Fitting pieces together – Pterodiscus Hooker (Pedaliaceae) in tropical NE Africa. A case study

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IHLENFELDT, H.-D. 2001. Fitting pieces together – Pterodiscus Hooker (Pedaliaceae) in tropical NE Africa. A case study. *Biol. Skr.* **54:** 63-74. ISSN 0366-3612. ISBN 87-7876-246-4.

The genus *Pterodiscus* presents difficult taxonomic problems, especially in tropical NE Africa, which are mainly due to: (1) high variability in nearly all characters, albeit the fruit morphology being the most stable character complex; (2) clines and character introgression, where distribution areas are in contact or overlap; (3) very inadequate type specimens, often not exhibiting the taxonomically important characters, and subsequent incomplete, sometimes even erroneous descriptions. Due to intensified collecting during the two last decades and the availability of living material and photographs taken in the natural habitat, it has now been possible to clarify the taxonomy of the tropical NE African species and to provide more complete descriptions. The presence of three fruit types that do not agree with the original generic description, necessitates a reconsideration of the concept of *Pterodiscus*. *Pterodiscus* in its present circumscription cannot be considered a natural group from a strictly phylogenetic point of view. The genus is a good example of the often irreconcilable conflict between practical (Linnaean) and phylogenetic (monophyletic or cladistic) taxonomy, currently a topic of discussion in the literature.

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Introduction

The family Pedaliaceae, comprising 13 genera (see Table 1) with approximately 70 species, is a comparatively small family, nevertheless a very interesting one in many respects.

It is an exclusively Old World family. Eight genera are confined to the African continent and one genus (*Uncarina*) is endemic to Madagascar. Four genera (*Sesamum*, *Josephinia*, *Pedalium*, *Dicerocaryum*) are mainly African, but have outliers to the east (Madagascar, India, Sri Lanka, Malayan Islands, N Australia).

The family belongs to what, in former times, has been called the Personatae; currently it is grouped either under Bignoniales (Thorne 1983) or Scrophulariales (Dahlgren 1983; Takhtajan 1980) or, quite recently, Lamiales (APG 1998).

The vast majority of the species are adapted to an arid climate, many of them preferring unstable, degraded or disturbed habitats. The African species occur in a large arc from the southern edge of the Sahara through East Africa to South Africa, Namibia and Angola (for details see Ihlenfeldt 1994).

It is well known that in the clade of Bignon-

iales/Scrophulariales the boundaries of many families are debatable. The family Pedaliaceae, however, is an exception: it is clearly delimited by an unspectacular anatomical feature, which, however, is *unique* within the Angiosperms: a remarkable type of hair. These hairs are composed of a generally short stalk of 1-3 cells and a head of invariably 4 cells (for details see Abels 1975: 28-50); after contact with water, the outer cell walls of the four cells forming the head completely dissolve, producing an enormous amount of mucilage, which is used as a lubricant in traditional medicine and for body care. The biological function of this unique structure is not yet understood.

This anatomical feature clearly separates the family from its closest relatives, the New World Martyniaceae with a similar ecology, the Old World Trapellaceae, water plants from East Asia, and the pantropical Bignoniaceae. In fact, the family Pedaliaceae has been interpreted as an ancient, highly specialised Old World branch of the Bignoniaceae (Ihlenfeldt 1967).

The family is well known for its highly specialised fruits adapted to quite diverse dispersal strategies: animal dispersal by the aid of burrs, which are either distributed by the feet (*Dicerocaryum, Harpagophytum, Josephinia)* or in the fur of passing animals (*Uncarina*); wind dispersal by the aid of winged fruits (*Holubia, Pterodiscus*), or by winged seeds (*Sesamothamnus, Sesamum* p.p.*)* or as so-called wind-ballists (*Ceratotheca, Rogeria)*. In wind-ballists the fruits only open in the upper part and stay on the plant, and the seeds are gradually expelled when the stems perform strong movements. In several cases the morphology of the fruit, adapted to a special mode of dispersal, is reflected in the generic name (see Table 1), and this implies that in this family the most important character for delimiting genera is the morphology of the fruits.

However, fruit morphology does not only serve to define the genera, but more subtle traits of the fruit types in question have also been used as important markers to delimit species within genera, *e.g.* in *Ceratotheca* and *Dicerocaryum* (Abels 1975), and in *Harpagophytum* (Ihlenfeldt & Hartmann 1970).

