized and keyed out Tetrapetalae earlier, also based on the number of petals. The purely artificial nature of this group involving the genera *Disepalum, Tridimeris,* and *Uvariopsis* is well demonstrated by Fries. Fries transfers *Tridimeris* to Uvarieae ("Pet. . . . zuerst warscheinlich dachig"). *Uvariopsis* (including *Tetrastemma* and the tripetalous (!) *Thonnera*), because of its single whorl of petals, is placed by Fries in the *Monanthotaxis*-group, and *Disepalum* is brought over to the *Artabotrys*-group; both these groups fall within Unoneae.

Also the genera with a single whorl of three petals placed in Tripetalae by Hutchinson are classified by Fries in different groups of genera (see Table 1), though all within Unoneae.

Sinclair (1955) already points at intrageneric variation in number of petals, e.g., in *Anaxagorea, Desmos,* and *Disepalum.*

Fries, in his introduction (1959), sees a classification based on number of perianth parts as done by Hutchinson as good for practical identification purposes only, and sees hardly any connection to phylogenetic relationships. The number of petals may vary within some genera, e.g., *Annona, Anaxagorea*; in other cases three petals result from reduction of either the inner whorl (*Dasymaschalon, Dennettia*) or the outer whorl (*Enantia*). The trimerous genus *Thonnera* is considered so close to the tetramerous *Uvariopsis* that Fries unites the two. In this context it should be noted that Hutchinson's placing of *Petalolophus* in Tripetalae apparently is due to misinterpretation: the outer petals are present, though very small.

Relative Size of Inner and Outer Petals

In many genera inner and outer petals are comparable in size. It should be remarked that this is not necessarily always clear during (early) stages of development. Moreover, what is "equal" and what is "unequal" often is a matter of subjective choice. All this explains how investigators may have come to different interpretations. Notwithstanding this, authors in the past attributed great systematic value to relative length of petals.

Table 1. Rough comparison of classifications of Annonaceae down to tribal level by different authors.

Bentham	Baillon[1]	Prantl	Engler/Diels	Hutchinson	Fries
	ANONEAE		UVARIOIDEAE	AN(N)ONOIDEAE	ANNONOIDEAE
			Uvarieae		Uvarieae
Uvarieae	Uvarieae	Uvarieae	Uvariinae	Uvarieae	(5 groups; see Table 2)
Unoneae	Unoneae	Unoneae	Unoninae		
					Unoneae
			Miliuseae		(9 groups; see Table 2)
Miliuseae	Miliuseae	Miliuseae	Milliusinae	Miliuseae	
Mitrephoreae	Oxymitreae	Mitrephoreae	Mitrephorinae		
Xylopieae	Xylopieae	Xylopieae	Xylopieae	Unoneae	
				Xylopi(i)neae	
			Xylopiinae	Hexapetalae[2]	
			Melodorinae	Tetrapetalae[2]	
	Rollinieae	Melodoreae		Tripetalae[2]	
			Anoninae	An(n)onineae	
			Hexalobeae		
					Tetramerantheae
	MONODOREAE	Monodoreae	MONODOROIDEAE	MONODOROIDEAE	MONODOROIDEAE
	EUPOMATIEAE	Eupomatieae	EUPOMATIOIDEAE		

[1] Baillon consistently used French endings.

[2] Called 'Series' by Hutchinson in 1923; in 1964 referred to by him as 'Group A', 'Group B', and 'Group C' respectively.

