Gomphocarpus (Apocynaceae: Asclepiadeae) in an African and a global context – an outline of the problem

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Aids to distinguish the species of *Gomphocarpus* found in Ethiopia and Eritrea are presented, together with a discussion on the wider relationships and systematic position of the genus, firstly in an African context, and secondly when New World taxa are taken into consideration.

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Introduction

Gomphocarpus is a familiar genus of somewhat weedy subshrubs in the derived, asclepiad, end of the Apocynaceae. The group has presented systematists with serious difficulties for decades, with no taxonomic consensus at either the species or the generic level. In the course of a study of the group over its entire geographic range, the author was able to delimit the taxa found in the Ethiopia and Eritrea Flora region. Results are presented in the form of a key to species and a stylised diagram of corona lobes, to illustrate that apparently intractable patterns of variation can be resolved by careful observation.

Controversy remains, however, in the delimitation of the genus, with North American authors including *Gomphocarpus* within a broadly defined *Asclepias*, and Old-World specialists retaining a narrower generic concept. The context for these differing views is discussed, and areas requiring further investigation are identified.

The account of *Gomphocarpus* for the Flora of Ethiopia and Eritrea is now in press, and a revision of the entire genus (as currently understood), treating African and Arabian taxa, is nearing completion.

Gomphocarpus in the Flora of Ethiopia and Eritrea region

The Flora region contains seven species of *Gomphocarpus*. Some of these were known in the mid-19th century, but the majority of taxa were described under *Asclepias* by N.E. Brown, in the *Flora of Tropical Africa* (Brown 1902-1903). Bullock (1952, 1953a, 1953b), disagreeing with Brown's broad generic concept, restricted *Asclepias* to the New World, and placed the Old World species in *Gomphocarpus*. He neither articulated his reasons for this view,