The 13 genera have been grouped in three tribes, which are well separated by a number of characters (Table 1).

Sesamothamneae with the sole genus *Sesamothamnus*. The species of this genus are large shrubs or even trees. The fruits are woody flattened capsules, which release seeds with broad wings. The most striking feature of this genus, however, is the succulence of the main stems.

Without any doubt, *Sesamothamnus* is the most primitive extant representative of the family. It combines certain features that are characteristic of the two remaining tribes, and could, therefore, well be the ancestor of these generally more advanced tribes. Moreover, this genus is very close to the family Bignoniaceae, and, in fact, inclusion in Bignoniaceae has been discussed in detail *e.g.* by Bruce (1953), but, in the end, rejected by the same author, mainly due to the occurrence of the mucilage hairs already described. Moreover, pollen morphology (Straka 1964; Straka & Ihlenfeldt 1965) clearly points to Pedaliaceae.

The author wishes to stress three features, which will play an important role in the further discussion:

(1) that the main stems are succulent,
(2) that the fruits are strongly sclerified (woody),
(3) and that the fruits are dehiscent.

Pedalieae: seven genera, including the genus *Pterodiscus*, which is part of a cluster of closely related genera and which will be discussed in some detail.

Sesameae: five genera including the important crop plant *Sesamum orientale* L.

Table 1. Classification and other data on Pedaliaceae.

1. The tribes and genera of Pedaliaceae R. Br.

Tribe Sesamothamneae Ihlenf.
Sesamothamnus Welw.

Tribe Pedalieae Meisn.
Uncarina (Baill.) Stapf
Rogeria J.Gay ex Del.
Pterodiscus Hooker
Pedalium Royen ex L.
Pedaliodiscus Ihlenf.
Harpagophytum DC. ex Meisn.
Holubia Oliv.

Tribe Sesameae (Endl.) Meisn.
Sesamum L.
Ceratotheca Endl.
Dicerocarum Bojer
Linariopsis Welw.
Josephinia Vent.

2. The closest relatives of Pedaliaceae and their geographical distribution and habitat:
Bignoniaceae Juss. – pantropic.
Trapellaceae Honda & Sakis – East Asian water plants.
Martyniaceae Stapf – New World, ecology similar to Pedaliaceae

3. The meaning of genus names with allusion to fruit structure:
Ceratotheca – *keras* = horn, *theke* = capsule.
Dicerocarum – *di* = 2, *keras* = horn, *karyon* = nut.
Harpagophytum – *harpago* = hook, *phyton* = plant.
Pedaliodiscus – *pedalion* = rudder, *discus* = disc.
Pedalium – *pedalion* = rudder of a ship.
Pterodiscus – *pteron* = wing, *discus* = disc.
Uncarina – *unca* = hook.

The genus Pterodiscus

The genus was established by Hooker (1844) based on a single species from South Africa, *P. speciosus* Hooker. Hooker, too, chose a name that alludes to the structure of the fruit (and, indirectly, to the mode of dispersal). He derived the generic name (in a latinised form) from the Greek *pteron* = wing, and *discos* = disk, thus characterising a fruit that is flattened and bears wings (Fig. 3).

Pterodiscus is restricted to the African continent and exhibits a distinctive NE (Somalia, Ethiopia, N Kenya, 5 species) – S (Zimbabwe, Zambia, Botswana. S Angola, Namibia, South Africa, 7 species) disjunction which, within the family, it shares with the genera *Sesamothamnus* and *Dicerocaryum* (Ihlenfeldt 1994). The two distribution centres are linked by a single, only sporadically occurring species (*P. angustifolius* Engl., Tanzania, N Mozambique).

Hooker defined his new genus by a combination of two remarkable features. These two features also occur individually (in different combinations) in related genera, *i.e.* they are not restricted to this genus.

Growth form. The plants possess as the perennating organ a thickened and ± succulent structure, termed a "caudex" (already used by Hooker in the generic description), which is partly aerial and partly subterranean. This succulent caudex ensures the survival of the plants during the dry season. Morphologically the caudex of *Pterodiscus* originates from the lower portion of the primary stem and the upper part of the taproot (Ihlenfeldt, unpublished data). The lower subterranean part of the caudex is always succulent and may form a large tuber, often bearing some lateral roots that are also swollen (Fig. 1); the upper part (at least partly aerial) also may be swollen and succulent (Fig. 2).