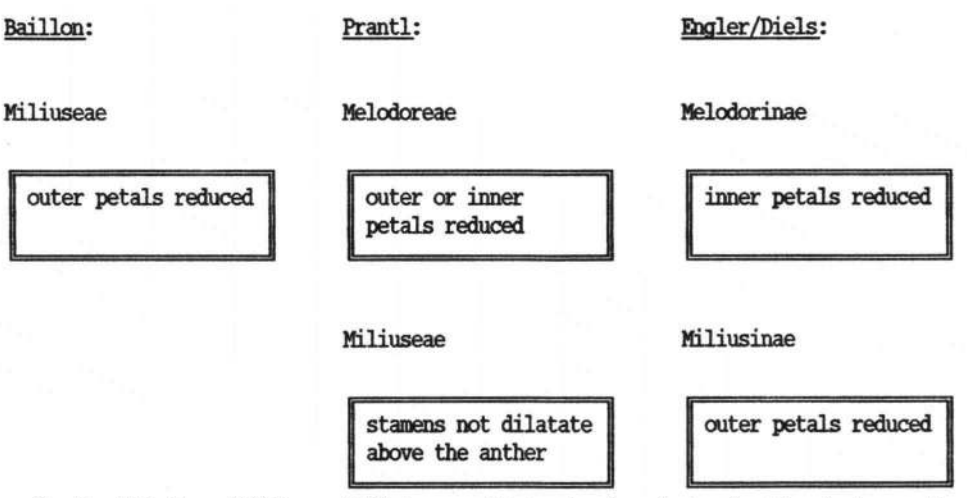

Fig. 1. Definition of Miliuseae/Miliusinae on the one hand, and role of petal reduction on the other hand, in classifications of Annonaceae by Baillon, Prantl, and Engler and Diels, respectively.

Only Fries (1959: 41) pointed out that relative length of petals may vary greatly within some genera. Therefore, in his opinion, this character is only incidentally useful in delimitation of genera. Its main value lies on the specific level.

1. Delineation of Miliuseae or Miliusinae: Outer petals much shorter than inner petals, about equalling sepals.—Bentham was the first to distinguish Miliuseae, characterized by small sepals and outer petals, and large, valvate inner petals. In this group Bentham also included *Eupomatia* R. Br. This genus was retained in Annonaceae by subsequent authors, though more and more in an isolated position, until Hutchinson restored it to the separate family of Eupomatiaceae still known today.

Circumscription of Miliuseae or Miliusinae, respectively, has not always been the same with various authors: this has been dependent upon priority of characters (see Fig. 1). Generally, the taxon included genera with reduced outer petals. Prantl, however, keyed out Miliuseae in the first place on stamens not dilatate above the anther (see also *Apex of the Connective,* part 1). Genera with either reduced inner or outer petals in Prantl's classification are grouped in Melodoreae. In the classification of Engler and Diels, however, Melodorinae stands for a group with lacking or reduced inner petals. Fries no longer recognized Miliuseae, which is the logical consequence of the low weight that he assigns to reduction of organs, as has been discussed before.

Orophea presents a problem in itself as it is distinguished by both unguiculate, mitriform inner petals and reduced outer petals. Baillon's transfer of *Orophea* from Miliuseae to Oxymitreae (≡Mitrephoreae), and the reverse action by Hutchinson, are therefore easy to understand. Baillon at the same time brought *Phaeanthus* (including *Heteropetalum* and *Piptostigma*) from Mitrephoreae sensu Bentham to Miliuseae. This remained there up to and including Hutchinson's classification.

Engler and Diels, and Hutchinson, also added genera to Miliuseae: *Anomianthus* and *Cymbopetalum,* as well as *Fenerivia* and *Marsypopetalum* that had been described in the meantime.

The genus *Bocagea* (with six equal, thin, petals) has been placed now in Miliuseae and at other times in Unoneae.

2. Melodorinae sensu Engler and Diels: Reduced inner petals.—As has already been mentioned in the preceding section, Engler and Diels alone recognized the Melodorinae as characterized by the lack or strong reduction of inner petals. This figures as a subgroup of Xylopieae which are characterized by thick petals. Melodorinae includes the genera *Ebu-*

Table 2. Position of Annonaceous genera in (sub-)tribes in various classifications. List of abbreviations used: Ann: An(n)onin(e)ae; He: Hexalobeae; Me: Melodoreae; Men: Melodorinae; Ml: Miliuseae; Mln: Miliusinae; Mt: Mitrephoreae; Mtr: Mitrephorinae; Ox: Oxymitreae; Ro: Rollinieae; Un: Unoneae; Unon: Unoninae; Uv: Uvarieae; Uvar: Uvariinae; X: Xylopieae; Xy: Xylopiinae; Xy-h: Xylopineae-Hexapetalae = Xylopiineae, Group A; Xy-t: Xylopineae-Tetrapetalae = Xylopiineae, Group B; Xy-tr: Xylopineae-Tripetalae = Xylopiineae, Group C; —: genus not yet described; ?: genus not mentioned.

