

# Tropical African Callitriche – a neglected and taxonomically difficult part of an evolutionary extremely interesting family

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Adaptation to life in water has implied so drastic reductions in flower morphology that it has been difficult to revise the genus *Callitriche* and to trace the taxonomic affinity of the monogeneric family Callitrichaceae. Morphological differences between the six species of *Callitriche* from tropical Africa are few and sometimes difficult to discern. The most useful ones are found in fruit and leaf shape, and in petiole venation. Additional evidence is provided by chromosome numbers, but so far counts from three species only are available. Pollen data support the distinctions between the species and provide a clue to the taxonomic affinities of the genus. Keys for the species based on gross morphology and on pollen morphology, respectively, are given. Information from studies in European and North American material reveals interesting similarities in chromosome number and in pollen characteristics. Phylogenetic studies on North American species are briefly touched upon and the need for a worldwide revision of the small but difficult family is pointed out.

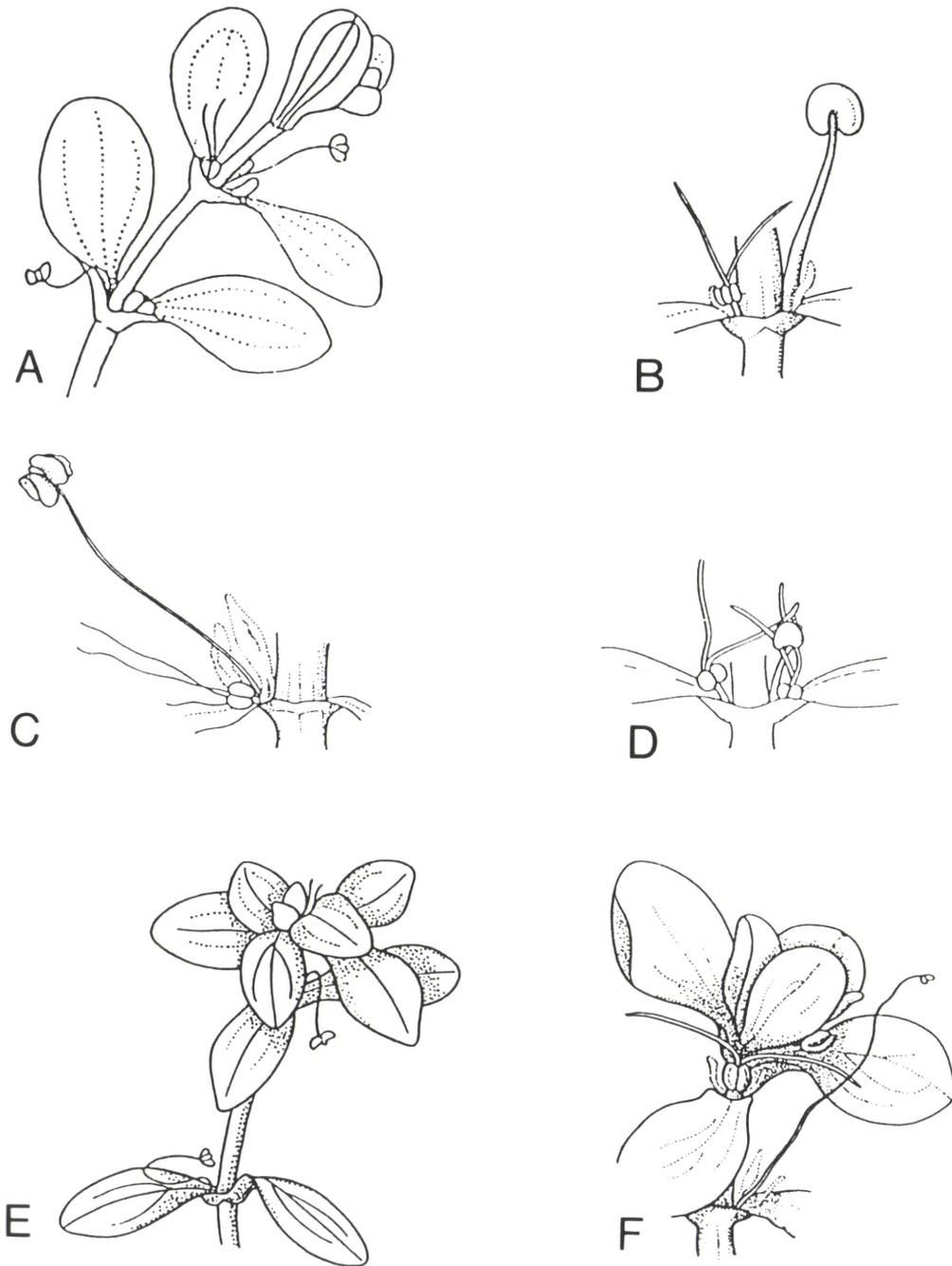
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## Introduction