Every rainy season the top of the caudex produces one to several erect annual shoots, which bear single axillary flowers, from which the characteristic fruits develop. Occasionally the upper part of the caudex may be branched. The usually unbranched annual shoots are mostly unliginified, only rarely slightly lignified, and usually disintegrate at the end of the season and decay. To spot a *Pterodiscus* during the dry season, therefore, may be difficult.

It is apparent that this remarkable structure evolved from the succulent main stem found in *Sesamothamnus* by miniaturising the succulent stem and extending succulence to the upper part of the taproot. The succulent stem of *Sesamothamnus* has a characteristic translucent papery bark, and the same type of bark is found in aerial parts of the caudex in *Pterodiscus*.

As has already been mentioned, the caudex structure is not restricted to the genus *Pterodiscus*, but also occurs *e.g.* in *Harpagophytum*, where it may reach an enormous size.

Fruit. According to the original generic description, the fruit consists of a coriaceous, laterally compressed, indehiscent oblong body (which is the fruit proper), which bears 4 pergamentaceous wings, longitudinally arranged in pairs in the median plane of the fruit (Fig. 3). The fruit has two locules, each of which (in the type species, see below) contains a single (very rarely 2) oblong seed with a smooth testa. The ripe fruits become detached and are blown around by the wind, rolling on the ground like wheels.

The author wishes to stress the following features: body coriaceous, wings pergamentaceous, fruit indehiscent, single oblong seed per locule.

Again, this highly adapted fruit type is not restricted to the genus, it is also found in the genus *Holubia*. *Holubia*, however, lacks a caudex, it is a strict annual, and the fruits contain numerous seeds.

Taxonomic problems in Pterodiscus, with special emphasis on the tropical NE African species

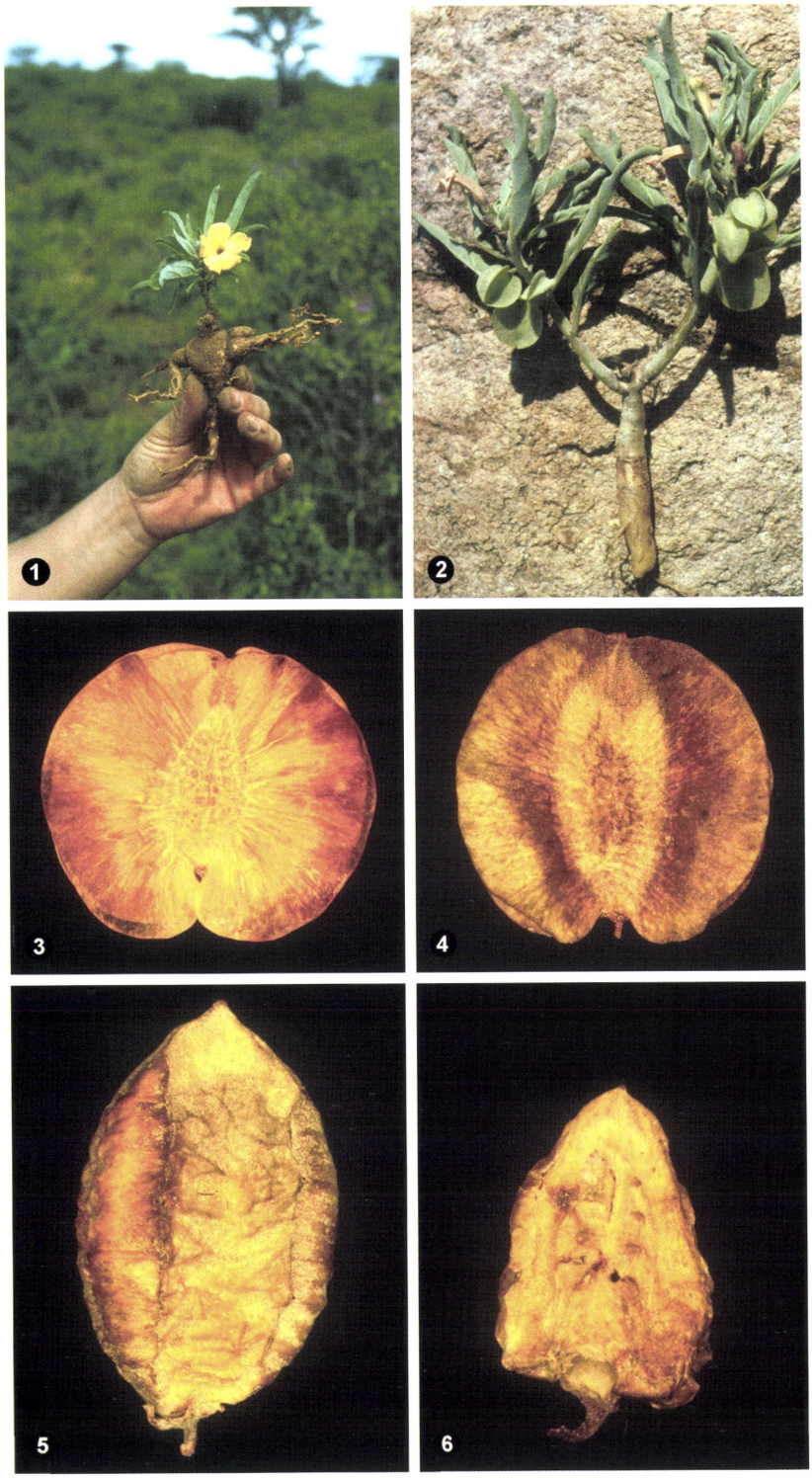
Of a total of 19 species (17 described in *Pterodiscus*, plus 2 species, originally described in related genera, but now considered as belonging to *Pterodiscus*), 10 species have been described from tropical NE Africa (Table 2).