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959
						ANNONOIDEAE-Uvarieae
						Uvaria-group
Mt	Uv[2]	Uv[2]	Uvar		Ml[8]	Anomianthus
—	—	—	—		—	Afroguatteria
—	—	—	—		Xy-h	Desmopsis
Uv	Uv[2]	Uv	Uvar		Uv	Ellipeia
—	—	—	—		Uv	Ellipeiopsis
—	—	—	—		Xy-h	Mischogyne
Uv[3]	Uv[2]	Uv[3]	?[7]		Uv	Sapranthus
—	—	—	—		Uv	Stenanona
—	Uv	Uv	Uvar		Uv	Tetrapetalum
—	—	—	—		Uv	Toussaintia
Uv	Uv	Uv	Uvar		Uv	Uvaria
						Duguetia-group
—	—	—	—		Uv	Duckeanthus
Uv	Uv[4]	Uv	Uvar		Uv	Duguetia[11]
—	Uv[5]	?	?		Uv	Fusaea
—	—	—	—		Uv	Letestudoxa
—	—	—	—	Uvar	Uv	Malmea
—	—	—	Uvar		Uv	Pachypodanthium
						Asimina-group
Un	Uv[2]	Uv	Uvar[2]		Xy-h	Asimina
—	—	Uv	Uvar		Uv	Cleistopholis
—	—	—	—		Uv	Cremastosperma
?	Un[6]	?	Unon		Uv	Cyathostemma
—	—	—	—		Xy-h	Deeringothamnus
—	—	Uv	Uvar		Uv	Enicosanthum[12]
—	—	Uv	Uvar		Uv	Ephedranthus

Table 2. Continued

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959
Uv[2]	Uv[2]	Uv[2]	?		Uv[2]	Fitzalania
?	Uv	Ml	Uvar		Uv	Oxandra
—	—	—	—		Uv	Pseudoxandra
—	—	—	—		Uv	Ruizodendron
Uv	Uv	Ml	Uvar		Uv	Sageraea
Uv	Uv[2]	Uv	Uvar		Uv	Stelechocarpus
—	—	Un	Unon		Xy-t	Tridimeris
						Hexalobus-group
—	—	—	—	Uvar	Uv	Asteranthe[13]
—	Uv	Uv	Uvar		Xy-h[9]	Cleistochlamys
Un	Ro	X	He		Xy-h	Hexalobus
—	—	—	—		Uv	Lettowianthus
—	—	—	—		Xy-h	Ophrypetalum
						Guatteria-group
Uv	Uv	Uv	Uvar		Uv	Guatteria
—	—	—	—		Xy-h	Guatteriella
—	—	—	—		Xy-h	Guatteriopsis
Mt	Ml[10]	Me	Mln		Ml	Heteropetalum
						ANNONOIDEAE-Unoneae
						Desmos-group
Ml	Un[14]	Ml	Unon		Xy-h	Alphonsea
—	—	—	—		Uv	Dasoclema
Un[6]	Un[6]	Un[6]	Unon[6]		Xy-h	Desmos
—	—	—	Uvar		Xy-h	Meiocarpidium
—	Un[6]	Un[6]	Unon		Xy-h[15]	Monocarpia
—	—	Mt	Unon		Xy-h	Rauwenhoffia
						Polyalthia-group
Un	Un[6]	Un	Unon		Xy-h	Cananga
—	—	—	—		Ml	Fenerivia
—	—	Ml	Uvar		Uv	Kingstonia[16]

