

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

H.E.K. HARTMANN\* and M. DEHN\*

**Keywords:** *Amphibolia*, lectotypification, Mesembryanthemaceae

### 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*.

### UITTREKSEL

Die holotipes van al vyf spesies wat in die genus *Amphibolia* L. Bol. ex Toelken & Jessop geplaas word, is ondersoek. Slegs twee van hulle stem ooreen met die diagnose van die genus, maar hulle is nie kongeneries nie. Daar word aangetoon dat die tipespesie wat deur Herre gekies is, ernstig met die protoloog in stryd is, en daarom word 'n nuwe lektotipe (*A. maritima* L. Bol. ex Toelken & Jessop) aangewys. Die ander vier spesies word uit *Amphibolia* uitgesluit.

### 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) has been re-examined. The results and taxonomic consequences are presented.

*Amphibolia* was first described by Bolus (1965). It was lectotyped 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 ...' (l.c. 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. gydouwensis*) 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 tanniferous 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.

\* Institut für Allgemeine Botanik und Botanischer Garten, Universität Hamburg, Ohnhorststrasse 18, D-2000 Hamburg 52.  
MS. received: 1989.02.10.

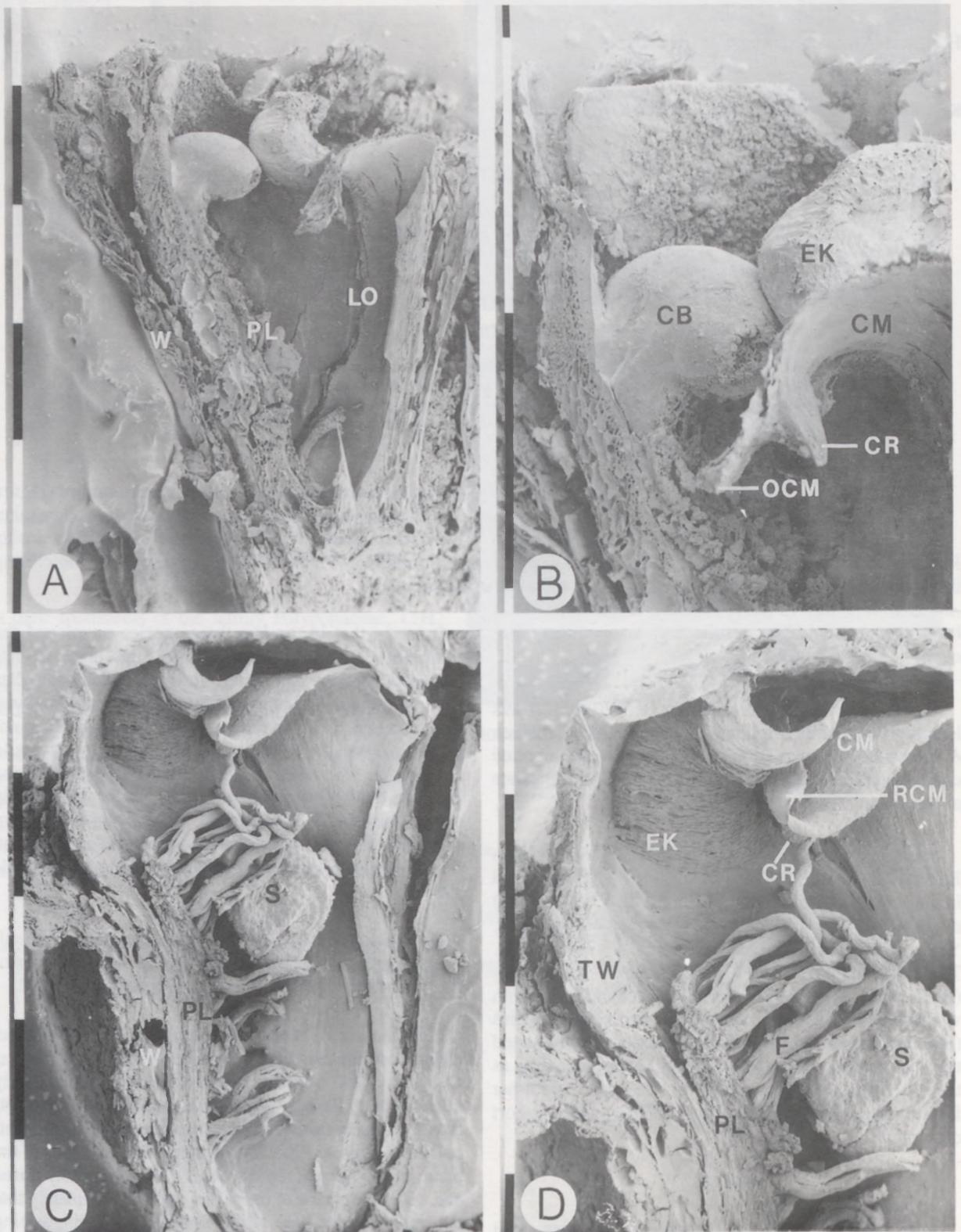


FIGURE 1.—Longitudinal sections of capsules. A, B, *Amphibolia maritima* (Hall 2885, BOL): locule (LO) blocked apically by closing body (CB) protruding from inner wall (W) of capsule; placenta (PL) torn to its base; in dry state (seen here) closing body touches expanding keel (EK) but not covering membrane (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 *Lampranthus*-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