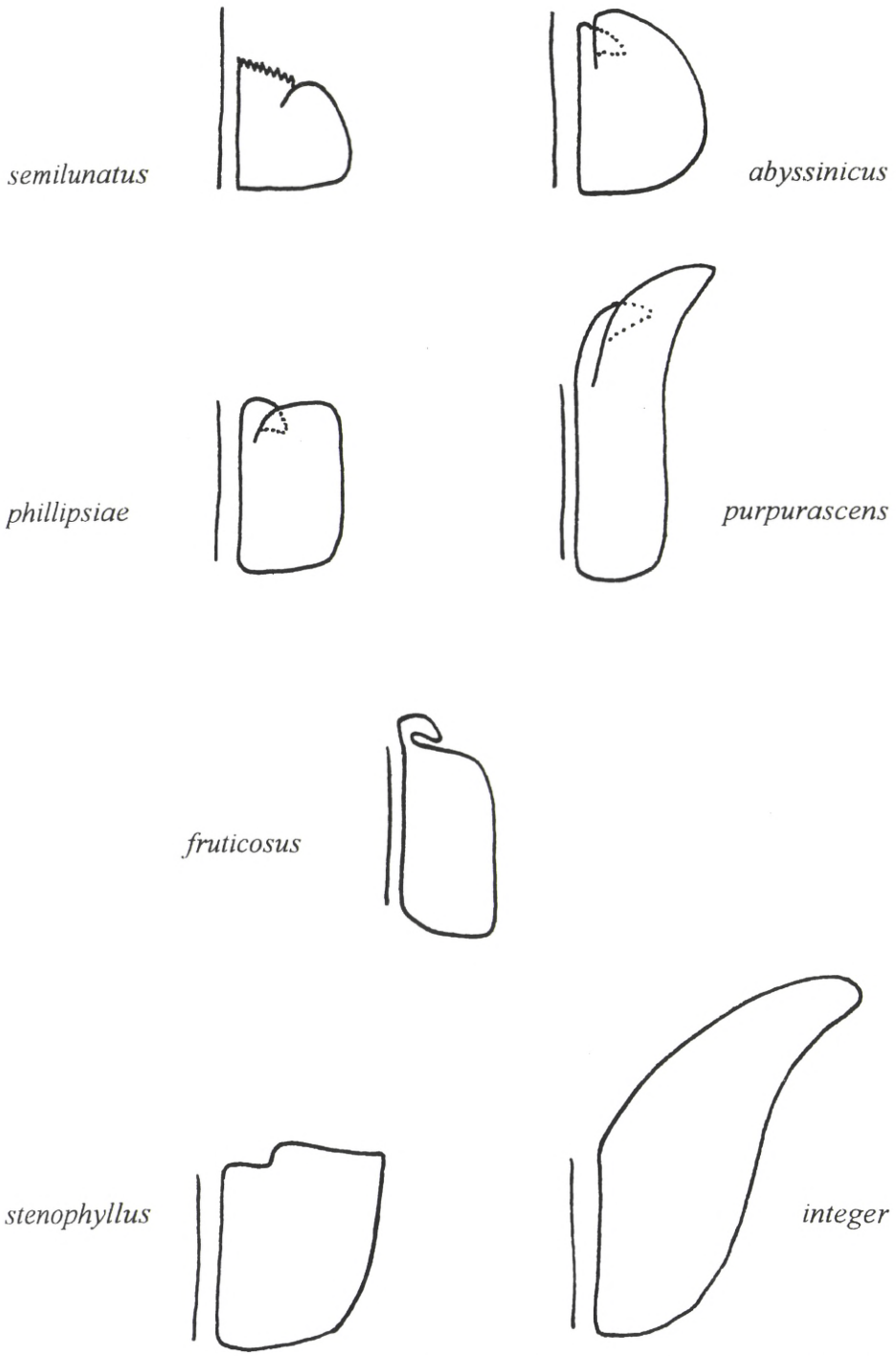

Fig. 1. Stylised corona lobes of *Gomphocarpus* species in Ethiopia and Eritrea, relative to the height of the staminal column (vertical line).

nor presented characters to support the treatment, but the two groups can generally be separated on the presence (*Asclepias*) or absence (*Gomphocarpus*) of a prominent tooth within the cavity of the corona lobe. Bullock's review of *Gomphocarpus* in tropical Africa identified some broad patterns of variation, but ultimately his treatment served only to confuse through an uneven mix of accurate nomenclature and inadequate observation of corona morphologies. Many critical but well-defined taxa were lumped into an extremely variable *G. fruticosus*, and his specific concept was never widely adopted. In the treatment presented here, many of Brown's taxa are reinstated. In a forthcoming revision (Goyder, in prep.); these will be placed in a pan-African context to reflect the wider patterns of variation.

The taxa are readily identifiable from corona morphology. A series of stylised corona lobes is presented in Fig. 1 to illustrate this point. These corona forms are correlated with features observable in nature, but which are frequently absent from herbarium sheets (growth form, branching patterns *etc.*). Collectors are encouraged to make accurate notes of such features or, even better, link photographs to herbarium specimens.

Key to species in Flora region:

1. Corolla rotate; corona lobes shorter than the column; follicles subglobose, not beaked 1. *G. semilunatus*
– Corolla reflexed; corona lobes as long as or longer than the column; follicles never subglobose, narrowing gradually or abruptly into a beak 2
2. Softly branched shrubby herbs; corona lobes ± entire; sepals ovate 3
– Stiffly branched shrubby herbs; corona lobes with a pair of proximal teeth pointing along or between upper margins; sepals lanceolate or triangular 4
3. Corona lobes oblong, taller than the column; follicles generally subglobose at the base, narrowing abruptly into an attenuate beak; corolla mostly white or cream 6. *G. integer*
– Corona lobes quadrate, ± as tall as the column; follicles more slender, narrowing gradually into the attenuate beak; corolla yellow 7. *G. stenophyllus*
4. Corona lobes brown or purple, without a distinct notch on upper margins at base of proximal teeth; corolla yellow or greenish yellow 2. *G. fruticosus*
– Corona lobes cream or green, upper margins with a distinct notch at base of proximal teeth; corolla white or cream, rarely green 5
5. Corona lobes 4.5-6 mm long, taller than the column; upper parts of the plant frequently tomentose 4. *G. purpurascens*
– Corona lobes 2-4 mm long, ± as tall as the column; upper parts of the plant pubescent but never tomentose 6
6. Corona lobes quadrate, upper margins rising gently from notch at base of proximal teeth; leaves mostly less than 5 cm long, with strongly revolute margins 3. *G. phillipsiae*
– Corona lobes D-shaped, upper margins forming an acute angle by the proximal teeth then falling away distally: leaves 7-14 cm long, margins weakly to strongly revolute 5. *G. abyssinicus*