Table 2. Continued

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959
–	Un[6]	Un[6]	Xy		Xy-h	Meiogyne
–	–	Ml	Unon		Xy-h	Mezzettia
Ml	Ml	Ml	Mln		Ml	Miliusa[17]
–	–	–	–		Xy-h	Papualthia
Un/Uv[18]	Un[6]/Uv[18]	Un/Uv[18]	Unon/Uvar[18]	Unon	Xy-h/Uv[18]	Polyalthia[19]
–	–	–	–		Xy-h[20]	Sphaerocoryne
–	–	–	–		Xy-h	Woodiella[21]
						Unonopsis-group
–	–	–	–		Xy-h	Bocageopsis
–	–	–	–		Xy-tr	Dennettia
–	–	–	–		Xy-h	Dielsiothamnus
–	–	–	–		Xy-h	Neouvaria
–	–	–	–		Xy-h	Onychopetalum
–	–	–	Xy		Xy-h	Polyceratocarpus
–	–	–	?		Xy-h	Unonopsis
–	–	–	–	Uvar	Xy-h	Uvariastrum
–	–	–	–		Xy-h	Uvariodendron
						Xylopia-group
Un	Un	Un/Mt[22]	Unon/Me[22]		Xy-h[23]	Anaxagorea
–	–	Un	Xy		Ann	Ararocarpus
–	Un[6]	Un[6]	Men		Xy-tr	Dasymaschalon
–	–	–	–		Xy-h	Diclinanona
X[24]	Un[6]	Un[25]/Me[26]	Men		Xy-h	Fissistigma[26]
–	–	–	–		Xy-h	Guamia
–	–	–	–	Men	Xy-h	Oncodostigma
–	Ml[10]	Me	Mln		Ml	Piptostigma[27]
–	–	–	–		Xy-h	Polyaulax
–	X[28]	?	?		Xy-h	Pseudannona
X	X	X	Xy		Xy-h	Xylopia
						Artabotrys-group
Un	Ro	X	Xy		Xy-h	Artabotrys

Table 2. Continued

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959
Un	Ro	X	Xy		Xy-h	Cyathocalyx
Un	Un	Un	Unon		Xy-t	Disepalum
–	–	X[15]	Xy[15]		Xy-h	Drepananthus
–	Ox	Un	Xy		Xy-tr	Enantia
–	–	Me	Mln		Ml	Marsypopetalum
–	–	–	Xy		Xy-h	Neostenanthera
–	–	–	–		Xy-h	Pseudartabotrys
						Orophea-group
–	–	–	–		Xy-h	Atopostema
–	–	–	–		Xy-h	Exellia
Mt	Ox[29]	Me[29]	Mtr[30]		Xy-h	Goniothalamus[4]
Mt	Ox	Mt	Mtr		Xy-h	Mitrephora
–	–	–	–	Mtr	Xy-h	Oreomitra
Ml	Ox	Mt	Mt	Unon[31]	Ml	Orophea[32]
–	–	–	–	Mtr	Xy-tr	Petalolophus
Mt	Ml	Me	Mln		Ml	Phaeanthus
–	–	–	Mtr		Xy-h	Platymitra
Un/Ml[33]	Un/?[33]	Mt/Ml[33]	Unon		Xy-h	Popowia
Mt[34]	Ox[34]	Mt[35]	?		Xy-h	Pseuduvaria
Mt	Ox[29]	Me[29]	Mtr/Men[36]		Xy-h	Richella[37]
–	–	–	–	Mtr	Xy-h	Schefferomitra
–	Un[6]	–	Mtr		Ml	Trivalvaria
						Annona-group
X	X	X	Ann		Ann	Annona
–	–	–	Uvar		Uv	Anonidium
–	–	–	–		Ann	Raimondia
X	Ro	X	Ann		Ann	Rollinia
–	–	–	–		Xy-h	Rolliniopsis
						Trigynaea-group
Ml	Un	Ml	Unon		Xy-h	Bocagea
–	–	Uv/X[38]	Uv[39]/Unon[38]		Xy-h	Cardiopetalum