Generally, the delimitation of the species, the interpretation of the descriptions and subsequently the correct naming of the species in *Pterodiscus* is difficult. This is mainly due to three reasons:

1. All species, especially those with a larger distribution area, exhibit a high variability in nearly all characters. In several cases single characters or complexes of characters may form topoclines (see example described below).

Fig 1-2: Habit and the two basic types of caudex in *Pterodiscus*. **Fig. 1**: *P. kellerianus* (*Specks* 804, Ethiopia, Sidamo). The lower part of the caudex forms a large succulent tuber with some lateral roots that are also swollen (succulent). The diameter of the upper part, which is partly aerial, is much less swollen and rather short; it bears a single annual shoot with a large flower. The plant has unusual oblong leaves with entire margins, apparently due to character introgression from *P. ruspolii* (see text). (Photo courtesy of E. Specks). **Fig. 2**: *P. aurantiacus* Welw. (*Wilke & Thiede* 104927, N Namiba). Subterranean and aerial parts of the caudex are of approximately the same diameter and length. The plant bears two annual shoots with flowers and several immature fruits. (Photo courtesy of J. Thiede). →

Fig. 3-6: Fruit types in *Pterodiscus* (see Table 3 and text). **Fig. 3**: *P. aurantiacus* (*Dinter* 7092, Namibia). The coriaceous body of the fruit (the fruit proper) is ovate and the upper part is much narrowed, forming a needle-like structure (compare with Fig. 4). The four pergamentaceous wings are very broad and overlap at the base of the fruit. Each locule contains a single oblong seed, and the fruit is indehiscent. Natural size: 33 x 39 mm. **Fig. 4**: *P. kellerianus* (*Friis et al.* 3260, Ethiopia, Sidamo). The coriaceous body is oblong and not narrowed in the upper part, the broad wings are pergamentaceous. Each locule contains *c.* 2-6 obovate seeds, and the fruit is tardily dehiscent. Natural size: 28 x 27 mm. **Fig. 5**: *P. coeruleus* (*Senni* 545, S Somalia). The body of the fruit is woody like the narrow wings (except their extreme margins). Each locule contains a single oblong seed, and the fruit is indehiscent. Natural size: 10 x 8 mm. **Fig. 6**: *P. saccatus* (*Bally* 9960, CN Somalia). The body of the fruit is woody, the *c.* 3 mm broad wings are pergamentaceous, but very indistinct as they are curled and pressed to the body. Each locule contains *c.* 6 obovate seeds, and the fruit is tardily deshiscent. Natural size: 20 x 13 mm.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Shape and size of the leaves are greatly influenced by the position of a given leaf within the leaf sequence of a season (the first leaves generally are much smaller and less divided, so that the plants have occasionally been described as "heterophyllous", *e.g. P. heterophyllus* from tropical NE Africa). The shape is also influenced by environmental conditions, especially by the amount of available water.

In many species size and coloration of the flower is also very variable, even within a single population.

The morphology of the taxonomically important caudex (Ihlenfeldt 1988) depends on the age of the plant. Only fully grown plants exhibit a caudex that is typical of the species in question.

