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The subfamilial and tribal classification of the family Asclepiadaceae

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A modified classification of the family Asclepiadaceae R. Br. *s.s.* into three tribes — Secamoneae, Asclepiadeae *s.l.* and Stapelieae *s.l.* — is proposed. The position of attachment of the caudicles to the pollinia is suggested as a criterion for defining the erect and pendulous stature of the pollinaria. The concept of the transverse stature of pollinaria has been abandoned. In addition to the stature of the pollinaria, the morphology of the anther sacs (whether or not embedded in the tissue of the anther wings) and the position of anther wings with respect to the anther sacs are suggested as supplementary characters for tribal classification of the family. The characters of the gynoecium, particularly the presence or absence of true styles and the sharp constriction between stigma-head and ovaries (i.e. clavuncular morphology) have also been suggested as useful in differentiating Asclepiadeae *s.l.* and Stapelieae *s.l.*, along with the stature of the pollinaria. The circumscription of Asclepiadeae is emended to accommodate taxa of the former tribe Gonolobeae as a subtribe. The circumscription of Stapelieae has been retained in a wider sense, as suggested by Decaisne (1844). The tribes Fockeeae Kunze, Liede & Meve (1994), Marsdenieae Benth. (1876), Ceropegieae Benth. (1876), and Stapelieae *s.s. sensu* Benth. (1876; non Decne., 1844) have been relegated to subtribe status in the tribe Stapelieae Decne. (1844). Homology of the different parts of the gynoecium in the Asclepiadeae (*s.l.*) with those in the Stapelieae (*s.l.*) has been drawn. Segments of the style have been distinguished into 'true style' and 'pseudostyle', the former as parts of the ovary segment in development, the latter as stigma segment in development. The genus *Tylophora* R. Br. which was formerly treated under Stapelieae Decne. has been transferred to Asclepiadeae based on the morphology of the pollinaria, gynoecium and seed coat architecture.

ADDITIONAL KEY WORDS:—gynoecium – morphology – pollinaria – seed – stamen – *Tylophora*.

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INTRODUCTION

In 1810, Robert Brown read a paper to the Wernerian Natural History Society in which he suggested segregating several members of the family Apocynaceae A. L. Jussieu, in which the pollen grains are collected in specialized structures called translators, into a separate family Asclepiadaceae. In erecting the new family, he also suggested natural groupings of the included genera thus providing a prototype of the modern infrafamilial, supra generic classifactory framework for the family (Swarupanandan, 1985).

In the 180 years since Brown's original proposal, there have not been many significant changes in the natural groupings of the genera of the family (Rosatti, 1989; Sundell, 1980). On the other hand, phylogeny of some of these groups has been questioned repeatedly (Schlechter, 1905, 1924; Hutchinson, 1959, 1969), the rank of some of them in the infrafamilial hierarchical system was often elevated (Schlechter, 1905, 1924; Bullock, 1956) and some were further subdivided (Dumortier, 1829; Don, 1838; Decaisne, 1844). Floral morphological, palynological and phytochemical evidence further contributed to these considerations (Safwat, 1962; Puri & Shiam, 1966; Huber, 1973, 1983; Nilsson, Endress & Grafstrom, 1993). Our present interest is to document further information on hitherto unconsidered aspects of the morphology of the androecium, gynoecium, fruit and seed, and to look at the implications of these characters in the infrafamilial classification of the family, especially at the subfamilial and tribal levels.

HISTORY OF THE CLASSIFICATION OF THE FAMILY

When aiming to improve the stability of supra generic names within the family, Sundell (1980) prepared an exhaustive inventory of available names within the family. An excellent review of the history of suprageneric classification of the family has been given by Rosatti (1989) and the more recent concepts about subfamilial and tribal categories recognized under the family are summarized by Bruyns & Forster (1991). For easy reference, the infrafamilal classification systems by various authors are provided in Table 1.

TABLE 1. A comparison of the classification schemes of different authors of the family Asclepiadaceae R. Br. *s.l.*

Decaisne (1844)	Bentham (1876)	Hooker (1883)	Schumann (1895)	Bruyns & Forster (1991)
	Suborder Periploceae	Suborder Periploceae	Subfamily Periplocoideae	Subfamily Periplocoideae
Periploceae	Periploceae	Periploceae	Periploceae	Periploceae
				Subfamily Secamonoideae
				Secamoneae
	Suborder Euasclepiadeae[1]	Suborder Euasclepiadeae[1]	Subfamily Asclepiadoideae	Subfamily Asclepiadoideae
Secamoneae	Secamoneae	Secamoneae	Secamoneae	
Cynancheae[2]	Cynancheae[2]	Cynancheae[2]	Asclepiadeae	Asclepiadeae
Gonolobeae	Gonolobeae	...[3]	Gonolobeae	Gonolobeae
	Marsdenieae	Marsdenieae		Marsdenieae
			Tylophoreae	
Stapelieae[4]	Ceropegieae			
		Ceropegieae[5]		
	Stapelieae			Stapelieae[6]

[1] Nomenclaturally correct name is subfamily Asclepiadoideae as it includes the genus *Asclepias*, the type genus of the family Asclepiadaceae.

[2] Nomenclaturally correct name is Asclepiadeae as it includes the genus *Asclepias*, the type genus of the family Asclepiadaceae.

[3] Hooker studied only the Indian elements: hence the absence of Gonolobeae in his classification.

[4] Stapelieae Decaisne (1844) encompasses taxa of the tribes Marsdenieae, Ceropegieae and Stapelieae of Bentham (1876).

[5] The circumscription of Ceropegieae of Hooker (1883) is different from that of Decaisne (1844) and Bentham (1876) as it includes the taxa of Stapelieae of Bentham too.

[6] Stapelieae *sensu* Bruyns & Forster (1991) is equivalent to Ceropegieae of Hooker (1883) in circumscription.

Robert Brown (1810) recognized three groups of genera under the family Asclepiadaceae R. Br. *s.l.* (1) Periploceae, characterized by granular pollen collected in solitary cornucopia-shaped pollen carriers, (2) Asclepiadeae Verae (true asclepiads), characterized by waxy pollinia and (3) an unnamed group with a single genus, *Secamone* R. Br. With the crystallization of the concepts of infra familial ranks, the Periploceae subsequently received the rank of a tribe (Periploceae Don, 1838) and subfamily (Periplocoideae Endlicher, 1838). Early twentieth century botanists argued that the Periplocoideae are phyletically more close to the Apocynaceae and therefore ascribed a separate family status (Periplocaceae Schlechter, 1905, 1924); this view was further supported by Hutchinson (1959, 1969) and more recently by Huber (1973, 1983). Thus the family Asclepiadaceae usually appears in most contemporary literature *sensu stricto*, i.e. excluding Periplocoideae, in the sense of the Asclepiadeae Verae plus the genus *Secamone* of R. Brown. The conflict over whether periplocoid genera should be given a subfamilial or a separate familial status is very much alive today (cf. Bruyns & Forster, 1991).

The unnamed group recognized by Brown (1810) comprising the single genus *Secamone* R. Br. was named Secamoneae by Reichenbach (1828) and was subsequently elevated to the rank of a tribe (Don, 1838) and subfamily (Subfam. Secamonoideae Endlicher, 1838). In general, the Secamoneae is considered as a tribe (Decaisne, 1844; Bentham, 1876; Hooker, 1883; Schumann, 1895), while

Bullock (1956), Puri & Shiam (1962) and Safwat (1962) supported the subfamily rank.

With the separation of Secamonoideae, the Asclepiadeae Verae of R. Brown thus circumscribe into a subfamily, Asclepiadoideae Meisner (1838; as 'Asclepiadeae'). Endlicher (1838) recognized three tribes within this subfamily — Cynancheae (correct name: Asclepiadeae). Gonolobeae and Pergularieae (correct name: Stapelieae Decne. 1844).

The integrity of Asclepiadeae remains undebated, while the Gonolobeae has been argued as an artificial assemblage, with many genera deserving transfer to Tylophoreae Schumann (correct name: Stapelieae Decne., 1844, *s.l.*) (Good, 1952).

Decaisne (1842) segregated the genus *Ceropegia* L. (and its allies?) from the Pergularieae Endl. (1838) (correct name: Stapelieae Decne., 1844), to constitute a separate tribe, Ceropegieae, although he did not recognize this tribe in his later publication (Decaisne, 1844). Bentham (1868) accepted Decaisne's (1842) tribe Ceropegieae, and added a further tribe to the list, Marsdenieae, by separating *Marsdenia* R. Br. and its allies from Stapelieae Decne. (1844), thus circumscribing the latter within the narrow sense (for nomenclature of the tribal names see: Swarupanandan, 1983; Bruyns & Forster, 1991).

Hooker (1883), while monographing the Indian Asclepiadaceae, found that the differences between the Ceropegieae and Stapelieae Decne., *s.s.* (*sensu* Bentham, 1868) are not as clear as stated by Bentham (1876) and therefore amalgamated them under his Ceropegieae, which according to the nomenclatural rules should bear the name Stapelieae Decne. (1844). More recently Bruyns & Forster (1991) also held this view. Schumann (1895) on the other hand, amalgamated all three tribes Marsdenieae, Ceropegieae and Stapelieae under his tribe Tylophoreae, which again should bear the name Stapelieae Decne., *s.l.*

To the list of tribal categories segregated from Stapelieae Decne. *s.l.*, Kunze, Meve & Liede (1994) added a third, Fockeeae, comprising two genera separated from Marsdenieae Benth. (1868) *viz.*, *Fockea* Endl. and *Cibirhiza* Bruyns.

Whether Stapelieae Decne. *s.l.* (1844) is to be considered as consisting of a single tribe, or several tribes, requires consideration.

In summary, eight natural groups of genera are recognized within the family Asclepiadaceae R. Br. (*s.l.*) at tribal rank and above: Periploceae/Periplocoideae/ Periplocaceae, Secamoneae/Secamonoideae, Asclepiadeae, Gonolobeae, Fockeeae, Marsdenieae, Ceropegieae and Stapelieae *s.s.* (cf. Table 2). In contemporary literature, some of these have been considered at familial or subfamilial ranks, while a few others have been considered not deserving any tribal status.

CHARACTER EVALUATION FOR SUPRAGENERIC CLASSIFICATION

Androecium

Within the Asclepiadaceae *s.l.* the androecium and its associated traits have been the major criteria used for infra familial classification.

Adnation of androecium and gynoecium

In the Periplocaceae the staminal filaments are invariably free and the anthers are

TABLE 2. Taxonomic categories available within the family Asclepiadaceae R.Br. *s.l.* and the characters by which they are distinguished

Taxonomic categories	Diagnostic characters
Family Asclepiadaceae R.Br. *s.l.*	Pollen grains collected in specialized pollen-carriers
Family Periplocaceae Schltr./ Subfamily Periplocoideae Endl./ Tribe Periploceae Don	Anther 4-celled, translator spoon-shaped
Family Asclepiadaceae R.Br. *s.s.*/ Subfamily Asclepiadoideae *s.l.*	Anther 4- or 2- celled, translator longitudinally bipartite
Subfamily Secamonoideae Endl./ Tribe Secamoneae Don	Anther 4-celled, translator devoid of caudicles
Subfamily Asclepiadoideae	Anther 2-celled, translator generally with caudicles, rarely absent
Tribe Stapelieae Decne. *s.l.*	Pollinaria erect
Tr. Fockeeae Kunze, Liede & Meve	Translator devoid of caudicles
Tr. Marsdenieae Benth.	Anther with a membranous tip, pollinia devoid of a pellucid margin/tip
Tr. Ceropegieae Benth.	Anther devoid of a membranous tip, pollinia with a pellucid margin/tip, leafy twiners with cylindric stems
Tr. Stapelieae Decne. *s.s.*	Anther devoid of a membranous tip, pollinia with pellucid margin/tip, stems succulent, leaves often reduced to scales
Tr. Asclepiadeae	Pollinaria pendulous
Tr. Gonolobeae Don	Pollinaria transverse

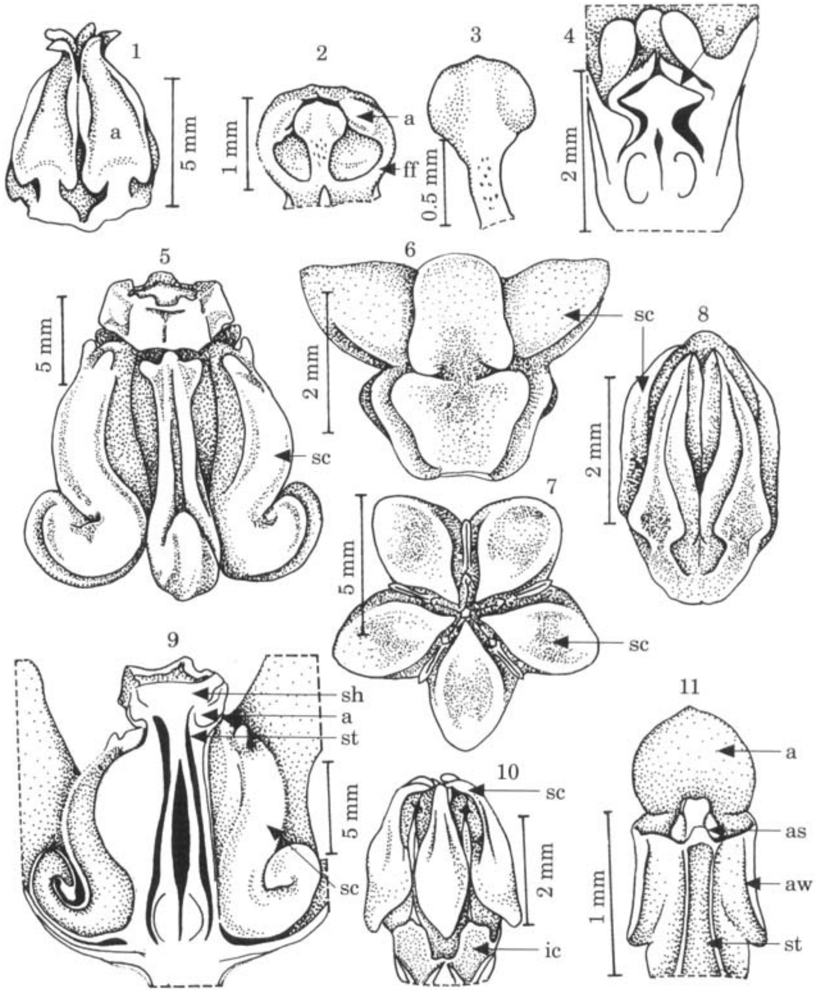
connate by their tips (Figs 1–3) but are in no way adnate to the stigma-head (Fig. 4). In the Asclepiadaceae *s.s.*, the staminal filaments are united to form a staminal tube covering the gynoecium (Fig. 9), and the anthers are free from one another (Fig. 11) but adnate to the stigma-head by their adaxial surface, just at the base of the anther sacs by the connective tissue (Figs 9, 11). Thus the stamens and the gynoecium together form a compound unit, usually called the '*gynostegium*' (Figs 5–10). This structural difference of the androecium was used as a criterion for the separation of the Periplocaceae from the Asclepiadaceae *s.s.* (cf Hutchinson, 1959).

Staminal corona

The stamens in the Asclepiadaceae *s.s.* are provided with various elaborations of the filament, anther and connective tissue collectively referred to as a *staminal corona* (cf. Woodson, 1941). The filaments carry appendages on their back which form a *gynostegial corona*; this is sometimes very elaborate and can contain an additional row of interstaminal corona (Kunze, 1982; Liede & Kunze, 1993; Fig. 10). The anther is provided with a sterile appendage on either margin, the *anther wings*, and the anther tip is extended to form a flat *membranous appendage* (Fig. 11) (cf. Woodson, 1941). All the above structures are absent from the Periplocaceae, except the apical appendage of the anther. This character difference of the two families is also not debated (*cf.* Schumann, 1895; Hutchinson, 1959). The innumerable variety of staminal corona exhibited by the Asclepiadaceae *s.s.* does not, however, seem to have any taxonomic importance above generic level (Woodson, 1941; Swarupanandan, 1985).

Anther tip

Bentham (1876) distinguished the Marsdenieae from the Ceropegieae and Stapelieae by the presence of two characters, the membranous apical appendage of the anther and the absence of pellucid margins for the pollinaria (Bruyns & Forster, 1991: pollimaria = pollimia + translator; cf. Bookman, 1981). In evaluating the



Figures 1–11. Androecium in Periplocaceae and Asclepiadaceae *s.s.* Figs 1–4. Periplocaceae. Figs 1, 2. The free but connivant stamens forming a cone around the gynoecium. Fig. 1. *Cryptostegia madagascariensis* Bojer Fig. 2. *Hemidesmus indicus* (L.) R. Br. Note the free staminal filaments here. Fig. 3. A stamen in *Hemidesmus indicus* (L.) R. Br. Fig. 4. Longitudinal section of the flower of *Cryptolepis buchananii* Roemer & Schultes showing the absence of fusion between the anthers and stigma-head. Figs 5–11. Asclepiadaceae *s.s.* Figs 5–8. Gynostegia in Asclepiadaceae *s.s.* Fig. 5. *Calotropis gigantea* (L.) R. Br. Fig. 6. *Wattakaka volubilis* (L. f.) Stapf. Fig. 7. *Hoya retusa* Dalz. Fig. 8. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 9. Longitudinal section of the flower of *Calotropis gigantea* showing the staminal tube and the adnation of the anther to the stigma-head. Fig. 10. Gynostegium in *Pergularia daemia* (Forsskal) Chiov. In many asclepiads, in addition to a row of staminal coronal scales, there is an additional row of interstaminal coronal scales, as seen here. Fig. 11. Adaxial view of a stamen in *Cynanchum tunicatum* (Retz.) Alston showing the membranous apical appendage and the anther wings. a - anther; ap - apical appendage of the anther; as - anther sac; aw - anther wing; ff - free filament; ic - interstaminal corona; s - stamen; sc - staminal corona; sh - stigma-head; st - staminal tube.

value of the apical appendage of the anther as a character in tribal classification, it will be worthwhile to make a survey of its occurrence in the various suprageneric categories within the family.

In the so-called Periplocaceae, appendages are largely extensions of the connective tissue (Figs 12, 13); in some cases they are differentiated as a separate subulate or cylindrical structure (Fig. 14). In the Secamoneae small connectival extensions are seen (Figs 15, 16). Members of the Asclepiadeae have a prominent, flat and foliaceous extension of the anther tip which is often transformed into a distinct structure, being separated from the anther proper by a constriction (Figs 17–21). The same morphology of the anther tip holds true for the Gonolobeae too (Kunze, 1995). Kunze has described the constriction between the anther proper and the apical appendage as 'transverse slit'.