Table 2. Continued

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959
Mt	Ox	Un	Mln		Ml	Cymbopetalum
—	—	—	—		Uv	Froesiodendron
—	—	—	—		Xy-h	Hornschuchia
Uv	Uv[2]	Uv	Uv[2]		Uv	Porcelia
Un	Un[6]	Un	Unon		Xy-h	Trigynaea
						Monanthotaxis-group
—	—	—	—		Xy-h	Enneastemon
—	—	—	—		Xy-h	Gilbertiella
—	—	Mt	Unon		Xy-h	Haplostichanthus
—	—	Ml	Unon		Xy-h	Monanthotaxis
—	—	—	—		Xy-h	Monocyclanthus
—	—	—	Unon		Xy-tr[40]	Uvariopsis[41]
						ANNONOIDEAE-Tetramerantheae
—	—	—	—		Uv	Tetrameranthus
						MONODOROIDEAE
Mt	MON	MON	MON		MON	Monodora
—	—	—	MON		MON	Isolona

[1] Prantl's classification of 1891 is supplemented by a paper by Engler in 1897; data from both publications are combined in one column. The column under "Engler" lists only genera dealt with by him in two papers (1908, 1915), and not mentioned in the publication by Engler and Diels in 1900. Hutchinson's classificatory scheme of 1964 is essentially based on that of 1923. *Cardiopetalum* has been moved from Uvarieae to Unoneae/Xylopiineae, Group A. *Orophea,* keyed out under two tribes in 1923 as well as in 1964, went from Unoneae/Xylopineae-Hexapetalae to Miliuseae. Other alterations concern delimitation of taxa and/or nomenclature, and addition of new taxa. In order to not unduly complicate the table, only Hutchinson's later version is shown.

[2] Included in *Uvaria.*

[3] Included in *Porcelia.*

[4] Included in *Aberemoa.*

[5] Included in *Aberemoa* as a separate section.

[6] Included in *Unona.*

[7] Probably included in *Uvaria.*

[8] Included in the keys of both Miliuseae and Uvarieae.

[9] Included in *Popowia.*

Table 2. Continued

Bentham 1862	Baillon 1868	Prantl[1] 1891, '97	Engler/Diels 1900	Engler 1908, '15	Hutchinson[1] 1964	Fries 1959

[10] Included in *Phaeanthus.*
[11] Including *Geanthemum.*
[12] Including *Griffithia, Griffithianthus,* and *Marcuccia*; see Engler and Diels, and Hutchinson.
[13] ≡*Asteranthopsis* O. Kuntze, illegitimate substitute name.
[14] Included in *Bocagea.*
[15] Included in *Cyathocalyx* (1964).
[16] ≡*Dendrokingstonia* Rauschert (not *Kingstonia* S. F. Gray 1821, Saxifragaceae).
[17] Including *Saccopetalum* (see Bentham, Engler and Diels, and Hutchinson).
[18] Refers to *Sphaerothalamus.*
[19] Including *Sphaerothalamus.*
[20] Included in *Polyalthia.*
[21] ≡*Woodiellantha* Rauschert (not *Woodiella* Saccardo and Sydow 1899, Fungi).
[22] Refers to *Eburopetalum.*
[23] *Anaxagorea,* including *Eburopetalum,* is mentioned in the keys to the genera of both Xylopiineae, Group A and Xylopiineae, Group B.
[24] Refers to *Melodorum.*
[25] Including *Ancana.*
[26] Including *Melodorum, Mitrella, Kentia,* and *Pyramidanthe.*
[27] Including *Brieya.*
[28] Included in *Xylopia.*
[29] Included in *Oxymitra..*
[30] Including *Atrutegia.*
[31] Refers to *Mezzettiopsis.*
[32] Fries omits the segregate genus *Phoenicanthus* Alston.
[33] Refers to *Clathrospermum.*
[34] Included in *Mitrephora.*
[35] Included in *Orophea.*
[36] Refers to *Oxymitra.*
[37] Including *Oxymitra* and *Friesodielsia.*
[38] Included in *Duguetia.*
[39] Refers to *Stormia.*
[40] Refers to *Thonnera.*
[41] Including *Tetrastemma* and *Thonnera.*

