A re-examination of the genus *Amphibolia* (Mesembryanthemaceae)

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**ABSTRACT**

The holotypes of all five species placed in the genus *Amphibolia* L. Bol. ex Toelken & Jessop have been examined. Only two of them agree with the generic diagnosis, but they are not congeneric. The type species chosen by Herre is shown to be in serious conflict with the protologue and a new lectotype (*A. maritima* L. Bol. ex Toelken & Jessop) is therefore designated. The other four species are excluded from *Amphibolia*.

**INTRODUCTION**

In the course of a comprehensive study of the subtribe Ruschiinae (M. Dehn) and the preparation of a survey of the genera of the Aizoaceae (H.E.K. Hartmann), the genus *Amphibolia* L. Bol. ex Herre (Toelken & Jessop 1976) have been re-examined. The results and taxonomic consequences are presented.

*Amphibolia* was first described by Bolus (1965). It was lectotypified and thus validated by Herre (1971). Toelken & Jessop (1976) reviewed the nomenclature and supplied correct names for all five species included in the genus at that time.

The history of the genus started earlier, though, when Bolus (1962) noticed that the two species she had described in the genus *Stoeberia* Schwant. (*S. hallii, S. littlewoodii*) did not conform with the generic characters of that genus. 'a new genus is therefore required for them...' (i.e. p. 14). The diagnosis of that new genus, namely *Amphibolia* (Bolus 1965), gives three characters: perennial, fruits with winged valves (like in *Lampranthus*) and closing bodies (like in *Ruschia* and *Stoeberia*). In addition Bolus stated that the capsules differ from those of *Stoeberia* insofar as they open spontaneously and do not close again. No further features were mentioned, but Herre (1971) provided a short description.

**RESULTS**

Since the diagnosis of *Amphibolia* stresses fruit characters, the present re-examination also concentrates on capsules. The holotypes of all five species placed in the genus were examined. Three different combinations of the relevant character expressions could be distinguished (Table 1). *A. maritima* and *A. littlewoodii* possess valve wings and closing bodies (CB), as well as closing rodlets (CR) at the distal end of the covering membranes (Figure 1B). The remaining three species lack closing bodies, but two of them (*A. hallii* and *A. gydowensis*) possess closing rodlets (CR in Figure 1D). *A. stayneri* shows no closing device at all.

It seems that in the last three species mentioned the prominent free end of the placenta (PL in Figure 1D) has been understood to represent a closing body (compare data from descriptions in Table 1). This interpretation, however, has to be rejected. The relevant placental structure is not in direct contact with the tangential endocarp, as would be necessary for an endocarpal closing body (Hartmann & Liede 1986). Furthermore, funicles occur up to the tip of the placenta (F in Figure 2), precluding, for lack of space, the formation of a placental tubercle (as described for *Pleiospilos* subgenus *Pleiospilos* by Hartmann & Liede 1986).

Remarkable, even though not mentioned in all descriptions, is the existence of closing rodlets in four of the five species (Table 1, CR in Figure 1B, D).

Examination of additional characters shows distinct differences between the two species with closing bodies. Capsules of *A. maritima* break off easily and regularly after ripening, leaving the persistent peduncle on the plant, thus forming a spine; capsules and peduncles are light-coloured, almost white, like all stems and branches of the plant; the margins of the valves are only moderately raised and, as a consequence, the valves open so completely that the tips touch the base of the fruit. Other distinguishing features of *A. maritima* are short, inflated, roundish leaves, small flowers and petals barely reaching the tips of the calyx lobes. In contrast, capsules of *A. littlewoodii* remain on the peduncles and they are dark reddish brown from numerous tanniniferous idioblasts, like all stems and branches. The margins of the valves are raised to high rims preventing the valves from opening further than 180°. Other characteristic features of *A. littlewoodii* are long, slender leaves and larger flowers with the petals exceeding the tips of the calyx lobes.
FIGURE 1.—Longitudinal sections of capsules. A, B, *Amphibolia maritima* (Hall 2885, BOL): locule (LO) blocked apically by closing body (CB) protruding from inner wall (W) of capsule; placenta (PL) torn to its base; in dry state (seen here) closing body touches expanding keel (EK) but not covering membrane (CM); closing rodlet (CR) and adjacent bend of outer part of covering membrane (OCM) pulled out from between valve proper and expanding keel at first opening of capsule. C, D, *Amphibolia hallii* (Hall 1741, BOL): placenta (PL) separates apically from endocarp and bears funicles (F) to its very tip; thickening of outer fruit wall (TW) above placenta (similar to condition in *Lamprothamnium*-type fruit; Hartmann 1988), distal end of covering membrane (CM) bent against expanding keel (EK), resembling position in unopened fruit. RCM, reflexed part of covering membrane; S, seed. Scale in mm.
TABLE 1.—Comparison of fruit characters of Amphibolia, Ruschia and Lampranthus as observed in the holotypes and as given in original description