Occurrence of intermediate forms (apparently due to character introgressions) in contact zones of allopatric species, or where partly sympatric species overlap (see example described below).

However, the morphology of the fruit represents the most stable and thus the taxonomically most reliable character complex (as in many other genera of the family), though the first fruits of the season may look different.

In many cases unambiguous identification is only possible if the following parts are available (an "ideal" herbarium specimen): caudex of an adult plant (plant collectors usually refrain from providing the caudex as preserving this succulent structure is troublesome); annual shoots with a full leaf sequence, at least leaves from the middle of the season; flowers; mature fruits (except the first ones). It is nearly impossible to match all these requirements in a collection made in the wild. Incomplete material, therefore, is one of the main reasons for the taxonomic problems in the genus, and this applies unfortunately also to the type specimens (see below).

A good example of problems caused by clines and character introgression, which is now fairly well documented, is the *P. kellerianus*-*P. ruspolii* complex from Somalia and Ethiopia. For the most part the two species are allopatric. *P. kellerianus* inhabits a comparatively narrow strip from NE Somalia (Bari) to C Somalia (Bakool and Gedo), then extending westward into Ethiopia (Sidamo). According to the type specimen, it is a medium-sized plant (about 15 cm high) with yellow flowers and pinnatifid leaves with a dense cover of mucilage hairs on the lower surface. *P. ruspolii* occurs in a parallel strip from N Somalia (Sanaag) through Ethiopia (Harerge, Bale, Sidamo), then extending into the whole of northern Kenya; that means, in Sidamo the areas of the two species overlap. *P. ruspolii* is a much more robust plant, with large elliptic leaves with entire margins, mucilage hairs are sparse, the long annual shoots (up to 50 cm) are often prostrate, and the fruits are larger. The flowers are yellow as in *P. kellerianus*.

Plants of *P. kellerianus* from NE Somalia are very tiny (only a few cm tall). The leaves are extremely pinnatifid, the cover of mucilage hairs extremely dense, so that the leaves appear grey, and in contrast to the type specimen, the flowers are red. Proceeding southwards, the plants become larger, the leaves less deeply pinnatifid, the cover of mucilage hairs less dense, and the colour of the flower gradually changes via pink to yellow, often tinged with orange. In the SE corner of Ethiopia the specimens nicely match the type. However, proceeding westwards into Sidamo, where the distribution area of the two species in question overlap, specimens are found with lanceolate, only slightly toothed leaves and even specimens with oblong leaves and completely entire margins (Fig. 1). In this area many specimens can no longer be identified unambiguously, as even the fruits, usually very distinctive in this genus and therefore taxonomically reliable, are very similar in these two species (and represent an aberrant type, see below).

Table 2: Availability of information on taxonomically important characters from the type specimens of the tropical NE African species of *Pterodiscus*. ex descr. = information available from the description. * = description apparently taken from another specimen.

Species	Caudex	annual shoot with flower	Fruit
P. coeruleus Chiov.	– ("annual" ex descr.)	+	+
P. kellerianus Schinz (2 syntypes)	± (seedling)	+	± (immature)
P. ruspolii Engl. (2 syntypes)	± (young plant)	+	–
P. somaliensis Baker ex Stapf	–	+	–
P. wellbyi Stapf	± (young plant)	+	–
P. saccatus S.Moore	–	+	–
P. heterophyllus Stapf	–	+	–
P. intermedius Engl. (type lost)	± (ex descr.)	+ (ex descr.)	–
P. undulatus Baker f.	± (incomplete)	+	+
P. purpureus Chiov.	+	± (no flower*)	–

2. Very incomplete or even lost type specimens. Many type specimens only consist of an annual shoot with poorly preserved flowers (Table 2), in one case even flowers are lacking, and especially mature fruits are missing. Subsequently the descriptions of the species are generally very incomplete, especially with respect to the taxonomically important characters.

Moreover, the type localities are often very vague and tracing of obsolete place-names is often difficult.

3. In some cases the descriptions are erroneous or even misleading by claiming certain characters as diagnostic ones which in reality are shared by all species of the genus. One example has already been cited, the succession of leaves in *P. heterophyllus*; another example is *P. saccatus* from NW Somalia. The epithet alludes to a sac-like protrusion at the base of the corolla tube, which can easily be identified as a reduced spur, found in several genera of the Pedaliaceae. This structure is found in all species of *Pterodiscus*, *i.e.* it is a generic character.