ropetalum (=*Anaxagorea*), *Dasymaschalon,* and *Fissistigma.* It is noteworthy that, in a sense, this idea is also adopted by Fries: *Xylopia* and the three genera just mentioned form part of the *Xylopia*-group is his classification, characterized by thick, ±wholly contiguous inner petals with concave bases.

3. Melodoreae sensu Prantl: Either reduced inner or outer petals.—This group, already mentioned above, cannot be but a highly artificial group. It is not surprising, therefore, that no other authors adopted it. Engler and Diels, in fact, rejected it and transferred the genera to Miliusinae, Mitrephorinae, and Melodorinae.

Shape of the Petals

Engler and Diels were the first authors to use this character on the tribal level. Their subdivision of Uvarioideae (Annonoideae of other authors) is given here:

–petals about equal, flat, rarely appendaged: Uvarieae;

–petals valvate, mostly unequal, inner petals often appendaged: Miliuseae (subdivided in Miliusinae and Mitrephorinae based on absence or presence of connivent inner petals);

–petals plicate: Hexalobeae;

–petals thick, valvate, inner petals smaller than outer petals, or lacking: Xylopieae.

The shape of the petals, however, is difficult to describe in terms useful for systematic purposes. There is only one group out of those just mentioned that, at first sight, seems quite natural (Mitrephorinae). The other three groups could hardly claim to be that.

1. Delineation of Mitrephoreae/Mitrephorinae: Inner petals hood-like.—In certain members of the Annonaceae, all with valvate petals, the distinctly smaller inner petals are contiguous apically, thereby forming a cap or mitre over the stamens and carpels. In all classification systems, except Hutchinson's, there is included a tribe or subtribe thus defined (Mitrephoreae, Mitrephorinae, Oxymitreae, *Orophea*-group).

Nevertheless, this character, too, appears open to various interpretations: what one person would call a "hood" will not necessarily be recognized as such by another! Table 2 shows that there is unanimity only in the case of comparatively few genera: *Goniothalamus, Mitrephora,* and *Richella* (*Oxymitra*). *Platymitra,* published somewhat later, can also be mentioned here.

Monodora was placed already by Baillon in a separate tribe, in which it has remained since. Other genera have been tossed to and fro between Mitrephoreae and other groups, such as Miliuseae (*Orophea, Phaeanthus,* and *Cymbopetalum*). *Popowia* and *Rauwenhoffia* are placed in Unoneae by, among others, Engler and Diels. *Anomianthus, Heteropetalum,* and *Enantia* fare even more oddly. Fries expands the *Orophea*-group with nine more genera, although with some doubts as regards two of these, viz., *Trivalvaria* and *Atopostema.*

2. Xylopia and its allies: Inner petals thick, valvate, more or less hollow at the base.—Xylopieae were defined by Bentham based on, among others, thick, valvate petals. Genera frequently mentioned in this context, beside *Xylopia,* are *Annona, Artabotrys, Cyathocalyx,* and *Rollinia* (Rollinieae sensu Baillon).

Other genera are placed incidentally in Xylopieae. Although with some generalization, one might say that the three subtribes of Xylopieae, viz., Unoninae, Xylopiinae, and Mitrephorinae sensu Engler and Diels agree with the *Xylopia*-, *Artabotrys*-, and *Annona*-groups sensu Fries.

Hutchinson has a different approach: the three subtribes by Engler and Diels just mentioned are united in Xylopi(i)neae, which is subdivided in three groups based on number of petals (already mentioned under the section *Number of Petals*), albeit with easy identification as the main goal.