<table>
<thead>
<tr>
<th>Taxon (holotype)</th>
<th>Valve wings</th>
<th>Closing bodies</th>
<th>Closing rodlets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>holo. descr.</td>
<td>holo. descr.</td>
<td>holo. descr.</td>
</tr>
<tr>
<td>A. maritima, Hall 2885 !</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>A. littlewoodii, Littlewood KG 522/59 !</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>A. hallii, Hall 174 !</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>A. gydouwensis, Leipoldt 480! !</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>A. stayneri, Stayner KG 258/65 !</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Ruschia</td>
<td>(+),-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Lampranthus</td>
<td>+</td>
<td>-</td>
<td>(+),-</td>
</tr>
</tbody>
</table>

( ) = Rare expression of characters.

CONCLUSIONS

In the light of recent findings in fruit typology (Hartmann 1988) and in generic delimitations in the wider relationship of the Ruschiinae (Dehn 1989, and in prep.), the groups described above can be allied to different fruit types and, consequently, to different genus groups.

Dehn (1989, and in prep.) has been able to show that valve wings may occur within the Ruschia-type of fruit. The possession of these structures can therefore not be used to exclude taxa from that group. Essential character expressions are the possession of small endocarpal closing bodies and of closing rodlets at the covering membranes.

A. maritima and A. littlewoodii agree with these requirements, but they differ in other characters not considered by Bolus (1965) in the delimitation of Amphibolia. Seeing that fruit characters are presently considered to be of great taxonomic importance in Mesembryanthema (e.g. Hartmann 1983; Dehn 1989; Ihlenfeldt & Bittrich 1985), the two species have to be understood as belonging to two different genera within the group characterized by the Ruschia-type of fruit. Whereas A. maritima shows several similarities to the genus Eberlanzia (valve wings, small closing body, widely opening valves, inflated short leaves, white stems, pedicels becoming spines; all data after Stüber unpublished), A. littlewoodii can be placed within the close relationship of the genus Ruschia (small closing body, narrow valve wings opening into an upright position, long slender leaves, dark reddish stems; Dehn in prep.).

Of the remaining three species, A. hallii and A. gydouwensis lack closing bodies but possess valve wings and closing rodlets (Table 1). This combination places them closest to the Lampranthus-type fruit (Hartmann 1988) which is characterized by valve wings and closing ledges in the absence of closing bodies; characteristic also is a thickened tissue within the outer wall above the zone where the placenta ends (similar to TW in Figure 1D). Preliminary investigations in the genus Lampranthus indicate that the taxon is probably heterogeneous and will have to be divided up, A. hallii and A. gydouwensis agreeing with a certain part of the material.

Superficially, A. stayneri may be placed in the vicinity of the Lampranthus-type fruit as well, but the complete absence of any closing device and the formation of rather fragile capsules indicates a closer relationship to the Drosanthenum-type of fruit (Hartmann 1988). Within this group, the nearest relative seems to be the genus Mestoklema (this hypothesis is supported by the formation of a remarkable storage root in A. stayneri, a feature common in Mestoklema, but further characters will have to be examined).

FIGURE 2.—Amphibolia hallii: distal opening of locule of capsule shown in Figure 1C,D seen from above after removal of valve, showing end of placenta (PL) which can be mistaken for a closing body. CM, covering membrane; EK, expanding keel; F, funicle; PL, placenta; RCM, reflexed part of covering membrane; W, wall. Scale in mm.
The results show that only two species, *A. maritima* and *A. littlewoodii*, conform with the generic diagnosis. This implies that the lectotype species (*A. hallii*) selected by Herre (1971) is in serious conflict with the protologue (Greuter et al. 1988, art. 8.2.b) and has to be replaced by one of the two species named above. *A. maritima* is selected as the new lectotype species because its valve wings are particularly broad, thus conforming best with the genus *Stoeberia* considered to be closest to *Amphibolia* by Bolus (1965) when she established the latter genus.

The taxonomy of the genus *Amphibolia*, as given below, reflects the present state of knowledge.

**TAXONOMY**


Species excluded


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**REFERENCES**


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