In the majority of the Marsdenieae Benth. the membranous anther tip is also foliaceous but unlike Asclepiadeae they are continuous with the staminal phyllome and generally not separated by a constriction to form a distinct structure (Figs 22, 23), except in rare cases. The closely related Ceropegieae and Stapelieae as a rule lack an apical appendage in the anther (Figs 24–26) although this is not universal. Two species of *Caralluma (C. sinaica* (Decne.) Benth. and *C. mireillae* Lavranos) belonging to the Stapelieae possess the membranous anther tip (Bruyns, 1987; Bruyns & Forster, 1991). Examination of the anther tip under low magnification in species of *Ceropegia* L. (*C. candelabrum* L.) belonging to the Ceropegieae shows the presence of rudiments of the membranous apical appendage which is elaborate in the Marsdenieae (Figs 24, 25).

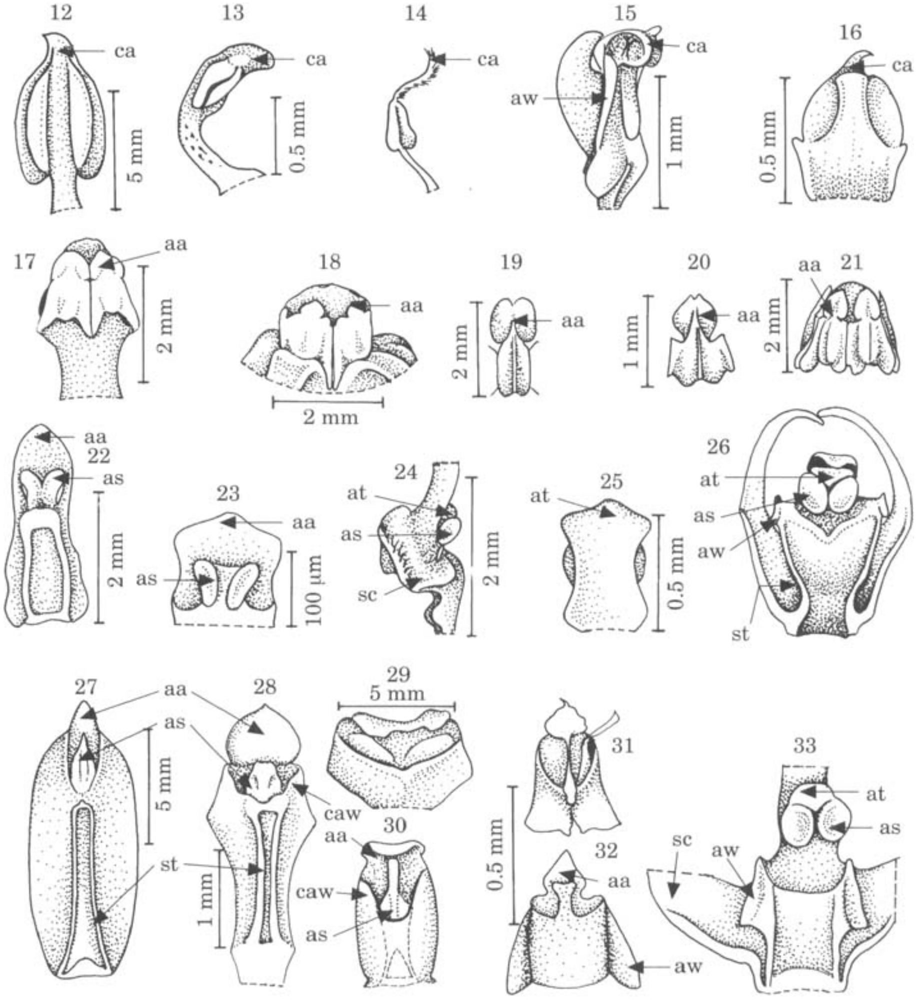
The presence/absence of apical appendages of the anther for tribal classification appears to be rather doubtful. Because of the overlap of the character state among members of Ceropegieae Benth. and Stapelieae Decne. *s.s*, the two were amalgamated to constitute a single tribe (Stapelieae Decne. *s.l.*) by Hooker (1883) and Bruyns & Forster (1991). Similarity of the apical appendage in Asclepiadeae and Gonolobeae also supports this view.

Anther cells

The number of microsporangia in the stamen has been an important criterion employed in the classification of the family *sensu lato*. The genera in Periplocaceae are easily distinguished by their 4-celled anther from the rest of the Asclepiadaceae, except for the Secamoneae. The Periplocaceae stand out from the latter because they possess a spoon-shaped translator.

Within the Asclepiadaceae *s.s.* the tribe Secamoneae is unique with its 4-celled anther, while the rest of the family possesses 2-celled anthers. Truly intermediate forms between the 4-celled and 2-celled anther have not yet been documented within the Asclepiadaceae, and the naturalness of the tribe Secamoneae is generally accepted.

The 4-celled anther is considered to be plesiomorphic and the 2-celled anther advanced, in all angiosperms and in the Asclepiadaceae (Stebbins, 1974). Although typical intermediaries between the 4-celled and 2-celled anther are wanting, the differing size of the pollinial pairs in one and the same pollinaria in some species of *Secamone* R. Br. (*S. attenuifolia* Goyder; Fig. 52) signifies the continuity of the two traits.



Figures 12–33.Androecium in Periplocaceae and Asclepiadaceae *s.s.*, showing the differences in the morphology of anther sacs and the apical appendage of the anther. Figs 12–14. Stamens in Periplocaceae showing the anther tip. Fig. 12. *Cryptostegia madagascariensis* Bojer. Fig. 13. *Hemidesmus indicus* (L.) R. Br. Fig. 14. *Pentamera sumatrana* Blume (redrawn from Schumann, 1895). Figs 15, 16. Stamen in Secamoneae (*Secamone emetica* R. Br.). Fig. 15. Lateral aspect of a stamen. Fig. 16. Dorsal aspect of the anther showing the apical appendage. Figs 17–21. Apical appendage of the anther in Asclepiadeae. Fig. 17. Gynostegium in *Cynanchum tunicatum* (Retz.) Alston showing the apical appendage of the anther. Fig. 18. Apex of the gynostegium in *Pergularia daemia* (Forsskal) Chiov. showing the apical appendage of the anther (the tip of the staminal coronal scales is forced down to expose the gynostegium proper). Fig. 19. Anther in *Schistogyne mosenii* (Malme) T. Meyer (redrawn from Meyer, 1950). Fig. 20. Anther in *Widgrenia corymbosa* Malme (redrawn from Meyer, 1947). Fig. 21. Gynostegium in *Funastrum flavum* (Decne.) Malme showing the apical appendage of the anther (redrawn from Meyer, 1943). Figs 22–26. Apical appendage of the anther in Stapelieae Decne. *s.l.* (i.e. incl. tribes Marsdenieae, Ceropegieae and Stapelieae *s. s.*). Fig. 22. Ventral aspect of a stamen in *Marsdenia tenacissima* (Roxb.) Moon. Fig. 23. Ventral aspect of the anther tip in *Gymnema sylvestre* (Retz.) R. Br. *ex* Schultes. Figs 24, 25. *Ceropegia candelabrum* L. Fig. 24. Lateral aspect of the stamen showing the anther tip; the tip of the staminal coronal scale is not shown. Fig. 25. Dorsal aspect of the anther. Fig. 26. Ventral aspect of a stamen and the corresponding coronal scales (the obsolete anther tip is still visible) in *Caralluma adscendens* (Roxb.) Haw. var. *geniculata* Grav. *et* Mayur. Figs 27–32. Ventral aspect of stamens/anthers in Asclepiadeae. Fig. 27. Stamen of *Holostemma annulare* (Roxb.) Schumann. Fig. 28. Stamen of *Cynanchum callialata* Buch.-Ham. *ex* Wight & Arn. Fig. 29. Anther of *Calotropis gigantea* (L.) R. Br. Fig. 30. Anther of *Asclepias curassavica* L. Fig. 31. Anther of *Asclepias subulata* Decne. (redrawn from Safwat, 1962). Fig. 32. Anther of *Tassadia valioi* Fontella (redrawn from Pereira, 1977). Fig. 33. Stapelieae *s.l.*: vertical aspect of a stamen and the corresponding gynostegial coronal scales (the tip of the staminal coronal scale has been trimmed off in *Ceropegia juncea* Roxb.) aa - apical appendage (of the anther); as - anther sac; at - anther tip; aw - anther wing; ca - connectival appendage; caw - collar formed by the anther wings; sc - staminal corona; st - staminal tube.

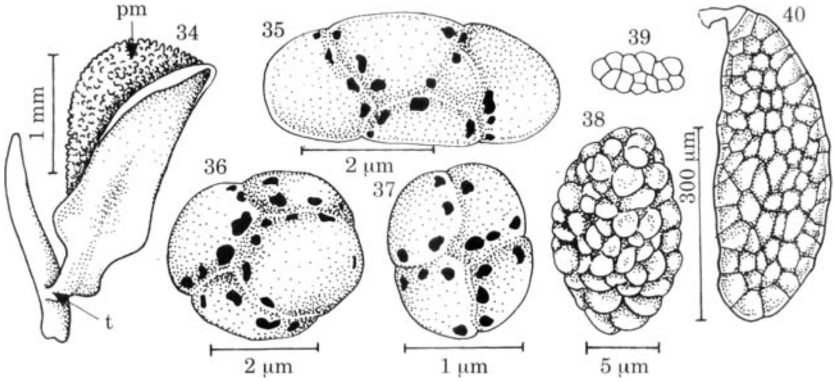
Anther wings

Some 20 years ago Huber (1973) documented a remarkable feature of the microsporangia in the Asclepiadaceae. He pointed out that in the Asclepiadeae the anther sacs are embedded in the tissue of the basal portion of the anther and in the rest (i.e. Stapelieae Decne.) embedded in the apical portion of the anther. This observation deserves attention.

The anther sacs (= anther cells) in the Asclepiadeae are embedded in the somewhat horny tissue of the anther wings, which form a collar around the apical portion of the anther sacs (Figs 27–32). For this reason, rupture of the anther sacs in this tribe is possible only apically or apico-laterally and hence the pollinaria have almost entirely become pendulous. In the Stapelieae (*s.l.*), the anther sacs are not embedded in the tissue of the anther wings as the anther wings are generally found below the level of the anther sacs (Fig. 26).

The anther wings are generally regarded as sterile outer anther sacs (Demetter, 1922; Huber, 1973). Members of the subfamily Apocynoideae of Apocynaceae, which are indeed primitive with respect to the Asclepiadaceae (due to the absence of gynostegium and pollinaria and the presence of 4-celled anther) also show the presence of anther wings, as in Asclepiadaceae. Size difference of the pollinial pairs in species of *Secamone* R. Br. (tribe Secamoneae; as explained in a previous section) is also an indication of the sterilization of the anther sacs that culminated in 2-celled anther in the rest of the Asclepiadaceae.

Whether the anther wings represent structures homologous to the outer anther sacs (Demetter, 1922) or structures *de novo*, their relative position in the stamen, with respect to the fertile anther sacs is characteristically uniform in all the members of the tribes, Asclepiadeae *s.l.* and Stapelieae *s.l.* The difference in the relative position of the anther wings in the two tribes remains a matter for further investigation. Despite the above fact, the morphological difference of the fertile anther sacs is an important criterion useful for tribal classification.



Figures 34–40. Pollen morphology in Periplocaceae and Asclepiadaceae. *s.s.* Figs 34–38. Periplocaceae. Fig. 34. Loose pollen mass in *Cryptolepis buchananii* Roemer & Schultes collected in the spoon shaped translator. Figs 35–37. Rhomboidal, tetrahedral and tetragonal pollen tetrads in *Raphionacme hirsuta* (E. Meyer) R.A. Dyer *ex* Phill. (redrawn from Nilsson, Endress & Grafstrom, 1993). Fig. 38. Pollen tetrads forming a loose massula in *Hemidesmus indicus* (L.) R. Br. (redrawn from Nilsson, Endress & Grafstrom, 1993). Figs 39, 40. Pollinia in Asclepiadaceae *s.s.* Fig. 39. Pollinium in Secamoneae (*Secamone alpinii* Schultes; redrawn from Kunze, 1993). Fig. 40. Pollinium in Asclepiadoideae (*Marsdenia tenacissima* (Roxb.) Moon). pm - pollen mass; t - translator.

Pollen/pollinia

In the Periplocaceae, the pollen grains on shedding are in tetrads of various kinds (Figs 35–37) and with an exine. In some members, the pollen tetrads are agglutinated to form loose pollen massula (*Hemidesmus indicus* (L.) R. Br.; Fig. 38). In the Asclepiadaceae, the pollen grains lack an exine. The pollen grains of each anther cell are united by a common wall, the *pollinial pellicle*, which is tapetal in origin (Vijayaraghavan & Shukla, 1976). This common wall has no homologue in the Periplocaceae and has been pointed out to be one of the major reasons for separating the latter family from the Asclepiadaceae *s.s.* (Hutchinson, 1959).

Woodson (1941) considered the excavated or depressed (concave) surface of the pollinia (Figs 102, 104) as the criterion for distinguishing the Gonolobeae from the rest. In fact, species of *Calotropis* R. Br. (Asclepiadeae; Fig. 70) and *Hoya* R. Br. (Stapelieae *s.l.*; Fig. 79) also show this character thus making it less reliable for suprageneric classification.

Within the Stapelieae *s.l.* most xerophytes have developed sterile pellucid margins or apices ('germinating mouth' of Schill & Jackel, 1978) for the pollinia (Figs 56, 61) while this is generally absent from the Asclepiadeae and Gonolobeae. Bentham (1876) used this character to differentiate the Ceropegieae and Stapelieae from the Marsdenieae; Marsdenieae are devoid of the pellucid tip/margin. However, genera like *Leptadenia* R. Br. and *Heterostemma* Wight & Arn. in the Marsdenieae Benth. have sterile pellucid margins for their pollinia (Bentham, 1876; Swarupanandan, Sasidharan & Mangaly, 1989), casting doubts on the value of the character for suprageneric classification.

Translator

The translator, although a part of the stigma-head in origin, is connected to the pollinia to become a single unit at maturity, and therefore is treated here.

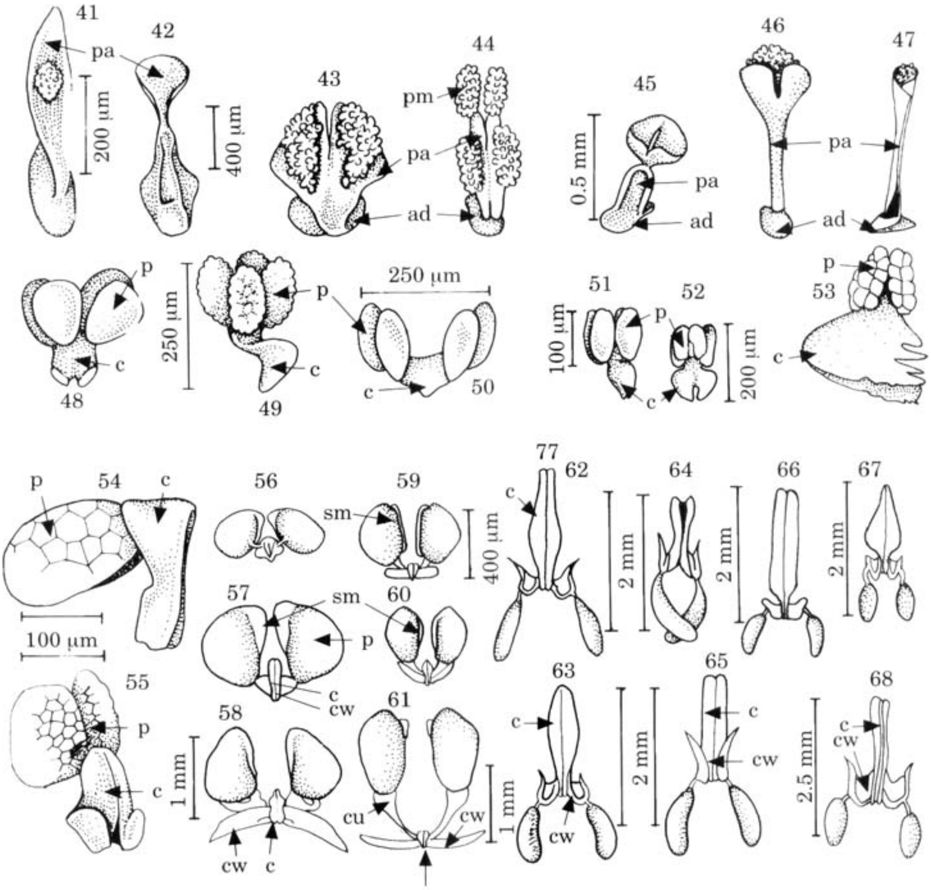
Brown (1810), when he distinguished Asclepiadeae Verae (= Asclepiadaceae R. Br. *s.s.*) from Periploceae (= Periplocaceae Schlecht.), the character that he used in segregating the two was the morphology of the translator. In the Periplocaceae, the translator apparatus invariably has a sticky adhesive disc, to which the pollen collecting arm - the spoon or cornucopia - is attached (Figs 41–47). In the Asclepiadaceae *s.s.*, the translator usually has a hard corpuscle ('corpusculum' of Corry, 1883; cf. Bookman, 1981) and two distinct 'caudicles' to which the pollinia are attached (Figs 56–68). Although homology of the periplocacean and asclepiadacean translators is often speculated (Demetter, 1922; Safwat, 1962; Schick, 1982), recent ontogenetic findings make this deduction untenable (for details see Kunze, 1993: 120). Whether the Periploceae is treated as a tribe, a subfamily or a distinct family, structural differences of the translator have been used as a diagnostic character for its separation from the rest without dissent.

Corpuscle

The corpuscle in Stapelieae, unlike the primitive lianous species, has developed wing-like appendages to which the caudicles are attached (Figs 56–67). Winged corpuscles also occur within the Asclepiadeae, e.g. in *Oxypetalum* R. Br. and *Calostigma* Decne. (Figs 64–68), and do not seem to be of any taxonomic value for suprageneric classification.