All these three factors are especially true for the tropical NE African species, and thus the taxonomy the tropical NE African species presents particularly difficult problems.

Due to intensified collecting during the last two decades and especially due the availability of living material and photographs taken in the natural habitat, it has been possible to present more complete descriptions and to clarify the taxonomy of these tropical NE African species. A detailed description of the fruits of all species has been published elsewhere (Ihlenfeldt 2001), and detailed specific descriptions will be included in the *Flora of Ethiopia and Eritrea* and in the forthcoming new *Illustrated Handbook of Succulent Plants* (Editor: U. Eggli, Zürich).

For the flora of Ethiopia and Somalia 4 species, now sufficiently well known, can be accepted: *P. kellerianus*, *P. ruspolii* (syn. *P. somaliensis* and *P. wellbyi*), *P. saccatus* (syn. *P. heterophyllus* and *P. intermedius*), *P. undulatus* (syn. *P. purpureus*). Only a single species, *P. coeruleus*, which is only known from the type collection from the extreme south of Somalia, remains

doubtful. This species has a strange woody fruit with equally sclerified wings (see below). The fruit is very similar to the that of *P. angustifolius* from Tanzania and N. Mozambique, and *P. coeruleus* might therefore be a purplish-flowered variety of this yellow-flowered species; however, this would extend the known area of this ecologically deviating species considerably.

Aberrant fruit types in Pterodiscus

The study of the fruits of *Pterodiscus* in tropical NE Africa revealed interesting novel facts, which shed completely new light on the relationships, the evolution and especially the genus concept of *Pterodiscus*.

There are three fruit types that do not agree with the original generic description (Table 3), two of them already known:

Stapf (1906) pointed out that at least some of the tropical NE African species contain several seeds per locule. This is true for *P. kellerianus, P. ruspolii* (and *P. saccatus*, see below) whose fruits contain 2-6 seeds per locule. In these fruits the upper part of the body is much broader (compare Fig. 3 with Fig. 4). Most of the species, including the type species, have only one seed per locule; in these species the seeds are invariably oblong and exhibit a smooth testa. In the polyspermous fruits, however, the seeds are obovate and have a sculptured testa. Moreover, what is much more interesting, these polyspermous fruits are not at all indehiscent (as claimed in the generic description), in fact they are dehiscent, though tardily so, a fact that has been overlooked until now. Against the background of the dispersal mode, it makes sense that these polyspermous fruits open some time after their detachment from the plant and gradually release their seeds while being dispersed, in contrast to those with only two seeds, which remain closed.

Another aberrant fruit type, already mentioned, has been described for *P. angustifolius* Engl. from Tanzania. This species has strongly sclerified, woody fruits with narrow wings which are also sclerified (except their extreme margins), not pergamentaceous. The locules contain a single oblong seed, and the fruit is indehiscent, which agrees with the generic description. Engler described this species twice: in 1894 as *P. angustifolius*, based on a specimen without fruits, and again in 1902, based on a specimen that possessed mature fruits, in a separate new monotypic genus as *Pedaliophyton busseanum* Engl. By choice of the generic name *Pedaliophyton* he apparently intended to indicate the similarity of the fruit of his new genus with the equally woody fruit of

Table 3: The four fruit types in *Pterodiscus*. Note the reticulate distribution of characters and character states. The fruits of the following species agree with the generic description: *P. aurantiacus* Welw., *P. brasiliensis* (DC.) Asch., *P. elliottii* Stapf, *P. luridus* Hooker f., *P. ngamicus* Stapf, *P. speciosus* Hooker, *P. undulatus* E.G. Baker; all except *P. undulatus* native af Southern Africa.

taxon & plant	fruit body	wings	dehiscent?	seeds per locule	shape of seeds
generic description (type species)	coriaceous	broad pergamentaceous	no	1	oblong
P. ruspolii *P. kellerianus*	coriaceous	broad pergamentaceous	yes	2-6	obovate
P. coeruleus *P. angustifolius*	woody	narrow woody	no	1	oblong
P. saccatus	woody	narrow pergamentaceous	yes	4-6	obovate

Pedalium, where the four (woody) wings are reduced to four spines at the base of the fruit. Bruce (1953) detected that *P. angustifolius* and *Pedaliophyton busseanum* are synonyms, and transferred *Pedaliophyton busseanum* in spite of the aberrant fruit to the genus *Pterodiscus*. As has already been mentioned, the structure of this fruit agrees with that of *P. coeruleus* (Fig. 5).