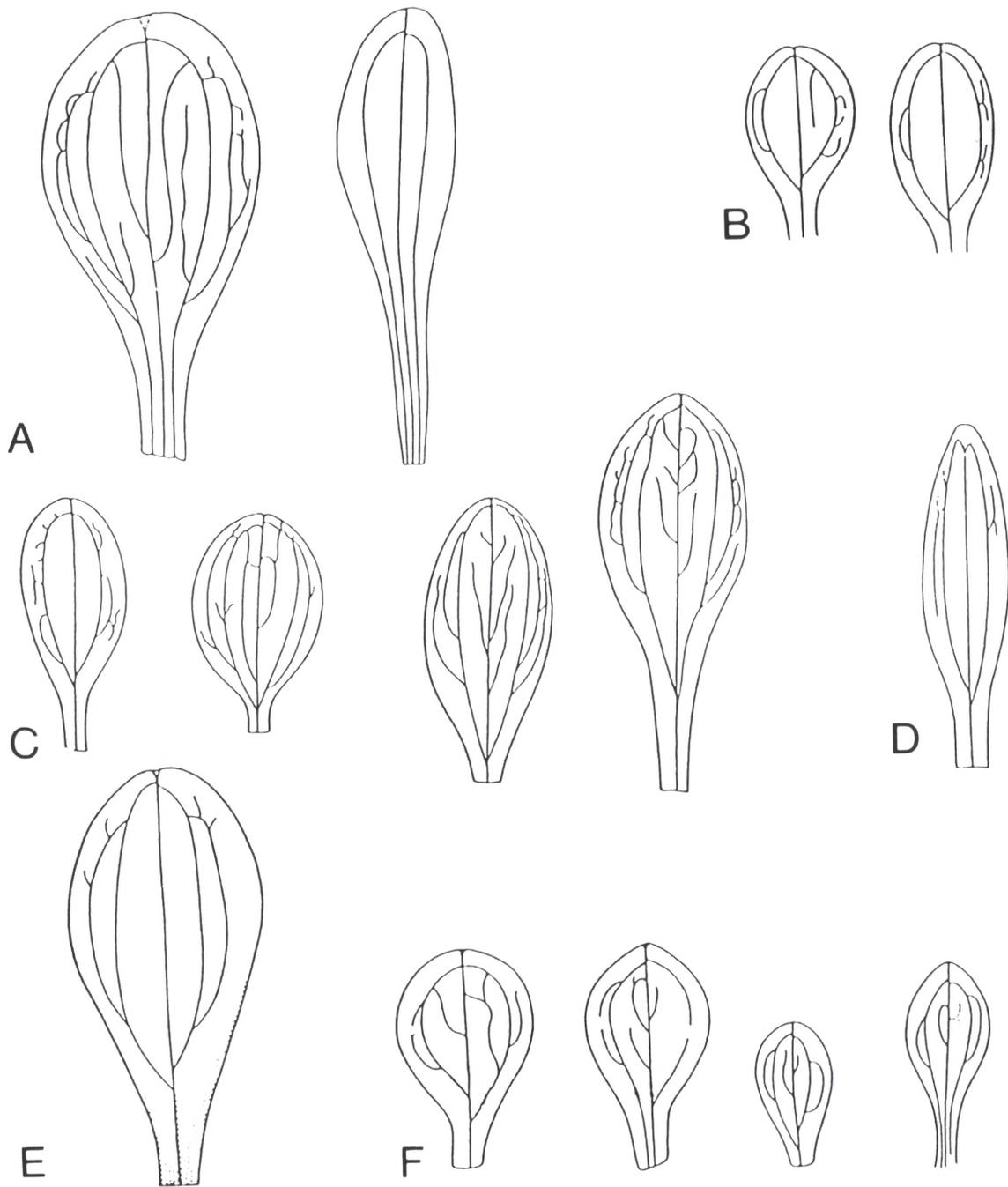
The family Callitrichaceae with the single genus *Callitriche* comprises monoecious herbs with opposite, entire leaves and axillary flowers. Adaptation to shoreline or submerged conditions has implied so widegoing reductions in flower morphology that few taxonomically useful characters remain – it is even difficult to find its closest relatives in the angiosperm system. The flowers are very inconspicuous with no perianth, and consist of only one stamen in the male ones and one pistil with a two-lobed style in the female ones. They are either solit-

ary or sometimes one male and one female together in the same leaf axil (Fig. 1). The stamens are usually very short but may elongate at maturation. The style-lobes are filiform, 1 to 4 mm long, and the fruit is a schizocarp, separating on maturity into two or four mericarps, which are winged, keeled or rounded.