Caudicles

Within the Asclepiadaceae, absence of caudicles distinguishes the Secamoneae and Fockeeae from the rest (Figs 54, 55). The possibility of this character being



Figures 41–68. Differences in the morphology of the translators in Periplocaceae and Asclepiadaceae. Figs 41–47. Periplocaceae. Fig. 41. *Cryptolepis buchananii* Roemer & Schultes. Fig. 42. *Periploca gracea* (redrawn from Kunze, 1993). Fig. 43. *Myriopteron paniculatum* Griffith (redrawn from Griffith, 1854). Fig. 44. *Streptocaulon griffithi* Hook. f. (redrawn from Griffith, 1854). Fig. 45. *Hemidesmus indicus* (L.) R. Br. Fig. 46. *Finlaysonia obovata* Wallich (redrawn from Griffith, 1854). Fig. 47. *Camptocarpus* sp. (redrawn from Kunze, 1993). Figs 48–68. Translators and pollinaria (= pollinia + translator; cf. Bookman, 1981) in Asclepiadaceae. Figs 48–53. Secamoneae. Fig. 48. *Toxocarpus roxburghii* Wight & Arn. (redrawn from Griffith, 1854). Fig. 49. *Secamone emetica* R. Br. Fig. 50. *Toxocarpus kleinii* Wight & Arn. Fig. 51. *Secamone leonensis* (Scott Elliot) N.E.Br. (redrawn from Goyder, 1992). Fig. 52. *Secamone attenuifolia* Goyder (redrawn from Goyder, 1992). Fig. 53. *Secamone alpinii* Schultes (redrawn from Kunze, 1993). Figs 54, 55. Tr. Fockeeae. Fig. 54. *Cibirhiza albersiana* Kunze, Meve & Liede (redrawn from Kunze, 1994). Fig. 55. *Fockea sinuata* (E. Meyer) Druce (redrawn from Kunze, 1994). Figs 56–61. Tr. Stapelieae *s.l.* showing the wing-like appendages of the corpuscles and sterile pellucid margins of the pollinia. Fig. 56. *Ceropegia elegans* Wallich. Fig. 57. *Brachystelma petraceum* Fourn. (redrawn from Dyer, 1977c). Fig. 58. *Stapelia grandiflora* Wight. Fig. 59. *Trichocaulon mossamedense* L.C. Leach (redrawn from Dyer, 1977a): Fig. 60. *Stapelianthus hardyi* Lavranos (redrawn from Dyer, 1977b). Fig. 61. *Duvalia sulcata* N.E. Br. (redrawn from Dyer, 1977a). Figs 62–68. Asclepiadeae (redrawn from Schumann, 1895). Fig. 62. *Oxypetalum coalitum* Fourn. Fig. 63. *O. lanatum* Decne. Fig. 64. *O. pannosum* Decne. Fig. 65. *O. erectum* Mart. & Zucc. Fig. 66. *Calostigma insigne* Decne. Fig. 67. *Oxypetalum minarum* Fourn. Fig. 68. *O. arachnoideum* Fourn. ad - adhesive disc; c - corpusculum; cu - caudicle; cw - corpuscular wing; p - pollinium; pa - pollen collecting arm; pm - pollen mass; sm - sterile margin (of the pollinium).

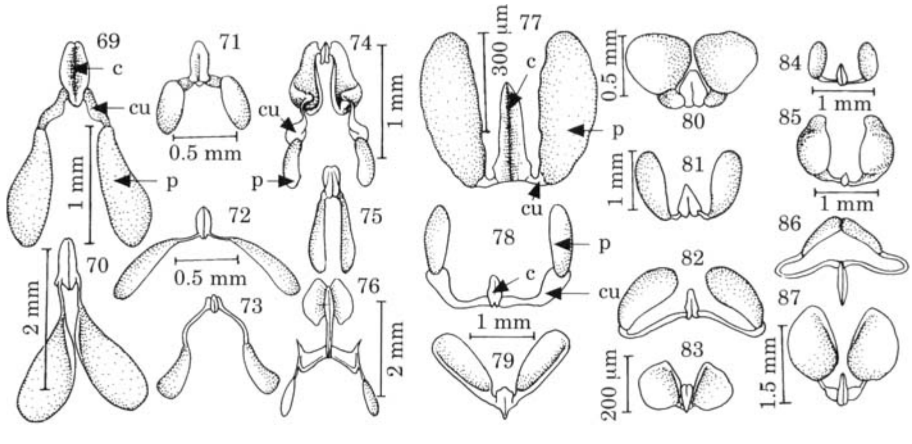
continuous with the primitive marsdenieaead taxa, which show feebly developed caudicles, is likely and therefore the value of the character in tribal classification is doubtful. The Secamoneae differ from the rest of the Asclepiadaceae in that the corpuscle is not horny.

Pollinaria

The pollinia together with the translator constitute the *pollinaria* (cf. Bookman, 1981). Since Don (1838) and Decaisne (1844), one of the important characters used in the segregation of tribes within Asclepiadaceae has been the pendulous (Figs 69–76), erect (Figs 77–87) or transverse stature of the pollinaria (Fig. 102). Although a tribal classification was not suggested by Robert Brown (1810), the use of this character (i.e. the stature of pollinaria) was indeed derived from his work; he used it for separating groups of genera that were subsequently raised to the rank of tribes or subfamilies by others.

The erect and pendulous statures of the pollinaria have been used to differentiate the Asclepiadeae and Stapelieae Decne. *s.l.* Although the value of these characters in differentiating the tribes is undisputable, in many instances the character states offer difficulties.

In most members of the Asclepiadeae, the attachment of the pollinia to the caudicles is by their apical (distal) end and hence the pollinia and pollinaria can be considered to be pendulous (Figs 69–76). On the other hand, the genus *Tylophora* R. Br. (which actually belongs to the Asclepiadeae, but which is at present erroneously placed under Stapelieae Decne.; discussed in detail below) has more or less



Figures 69–87. Stature of pollinaria in Asclepiadaceae. Figs 69–76. The pendulous pollinaria in Tr. Asclepiadeae. Fig. 69. *Asclepias curassavica* L. Fig. 70. *Calotropis gigantea* (L.) R. Br. Fig. 71. *Cynanchum callialata* Buch.-Ham. *ex* Wight & Arn. Fig. 72. *Sarcostemma acidum* (Roxb.) J. Voigt. Fig. 73. *Pachycarpus lineolatus* (Decne.) Bullock (redrawn from Bullock, 1953). Fig. 74. *Stathmostelma rachodes* Schumann (redrawn from Bullock, 1953). Fig. 75. *Oxystelma esculentum* (L. f.) R. Br. *ex* Schultes. Fig. 76. *Oxypetalum appendiculatum* Mart. & Zucc. (redrawn from Schumann, 1895). Figs 77–87. The erect pollinaria in Tr. Stapelieae *s.l.* Fig. 77. *Wattakaka volubilis* (L. f.) Stapf. Fig. 78. *Marsdenia tinctoria* (Roxb.) R. Br. (redrawn from Griffith, 1854). Fig. 79. *Hoya ovalifolia* Wight & Arn. Fig. 80. *Telosma cordata* (Burm. f.) Merr. Fig. 81. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 82. *Cosmostigma racemosum* (Roxb.) Wight. Fig. 83. *Brachystelma alpinum* R.A. Dyer (redrawn from Dyer, 1977c). Fig. 84. *Gymnema sylvestre* (Retz.) R. Br. *ex* Schultes. Fig. 85. *Leptadenia reticulata* (Retz.) Wight & Arn. Fig. 86. *Sarcolobus carinatus* (Retz.) R. Br. *ex* Schultes (redrawn from Griffith, 1854). Fig. 87. *Piaranthus parvulus* N.E. Br. (redrawn from Dyer, 1977b). c - corpusculum; cu - caudicle; p - pollinium.

subglobose anther sacs and therefore the pollinia (Fig. 227) lack definite polarity. For this reason, it is difficult to distinguish whether the pollinia and pollinaria here are actually erect or pendulous. In fact, all three statures of pollinaria - erect, pendulous and transverse - have been described for different species of the genus *Tylophora* R. Br. (Bentham, 1876; Hooker, 1883).

Within the Stapelieae the attachment of the pollinia to the caudicle is by their basal end and thus the pollinia and pollinaria can be said to be erect (Figs 77–87). While this is true for most taxa of the tribe, within the genus *Ceropegia* L. itself there are species with pollinia attached to the caudicles by their medio-lateral (in between the base and tip) and ventro-lateral positions (Figs 89–92). Similar situations exist in *Lagoa calcarata* (Decne.) Durand *ex* Schumann, *Petalostelma martianum* (Decne.) Fourn. (cf. Figs 50 & 54 in Pereira, 1980).

The members of the Gonolobeae are generally distinguished by their transverse pollinaria. Woodson (1941) however noted that the pollinaria in many members of this tribe are indeed pendulous and used yet other characters for circumscribing the tribe, thus indicating the unreliability of the transverse stature of the pollinaria. Good's (1952) suggestion that the Gonolobeae is an artificial assemblage of genera, many of which require transfer to other tribes, actually supplements Woodson's (1941) observations. In fact, the transverse stature of the pollinaria is not really separable from the pendulous stature. Critical observations on the morphology of the stamen in the subfamily leads us to this conclusion.

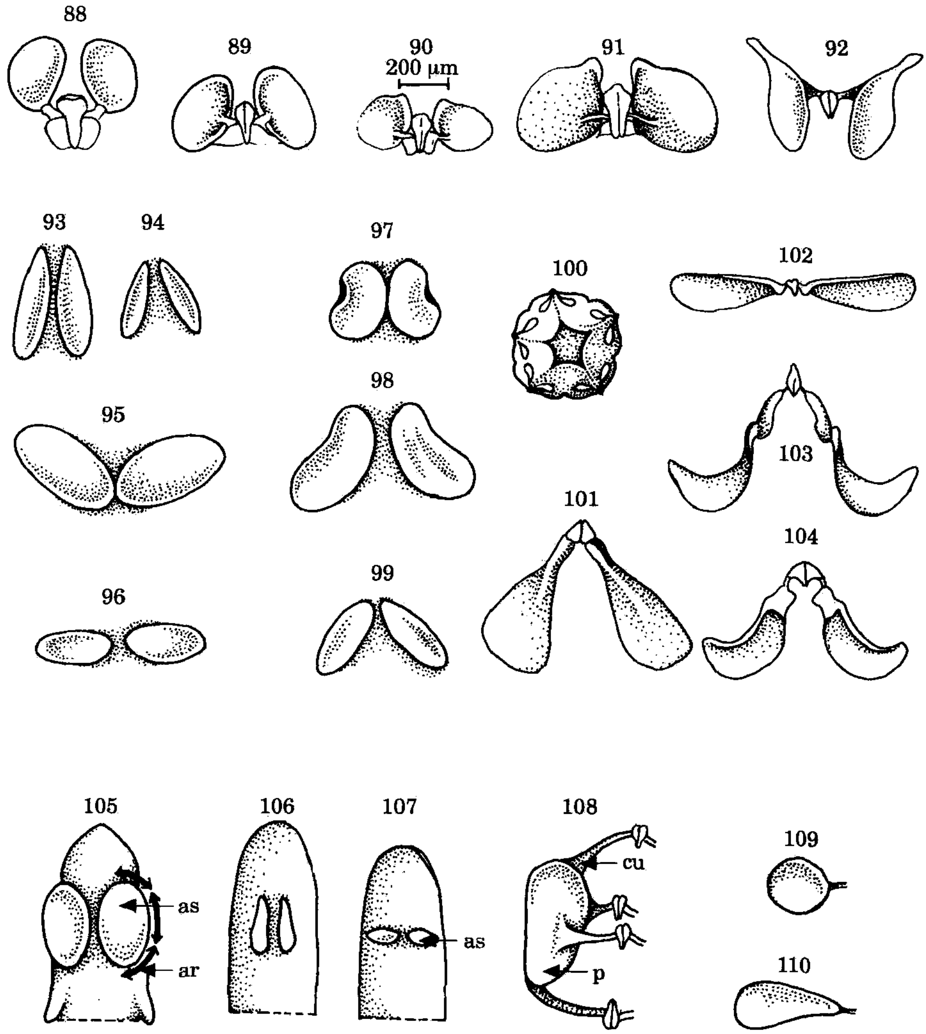
Within both the Asclepiadeae and Stapelieae (*s.l.*) the orientation of the anther sacs with respect to the filament varies considerably (Figs 93–99). In some they are parallel and lengthwise (Figs 93, 94), while they are divergent in many others (Figs 95, 96, 98, 99). In the Gonolobeae the anther sacs have reached extreme divergence and therefore are arranged horizontally with respect to the filament (Fig. 100).

Generally, the dehiscence of the anther in the Gonolobeae is described as transverse and consequently the pollinia and pollinaria are also described as horizontal or sub-pendulous (Bentham, 1876). Kunze's recent observations (1995) are also very relevant in this context. He has pointed out that anther sacs in Gonolobeae are concealed, being flanked by the anther wings and the apical appendage and the slit (constriction or incision) separating them has been confused as the line of dehiscence in earlier literature (for example: Bentham, 1876; Schumann, 1895; Bruyns & Foster, 1991). Kunze also notes that, contrary to the earlier documentation, the anther dehiscence in the Gonolobeae is actually along the dorso-lateral line in vertical direction. But presumably it is also true that the lengthwise dehiscence of the horizontal anther sacs appears to be transverse. Owing to the horizontal orientation of the anther sacs, the pollinia are connected to the caudicles by their apices and thus the pollinaria are actually pendulous as in Asclepiadeae (see Figs 101–104).

A closer examination of the statures of the Asclepiadacean pollinaria [erect, pendulous and transverse] necessitates the following considerations on the statures.

(1) *The dehiscence of the anther sacs*: whether baso-lateral, lateral or apico-lateral (Fig. 105).

(2) *The attachment of the pollinia to the caudicle*: to the base, tip or in between (Fig. 108).



Figures 88–110. Factors affecting the stature of the pollinaria. Figs 88–92. Morphology of pollinaria in some asclepiads, where the pollinarial stature can be questionable, pointing to the necessity of redefinition of statures. Fig. 88. Typical erect pollinaria in *Ceropegia juncea* Roxb. Fig. 89. *C. decaisneana* Wight. Fig. 90. *Caralluma pauciflora* (Wight) Berger. Fig. 91. *Ceropegia candelabrum* L. In Figs 89–91, the pollinia are attached to the caudicles not by their base, but by their lateral margins or by the ventro-lateral facets. Fig. 92. *Trichosacme* sp. Here the pollinia are attached to the caudicles by medio-lateral positions. Figs 93–104. Interpretation of the morphology of the anther pads in Asclepiadaceae *s.s.* and its bearing on the pollinarial stature in Tr. Gonolobeae. Figs 93–99. The orientation of anther sacs in the stamen of Asclepiadaceae. Across these taxa, a change from vertically arranged anther sacs to horizontal positions can be seen. Figs 93–96. Asclepiadeae. Fig. 93. *Asclepias curassavica* L. Fig. 94. *Asclepias fruticosa* L. Fig. 95. *Calotropis gigantea* (L.) R. Br. Fig. 96. The horizontal anther sacs in Gonolobeae. Figs. 97–99. Stapelieae *s.l.* Fig. 97. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 98. *Dolichopetalum kwangsiense* Tsiang (redrawn from Tsiang, 1973). Fig. 99. *Gymnema sylvestre* (Retz.) R. Br. *ex* Schultes. Figs 100–104. Gynostegium and pollinaria in Gonolobeae (all figures redrawn from Delessert, 1846). Fig. 100. Gynostegium in *Matelea latifolia* Aubl. showing the horizontal orientation of anther sacs in the stamen. Figs 101–104. Pollinaria in some taxa of the Gonolobeae showing their truly pendulous nature. Fig. 101. *Matelea latifolia*. Fig. 102. *Fischeria scandens* Decne. Fig. 103. *Lachnostoma balbisii* Decne. Fig. 104. *Polystemma viridiflora* Decne. Figs 105–110. Factors affecting the stature of pollinaria: the location of rupture of anther sacs, position of attachment of caudicles to pollinia and the shape of pollinia. Fig. 105. Diagrammatic sketch of anther showing possible anther sac rupture patterns in Asclepiadaceae; apical, lateral and basal ruptures are shown. Figs 106, 107. Diagrammatic sketch of stamen showing vertical and transverse position of anther sacs. Fig. 108. Observed points of attachment of pollinia to the caudicles; apical, basal, medio-lateral and ventro-lateral attachments are shown. Figs 109, 110. Sphaeroid and elongate shapes of pollinia. a - anther; ar - anther rupture position; as - anther sac; cu - caudicle; p - pollinium.

TABLE 3. Definitions of anther sac apex and base and pollinial attachment and redefinition of pollinarial statures.

ANTHER SACS

Base of anther sac: The lower end of the anther sacs (and thereby of the pollinia) when they are orientated lengthwise on the stamen, or the inward end when orientated horizontally in the stamen (Figs 106, 107).

Apex of anther sac: The upper end of the anther sacs (and thereby of the pollinia) when they are orientated lengthwise on the stamen or the outward end when orientated horizontally in the stamen (Figs 106, 107).

POLLINIAL ATTACHMENT

Apical attachment: When pollinia are attached to the translator arms (caudicles) by their apex [as defined above]. This stature belongs to the pendulous [Tr. Asclepiadeae] and partly transverse [Tr. Gonolobeae and the genus *Tylophora*] pollinial statures described by earlier authors (Figs 62–68, 69–76, 101–104).

Basal attachment: When pollinia are attached to the translator arms (caudicles) by their base [as defined above]. This situation can be considered equivalent to erect pollinial stature described by earlier authors (Figs 56–61, 77–88).

Lateral attachment: When pollinia are attached to the translator arms (caudicles) not by their apex or base but by the lateral margins. This may be apico-lateral, baso-lateral, medio-lateral or rarely ventro-lateral (Figs 89–92).

Apico-lateral attachment: When pollinia are attached to the translator arms (caudicles) by their lateral margins below their apex proper but above the mid point [*Ibatia albiflora*] or when the attachment extends from the apex through the lateral margin [Tr. Gonolobeae]. This stature belongs to the transverse pollinial stature described by earlier authors (Figs 102–104).

Baso-lateral attachment: When pollinia are attached to the translator arms (caudicles) by their lateral margins above the base proper, but below the mid point. This situation (as seen in many species of *Ceropegia*) belongs to the erect pollinial stature described by earlier authors.

Medio-lateral attachment: When pollinia are attached to the translator arms (caudicles) by their lateral margins medianly (Fig. 92).

Ventro-lateral attachment: When pollinia are attached to the translator arms (caudicles) by their ventral surface (Figs 89–91).

POLLINARIAL STATURE

Erect pollinaria (redefinition): when the attachment of pollinia to the caudicles is basal or baso-lateral as defined above.

Pendulous pollinaria (redefinition): when the attachment of the pollinia to the caudicle is apical or apicolateral.

(3) *The position of the corpuscle on the stigma*: with respect to the position of the pollinia (Fig. 108).
(4) *The orientation of the anther sacs*: with respect to the filaments (Figs 106, 107).
(5) *The position of the caudicles*: with respect to the pollinia (Fig. 108).
(6) *The shape of pollinia*: whether they are globose or elongate (Figs. 109 110).

The confusion existing in the tribal classification within the Asclepiadaceae partly results from the absence of clear cut definitions for the erect, pendulous and transverse statures of pollinaria. This can be resolved by defining the base and the apex of the anther sacs and pollinia in the stamen and the point of attachment of the pollinia to the caudicles. Proposed definitions for anther tip, anther base, pollinial attachment and redefinition of the pollinarial statures are given in Table 3.

Pollinaria in three species of the genus *Matelea* (*sensu* Woodson, 1941), a member of the Gonolobeae, are reproduced in Figures 101–104. In accordance with the redefinition of the pollinarial statures they are indeed pendulous and therefore are typical of the asclepiadeaen type.