The third, still undescribed aberrant fruit type was first collected by Bally in 1954 (*Bally* 9960, K) in N Somalia. Unfortunately the collection in question only consisted of fruits and some leaves. The body of this fruit is also strongly sclerified (as in *P. angustifolius* and *P. coeruleus*), but has four narrow pergamentaceous wings, which in the mature fruit are curled and pressed to the body of the fruit and are therefore very indistinct (Fig. 6). Each locule contains several obovate seeds with a sculptured testa, and the fruit is tardily dehiscent (as in the *P. kellerianus-P. ruspolii* complex). Only recent collections revealed that this aberrant fruit type belongs to *P. saccatus* (with the two synonyms *P. heterophyllus* and *P. intermedius*, see above), already described by Moore in 1899.

Comments on the circumscription of Pterodiscus

The existence of four different fruit types within the genus, three of them basically differing from the fruit of the type species, led the present author to re-evaluate the genus concept of *Pterodiscus*.

Attempts to produce a computer-generated cladogram of the "core genera" of the tribe *Pedalieae* (*i.e.* excluding the genera *Uncarina* and *Rogeria* which apparently represent early side branches, see Ihlenfeldt 1967) failed due to the impossibility of setting up a usable matrix which would at least meet the minimum requirements. The main reasons are:

1) Nearly all characters and character states that could be used, form parts of the highly evolved dispersal systems, that means that they are functionally interdependent and, therefore, cannot evolve independently (see Ihlenfeldt 1967). These complex character syndromes are even not restricted to the fruits, but they also integrate growth form and life strategy, the latter in turn being connected with ecological constraints. This drastically reduces the number of available characters.
2) There are uncertainties about the homology (in a strict sense) of the morphological fruit structures, *i.e.* they may represent homoplasies.
3) There are uncertainties about the correct coding of the character states.

Diagram 1 ("phylogenetic tree") illustrates the putative phylogeny of the core genera of the Pedalieae. It has been constructed on the basis of a number of plausible assumptions. It is mainly based on life forms and fruit morphology, and the underlying evolutionary steps are indicated in the diagram. The starting point (bottom) is *Sesamothamnus,* with succulent stems and a sclerified dehiscent capsule containing numerous seeds with broad wings. The first step would be the formation of a caudex with annual shoots by miniaturising the whole plant, reduction of the seed wings and especially the formation of four longitudinal emergences ("wings") on the fruit, and the fruit becomes tardily dehiscent. The wings may be sclerified or pergamentaceous, the latter state is considered as derived.

What comes out clearly, even if one tries other versions, is that the species of *Pterodiscus* appear in different lineages; that means *Pterodiscus* in its present circumscription cannot be considered a natural group applying the concept of cladistics, as the species are kept together by a (relatively) primitive (plesiomor-