The wider African picture

Gomphocarpus comprises a series of critical complexes containing 25 taxa in Africa and the Arabian Peninsula. There is a core group of 15 shrubby species, with a satellite group of 5 species with one or more annual stems arising from a woody rootstock. A revision of the genus is nearing completion (Goyder, in prep.). More distant, but clearly related, are genera such as *Pachycarpus* (revised by Goyder

(1998a) for tropical Africa and Smith (1988) for South Africa), *Stathmostelma* (Goyder 1998b), *Trachycalymma* (Goyder 2001) and *Xysmalobium*, each with their own distinctive suites of morphological characters. Further groups of species occur in southern Africa, although many of these have not yet been given generic rank. See Appendix 1 for a summary of the Old World genera that form a natural group around *Gomphocarpus*.

Asclepias in the Americas

Asclepias in the New World comprises *c.* 120 species, mostly in Mexico and the southern United States (Woodson 1954), but with a dozen species in drier parts of South America (Bollwinkel 1969). Vegetative diversity parallels or even exceeds that in African genera, but the floral morphology is relatively conservative, with far fewer species diverging markedly from the basic coronal plan. There are, nevertheless, some species groups with highly derived coronas analogous to Old World forms – for example, subgenus *Asclepiodora* has parallels with some of the more extreme *Trachycalymma* species from Africa. The New World treatment of *Asclepias* in outlined in Appendix 1.

How do the two systems relate?

Can the two systems be integrated and what are the factors that limit our understanding of the group as a whole? Huge morphological diversity in *Gomphocarpus* and related groups in Africa has resulted in their recognition at generic rank, while a lower, but still substantial, degree of diversity in the Americas is recognised taxonomically within a single variable genus *Asclepias*. Morphologically, the African genera that appear most closely allied to American *Asclepias* are *Gomphocarpus* and *Stathmostelma*, with the other African groups showing progressively less affinity.

Little attempt has been made to unify the classification globally and, as most potentially useful morphological characters are inextricably linked to functional pollination syndromes, it is not at all clear whether the morphological similarities displayed by a number of Old and New World species pairs are a result of close phylogenetic relation or are due to convergence. The latter is thought to be more likely in the case of *Asclepias lynchiana* (NW) and *Pachycarpus lineolatus* (OW), which show both vegetative and floral similarities; *Asclepias subulata* (NW) and *Gomphocarpus filiformis* (OW), both adapted vegetatively to extreme desert conditions; and *Asclepias tuberosa* or *A. barjoniaefolia* (NW) and *Stathmostelma pauciflorum* (OW) which share the same brightly coloured visual attraction mechanisms.

Traditional floral characters are invaluable for delimiting species, but have severe limitations at higher rank when they are so closely linked to, and are probably driven by, pollinator pressures. There is a serious danger that a global classification of the *Asclepias* group based purely on morphology would in effect be a classification of pollination syndromes rather than reflecting the evolutionary history of the group. Disparities of basic data and understanding of the mechanisms on the two continents are striking. Pollination data is all but unknown for African taxa in their native environment, whereas the American literature is replete with studies on pollinators and population studies of North American species. See Appendix 2 and 3 for a comparison.

Fishbein (1996) analysed the morphology of many of the relevant taxa cladistically, but the results are still arguably skewed by heavy reliance on pollination-related organs. His results place the four African *Gomphocarpus* taxa sampled in widely separate parts of American *Asclepias*, a situation not easy to explain convincingly, and with the remaining African genera more basal. Fishbein, Goyder, Liede and

Nicholas are now sampling across the spectrum to investigate the molecular systematics of the group in the expectation that a more independent source of data will shed some light on evolutionary relationships in the group.