The redefinition of pollinarial statures removes the ambiguity of the transverse pollinaria to a great extent as many of these can be definitely identified as erect and others as pendulous. This allows the classification of the Asclepiadaceae into two natural groups, one with erect pollinaria and the other with pendulous pollinaria. Problems arise only when the pollinial attachment is medio-lateral indicating that the pollinarial stature alone is not foolproof in defining natural groups within the family when other characters such as that of the gynoecium (discussed in a later section) and the number of anther cells will have to be used.

Gynoecium

Starting from Brown (1810), staminal characters alone were considered for higher level classification of the family. Our observations however indicate that the gynoecium also possesses sufficient characteristics for that purpose.

The features of the gynoecium in Asclepiadeae are shown in Figures 111–121 and of Gonolobeae in Figures 122–124. In both tribes, the upper portion of the two apocarpous ovaries gradually narrows to join the style(s). The styles unite at the tip to join the stigma-head directly (Figs 112, 113, 122, 123) and in others unite and continue upwards as a single style for some distance to form the stigma-head (Figs 114, 115, 117, 124). Thus, depending upon the length of the united upper portion, the style in the tribe may be single or double. But in fact, the united upper portion(s) of the style beneath the dilated stigma-head is stigmatic in origin, as evident from ontogenetic studies.

The ontogeny of the gynoecium in three species of the Asclepiadeae - *Asclepias curassavica* L., *Calotropis gigantea* (L.) R. Br. and *Pergularia daemia* (Forsskal) Chiov. - was studied by the present authors. The details of development and differentiation of the gynoecium are the same in all three species, and the sequence for *Calotropis gigantea* is depicted in Figures 125–133. The carpellary primordia fold conduplicately very early in development and the ovarian and stigmatic segments differentiate (Figs 128, 129). The stigmatic segments of the two carpels then fuse to make the single stigma-

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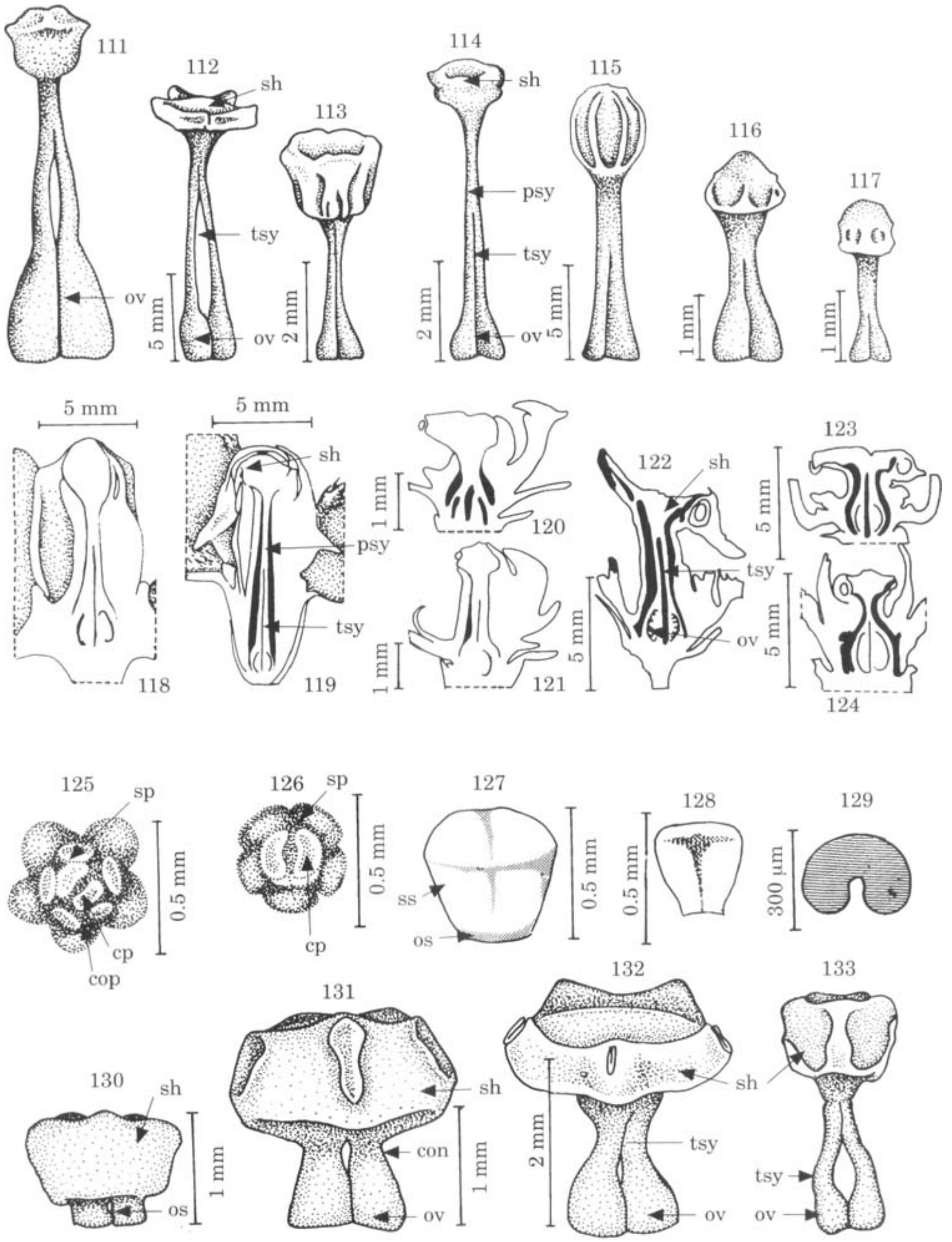
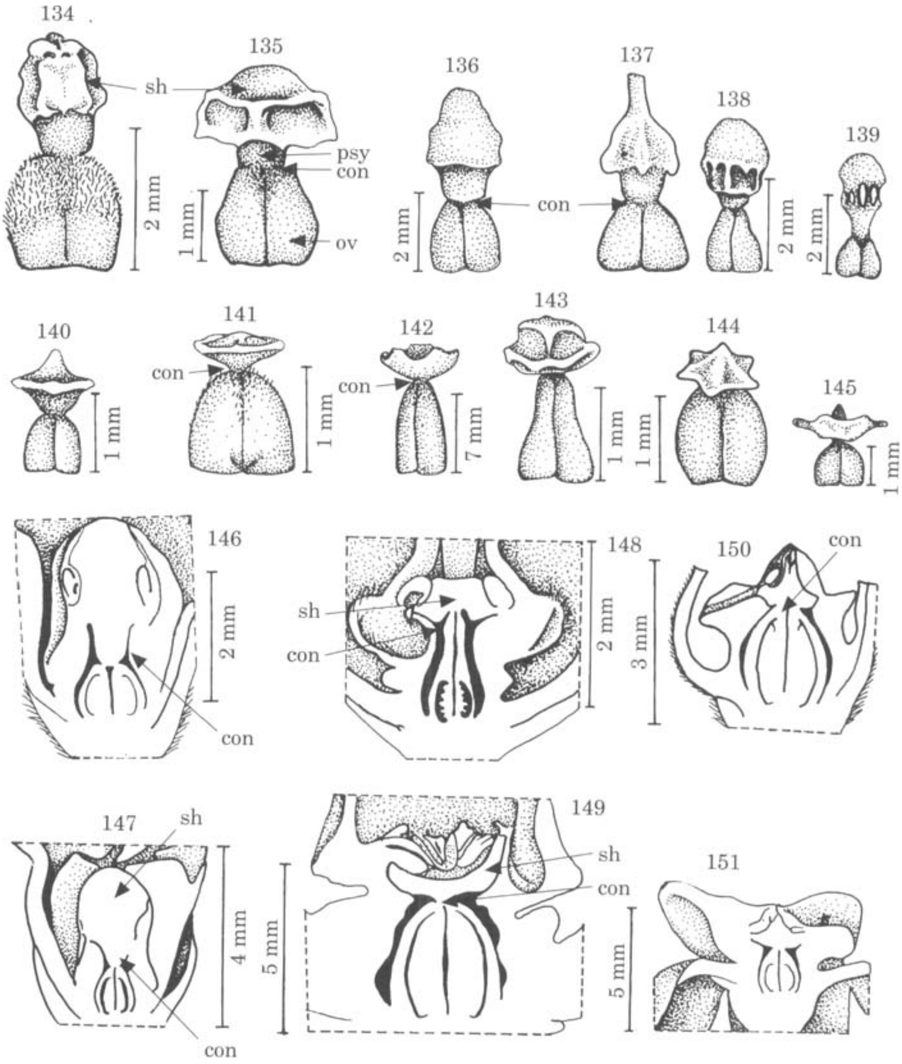
Figures 111–133. Morphology of gynoecium and its development in Asclepiadeae *s.l.* (incl. Gonolobeae). Figs 111–117. Pistil as dissected out from the gynostegium. Fig. 111. *Oxystelma esculentum* (L. f.) R. Br. *ex* Schultes. Fig. 112. *Calotropis gigantea* (L.) R. Br. Fig. 113. *Asclepias curassavica* L. Fig. 114. *Pergularia daemia* (Forsskal) Chiov. Fig. 115. *Holostemma annulare* (Roxb.) Schumann. Fig. 116. *Sarcostemma acidum* (Roxb.) Voight. Fig. 117. *Cynanchum callialata* Buch.-Ham. *ex* Wight & Arn. Figs 118–124. Longitudinal sections of the flowers in Asclepiadeae showing the morphology of the gynoecium. Fig. 118. *Holostemma annulare*. Fig. 119. *Pergularia daemia* (Forsskal) Chiov. Fig. 120. *Pentarrhinum insipidum* E. Meyer (redrawn from Kunze, 1990). Fig. 121. *Sarcostemma australe* (R. Br.) Forster (redrawn from Kunze, 1990). Fig. 122. *Gonolobus barbatus* H.B. & K. Fig. 123. *G. cteniophorus* (Blake) Woodson. Fig. 124. *Matelea carolinesis* (Jacquin) Woodson (Figures 122 & 124 redrawn from Puri & Shiam, 1966). Figs 125–133. Successive stages in the development of gynoecium in Asclepiadeae (*Calotropis gigantea* (L.) R. Br.). Developmental studies show the presence of true styles in Asclepiadeae. The narrowed upper portions of the carpels as seen in Asclepiadeae have no homologue in Stapelieae *s.l.* Fig. 125. Corolline, staminal and carpellary primordia at an early stage of development. Fig. 126. Staminal and carpellary primordia at a later stage. Fig. 127. Carpellary primordia showing the differentiation of the stigmatic and ovarian segments at an early stage of development. Fig. 128. A carpel at the stage of gynoecium as in Fig 127. Fig. 129. Transverse section of the ovary at the stage of the carpel as in Fig. 128. Fig. 130. Young gynoecium showing the fusion of the stigmatic segments of the two carpels to become the stigma-head. In the fusion between the carpels, only the stigmatic segments participate; ovary portions do not participate in the fusion. Fig. 131. A later stage of the gynoecium showing the incipient constriction between the ovaries and the stigma-head. Fig. 132. Late development of the true styles by intercalary growth of the apical portion of the ovary segment below the stigma-head and the constriction. Fig. 133. A submature gynoecium showing the constriction between the stigma-head and the true styles/ovary which gets obliterated at maturity (see Fig. 112) owing to growth adjustments. con - constriction (feeble here) between the ovaries and the stigma-head; cop - corolline primordium; cp - carpellary primordium; ov - ovary; os - ovary segment (of the carpellary primordium); psy - pseudostyle; sh - stigma head; sp - staminal primordium; ss - stigmatic segment (of the carpellary primordium); tsy - true style.

head (Fig. 130). In a slightly advanced stage of development, the stigma-head is found separated from the ovary portion by a constriction. The '*true styles*' (the sterile narrow portion of the ovaries) differentiate later in development by an intercalary elongation of the apical portion of the ovary segments below the constriction separating the ovaries and the stigma-head. Here, it is to be noted that the stigmatic segments of the carpellary primordia alone participate in the fusion process, and no



part of the ovaries is involved in the fusion. Thus, the solitary portion of the gynoecium between the dilated stigma-head and the ovaries (Stapelieae: Figs 134–137, 140; Asclepiadeae: Figs 114, 115, 117, 119, 124) actually belongs to the



Figures 134–151. Morphology of the gynoecium in Tr. Stapelieae (*s.l.*). Figs 134–145. Gynoecium as dissected out from the gynostegium. Fig. 134. *Wattakaka volubilis* (L. f.) Stapf. Fig. 135. *Cosmostigma racemosum* (Roxb.) Wight. Fig. 136. *Telosma cordata* (Burm. f.) Merr. Fig. 137. *Gymnema malayana* Griffith (redrawn from Griffith, 1854). Fig. 138. *G. sylvestre* (Retz.) R. Br. *ex* Schultes. Fig. 139. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 140. *Hoya retusa* Dalz. Fig. 141. *Heterostemma vasudevanii* Swarup. & Mangaly. Fig. 142. *Caralluma crenulata* Wallich. Fig. 143. *Ceropegia candelabrum* L. Fig. 144. *Leptadenia reticulata* (Retz.) Wight & Arn. Fig. 145. *Hoya ovalifolia* Wight & Arn. Figs 146–151. Longitudinal sections of flowers in the Stapelieae *s.l.* showing the morphology of the gynoecium. Fig. 146. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 147. *Gymnema sylvestre*. Fig. 148. *Ceropegia candelabrum*. Fig. 149. *Tavaresia barklyi* (Dyer) N.E. Br. (redrawn from Bruyns & Forster, 1991). Fig. 150. *Orthanthera jasminiflora* (Burch.) Schumann (redrawn from Bruyns & Forster, 1991). Fig. 151. *Hoya ovalifolia*. con - constriction between the ovaries and the stigma-head; ov - ovary; psy - pseudostyle; sh - stigma head.

stigmatic segments of the carpellary primordia and is therefore distinct from the true style(s) (that are portions of the ovarian segments in origin). In order to differentiate this stigmatic-element portion of the style from true styles, the term 'pseudostyle' is used here. In all the illustrations of the gynoecium in Asclepiadeae provided here (Figs 111–124) are seen true styles, the sterile narrow upper portions of the ovaries which are ovarian in development.

Features of the gynoecium in Stapelieae Decne. *s.l.* are shown in Figures 134–151. In primitive lianous genera of this tribe, thick pseudostyles are very much evident (Figs 134–139, 146). In advanced succulent herbaceous genera like *Caralluma* R. Br., *Tavaresia* Welw., etc. (Figs 149, 150) even the pseudostyle has been eliminated and the stigma-head is of the same morphology as the '*clavuncle*' of Apocyneae (Apocynaceae) where a definite differentiation into style and stigma-head is lacking (cf. Rosatti, 1989). What is more interesting here is that the stigma-head and ovaries are separated by a sharp constriction. This constriction is observable in the gynoecium of some members of the Asclepiadeae too, but feebly (Fig. 133). From developmental studies in the latter tribe, it appears that such a constriction exists early in development, but gets obliterated at maturity (Figs. 133, also see 112). Most taxa of the Stapelieae Decne. *s.l.* (i.e. including Marsdenieae Benth., and Ceropegieae Decne.) can easily be distinguished from the Asclepiadeae and Gonolobeae in the extreme exomorphy of the gynoecium, i.e. in the absence of true styles and the presence of a pronounced constriction between the ovaries and the stigma-head/pseudostyle. In the Indian species we have studied, no taxa in Stapelieae are known to have true styles except perhaps in species of *Ceropegia* L. (*C. candelabrum* L.; Fig. 148), where the sharp constriction between the ovaries and the stigma-head clearly signifies the stapelieaean morphology of the gynoecium.

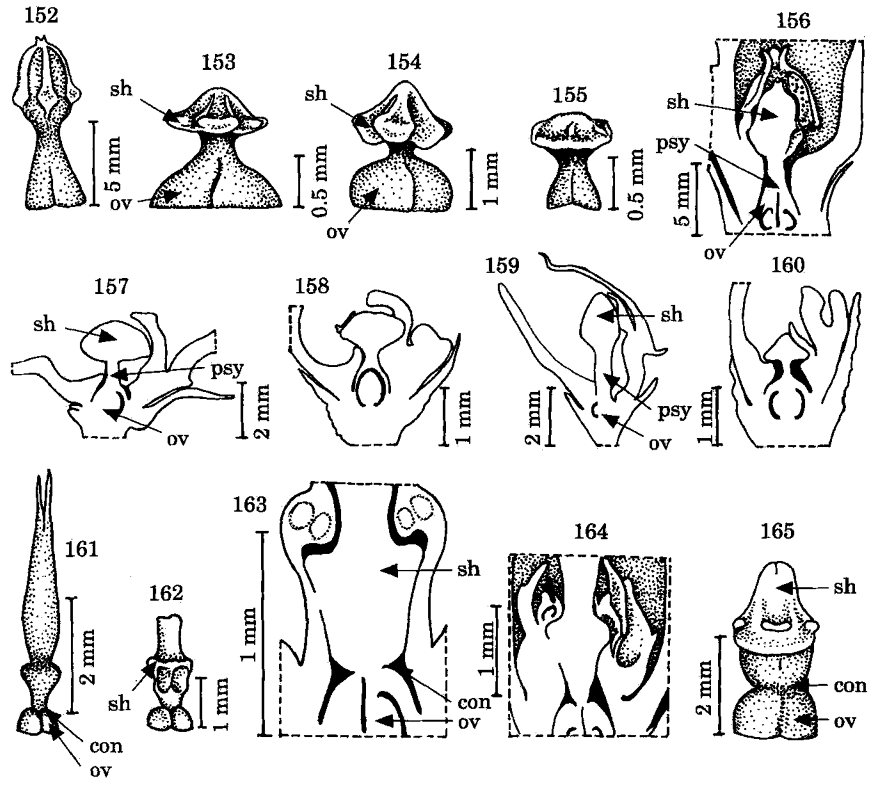
In summary, within the Asclepiadaceae there are two basic types of gynoecium: one with a sharp constriction between the ovary and the stigma-head and without true style(s), as exhibited by the Stapelieae Decne. *s.l.* and the other with true style(s), characteristic of the group comprising Asclepiadeae and Gonolobeae. Very rarely, difficulties arise with some members of the Asclepiadeae where the true styles are not well developed and pseudostyle is obsolete so that the ovaries and the stigma-head appear as if separated by a sharp constriction.