Sympetalous Flowers

In most genera petals are free. Although sympetaly occurs in Annonaceae, there is no author, with the exception of Fries (see below), who distinguishes major groups based on

this character state. Occurrence of both choripetalous and sympetalous flowers is found in *Annona.* The same holds for the small genus *Fusaea.* The fully sympetalous state may be seen in such widely divergent genera as *Rollinia* and *Isolona.*

1. The Monanthotaxis*-group sensu Fries.*—The group with the largest concentration of genera with sympetaly (though in various degree) is the *Monanthotaxis*-group of Fries. This group also includes genera with free petals, however. On the other hand Fries moves the manifestly sympetalous *Disepalum* to the *Artabotrys*-group, where it admittedly remains a heterogeneous element.

Apex of the Connective

In most Annonaceae the apex of the connective characteristically is prolonged into a dilatation that is usually shield-like. This connective shield has a protective function: it keeps the developing fertile parts of the flower away from voracious insects (Gottsberger, 1970).

1. Miliuseae sensu Prantl.—In Prantl's (1891) concept Miliuseae are keyed out in the first place on stamens not dilatate above the anther (though the connective may still be prolonged into an appendage of very distinct shape). This group includes seven genera, among them *Oxandra* and *Sageraea,* genera placed in the Uvarieae in all other classifications.

No other authors, however, assign such importance to the apex of the connective as did Prantl. Sinclair perhaps comes closest to Prantl's concept in defining Miliuseae (six genera) as having, among other things, "stamens few, loosely imbricate, anther cells not covered by the flat-topped, rounded or pointed connectives" (Sinclair, 1955: 178). Engler and Diels use this character well below tribal level, to key out genera. Hutchinson characterizes the connective in Uvarieae as "almost invariably truncate and hiding the loculi"; in both the other tribes, viz., Miliuseae and Unoneae, he considers this character as inconstant.

Fries points out that stamen shape may vary even within a genus, for instance in *Annona* where the connective shield varies from large to strongly reduced, and *Duguetia* where some species lack the connective shield typical for the genus.

Placentation and the Number of Ovules

In Annonaceae, both lateral (marginal) and basal placentation are found. Monodoroideae, with numerous parietal ovules, are aberrant in this regard. Contradictory views as to the morphological nature of the fruit of Monodoroideae have already been mentioned in the first section. At present, the increasingly popular opinion seems to be that this fruit consists of a single carpel with laminally attached ovules (van Setten, pers. comm.).

Most authors use the number of ovules per carpel as a differentiating character at the genus level or below. All authors seem to admit that lateral and basal placentation may occur together in the same taxon and, thus are of little general taxonomic value. In this context it should be remarked that in actual practice it is often hard to determine whether a single ovule that one observes at the bottom of the ovary is basal or lateral! Uvarieae and Unoneae in the sense of Fries are also heterogeneous in this respect. Fries (1959), however, uses placentation to define generic groups, with the exception of the *Artabotrys* and *Asimina* groups. Yet Fries admits, giving *Ephedranthus* and *Unonopsis,* among others, as examples, that it is often difficult to determine if a basal ovule should not rather be taken as a derived condition from an ancestral form with lateral ovule(s), and that ". . . Gattungen mit basalen oder parietalen Samen vom phylogenetischen Gesichtspunkt oft in eine und dieselbe Gattungsgruppe aufgenommen werden können" (Fries, 1959: 42).

Inflorescence Position

This character, curiously enough, drew little attention from authors prior to Fries. Inflorescence position and structure is discussed at some length in two papers by Fries (1919,

1959), to which the reader is referred. Flowers in Annonaceae appear singly or in monochasial structures. These originate from leaf axils or from the internode (leaf-opposed, supra-axillary, infra-axillary). Both conditions may be explained as derivations from a terminal anthotaxis.