Taxon (holotype)	Valve wings		Closing bodies		Closing rodlets	
	holo.	descr.	holo.	descr.	holo.	descr.
<i>A. maritima</i> , Hall 2885 !	+	+	+	+	+	-
<i>A. littlewoodii</i> , Littlewood KG 522/59 !	+	+	+	+	+	+
<i>A. hallii</i> , Hall 1741 !	+	+	-	+	+	+
<i>A. gydouwensis</i> , Leipoldt 4801 !	+	+	-	-	+	+
<i>A. stayneri</i> , Stayner KG 258/65 !	+	+	-	+	-	-
<i>Ruschia</i>		(+),-		+		+
<i>Lampranthus</i>		+		-		(+),-

( ) = 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 *Drosanthemum*-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).

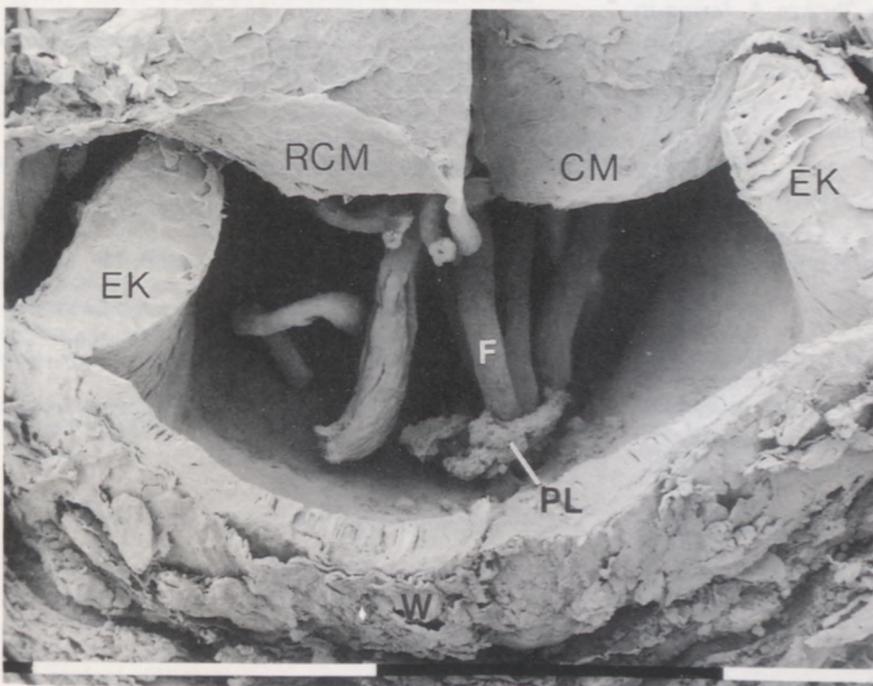


FIGURE 2.—*Amphibolia hallii*: distal opening of locule of capsule shown in Figure 1C,D seen from above after removal of valve, showing end of placenta (PL) which can be mistaken for a closing body. CM, covering membrane; EK, expanding keel; F, funicle; PL, placenta; RCM, reflexed part of covering membrane; 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

**Amphibolia** L. Bol. ex Herre, The genera of Mesembryanthemaceae: 70 (1971); L. Bol.: 169 (1965); Toelken, H.R. & Jessop, J.P.: 64 (1976). Lectotype species (here designated): *A. maritima* L. Bol. ex Toelken & Jessop. This lectotypification supercedes the lectotypification of Herre (1971), *A. hallii*, because the character expressions of that species are in serious conflict with the protologue.

**A. maritima** L. Bol. ex Toelken & Jessop in Bothalia 12: 64 (1976); L. Bol.: 169 (1965). Lectotype species. Holotype: Hall 2885 (BOL!). Nomenclatural synonym: *Ruschia maritima* Rowley: 62 (1978b).