It is indeed surprising that the characters of the gynoecium go hand in hand with the morphology of the anther sacs and the erect and pendulous statures of the pollinia. The Asclepiadeae and Gonolobeae characterized by true styles always have pendulous pollinaria (as redefined in the previous section) and anther sacs embedded in the tissue of the anther wings, while the Stapelieae which are devoid of true styles have erect pollinaria and the anther wing situated well below the level of the anther sacs. Wherever the stature of the pollinaria and the morphology of the anther are confusing, the characteristics of the gynoecium can be used as diagnostic and *vice versa*. Thus, rather than taking the stature of pollinaria or the morphology of the anther or the characteristics of the gynoecium in isolation, their combination provides sound ground for recognizing natural suprageneric groups within Asclepiadaceae *s.s.*

In analysing the morphology of the gynoecium in Asclepiadaceae *s.s.*, the two groups of genera seem to have progressed in opposite directions, one towards bringing the stigma-head closer to the ovary and the other towards moving the stigma-head away from the ovary, signifying different selective pressures. Whatever the nature of the selective pressures involved, intermediate morphology between the typical asclepiadeaean and stapelieaean types of gynoecium is likely to occur in some primitive members of both the tribes and this aspect requires further research.

The gynoecium in the Secamoneae (Figs 161–164) is again homomorphic to that of the Stapelieae, but the former differs in the 4-locular anther. In the Periplocaceae, although the gynoecium lacks true styles in the strict sense of the narrowed upper portions of the ovary, its morphology is asclepiadeaean, in the absence of a sharp constriction between the ovaries and the style/stigma-head.

Information on features of the gynoecium, with true styles, pseudostyle or without both, and the features of the anther, whether embedded in the tissue of the anther wing or not, etc, are generally not found in floras. There is every relevance for documentation of such details in the family so that relationships between genera and species can be speculated. In fact, comparative anatomical and developmental



Figures 152–165. Morphology of the gynoecium in Periplocaceae, Secamoneae, and the Apocynineae of Apocynaceae. Figs 152–155. Gynoecium in Periplocaceae. Fig. 152. *Cryptostegia madagascariensis* Bojer. Fig. 153. *Cryptolepis buchananii* Roemer & Schultes. Fig. 154. *C. grandiflora* Wight. Fig. 155. *Hemidesmus indicus* (L.) R. Br. Figs 156–160. Longitidunal sections of flowers in Periplocaceae depicting the morphology of the gynoecium. Fig. 156. *Cryptostegia madagascariensis* Bojer. Fig. 157. *Periploca gracea* L. Fig. 158. *Hemidesmus indicus* (L.) R. Br. Fig. 159. *Raphionacme zeyheri* Harvey. Fig. 160. *Cryptolepis buchananii* Roemer & Schultes (Figs 157–160 redrawn from Kunze, 1990). Figs 161–164. Secamoneae. Figs 161, 162. Gynoecium, as dissected out from the gynostegium. Fig. 161. *Toxocarpus kleinii* Wight & Arn. Fig. 162. *Secamone emetica* R. Br. Figs 163–164. Transverse sections of flower depicting the morphology of the gynoecium. Fig. 163. *Secamone zambesiaca* Schultes (redrawn from Safwat, 1962). Fig. 164. *Toxocarpus kleinii* Wight & Arn. Fig. 165. Gynoecium in *Apocynum cannabinum* L. (Apocynineae: Apocynaceae; redrawn from Safwat, 1962). con - constriction between the ovaries and the stigma-head; ov - ovary; psy - pseudostyle; sh - stigma head.

studies of the gynoecium in Apocynaceae, Periplocaceae and Asclepiadaceae are highly desirable.

Fruit and seed

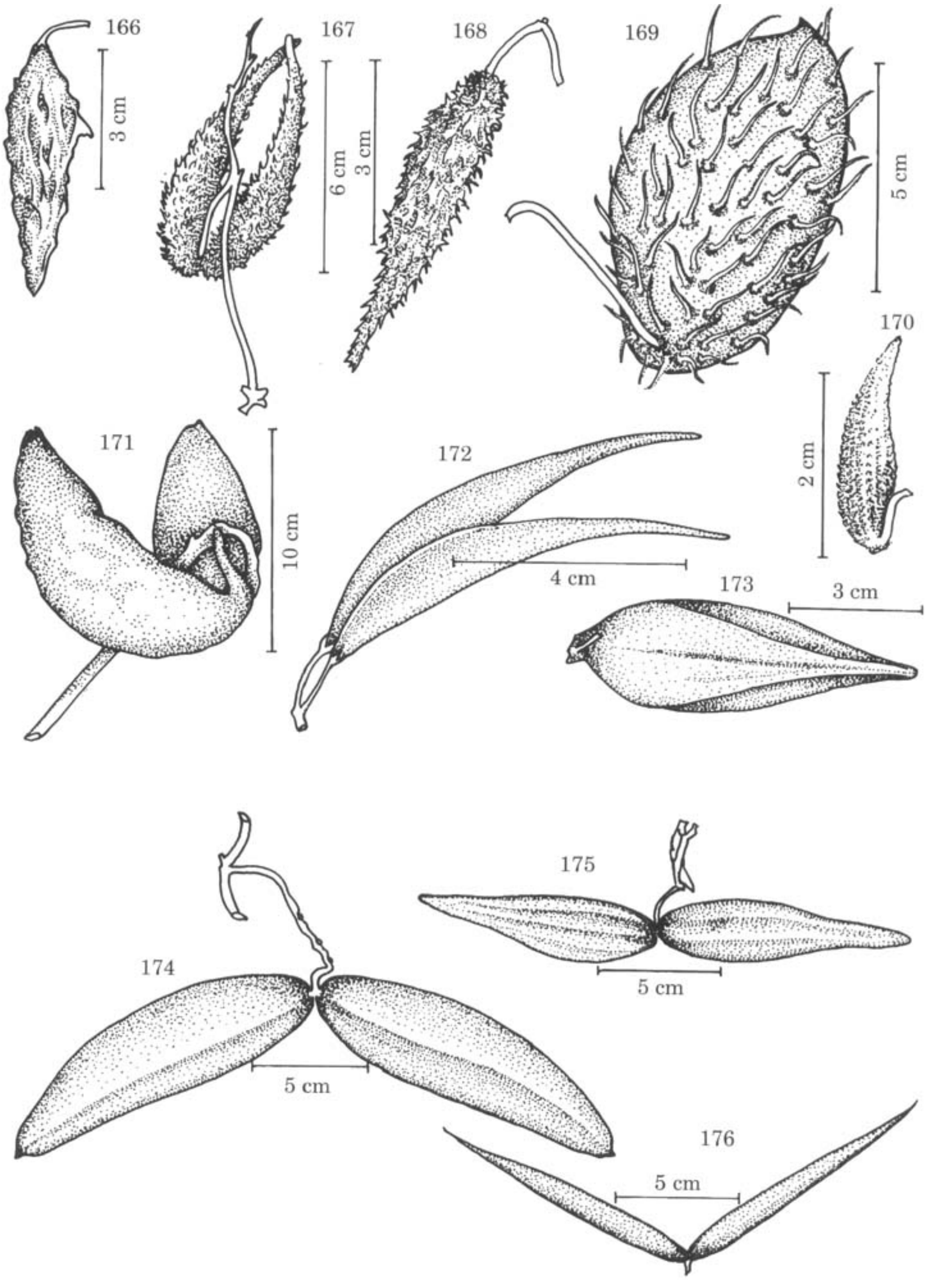
Characteristics of the fruits and seeds do not seem to have been employed for suprageneric classification. Neither the exomorphy nor the internal morphology has been helpful in this regard, perhaps for want of relevant directed research. In a number of genera in the Asclepiadeae *s.l.* (incl. Gonolobeae), the surface of the follicles is thrown into protuberances, echinations, and bristles (*Holostemma* R. Br., *Seshagiria* Ansari & Hemadri, *Pergularia* R. Br., *Gomphocarpus* R. Br. (= *Asclepias* L.), *Matelea* Aubl. and *Schubertia* Mart.; Figs 166–170; Ansari & Hemadri, 1971; Pereira, 1980; Rosatti, 1989; Swarupanandan, 1985). Such echinations although not universal in the tribe, are totally absent from the Stapelieae (Figs 166–176). Perhaps, going along with this, there exist corresponding differences in the distribution of vascular bundles in the pericarp (see paragraph below).

Transverse sections of follicles of selected taxa from different suprageneric groups are illustrated in Figures 177–184. The vascular bundles of both species of Periplocaceae studied by the present authors have crescentic vascular bundles arranged in a single row (Figs 176, 177). The vascular bundles in the pericarp of Asclepiadaceae *s.s.* are not crescentic in cross section but the number of their rows range from many to one (Figs 168–173). The number of rows of vascular bundles in the pericarp across the various suprageneric categories within Asclepiadaceae, its relationship to the echinations of the pericarp, and the taxonomic significance to these traits are yet to be ascertained.

Further characters of the fruit that might be of value in classification perhaps might be the morphology and vasculature of the placental flaps. The mature fruit-placentum in the Periplocaceae is a solid structure to which the seeds are attached on denticles in definite rows (Figs 185, 186). In the Asclepiadaceae, the placentum has lost its solid structure; it consists of a thin cylindrical structure to which several flat and papery flaps are attached. The outer margin of these flaps are dentate and the seeds are borne on these dentations (Figs 187–190). The number and ramification of the vascular traces contributing to each dentation or seed varies. In the Asclepiadeae, more than one vascular trace contributes to a seed and they ramify forming a sparse to dense reticulum in the placental ridge (Figs 195–197). In the Stapelieae *s.l.* they are mostly 1-traced (Figs 192–194). The Secamoneae shows a more or less intermediate condition. The Periplocaceae and Gonolobeae were not studied from this viewpoint and a proper survey within the various tribes and suprageneric categories may yield supplementary characters useful for classification.

Seeds

The seeds in Asclepiadaceae *s. l.* are flattened ovate structures closely imbricated within the fruit cavity and with the long silky coma arranged longitudinally inside the grooves between the seed-bearing ridges of the placenta. In Periplocaceae and Secamoneae, the seeds are biconvex in transverse section. In the rest of the tribes of the family Asclepiadaceae, the seed has essentially the same morphology but, in addition, is differentiated into a 'seed area' enclosing the embryo and a thin wing

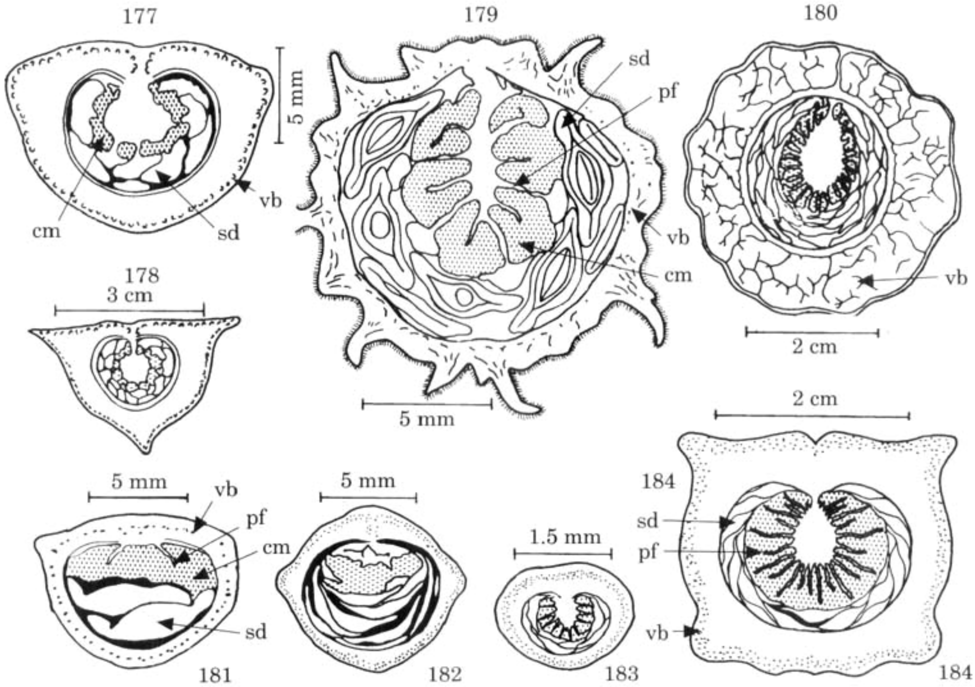


Figures 166–176. Morphology of the follicles in Asclepiadaceae *s.s.* Figs 166–173. Tr. Asclepiadeae *s.l.* Fig. 166. *Seshagiria sahyadrica* Ansari & Hemadri (redrawn from Ansari & Hemadri, 1971). Fig. 167. *Pergularia daemia* (Forsskal) Chiov. Fig. 168. *Matelea carolinensis* (redrawn from Rosatti, 1989). Fig. 169. *Asclepias fruticosa* L. Fig. 170. *Asclepias syriaca* L. (redrawn from Rosatti, 1989). Fig. 171. *Calotropis gigantea* (L.) R. Br. Fig. 172. *Asclepias curassavica* L. Fig. 173. *Cynanchum callialata* Buch.-Ham. *ex* Wight & Arn. Figs 174–176. Stapelieae *s.l.* Fig. 174. *Cosmostigma racemosum* (Roxb.) Wight. Fig. 175. *Wattakaka volubilis* (L. f.) Stapf. Fig. 176. *Sarcostemma acidum* (Roxb.) J. Voigt.

surrounding it, the 'seed-wing' (Fig. 198). Such a seed wing is absent in the Periplocaceae and Secamoneae. The seed wing is entirely made up from the seed coats. In the primitive lianous taxa, the seed wing is unspecialized and thin (Fig. 200). In more advanced taxa of both the Stapelieae and Asclepiadeae, the seed wing is thick owing to the development of special layers of cells (Figs 201–207).

The thickening of the seed-wing relies on two different types of architecture. The *first* is by the development of an internal parenchymatous core, a *columella* (Fig. 202). As far as our current knowledge goes, this kind of architecture is known only in the Asclepiadeae (Sylla & Albers 1989). The second type of architecture is formed by the columnar outward expansion of the cells of the testa and is exhibited by members of both tribes, Asclepiadeae *s.l.* and Stapelieae *s.l.* (Figs 201, 203–207). The Ceropegiae *s.s.* and Stapelieae *s.s.* have a modified architecture of the second type, in which the columnar expansion of testal cells is unequal on opposite sides, and the wings fold on to the seed area (Figs 203–208). Such unequal morphology of the seed wings never occurs within the Asclepiadeae.

Relative to the internal morphology of the pericarp, architecture of the seed coat could be a very useful character in suprageneric classification, but a survey of this feature across the different categories of genera is needed before its value in classification can be assessed.



Figures 177–184. Transverse sections of follicles in Periplocaceae and the tribes Asclepiadeae and Stapelieae *s.l.* Figs 177, 178. Periplocaceae; note the crescentic or gutter-shaped vascular bundles. Fig. 177. *Cryptolepis buchananii* Roemer & Schultes. Fig. 178. *Cryptostegia madagascariensis* Bojer. Figs 179, 180. Asclepiadeae. Fig. 179. *Pergularia daemia* (Forsskal) Chiov. Fig. 180. *Calotropis gigantea* (L.) R. Br. Figs 181–184. Stapelieae *s.l.* Fig. 181. *Caralluma adscendens* (Roxb.) Haw. Fig. 182. *Gymnema sylvestre* (Retz.) R. Br. *ex* Schultes. Fig. 183. *Marsdenia tenacissima* (Roxb.) Moon. Fig. 184. *Telosma cordata* (Burm. f.) Merr. cm - coma (of the seeds); pf - placental flap; sd - seed; vb - vascular bundle(s) (of the pericarp).

Accessory floral appendages

Accessory appendages of the corolla and stamen have also been occasionally used as characters in differentiating Periplocaceae and Asclepiadaceae *s.s.*, although not in a very definitive way (cf. Bentham, 1876). Members of the Periplocaceae are generally provided with a corolline corona of various kinds and lack a staminal corona (Bentham, 1876; Hooker, 1883). The Asclepiadaceae *s.s* is generally devoid of a corolline corona, but genera like *Gymnema* R. Br., and *Leptadenia* R. Br. possess both corolline and staminal corona; some like *Sarcolobus* R. Br., lack both corolline and staminal corona. The variability of staminal corona and its implications on classification have already been dealt with above in the section *Androecium*.

Vegetative morphology

Stem

Many members of the Asclepiadaceae *s.l.* have a succulent shoot morphology with the leaves reduced to scales (Figs 209–213) as adaptations in arid environments. These xerophytic stems are of two types: the first includes cylindrical photosynthetic stems with long internodes (e.g. *Ceropegia juncea* Roxb., *Orthanthera viminea* (Wallich) Wight, Figs 209, 210). The second type is found in many stapeliad genera like *Caralluma* R. Br., *Stapelia* L., *Tavaresia* Welw., *Hoodia* Sweet, *etc.* (Figs 211–213), where, owing to extreme condensation of internodes, the shoot appears four to many angled in cross section (Fig. 212; cf. Albers *et al.*, 1989).