Acknowledgements

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Appendix 1. A survey of *Asclepias* sensu latissimo.

<table>
<tr><th colspan="4">Asclepias sensu latissimo – c. 380 spp.</th></tr>
<tr><th colspan="2">a. Old World</th><th colspan="2">b. New World</th></tr>
<tr><td>Gomphocarpus</td><td>25 spp. in 2 informal grups (Goyder in prep.)</td><td>Asclepias</td><td>c. 120 spp. in 9 subgenera (Woodson 1954); Bollwinkel 1969)</td></tr>
<tr><td>Stathmostelma</td><td>13 spp. (Goyder 1998)</td><td>subgen. Asclepias</td><td>in 9 series – includes Gomphocarpus fruticosus</td></tr>
<tr><td rowspan="2">Asclepias
Xysmalobium</td><td rowspan="2">A polyphyletic assemblage of c. 80 spp. In 7 major groups (Nicholas & Goyder unpubl.) remaining in these two genera from Brown (1902-1903 & 1907-1909)</td><td>subgen. Podostemma</td><td></td></tr>
<tr><td>subgen. Anantherix</td><td></td></tr>
<tr><td>Trachycalymma</td><td>10 spp. (Goyder 2001)</td><td>subgen. Asclepiodella</td><td></td></tr>
<tr><td>Glossostelma</td><td>12 spp. (Goyder 1995)</td><td>subgen. Acerates</td><td></td></tr>
<tr><td rowspan="2">Pachycarpus</td><td rowspan="2">37 spp. (Smith 1988; Goyder 1998)</td><td>subgen. Solanoa</td><td></td></tr>
<tr><td>subgen. Polyotus</td><td></td></tr>
<tr><td>Kanahia</td><td>2 spp. (Field et al. 1986)</td><td>subgen. Asclepiodora</td><td></td></tr>
<tr><td>Aspidonepsis</td><td>5 spp. (Nicholas & Goyder 1992)</td><td>subgen. Podostigma</td><td></td></tr>
<tr><td>Aspidoglossum
Schizoglossum
Miraglossum</td><td>34 spp.
12 spp. (Kupicha 1984)
7 spp.</td><td colspan="2" rowspan="4"></td></tr>
<tr><td>Stenostelma</td><td>3 spp. (Bullock 1952; 1957)</td></tr>
<tr><td>Parapodium
Woodia
Periglossum
Cordylogyne
Fanninia</td><td>3 spp.
3 spp.
4 spp. (Brown 1908)
1 sp.
1 sp.</td></tr>
<tr><td colspan="2">Undescribed or unplaced c. 15 spp.</td></tr>
</table>

Appendix 2. Inferred pollination of the New World species. A list of insects observed with pollinia attached under natural conditions.