#### Species excluded

##### 1. Species close to the genus *Ruschia* Schwant.:

**A. littlewoodii** (L. Bol.) L. Bol. ex Toelken & Jessop in Bothalia 12: 64 (1976); L. Bol.: 170 (1965). Basionym: *Stoeberia littlewoodii* L. Bol.: 162 (1960). Holotype: Littlewood KG 522/59 (BOL!). Nomenclatural synonym: *Ruschia mutata* Rowley: 7 (1978a) non *Ruschia littlewoodii* L. Bol.

##### 2. Species close to the genus *Lampranthus* N.E. Br.:

**A. hallii** (L. Bol.) L. Bol. ex Toelken & Jessop in Bothalia 12: 64 (1976); L. Bol.: 161 (1960). Basionym: *Stoeberia hallii* L. Bol.: 161 (1960). Holotype: Hall 1741 (BOL!). Nomenclatural synonym: *Ruschia amphibolia* Rowley: 7 (1978a) non *Ruschia hallii* L. Bol.

**A. gydouwensis** (L. Bol.) L. Bol. ex Toelken & Jessop: 64 (1976), L. Bol.: 306 (1967). Basionym: *Lampranthus gydouwensis* L. Bol.: 13 (1963). Holotype: Leipoldt 4801 (BOL!). Nomenclatural synonym: *Ruschia gydouwensis* Rowley: 7 (1978a).

##### 3. Species perhaps close to *Mestoklema* N.E. Br.:

**A. stayneri** L. Bol. ex Toelken & Jessop in Bothalia 12: 64 (1976); L. Bol.: 126 (1966). Holotype: Stayner KG

258/65 (BOL!). Nomenclatural synonym: *Ruschia dissimilis* Rowley: 62 (1978b) non *Ruschia stayneri* L. Bol.

#### ACKNOWLEDGEMENTS

We are indebted to the Director of the Bolus Herbarium for the loan of all type sheets of all species of *Amphibolia* and for permission to examine the material.

Our work on Mesembryanthemaceae has been made possible through grants from the Deutsche Forschungsgemeinschaft and financial support from the National Botanic Gardens. For both we are most grateful. Work on fruits has been funded also by the Cactus and Succulent Society of America through a Research Grant. We should like to thank all donors.

We are also thankful to Horst Gölling for help with SEM-graphs of fruits.

#### REFERENCES

- BOLUS, H.M.L. 1960. Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 26: 155–164.
- BOLUS, H.M.L. 1962. Corrections and additional notes (notes on *Stoeberia hallii* and *S. littlewoodii*). *Journal of South African Botany* 28: 14.
- BOLUS, H.M.L. 1963. Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 29: 11–19.
- BOLUS, H.M.L. 1965. Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 31: 169–174.
- BOLUS, H.M.L. 1966. Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 32: 125–128.
- BOLUS, H.M.L. 1967. Notes on *Mesembryanthemum* and allied genera. *Journal of South African Botany* 33: 305–309.
- DEHN, M. 1989. Untersuchungen zum Merkmalsbestand und zur Stellung der Gattung *Antimima* N.E. Br. (Mesembryanthemaceae). *Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg* 22: 195–232.
- DEHN, M. in prep. Untersuchungen zum Verwandtschaftskreis der Subtribus Ruschiinae (Mesembryanthemaceae).
- GREUTER, W. *et al.* 1988. International Code of Botanical Nomenclature. *Regnum Vegetabile* 118.
- HARTMANN, H.E.K. 1983. Untersuchungen zum Merkmalsbestand und zur Taxonomie der Subtribus Leipoldtiinae (Mesembryanthemaceae). *Bibliotheca Botanica* 136: 1–67.
- HARTMANN, H.E.K. 1988. Fruit types in Mesembryanthema. *Beiträge zur Biologie der Pflanzen* 63: 313–349.
- HARTMANN, H.E.K. & LIEDE, S. 1986. Die Gattung *Pleiospilos* s. lat. (Mesembryanthemaceae). *Botanische Jahrbücher* 106: 433–485.
- HERRE, H. 1971. *The genera of Mesembryanthemaceae*. Tafelberg, Cape Town.
- IHLENFELDT, H.-D. & BITTRICH, V. 1985. Morphologie, Gliederung und Abgrenzung der Gattung *Psilocaulon* N.E. Br. s.l. (Mesembryanthemaceae). *Botanische Jahrbücher* 105: 289–322.
- ROWLEY, G.D. 1978a. Reunion of some genera of Mesembryanthemaceae. *National Cactus and Succulent Journal* 33: 6–9.
- ROWLEY, G.D. 1978b. Reunion of some genera of Mesembryanthemaceae — a postscript. *National Cactus and Succulent Journal* 33: 62.
- TOELKEN, H.R. & JESSOP, J.P. 1976. Mesembryanthemaceae. Nomenclature of the genus *Amphibolia*. *Bothalia* 12: 64.