Bentham (1876) used the differences in the above character to separate the Stapelieae *s.s.* from the Ceropegieae Decne. (1842) and Marsdenieae Benth. (1868) along with the characteristics of the pollinia. The succulent angular stem with leaves born on raised tubercles is characteristic of Stapelieae *s.s.* However, several species of *Ceropegia* L. such as *C. stapeliformis* Haw., *C. cimiciodora* Obern., *C. armandii* Raugh, *C. dimorpha* Humbert and *C. variegata* Decne. (Ceropegieae *s.s.*) the leaves are born on

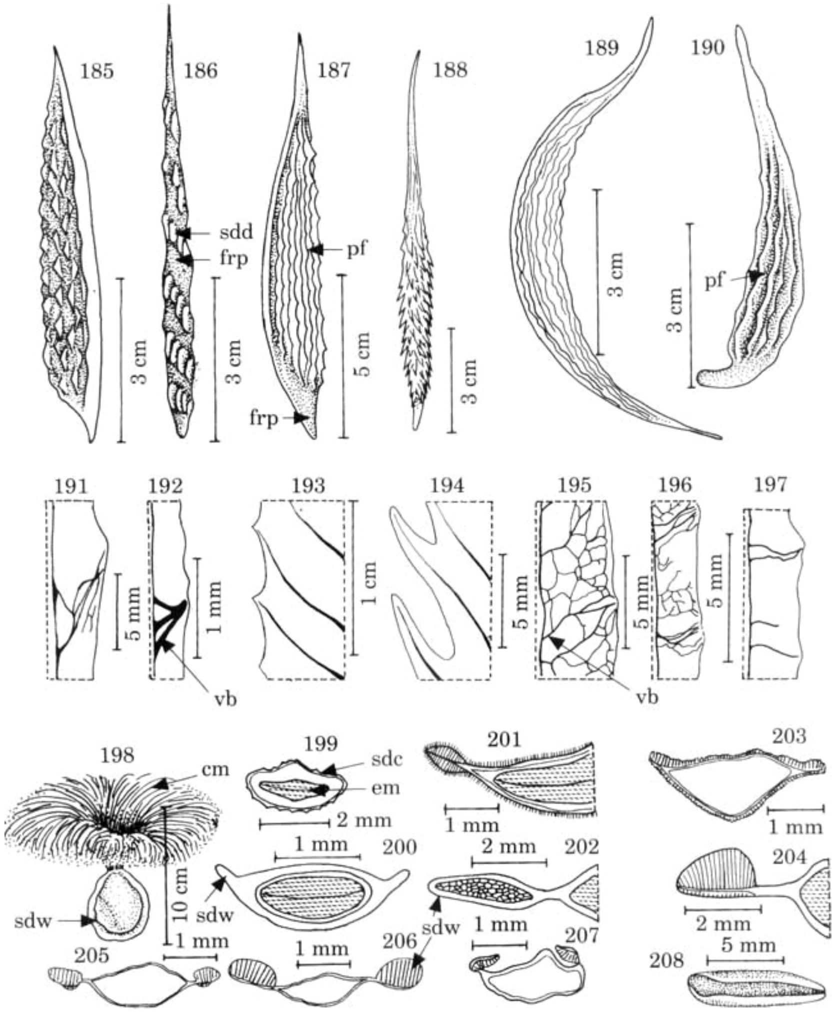
Figures 185–208. Fruit-placenta, vasculature of fruit-placenta and seed morphology of Periplocaceae and Asclepiadaceae *s.s.* Figs 185–190. Fruit-placenta as in dehisced follicles. In Periplocaceae the fruit-placentum is a thick solid cylinder upon which the seed bearing denticles are born in rows. In Asclepiadaceae, the central placental cylinder, to which several flat papery flaps are attached is thin; the outer margin of these flaps is thrown into denticles upon which the seeds are borne. The number of seed-bearing placental flaps and the extent of dentation vary between species. Figs 185, 186. Periplocaceae. Fig. 185. *Cryptostegia madagascariensis* Bojer. Fig. 186. *Cryptolepis buchananii* Roemer & Schultes. Figs 187, 188. Stapelieae *s.l.* Fig. 187. *Cosmostigma racemosum* (Roxb.) Wight. Fig. 188. *Telosma cordata* (Burm. f.) Merr. Figs 189, 190. Asclepiadeae. Fig. 189. *Calotropis gigantea* (L.) R. Br. Fig. 190. *Pergularia daemia* (Forsskal) Chiov. Figs 191–197. Vasculature of the seed-bearing placental flaps in Asclepiadeae. Fig. 191. *Toxocarpus kleinii* Wight & Arn. (Secamoneae). Figs 192–194. Stapelieae *s.l.* Fig. 192. *Ceropegia candelabrum* L. Fig. 193. *Cosmostiga racemosum* (Roxb.) Wight. Fig. 194. *Telosma cordata* (Burm. f.) Merr. Figs 195–197. Asclepiadeae. Fig. 195. *Calotropis gigantea* (L.) R. Br. Fig. 196. *Pergularia daemia* (Forsskal) Chiov. Fig. 197. *Cynanchum tunicatum* (Retz.) Alston. Figs. 198–208. Morphology of the seeds in Periplocaceae and Asclepiadaceae *s.s.* Fig. 198. A comate seed of *Cosmostigma racemosum* (Roxb.) Wight showing the seed wing. Figs 199–204. Transections of seeds in Periplocaceae and Asclepiadaceae *s.s.* Fig. 199. Cross section of a seed of *Cryptostegia madagascariensis* Bojer (Periplocaceae) showing the absence of a seed wing. Fig. 200. Tranverse section of a typical Asclepiadacean seed with seed wing. Figs 201, 202. Asclepiadeae. Fig. 201. *Pergularia tomentosa* L. (redrawn from Bruyns, 1993). Fig. 202. *Asclepias syriaca* L. (redrawn from Sylla & Albers, 1989). Fig. 203. *Quaqua pruinosa* (Masson) P.V. Bruyns. Fig. 204. *Duvalia pubescens* N.E. Br. (redrawn from Sylla & Albers, 1989). Fig. 205. *Lavrania picta* (N.E. Br.) Bruyns. Fig. 206. *Huernia plowesii.* Fig. 207. *Richteranthus columnaris* (Figs 205–207 redrawn from Bruyns, 1993). Fig. 208. A seed of *Ceropegia candelabrum* L. (coma excised), showing the folding of the seed wings over the seed-proper, owing to the unequal expansion of the epidermal cells of the wing on either sides. cm - coma (of the seed); em - embryo; frp - fruit-placentum; pf - placental flap(s); sdc - seed coat; sdd - seed-bearing denticles of the placentum; sdw - seed-wing; vb - vascular bundle(s) (of the placental flap).

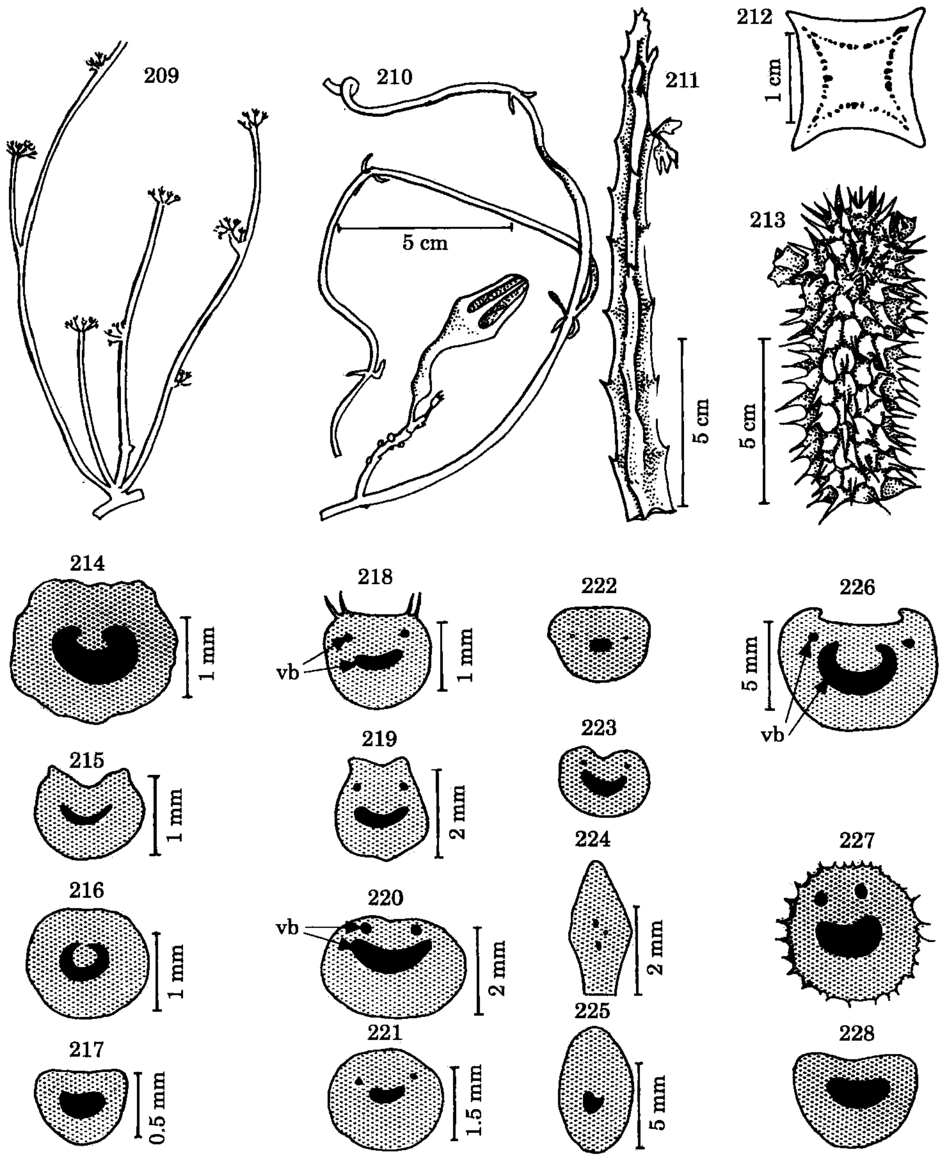
raised tubercles and in *Frerea* Dalz., a member of the Stapelieae, the stem is indeed cylindrical (Bruyns & Forster, 1991). Thus the distribution of the stem character across the tribes is not clear-cut making it of limited taxonomic value in higher level classification.

Succulent morphology is similarly unhelpful in separating the Ceropegieae and Stapelieae from the rest. Cladode formation occurs in the Asclepiadeae too. Cladodes with long internodes similar to those in *Ceropegia juncea* Roxb. (Tr. Ceropegieae), are seen in genera such as *Sarcostemma* R. Br. (*S. acidum* (R. Br.) J. Voight, *S. brunonianum* Wight & Arn. *etc.*) (Fig. 176). The angular stem type with condensed nodes, although widespread in the Stapelieae, *Cynanchum rossii* Rauh (Tr. Asclepiadeae) comes quite close to it (Liede, 1995. Pers. comm.).

Petiole

The vascular structure of the node and petiole has not been studied to any



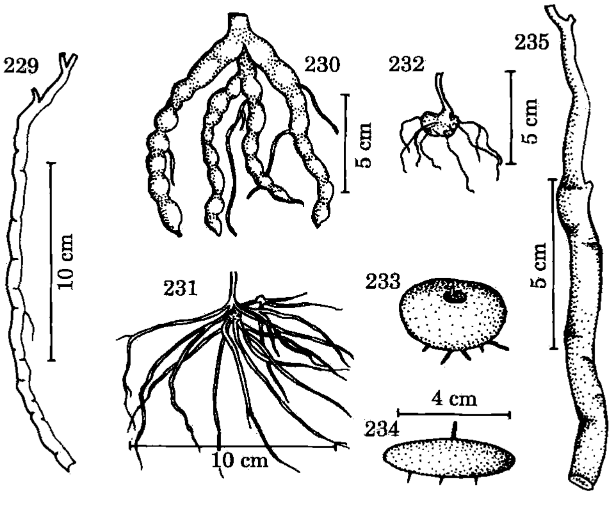


Figures 209–228. Morphology of the stem and petiole in Periplocaceae and Asclepiadaceae. Figs 209–213. Succulent stem morphology in Asclepiadeae. Fig. 209. *Cynanchum decaisneanum* (Syn.: *Decanema bojerianum* Decne.; redrawn from Delessert, 1846). Figs 210–213. Stem morphology in the Stapelieae. Fig. 210. A branch of *Ceropegia juncea* Roxb. Fig. 211. *Caralluma adscendens* (Roxb.) Haw. var. *adscendens*. Fig. 212. Transverse section of the stem in *Caralluma umbellata* showing the angular stem. Fig. 213. A branch of *Hoodia gordonii* (Masson) Sweet *ex* Decne. (Syn.: *H. pillansii* Haw.; redrawn from Dyer, 1978). Figs 214–228. Vascular morphology of the petiole in Periplocaceae and Asclepiadaceae. Figs 214, 215. Periplocaceae. Fig. 214. *Baeolepis nervosa* (Wight & Arn.) Moq. Fig. 215. *Hemidesmus indicus* (L.) R. Br. Figs 216, 217. Secamoneae. Fig. 216. *Toxocarpus kleinii* Wight & Arn. Fig. 217. *Secamone emetica* R. Br. Figs 218–225. Stapelieae *s.l.* Fig. 218. *Ceropegia candelabrum* L. Fig. 219. *Heterostemma vasudevanii* Swarup. & Mangaly. Fig. 220. *Telosma cordata* (Burm. f.) Merr. Fig. 221. *Hoya ovalifolia* Wight & Arn. Fig. 222. *Ceropegia juncea* Roxb. Fig. 223. *Gymnema sylvestre* (Retz.) R. Br. *ex* Schultes. Fig. 224. *Caralluma umbellata* Haw. Fig. 225. *C. crenulata* Wallich. Figs 226–228. Asclepiadeae. Fig. 226. *Calotropis gigantea* (L.) R. Br. Fig. 227. *Pergularia daemia* (Forsskal) Chiov. Fig. 228. *Asclepias fruticosa* L. vb - vascular bundle(s) (of the petiole).

significant extent in the family (Metcalfe & Chalk, 1972), to provide any categorical information on the different suprageneric taxa. Preliminary observation of the petiolar vasculature in the Indian Asclepiadaceae *s.l.* shows that Periplocaceae is invariably 1-traced. Metcalfe & Chalk (1972) reported the petiole in *Periploca* L. as 1-traced and that in *Cryptostegia* R. Br. as 3-traced. Anatomical observations of the petiole in *Cryptostegia madagascariensis* Bojer proved to be 1-traced, contrary to the earlier report. Species of *Baeolepis* Decne. *ex* Moq. (*B. nervosa* (Wight & Arn.) Decne. *ex.* Moq.), *Cryptolepis* R. Br. (*C. buchananii* Roemer & Schultes and *C. grandiflora* Wight) and *Hemidesmus* R. Br. (*H. indicus* (L.) R. Br.), all have a 1-traced petiole (Figs 214, 215). Apparently, in Periplocaceae the 3-traced condition is unknown. The few species of Secamoneae studied also have 1-traced petioles. Asclepiadeae shows both 1-traced and 3-traced conditions (Figs 226–228) as is the case with Stapelieae *s.l.* (Figs 218–225), but in the latter, the 1-traced condition is associated with succulence and reduction of foliar leaves to scales. Thus, except for the separation of Periplocaceae, the vascular morphology of the petiole is not taxonomically significant.

Root

As for stem succulence, tuberization of root is an adaptation to the seasonal environment. Tuberous roots are occasional in Periplocaceae, Asclepiadeae *s.s.* and Ceropegieae *s.s.* (Figs 229–235), and conform to two different types: (1) long cylindrical/tuberous roots, (2) napiform/subglobose tuber. Type-1 morphology is widespread in Periplocaceae (*Hemidesmus indicus* (L.) R. Br., *Janakia arayalpathra* Joseph & Chandr. (Figs 229, 230) and is known in Asclepiadeae (*Holostemma annulare* (Roxb.) Schumann; Fig. 235). Root tubers of Type-2 morphology are almost unknown in Periplocaceae, but occur in both Asclepiadeae (*Cynanchum madagascariense* Schumann, *C. lineare* Tsiang & Zang and *Aidomene parvula* Stopp) and Ceropegieae (most species



Figures 229–235. Morphology of tuberous roots in Periplocaceae and Asclepiadaceae. Figs 229, 230. Periplocaceae. Fig. 229. *Hemidesmus indicus* (L.) R. Br. Fig. 230. *Janakia arayalpathra* Joseph & Chandr. Fig. 231. *Ceropegia candelabrum* L. Fig. 232. *C. juncea* Roxb. Fig. 233. *Brachystelma arnottii* Baker (redrawn from Schumann, 1895). Fig. 234. *Tenaris volkensii* Schumann (redrawn from Schumann, 1895). Fig. 235. Asclepiadeae (*Holostemma annulare* (Roxb.) Schumann).

of *Ceropegia* L. and *Tenaris* E. Meyer; Figs 231–234); they are therefore of no value in tribal classification of the family.

Proposed classification

Comparison of the different classification schemes for Asclepiadaceae *s.l.* (cf. Table 1) shows that these schemes differ in three salient points. They are:

(1) *The position of the periplocoid genera*: either as a subfamily within the Asclepiadaceae, or as a family, Periplocaceae, separated from the former.
(2) *The taxonomic status of the secamonad genera*: either as a tribe or as a subfamily.
(3) *The number of tribes in the residual genera of the F. Asclepiadaceae*: i.e. whether they recognize Marsdenieae and Ceropegieae as being separate from the Stapelieae.

Using an entirely different logic, some even suggest the inclusion of the three groups — the periplocs, the secamonads and the asclepiads (*s.s.*) — as subfamilies: Periplocoideae, Secamonoideae and the Asclepiadoideae (*s.l.*) within the Apocynaceae A.L. Jussieu *s.l.* along with Apocynoideae and Plumerioideae (Safwat, 1962; Stevens, 1983).

The above differences between the different classification schemes reflect the lack of clarity of the existing apomorphies and synapomorphies within the Asclepiadaceae in particular, and within the suborder Apocynineae (incl. Apocynaceae, Periplocaceae and Asclepiadaceae; cf. Rosatti, 1989) in general. It also informs us of the disagreement among botanists on the characters that can be employed for classification at different hierarchical levels within the family.

Systematics is one of the oldest information sciences in the sense that its core is a huge global database which has proper documentation and allows quick retrieval of information on individual taxa. It also provides the opportunity to pool data at various levels of magnitude and to derive inferences. Handling the huge bulk of information on millions of organisms is its most fundamental purpose (Hawksworth, 1991; Swarupanandan *et al.*, 1996).

The family Apocynaceae A.L. Jussieu, comprising as many as 1500 species (Willis, 1973), is fairly large. The family Asclepiadaceae *s.l.* comprises nearly 2000 species (Willis, 1973). Amalgamation of the two families would result in a doubly large family, with information handling more problematic than when they are treated as separate. In this context it is worth recalling here that it was the large size of Apocynaceae A.L. Jussieu that prompted Robert Brown (1810) to segregate the members possessing mass transference to pollen into a separate family, the Asclepiadaceae. Understanding the information role of systematics as primary, we are more inclined to recognize the identity of Asclepiadaceae as being separate from the Apocynaceae A.L. Jussieu.

In order that the discussion on the high level classification of the family Asclepiadaceae is well informed, we give a summary of the discussion on various characters employed and their potential for classification at various levels in a comprehensive table (Table 4).

The free staminal filaments, anthers without sterile anther wings, the spoon-shaped translators, and the absence of pollinia and a pollinial pellicle have been used to distinguish the periplocoid genera from the rest of the Asclepiadaceae *s.l.*, (Tables

TABLE 4. Characters used by various authors and other prospective characters† useful in the supra-generic classification of the family Asclepiadaceae *s.l.*

Contrasting characters	Competing taxa	Value of characters*
ANDROECIUM		
Staminal corona (on the back of the stamens)		
1. Absent *vs.* present	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive
Anther filaments		
1. Free *vs.* united into a staminal tube	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive
Anthers		
1. Not adnate to stigma-head *vs.* adnate to stigma-head	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive
Anther tip		
1. Membranous anther tip present *vs.* absent	1. Tribe Marsdenieae *vs.* Tribe Ceropegieae *s.s.*	Intergrading, some overlap recorded
	2. Tribe Marsdenieae *vs.* Tribe Stapelieae *s.s.*	Intergrading, some overlap recorded
Anther cell number		
1. Four *vs.* two	1. Subfamily Secamonoideae *vs.* Subfamily Asclepiadoideae	Both states definitive
Anther sac morphology		
1. Embedded in the tissue of the anther wings *vs.* not embedded	1. Tribe Asclepiadeae *s.l.* *vs.* Tribe Stapelieae *s.l.*	Both states definitive as far as taxa examined, some overlap expected in primitive taxa†
Anther wings		
1. Absent *vs.* present	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive
	[2. Within the Apocynaceae] Subfamily Apocynoideae *vs.* Subfamily Plumerioideae	Both states definitive(?)
2. Forming a collar around the anther sacs *vs.* not forming a collar	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive†
3. Below the level of anther sacs *vs.* at the level of the anther sacs	1. Tribe Stapelieae *s.l.* *vs.* Tribe Asclepiadeae *s.l.*	Both states definitive, some overlap expected in primitive taxa†
Pollinaria		
1. Erect *vs.* pendulous	1. Tribe Stapelieae *s.l.* *vs.* Tribe Asclepiadeae *s.l.*	Both states definitive (as redefined in the present paper)
2. Erect *vs.* horizontal	1. Tribe Stapelieae *s.l.* *vs.* Tribe Gonolobeae	Intergrading (abandoned)
3. Pendulous *vs.* horizontal	1. Tribe Asclepiadeae *s.s.* *vs.* Tribe Gonolobeae	Intergrading (abandoned)
Translators		
1. Spoon shaped *vs.* with a hard corpuscle and two caudicles	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive

*across competing taxa; †prospective character states.