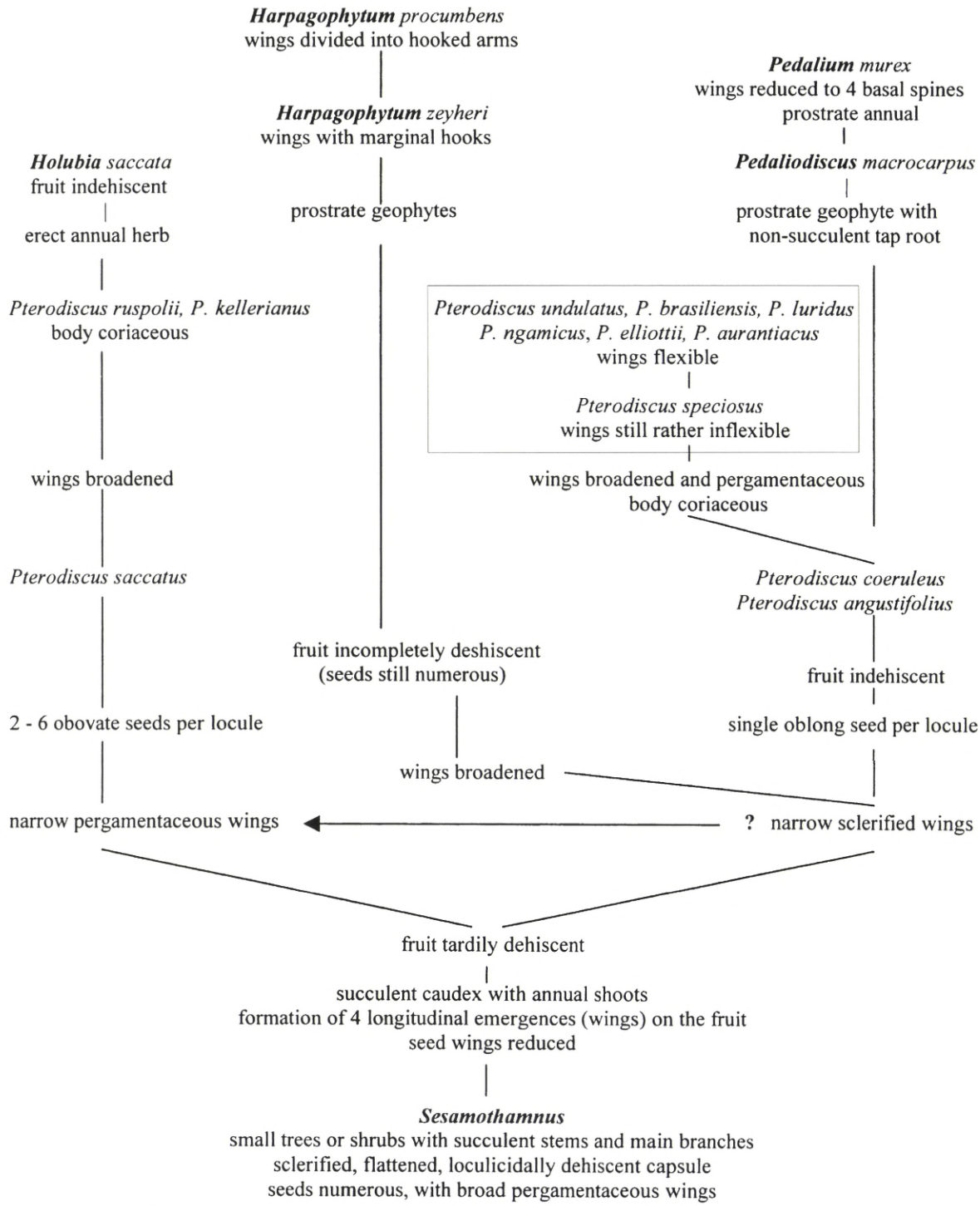

Diagram 1. Possible phylogeny of *Pterodiscus* and related genera. For details compare text.

phic) character only, namely life form based on a caudex. Only a cluster of 7 species (mainly from southern Africa), whose fruits agree with the original generic description and which includes the type species *P. speciosus*, can be considered a natural ("monophyletic") unit.

One can put it this way: *Pterodiscus* in its present circumscription appears to represent a moderately advanced evolutionary layer within the tribe Pedalieae, from which several highly specialised genera (*Holubia*, *Harpagophytum*, *Pedaliodiscus* and *Pedalium*) evolved.

Pterodiscus in the generally accepted present circumscription, is a good example of the conflict between practical (Linnaean) taxonomy and phylogenetic (monophyletic or cladistic) taxonomy. Quite recently Sosef (1997) gave convincing reasons for this irreconcilable conflict. For the case of *Pterodiscus* this means: it is easy to assign a specimen, even if the material is incomplete, if *e.g.* the taxonomically extremely important fruits are lacking, to the genus *Pterodiscus*. Strict application of phylogenetic concepts, however, would require redefinition of most of the genera in the tribe Pedalieae and produce groups difficult to circumscribe and difficult to handle with regard to the easy identification of taxa.

Acknowledgements

The author wishes to thank the directors of numerous herbaria for the loan of valuable material. Several persons contributed information and material, especially for tropical NE Africa: Mrs. Susan Carter Holmes (Royal Botanic Gardens Kew, England), Mr. John Lavranos (Loulé, Portugal), Mr. Ernst Specks (Erkelenz, Germany), Prof. Ib Friis (Botanical Museum and Library, Copenhagen, Denmark), Mr. Chuck Hanson (Glenwood, USA), Dr. Joachim Thiede (Botanical Institute, Universität Hamburg); without their generous support it would not have been possible to clarify the taxonomy of the tropical NE African species of the genus *Pterodiscus*. Special thanks are due to Dr. Roger Polhill (Royal Botanic Gardens Kew) for improving the English text.

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