The character, though variable at tribal level, is usually very constant at the level of Fries's groups, and plays an important role in keying out groups, particularly in Uvarieae. Only in a few genera are both character states found, such as in *Anaxagorea* (Maas and Westra, 1984, 1985).

Phyllotaxis

One of the distinct features of Annonaceae is the phyllotaxis: all genera (except for *Tetrameranthus*) are characterized by leaves in two rows (1/2). As already mentioned in the section *Number of Petals,* this genus is also exceptional in having 4-merous perianth whorls. There are additional characters which place that genus in an isolated position within the family and which need not be mentioned in detail here. The reader is referred to Fries (1939, 1959), Westra (1985), and Koek-Noorman et al. (1988).

Apart from *Tetrameranthus,* there are few reported cases of a phyllotaxis other than 1/2. Treub (1883) described leaves in three rows on branches in certain species of *Artabotrys.* The same occurs possibly in *Annona crotonifolia* (Fries, 1959: 8). The latter two genera are unrelated; moreover, both normally have leaves in two rows. Wagner's (1906) report of a 2/5 phyllotaxis in *Disepalum anomalum* is based on a wrong assumption from herbarium study of flowering shoots, as is discussed by Johnson (in press).

Indument

Most genera in Annonaceae, if not glabrous, possess simple trichomes. Stellate trichomes have been reported in several genera by now. A few genera have a very distinctive indument of scales.

Hutchinson (1964: 73, 76) suggests that the majority of genera (seven) with stellate or lepidote indument is found in Uvarieae. Only four genera remain in other tribes. This is definitely not true. Generic descriptions by Fries (1959) show that stellate hairs occur in at least four more genera beside those mentioned by Hutchinson. These genera are all classified by Hutchinson in tribes other than Uvarieae.

In Fries's classification, genera with stellate and/or lepidote indument are found in six groups. Four genera out of these are mentioned as heterogeneous in the sense that they contain both species with simple and with stellate hairs.

Although it is possible that stellate trichomes may emerge in more genera than are now known to possess them, it seems unlikely that this feature is ever going to play an important role on the tribal level.

Conclusion

The foregoing has illustrated clearly that there is no consensus among previous authors on classification of the Annonaceae. It hardly seems possible to indicate which one of the classifications is the best. Altogether there seems to be agreement most on Uvarieae, although size and contents of this tribe vary somewhat.

There is much confusion about relationships among genera that are grouped under Unoneae by Fries, as a result of apparent lack of correlation of characters. Whether focus is on reduction (suppression) of one whorl of petals, or variation in shapes of petals, or variation in shapes of stamens, etc., in each case the resulting classification is a different one. It then largely becomes a matter of taste which character one wants to assign the most value, and, consequently, what classification one will prefer. All authors have had to admit, in one way or another, that their classificatory schemes were unsatisfactory.

The seven classifications mentioned in the introduction are all based, for the most part,

on floral characters listed there (nos. 1–8). Much less attention was paid to inflorescence structure and vegetative characters (nos. 9–11). Fruits and seeds also have been much neglected. The seeming uniformity of fruits and seeds as well as their paucity in older collections may account for this.

Since Fries and Hutchinson published their last classifications in the late 1950's and early 1960's, respectively, much new material has been brought in. More complete datasets may now be available for taxa still very incompletely known 25 years ago. This applies to fruits not in the least. Furthermore, after Fries's integral treatment, nine new genera were described. One of the urgent studies needed now is a worldwide survey of fruit and seed characters. The greatly increased number of collections, however, has also brought much new data on flowers and, or course, the other structures mentioned in the foregoing sections as well. This makes the need for a modern worldwide survey of floral characters equally important.

As part of the recent research activities by the Annonaceae Project group in Utrecht (Maas, 1983, 1984), two publications will appear in this context. One will feature a descriptive study of flowers of Annonaceous genera from the whole world (van Heusden, in prep.). The second one will provide descriptions and character analyses of fruits and seeds of Annonaceae on the generic level also worldwide (van Setten, in prep.).

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