TABLE 4. (continued)

Contrasting characters	Competing taxa	Value of characters*
Translators (continued)		
2. Caudicles absent *vs.* present	1. Tribe Secamoneae *vs.*: 1. Tribe Marsdenieae *s.s.*	Definitive (?), intermediate conditions expected
	2. Tribe Ceropegieae	Both states definitive
	3. Tribe Stapelieae *s.s.*	Both states definitive
	4. Tribe Asclepiadeae *s.l.*	Both states definitive
	2. Tribe Fockeeae *vs.*: 1. Tribe Marsdenieae *s.s.*	Definitive, intermediate conditions expected
	2. Tribe Ceropegieae	Both states definitive
	3. Tribe Stapelieae *s.s.*	Both states definitive
	4. Tribe Asclepiadeae *s.l.*	Both states definitive
Cytokinesis of microspore mother cells		
1. Simultaneous *vs.* successive	1. Family Periplocaceae *vs.* Subfamily Asclepiadoideae *s.s.*	Definitive (?)
	2. Subfamily Secamonoideae *vs.* Subfamily Asclepiadoideae *s.s.*	Definitive (?)
Pollen grains		
1. Released in tetrads *vs.* in pollinia with a common pellicle	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive
2. Microspore tetrads tetrahedral/T-shaped/rhomboid *vs.* linear	1. Family Periplocaceae *vs.* Family Asclepiadoideae *s.s.*	Both states definitive, few intermediate conditions recorded
3. Microspore tetrads rhomboid *vs.* linear	1. Subfamily Secamonoideae *vs.* Subfamily Asclepiadoideae	Both states definitive
Pollinial morphology		
1. Biconvex *vs.* biconcave	1. Tribe Gonolobeae *vs.* Tribe Asclepiadeae	Intergrading
2. With pellucid margin *vs.* devoid of pellucid margin	1. Tribe Marsdenieae *vs.* Tribe Ceropegieae *s.s.*	Intergrading
	2. Tribe Marsdenieae *vs.* Tribe Stapelieae *s.s.*	Intergrading
Attachment of caudicles to pollinia		
1. At a point *vs.* along a longer margin	1. Tribe Gonolobeae *vs.* Tribe Asclepiadeae	Intergrading
Attachment of pollinia to caudicles		
1. By their base *vs.* tip	1. Tribe Asclepiadeae *s.l.* *vs.* Tribe Stapelieae *s.l.*	Both states definitive†
GYNOECIUM		
1. True styles present *vs.* absent [non-clavuncular *vs.* clavuncular gynoecium]	1. Tribe Asclepiadeae *vs.* Tribe Stapelieae *s.l.*	Presence definitive, absence not definitive†
2. Sharp constriction between ovary and gynoecium present *vs.* absent	1. Tribe Stapelieae *s.l.* Tribe Asclepiadeae	Both states definitive†

*across competing taxa; †prospective character states.

TABLE 4. (continued)

Contrasting characters	Competing taxa	Value of characters*
FRUIT AND SEED		
Pericarp		
1. Provided with protuberances, echinations, bristles *vs.* devoid of appendages	1. Tribe Asclepiadeae *s.l.* *vs.* Tribe Stapelieae *s.l.*	Presence definitive, absence not definitive†
2. Vascular traces gutter-shaped, in 1 row *vs.* not gutter-shaped, in more than 1 row	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Definitive (?)†
Fruit-placentum		
1. Thick, seeds born on denticles *vs.* thin, seeds born on the margin of thin papery flaps	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	Both states definitive†
2. Vascular traces to the seed-bearing denticles more than 1, reticulate *vs.* 1, not reticulate	1. Tribe Asclepiadeae *s.l.* *vs.* Tribe Stapelieae	Intergrading (?)
ACCESSORY FLORAL APPENDAGES		
1. Corolline corona absent *vs.* present	1. Family Asclepiadaceae *s.s.* *vs.* Family Periplocaceae	Intergrading
VEGETATIVE MORPHOLOGY		
Stem		
1. Angular vs. cylindric	1. Tribe Stapelieae *s.s.* *vs.* Tribe Ceropegieae	Intergrading
	2. Tribe Asclepiadeae *s.l.* *vs.* Tribe Stapelieae *s.l.*	Mostly definitive, some intermediaries recorded
Petiole		
1. Vasculature 1-traced *vs.* 3-traced	1. Family Periplocaceae *vs.* Family Asclepiadaceae *s.s.*	1-traced condition definitive for Family Periplocaceae†
Colleters		
1. Present *vs.* absent	1. Family Asclepiadaceae *vs.* Family Periplocaceae	Definitive (?)

*across competing taxa; †prospective character states.

3, 5). The naturalness of the periplocs is generally agreed by systematists. The above apomorphies also indicate the polyphylesis of the periplocs and asclepiads (*s.s.*). Further details on the subject are discussed under the section Periplocaceae. Accepting the concept of polyphylesis, as advocated by Huchinson (1959), we recognize the periplocs as a separate family.

Within the Asclepiadaceae *s.s.*, the 4-celled anther has been used to distinguish the secamonads from the rest. The secomonads also have been understood as a natural group since Brown (1810). The variation in size of pollinial pairs in one and the same pollinarium as seen in some species of *Secamone* R. Br. is evidence of the progressive sterilization of the anther sacs to the 2-celled state in the rest of the Asclepiadaceae. The translators in Secamoneae are very close to those in the primitive members of the Stapelieae (cf. Kunze, 1993; Safwat, 1962) and the clavuncular morphology of the gynoecium is common to both. In the light of the above evidence, one is forced to think of the Secamoneae as a group lying at the bottom of a morphological continuum extending into the rest of the Asclepiadaceae, especially to the Stapelieae. Therefore, despite the differences in the ontogenetic details of the translator, the

TABLE 5. Proposed classification of the family Asclepiadaceae R. Br. (1810), *s.l.*

Family, Tribe, Author, (Year)
Family Periplocaceae Schltr. (1905, 1924)
Family Asclepiadaceae R. Br. (1810) *s.s.* [excl. Periplocoideae Endl., 1838]
Tribe Secamoneae Don (1838)
Tribe Stapelieae Decne. (1844), *s.l.* [incl. Tribe Ceropegieae (Decne. *ex* Benth., 1868), Tribe Marsdenieae Benth. (1876) and excl. *Tylophora* R. Br.]
Tribe Asclepiadeae *s.l.* [incl. Tribe Gonolobeae Don (1838); incl. *Tylophora* R. Br.]

particulars of cytokinesis of the microspore mother cells (Safwat, 1962) and the organization of the pollen tetrads, we reject the subfamilial concept of the group (Bullock, 1956) and rank it as a primitive tribe within the Asclepiadaceae, along with Stapelieae and Asclepiadeae.

Apart from the Secamoneae, six tribes have been described within the residual genera of the Asclepiadaceae sharing the 2-celled anther: (1) Asclepiadeae, (2) Gonolobeae, (3) Fockeeae, (4) Marsdenieae, (5) Ceropegieae and (6) Stapelieae (see Table 2). The diagnostic characters that have been used in the classification of the tribes as above have been erect, pendulous and transverse pollinaria, and presence/absence of: (1) caudicles for the translators, (2) membranous apical appendage for the anther, (3) pellucid margin for the pollinia, and (4) the aphyllous succulent stem morphology.

Following the discussions on the stature of pollinaria and their redefinition in a previous section, the transverse pollinaria are actually pendulous. Thus we prefer to include the Gonolobeae with transverse pollinaria in the Asclepiadeae, which share the pendulous pollinaria, by assuming a wider circumscription of the latter.

The use of the presence/absence of a membranous apical appendage of the anther for tribal classification has been criticized as not providing satisfactory demarcation of groups. Hooker (1883) and Bruyns & Forster (1991) found that the aphyllous succulent stem morphology segregating the Ceropegieae and Stapelieae is not reliable as they intergrade. The membranous apical appendage of the anther demarcating the Marsdenieae and Ceropegieae suffers from the same weakness. The absence of caudicles in the Fockeeae is speculated as very distinctive, but many members of the Marsdenieae approach the same condition with very poorly developed, almost indistinct caudicles. On the other hand, the clavuncular morphology of the gynoecium unify all these tribes into a single natural group assuming a circumscription equalling the Stapelieae Decne. (1844), and we have incorporated this taxonomic decision into our scheme.

Further details on each of the points discussed above can be found in the sections concerning the characters, and their inferences discussed under the taxonomic part of each category. A table of suprageneric categories recognized in the proposed classification system is given in Table 5.

KEY TO THE FAMILIES (*s.s.*) OF THE ASCLEPIADACEAE R. BR. (*s.l.*)

I. Staminal filaments free, pollen grains shed in tetrads, collected in spoon-shaped translators, anther wings absent (petiole 1-traced, staminal corona absent). .... *Family Periplocaceae.*

II. Staminal filaments united to form a staminal tube, pollen grains shed as compound grains, the *pollinia* (never in tetrads), translators not spoon-shaped, anther wings present (petiole 3- or 1-traced, staminal corona present, rarely absent) .... *Family Asclepiadaceae s.s.*

Family Periplocaceae nom. fam. conserv.

Fam. Periplocaceae Schltr. in Schumann & Lauterb., *Fl. Schutzgeb. Sudsee* 351. 1905; Hutch., *Fam. Fl. Pl., ed. 2.*, 1: 381. 1959; Huber in Abeywickrama, *Revd. Hbk. Fl. Ceylon* 1: 28. 1973. Type genus: *Periploca* L.

Fam. *Apocynaceae* De Jussieu, *Gen. Pl.* 143. 1789, *pro parte*. Type genus: *Apocynum* L.

Tr. *Periploceae* R. Br. *ex* Don, *Gen. Hist.* 4: 161. 1838; Decne. in DC., *Prodr.* 4: 491. 1844. Type genus: *Periploca* L.

Subfam. *Periplocoideae* (R. Br.) *ex* Endlicher, *Gen. Pl.* 2: 587. 1838 (as 'Periploceae'); Schumann in Engl. & Prantl, *Naturl. Pflanzenfam.* 4: 209. 1895 (as Unterfam); Rendle, *Classific. Flr. Pl., revd. ed.*, 2: 478. 1938; G. Lawr., *Taxon. Vascul. Pl.* 674. 1951; Bruyns & Forster in *Taxon* 40: 387. 1991. Type genus: *Periploca* L.

Serie des *Periploca* Baillon, *Hist. Pl.* 10: 238, 241, 293. 1890, misplaced term. Type genus: *Periploca* L.

PETIOLE : vascular trace 1, gutter-shaped. COROLLINE CORONA: as thickenings or appendages on the corolla tube or at the sinuses between petal lobes. ANDROECIUM: staminal filaments free, anthers connate, pollen grains in tetrads, rarely forming loose massula (*Hemidesmus indicus* (L.) R. Br.), translator with an adhesive disc and a spoon-shaped pollen collecting arm. GYNOECIUM: devoid of a strong constriction between the carpels and stigma-head. SEEDS: born on small denticular emergences on the thick cylindric placentum, devoid of a marginal wing.

Chromosome number. Only a few species are known cytologically; $2n = 22$ and 24.

Distribution. Approximately 50 genera and 200 species (Gunn *et al.*, 1992; Willis, 1973) distributed along the warmer parts of the tropical Old World, between the latitudes of 40° N and 40° S (Good, 1952).

Taxonomic notes. Schlecther's (1905) suggestion that this group may be raised to the rank of a family is justified. The affinity of the periplocoid genera to the subfamily Apocynoideae of Apocynaceae had long been proposed by Schumann (1895) in the absence of sterile anther wings in both the groups, whereas the presence of this structure is common to both Asclepiadaceae (*s.s.*) and the subfamily Plumerioideae (Syn.: Echitoideae) of Apocynaceae. The Periplocaceae does not have a structural homologue of the common pollinial wall as seen in Asclepiadaceae. This indicates that the mass transference of pollen through pollen carrier mechanism although is

TABLE 6. A comparison of character states in the two families Periplocaceae and Asclepiadaceae *s.s.*

No.	Characters	Periplocaceae	Asclepiadaceae
1.	Colleters/scales at leaf juncture	Absent	Present
2.	Petiolar vascular traces	1 [Figs 214, 215]	3 or 1 [Figs 216–228]
3.	Corolline corona	Present	Absent; Present in a few
4.	Staminal corona	Absent	Present [Figs 5–10]
5.	Staminal tube	Absent [Figs 1–4]	Present [Figs 9, 118–124, 146–151]
6.	Connation between anthers	Present [Figs 1 & 2]	Absent
7.	Anther cells	4 [Fig. 12]	2 [Figs 23, 26, 33]
8.	Anther wings	Absent [Figs 12–14]	Present [Figs 11, 17, 26, 32, 33]
9.	Pollen grains	granular, in tetrads [Figs 34–37]	aggregated into pollinia [Figs 38–40, 48–92]
10.	Pollen carriers	spoon-shaped [Figs 41–47]	bipartite, usually with caudicles [Figs 56–92]
11.	Fusion between stamens and stigma	Absent [Fig. 4]	Present [Figs 9, 118, 119, 123, 146, 151, 164]
12.	Seeds	Born on denticles on thick cylindric fruit placenta [Figs 185, 186]	Born on the margin of papery placental flaps [Figs 187–190]
13.	Seed wings	Absent [Fig. 199]	Present [Figs 200–208]

common to both Periplocaceae and Asclepiadaceae *s.s.*, is a result of parallel development.

Kunze's (1990) studies on the morphology of the corona in Apocynaceae, Periplocaceae and Asclepiadaceae refute the homology of the corolline and staminal corona. The absence of glandular scales (‘*colleters*’ of Gluck, 1919; cf. Kunze, 1990) at leaf juncture in the Periplocaceae and their presence in Asclepiadaceae is also striking. All these point to the probable polyphylesis of the two groups and support the views held by Schlechter (1905, 1924) and Hutchinson (1959, 1969). More recently, Kunze (1993) suggested the possibility of common ancestry of Periplocaceae and Asclepiadaceae. In drawing this conclusion, Kunze considered only the characters of the translators.

The above finding does not mean that there are no relationships between Periplocaceae and Asclepiadaceae (*s.s.*). Phyletically the former is more closely related to Plumerioideae (of Apocynaceae) than to the Asclepiadaceae (*s.s.*). (cf. Huber, 1973, 1983; Hutchinson, 1969; Nilsson, Endress & Grafstrom, 1993). Based on differences in the ultrastructure and stratification of the exine of pollen grains in Periplocaceae and Apocynoideae Kubitzski, Sengbusch & Poppendieck (1991) and Nilsson, Endress & Grafstrom (1993) argue that derivation of the former from Apocynoideae is unlikely. They interpret the two groups as a result of parallel evolution from a common ancestral stock. A comparison of the character states of the families Periplocaceae and Asclepiadaceae is given in Table 6.

Family Asclepiadaceae R. Br., *s.s.*, nom. fam. conserv.

Family Asclepiadaceae R. Br. in *Mem. Wern. Soc.* 1: 12. 1811, prep. 1810 (as '*Asclepiadeae*'), *pro parte,* excl. Periploceae; Decne. in DC., *Prodr.* 8: 490. 1844, *pro parte*; Woodson in *Ann. Missouri Bot. Gard.* 28: 193. 1941. Gunderson, *Fam. Dicot.* 190. 1950; Hutch., *Fam. Fl. Pl., ed.* 2, 2: 383. 1959. Type genus: *Asclepias* L.

Family *Apocynaceae* De Jussieu. *Gen. Pl.* 143. 1789, *pro parte.* Type genus: *Apocynum* L.

Suborder *Euasclepiadeae* Benth., *Fl. Austral.* 4: 324. 1868 *et* in Benth. & Hook. f., *Gen. Pl.*, 2: 728. 1876; Boiss., *Fl. Orient.* 4: 49. 1879; Hook. f., *Fl. Brit. India* 4: 1. 1883. Type genus: *Asclepias* L.

Unterfamily *Cynanchoideae* Schumann in Engl., *Bot. Jaharb.* 17. 114. 1893 *et* in Engl. & Prantl, *Naturl. Pflanzenfam.* 4: 209. 1895; Rendle, *Classific. Flr. Pl.* 2: 478. 1938; G. Lawr., *Taxon. Vascul. Pl.* 674. 1951. Type genus: *Cynanchum* L., *nom. superfl.*, incl. *Asclepias* L.

PETIOLE: vascular traces 1 or 3, not gutter-shaped. COROLLINE CORONA: generally absent, rarely present (*Gymnema* R. Br., *Leptadenia* R. Br., *Oxystelma* R. Br.). ANDROECIUM: staminal filaments united to form a tube, anthers 2-celled or 4-celled (Secamoneae), free, basally united with the stigma-head forming a gynostegium; staminal corona present, rarely absent (*Orthanthera* Wight), anther wings present, pollinia 2, 4 (in Secamoneae; translators with a corpuscle ('*corpusculum*') and two caudicles, caudicles rarely absent (Secamoneae, and the genera *Cibirhiza* Bruyns, *Fockea* Endl.). SEEDS: born on the marginal denticles of the flat fruit-placental flaps, generally provided with a marginal wing all around.

Chromosome number. Basic chromosome number, $n = 11$, rarely 10 and 12; nearly 240 species are known cytologically, 45 are polyploids, polyploidy varies from $3n$ to $12n$, $3n$ is the most common (35 taxa), most genera have more than one polyploid species; reported $x = 18, 20, 22, 24, 33, 44, 46, 48, 55, 66, 77, 88, 110, 132$ (Federov, 1969; Albers, 1979, 1983; Albers & Meve, 1991).

Distribution. Approximately 2000 species in *c.* 250 genera (Willis, 1973; Gunn *et al.*, 1992) distributed in both the hemispheres between the latitudes 61° N and 50° S (Good, 1952). Largely inhabiting the tropics and to a lesser extent the warmer temperate; two thirds of the genera are distributed in the Old World, South Africa being the richest and Madagascar and Malesia being the next highest (Good, 1952).

Taxonomic notes. The 4-celled or 2-celled anther and pollinial statures as redefined in an earlier section in this paper, when combined with the morphology of the anther sacs and gynoecium, categorize the Asclepiadaceae *s.s.*, into three natural groups. These suprageneric groups are recognized as tribes: Secamoneae, Stapelieae and Asclepiadeae.