Asclepias cornuti **Coleoptera:** Scarabaeidae. **Diptera:** Midasidae. **Hymenoptera:** Apidae; Scoliidae; Sphecidae; Vespidae. **Lepidoptera:** Danaidae; Hesperiidae; Nymphalidae; Papilionidae; Pieridae	Robertson (1891)
A. cryptoceras **Hymenoptera:** Apidae	Payson (1916)
A. curassavica **Hymenoptera:** Formicidae; Vespidae. **Lepidoptera:** Danaidae; Heliconiidae; Nymphalidae; Papilionidae; Pieridae	Atsatt (1969); Bierzychudek (1981); Chaturvedi & Pant (1986); Ule (1897)
A. exaltata **Hymenoptera:** Apidae. **Coleoptera:** Cantharidae	Queller (1985)
A. incarnata **Coleoptera:** Cantharidae; Scarabaeidae. **Diptera:** Conopidae; Midasidae; Stratiomyidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Colletidae; Eumenidae; Halictidae; Nyssonidae; Pompilidae; Scolidae; Sphecidae; Tiphiidae; Vespidae. **Lepidoptera:** Arctiidae; Danaidae Hesperiidae; Libytheidae; Nymphalidae; Papilionidae; Pieridae	Kephart (1979); Macior (1965); Robertson (1887, 1891 & 1928)
A. longifolia **Coleoptera:** Scarabaeidae. **Hymenoptera:** Apidae; Megachilidae; Pompilidae; Sphecidae	Robertson (1887, 1891 & 1928)
A. purpurascens **Diptera:** Conopidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Megachilidae. **Lepidoptera:** Hesperiidae; Nymphalidae	Robertson (1887, 1891 & 1928)
A. solanoana **Hymenoptera:** Apidae	Lynch (1977)
A. sullivantii **Diptera:** Conopidae; Stratiomyidae. **Hymenoptera:** Apidae; Ichneumonidae; Megachilidae; Sphecidae. **Lepidoptera:** Danaidae Hesperiidae; Lycaenidae; Nymphalidae; Papilionidae; Pieridae	Robertson (1887, 1891 & 1928)
A. syriaca **Coleoptera:** Lampyridae. **Diptera:** Anthomyidae; Calliphoridae; Conopidae; Midasidae; Syrphidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Colletidae; Eumenidae; Formicidae; Halictidae; Megachilidae; Scolidae; Sphecidae; Vespidae. **Lepidoptera:** Arctiidae; Ctenuchidae; Danaidae; Geometridae; Hesperiidae; Lycaenidae; Noctuidae; Nymphalidae; Pentatomidae; Pieridae; Satyridae; Sphingidae. **Neuroptera:** Chrysopidae	Jennersten & Morse (1991); Kephart (1979); Macior (1965); Morse (1981 & 1982); Robertson (1928); Willson & Bertin (1979); Willson & Rathcke (1974)
A. tomentosa **Hymenoptera:** Apidae	Krombein et al. (1979)
A. tuberosa **Diptera:** Conopidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Halictidae; Megachilidae; Scolidae; Sphecidae; Vespidae. **Lepidoptera:** Ctenuchidae; Danaidae; Hesperiidae; Lycaenidae; Noctuidae; Papilionidae; Pieridae	Fishbein & Venable (1996); Robertson (1887, 1891 & 1928)
A. verticillata **Coleoptera:** Cantharidae. **Diptera:** Conopidae; Midasidae; Muscidae; Sarcophagidae; Syrphidae; Tachinidae. **Hemiptera:** Lygaeidae. **Hymenoptera:** Apidae; Argidae Colletidae; Eumenidae; Halictidae; Megachilidae Pompilidae; Scolidae; Sphecidae; Tiphiidae; Vespidae. **Lepidoptera:** Arctiidae; Danaidae Hesperiidae; Noctuidae; Nymphalidae; Pieridae	Kephart (1979); Macior (1965); Robertson (1887, 1891 & 1928); Willson & Bertin (1979)
A. viridiflora **Hymenoptera:** Apidae; Sphecidae	Robertson (1887 & 1928)
A. viridis **Hymenoptera:** Apidae	Bernhardt (1990)

Data from ASCLEPOL (http:\\www.uni-bayreuth.de) compiled by Jeff Ollerton (Nene-University College, Northampton, UK) & Sigrid Liede (University of Bayreuth, Germany).

Appendix 3. Inferred pollination of Old World species. A list of insects observed with pollinia attached under natural conditions

Gomphocarpus physocarpus (Australia – introduced) **Hymenoptera:** Apidae; Formicidae; Ichneumonidae; Pompilidae; Vespidae **Lepidoptera:** Danaidae	Forster (1994)
Gomphocarpus sp. (Europe – introduced) **Hymenoptera:** Apidae; Vespidae	Ollerton (unpublished, 1995)
Gomphocarpus 2 spp. (South Africa) **Coleoptera:** Lycidae **Hymenoptera:** "several species of winged Hymenoptera" **Lepidoptera:** Nymphalidae	Weale (1873)

Data from ASCLEPOL (http:\\www.uni-bayreuth.de) compiled by Jeff Ollerton (Nene-University College, Northampton, UK) & Sigrid Liede (University of Bayreuth, Germany). See database for Ollerton reference cited above.