KEY TO THE TRIBES OF THE ASCLEPIADACEAE R. BR. (*s.s.*)

1. Anther 4-celled, pollinia 4 per stamen, translators devoid of caudicles.... ....*Tribe Secamoneae*

1\. Anther 2-celled, pollinia 2 per stamen, translators generally with caudicles (rarely absent) ....*:2*

2\. Pollinia attached to the caudicles by their base (base as defined in this paper; rarely by their lateral margins or ventro-laterally), caudicles lacking in some (*Cibirhiza* Bruyns, *Fockea* Endl.); anther sacs not embedded in the tissue of the anther wings, anther wings always below the level of the anther sacs and not forming a collar around them; gynoecium devoid of true styles (sterile narrowed upper portions of the ovary below the stigma-head), pseudostyle (united solitary portion of the style below the dilated stigma-head and above the ovary) present or absent, pseudostyle/stigma-head separated from the ovaries by a sharp constriction, stigma-head clavuncular .... *Tribe Stapelieae*

2\. Pollinia attached to the caudicles by their apex (apex as defined in this paper in a previous section; rarely by their lateral margins); anther sacs partly embedded in the tissue of the anther wings, anther wings often forming a collar around the anther sacs; gynoecium generally with two true styles and a pseudostyle, very rarely both true styles and pseudostyle absenting, constriction between the styles and pseudostyle/stigma-head absent or if present very feeble, stigma-head not clavuncular ....*Tribe Asclepiadeae*

Don Tribe Secamoneae Don

Tribe Secamoneae Reichb. *ex* Don, *Gen. Hist.* 4: 109, 159. 1838; Decne. in DC., *Prodr.* 8: 500. 1844; Benth. in Benth. & Hook. f., *Gen. Pl.* 2: 730. 1876; Hook. f., *Fl. Brit. India* 4: 3. 1883; Schumann in Engl. & Prantl, *Naturl. Pflanzenfam.* 4(2): 209. 1895. Type genus: *Secamone* R. Br.

Subfamily Secamonoideae Endlicher, *Gen. Pl.* 589. 1838 (as 'Secamoneae'); Bruyns & Forster in *Taxon* 40: 387. 1991. Type genus: *Secamone* R. Br.

Serie des *Secamone* Baillon, *Hist. Pl.* 10: 221–304. 1890, misplaced term. Type genus: *Secamone* R. Br.

Chromosome number. $2n = 22$.

Distribution. Three or four genera and *c.* 100 species distributed along tropical and South Africa, Asia, Far East and tropical Australia (Forster & Harold, 1989; Goyder, 1992).

Taxonomic notes. The 4-celled stamen and the poorly developed translator without any differentiation into corpuscle and caudicles in the secamoneaean genera represent a primitive stage. Ontogenetically the secamoneaean translator devoid of caudicles is a single unit; on the other hand, the translator in the rest of the family Asclepiadaceae *s.s.* is developmentally a joint structure of four individual pieces, two making the corpuscle and the other two contributing to the caudicles (Safwat, 1962; Kunze, 1994).

This tribe, in addition to its characteristic 4-celled anther, differs in having simultaneous cytokinesis of the microspore mother cells similar to Apocynaceae and Periplocaceae and the T-shaped or rhomboidal tetrad formation, whereas the rest of the Asclepiadaceae have successive cytokinesis and linear microspore tetrads (Safwat, 1962; Puri & Shiam, 1966).

Within the Asclepiadaceae *s.s.* the tribes Secamoneae and Stapelieae *s.l.* have ovaries separated from the stigma-head by a strong constriction and lack true style(s) (i.e. clavuncular morphology). Taking into account the above observation, it seems that the Secamoneae is closer to Stapelieae. The tribe Fockeeae Kunze, Liede & Meve, another group within the tribe Stapelieae Decne. *s.l.*, is devoid of caudicles, evincing the closer affinities between Secamoneae and Stapelieae (Kunze, 1993). Genera in the tribe Apocyneae in the Apocynaceae (Subfamily Apocynoideae) have sterile anther wings as in Asclepiadaceae and share the clavuncular morphology of the stigma-head, as in the Secamoneae and Stapelieae. All the above tribes, Apocyneae, Secamoneae and Stapelieae *s.l.*, probably share a common ancestry.

Tribe Stapelieae Decne. *s.l.*

Tribe Stapelieae Reichb. *ex* Decne. in DC., *Prodr.* 8: 606. 1844; Bruyns & Forster in *Taxon* 40: 387. 1991. Type genus: *Stapelia* L.

Tribe Orthophuramiae Don, *Gen. Hist.* 4: 106, 109. 1838, *nom. inadmiss.*

Tribe Hoyeae Graham, *Cat. Pl. Bombay* 118. 1839 (as 'Hoyaceae'), *nom. nud.* Type genus: *Hoya* R. Br.

Tribe Ceropegieae Decne. [in d'Orbig., *Dict. Univ. d'Hist. Nat.* 2: 211. 1842 (as 'Ceropegiees')] *ex* Benth., *Fl. Austral.* 4: 738. 1868 *et* Benth. & Hook. f., *Gen. Pl.* 2: 738. 1876; Hook. f., *Fl. Brit. India* 4: 3. 1883. Type genus: *Ceropegia* L.

Tribe Marsdenieae Benth., *Fl. Austral.*, 325, 333. 1868 *et* in Benth. & Hook. f., *Gen. Pl.* 2: 730, 736, 1876; Hook. f., *Fl. Brit. India* 4: 3. 1883; N. E. Br. in Dyer, *Fl. Trop. Afr.* 4(1): 237. 1902. Type genus: *Marsdenia* R. Br.

Serie des *Marsdenia* Baillon, *Hist. Pl.* 10: 228. 1890, misplaced term. Type genus: *Marsdenia* R. Br.

Serie *des Stapeliea* Baillon, *Hist. Pl.* 10: 228. 1890. Type genus: *Stapelia* L.

Tribe Tylophoreae Schumann in Engl., *Bot. Jaharb.* 17: 114. 1895 *et* in Engl. & Prantl, *Nat. Pflanzenfam.* 4(2): 209. 1895 (*nom superfl.*, includes *Stapelia* L.; excluding the type genus *Tylophora* R. Br.); Woodson in *Ann. Missouri Bot. Gard.* 28: 203. 1941.

Tribe Fockeeae Kunze, Liede & Meve in *Taxon* 43: 373. 1994. Type genus: *Fockea* Endl.

Chromosome number. $x = 22, 24, 33, 43, 44, 46, 66, 121, 130, 132$ (cf. Fedorov, 1969; Albers, 1979).

Distribution. Approximately 100 genera (Gunn *et al.*, 1992); mainly pantropical, the majority within Africa.

Taxonomic notes. To date, four suprageneric categories considered to be of tribal rank by various authors constitute the Stapelieae Decne. *s.l.* (1) Fockeeae Kunze, Liede & Meve (1994) characterized by leafy shoots and the absence of caudicles; (2) Marsdenieae Benth. (1868) with leafy shoot and anthers with membranous apical appendage [Figs 94, 95]; (3) Ceropegieae Decne. (1842) characterized by leafy shoots and the absence of apical appendages on the anther, and (4) Stapelieae Decne. *s.s.* (*sensu* Bentham, 1876) with succulent, aphyllous stems, reduced scale-like leaves and the absence of membranous apical appendages on the anther.

Genera like *Heterostemma* Wight & Arn. in the Marsdenieae Benth. are characterized by pollinia with sterile margins/tips, similar to the genera of Ceropegieae Benth. Moreover, the staminal corona in *Heterostemma vasudevanii*

Swarup. & Mangaly, with collaterally split connate scales and the corolla tube with verrucose rugations, is more similar to that of the Ceropegieae *s.s.* (Swarupanandan, 1985).

The anther tip in *Ceropegia* L. shows the presence of rudiments of membranous apical appendages on the anther that are elaborate in members of the Marsdenieae Benth. Membranous apical appendages are also rarely encountered in some species of *Caralluma* R. Br., belonging to the Stapelieae *sensu* Benth. (Hooker, 1883; Bruyns, 1987; Bruyns & Forster, 1991) making the character unreliable. For further details on this respect, see section Anther tip.

The gynoecium devoid of true style(s), the clavuncular morphology of the stigma-head and the erect pollinaria unify all the four groups (including Fockeeae) and better circumscribe them into a single tribe, the Stapelieae Decne. with the same circumscription as Tylophoreae Schumann (1895).

Tribe Asclepiadeae *s.l.*

Tribe Asclepiadeae, *s.l.* (incl. Tr. *Gonolobeae* Don). Type genus: *Asclepias* L.

Asclepiadeae Verae R. Br. in *Mem. Wern. Nat. Hist. Soc.* 1: 10. 1811. prep. 1810, *pro parte, nom. inadmiss.* Type genus: *Asclepias* L.

Tribe Cynacheae Reichb. *ex* Dumort., *Anal. Fam. Pl.* 26. 1829, *nom. nud., nom. inadmiss.* Type genus: *Cynanchum* L.

Tribe Gonolobeae Reichb. *ex* Don, *Gen. Pl.* 107, 136. 1838; Decne. in DC., *Prodr.* 8: 591. 1844; Benth. in Benth. & Hook. f., *Gen. Pl.* 2: 735. 1876; Schumann, *Nat. Plazenfam.* 4(2): 297. 1895, Woodson in *Ann. Missouri Bot. Gard.* 28: 203. 1941. Type genus: *Gonolobus* Mich.

Serie des *Gonolobus* Baillon, *Hist. Pl.* 10: 235, 241, 285. 1890, misplaced term. Type Genus: *Gonolobus* Mich.

Tribe Tylophoreae Schumann in Engl., *Bot. Jaharb.* 17: 114. 1895 *et* in Engl. & Prantl, *Nat. Plfanzenfam..* 4(2): 209. 1895 (*nom. superlf.*, includes *Stapelia* L.; excluding all genera except the type genus *Tylophora* R. Br.); Woodson in *Ann. Missouri Bot. Gard.* 28: 203. 1941.

Chromosome number. Compared to the Stapelieae, the Asclepiadeae is only poorly known cytologically, reported $x = 18, 20, 22, 24, 33, 44, 48$ (Fedorov, 1969).

Distribution. Over 100 genera (Gunn *et al.*, 1992); pantropical, a large number inhabiting the New World.

Taxonomic notes. There has not been much dispute with regard to the naturalness of the Asclepiadeae, which is indeed circumscribed by the pendulous stature of the pollinaria. Nevertheless, the status of the Gonolobeae has a bearing on the circumscription of the Asclepiadeae.

Brown's (1810) group of the gonoloboid genera were given the name Gonolobeae by Reichenback (1828) which was subsequently circumscribed as a tribe by Don (1838). Don constituted the Gonolobeae based on the transverse pollinaria and transverse dehiscence of the anther sacs; so did Bentham (1876), Schumann (1895) and Baillon (1890). Woodson (1941) and Good (1952) were of the opinion that this is an unnatural group.

Many species of the typical gonolobeaean genera *Gonolobus* Mich. and *Matelea* (*sensu* Woodson, 1941) were originally described under *Cynanchum* L. and *Vincetoxicum* Moench. (Asclepiadeae). Bentham (1876) considered *Metalepis* Griseb. under the Asclepiadeae. According to Woodson (1941) there are only three genera *Gonolobus, Matelea* Aubl. and *Fischeria* Decne. in the tribe Gonolobeae. The other genera included by earlier authors in this tribe have either been synonymized under the above three genera or have been transferred to Asclepiadeae. Occasional transfer of the above genera across the two tribes Asclepiadeae and Gonolobeae suggests unsatisfactory tribal circumscription.

According to the redefinition of the pollinarial statures in this paper, the gonoloboid pollinaria are indeed pendulous. Likewise, the characters of the gynoecium also conform to the asclepiadeaean type. The similar morphology of the gynoecium and the pollinaria suggests that the Gonolobeae does not deserve a separate tribal identity; however, we feel a subtribal recognition of the group may be meaningful.

Position of the genus Tylophora *R.Br.*

The genus *Tylophora* as constituted by Robert Brown (1810) was included in the Stapelieae by Decaisne (1844) and was treated likewise by all subsequent asclepiadologists including Bentham (1876), Hooker (1883) and Schumann (1895).

Because of the pendulous stature of the pollinaria in two species of *Tylophora* R. Br., Liede (1994) transferred them to the genus *Tylophoropsis* N.E. Br. in the Asclepiadeae. Examination of the gynoecium in several Indian species of the genus *Tylophora* (Figs 240, 241) proved that it conforms to the asclepiadeaean morphology with true styles. The structure of the stamens (Figs 236, 237), and the remarkable similarity of the translators and pollinia (Fig. 238) to those in the members of Asclepiadeae (like *Blepharodon* Decne.; Fig. 239), definitely prove the asclepiadeaean affinity and the right placement of the genus in the Asclepiadeae.

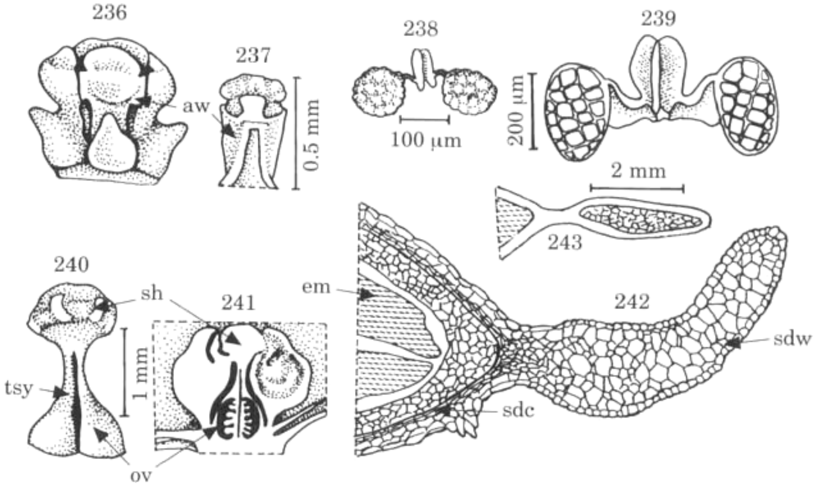
Internal morphology of the seed coat also provides evidence for the same conclusion. A cross section of the seed of *Tylophora tetrapetala* (Dennst.) Suresh is given in Figure 242. Here, the seed wing is composed of a parenchymatous columella as in the asclepiadeaean genus *Asclepias* L. (Fig. 243). This composition of the seed coat is not yet known in the Stapelieae (cf. Sylla & Albers, 1989). The simple staminal corona of the genus indicates the relatively primitive position within the Asclepiadeae perhaps closer to *Astephanus* R. Br. and *Microloma* R. Br., which completely lack a staminal corona.

CONCLUDING REMARKS

Asclepiadaceae *s.l.* comprising nearly 2000 species and around 300 genera (Willis, 1973) is a large family. Leaving the suprageneric categories Periplocaceae (50 genera and 200 species) and Secamoneae (three or four genera and 100 species) the tribes Asclepiadeae *s.l.* (over 100 genera) and Stapelieae *s.l.* (approximately 100 genera) (cf. Gunn *et al.*, 1992), are large taxonomic groups. Several suprageneric categories have been recognized in each of these tribes (see the paragraph below), but Woodson (1941) and Rosatti (1989) caution against subtribal classification in that it tends to be unnatural. However, classification, apart from reflecting the natural relationship between taxa, also serves the purpose of providing conventions for proper documentation and quick and accurate retrieval of information (Swarupanandan *et al.*, 1996). In this sense, subtribal classification of these two tribes is certainly desirable, so that the groups become taxonomically manageable, and information on the included taxa does not become unwieldy (Liede, 1994).

Within the tribe Asclepiadeae, five subtribes have been recognized by Schumann (1895): (1) Asclepiadinae, (2) Astephaninae Meisner (1838), (3) Glossonematinae Schumann (1895) (corr. name: Araujinae Fourier, 1885), (4) Cynanchinae Schumann (1895), and (5) Oxypetalinae Fourier (1885). Perhaps the gonoloboid genera also deserves a subtribal recognition. In addition, the subtribes Calotropidinae Meisner (1838) and Ditassinae Meisner (1838), Haplostemmatinae Miquel (1856), Metastelmatinae Meisner (1838), Sarcostemmatinae Miquel (1856) also exist. Likewise, within the tribe Stapelieae Decne. *s.l.* four groupings of genera are recognized: (1) Fockeeae Kunze, Liede & Meve (1994), (2) Marsdenieae Benth. (1868), (3) Ceropegieae Decne. (1842), and (4) Stapelieae Decne. (1844) *s.s.* In addition, the subtribes Hoyinae Don (1838), Gymnematinae Miq. (1856) also exist. Many of the categories mentioned above may be taxonomically synonymous, but their importance in subtribal nomenclature cannot be overlooked (cf. Sundell, 1980).

Invariably, in both the tribes Asclepiadeae *s.l.* and Stapelieae *s.l.*, subtribal classification would demand reasonably sound knowledge of intergeneric relation-



Figures 236–243. Morphology of the genus *Tylophora* R. Br. and its comparison to other members of the Tr. Asclepiadeae. Figs 236–238. *Tylophora indica* (Burm. f.) Merr. var. *indica*. Fig. 236. An early stage in the development of gynostegium. The anther wings and apical appendage are visible. Fig. 237. A mature anther showing the anther wings and apical appendage of the anther. Fig. 238. The so-called transverse pollinaria, which is actually pendulous according to the redefinition (in this paper). Fig. 239. Pollinaria in *Blepharodon hetschbachii* Fontella & Marquand belonging to the Asclepiadeae (redrawn from Peirera & da Silva, 1974); note the resemblance to that in *Tylophora*. Figs 240, 241. *Tylophora indica* var. *indica*. Fig. 240. Gynoecium as dissected from the gynostegium, showing the true styles characteristic of the Tr. Asclepiadeae. Fig. 241. Longitudinal section of the flower showing the morphology of the gynoecium. Fig. 242. A diagrammatic sketch of seed wing architecture in *Asclepias syriaca* L. (Asclepiadeae; redrawn from Sylla & Albers, 1989). Fig. 243. Seed wing structure in *Tylophora tetrapetala* (Dennst.) Suresh, showing the identity of architecture with that in the Tr. Asclepiadeae, and confirming the position of the genus in the latter. aa - apical appendage of the anther; aw - anther wing; em - embryo; sdc - seed coat; sdw - seed wing; sh - stigma head tsy - true style(s); ov - ovary.

ships within each tribe. While morphology of the staminal corona could provide evidence for intergeneric relationship, morphology of the gynoecium, anther sacs, anther wings and internal morphology of the seeds are also of great significance in this context. Documentation of these characters for species and genera is needed, as are comparative anatomical and developmental studies of the gynoecium, anther and seed across the families Apocynaceae, Periplocaceae and Asclepiadaceae.

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