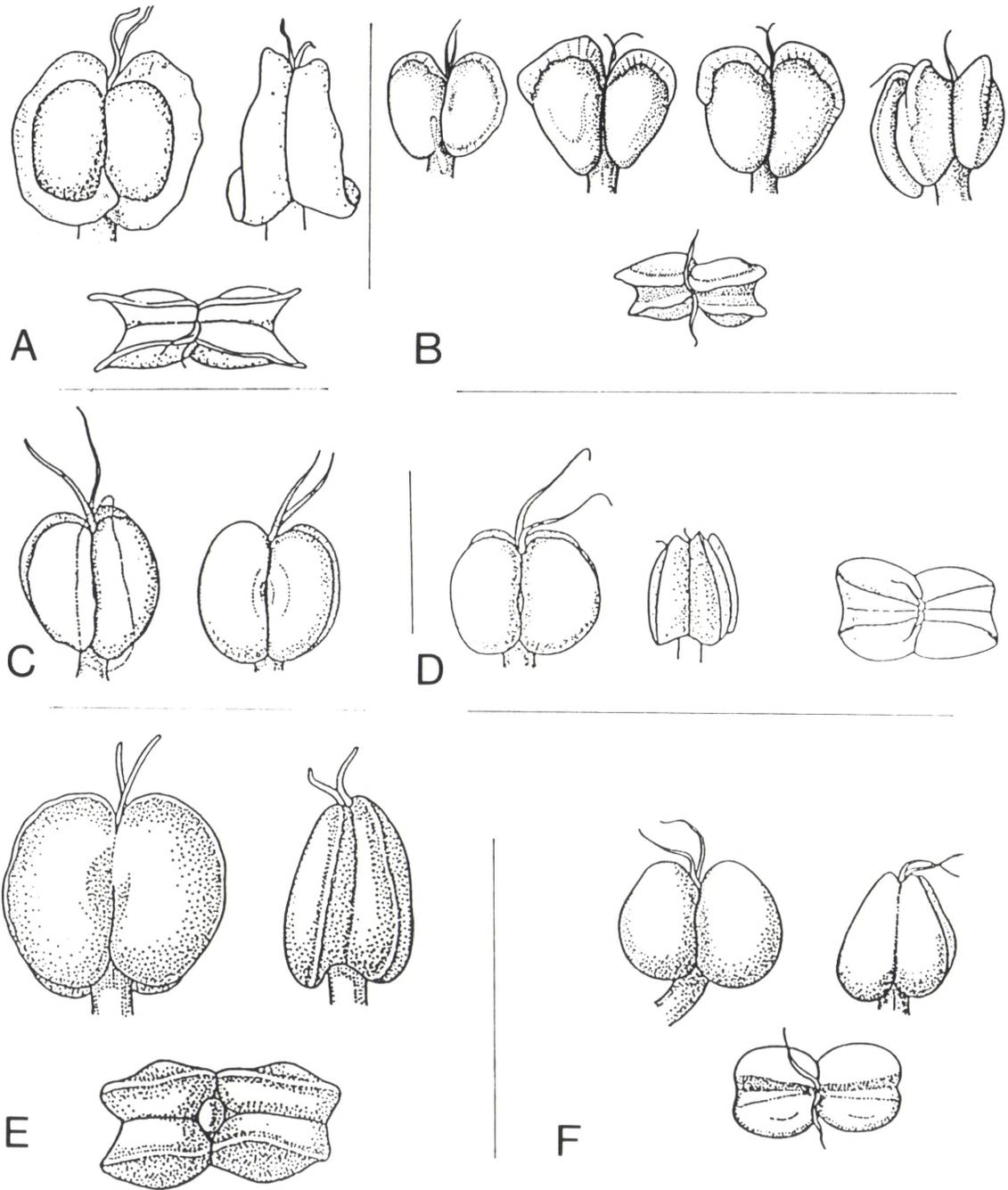
The genus has an almost cosmopolitan distribution and is claimed to comprise from 17 species (Mabberley 1997) up to 50 (Philbrick 1994). It occurs in three different growth habits: terrestrial, amphibious and submerged, and is evolutionary interesting because of the



**Fig. 1.** Flower arrangements in Tropical East African *Callitriche*. **A:** *C. oreophila* (x 6). **B:** *C. anisoptera* (x 9). **C:** *C. keniensis* (x 8). **D:** *C. favargeri* (x 13). **E:** *C. vulcanicola* (x 4). **F:** *C. hedbergiorum* (x 7). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.)



**Fig. 2.** Variation in leaf shape and venation in Tropical East African *Callitriche*. **A:** *C. oreophila* (x 7). **B:** *C. anisoptera* (x 6). **C:** *C. keniensis* (x 4). **D:** *C. javargerii* (x 10). **E:** *C. vulcanicola* (x 7). **F:** *C. hedbergiorum* (x 6). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.)



**Fig. 3.** Fruit shape (front view, side view and top view) in Tropical East African *Callitriche*. **A:** *C. oreophila* (x 15). **B:** *C. anisoptera* (x 15). **C:** *C. keniensis* (x 15). **D:** *C. javareri* (x 20). **E:** *C. vulcanicola* (x 20). **F:** *C. hedbergiorum* (x 15). A and E from Schotsman 1985 (Courtesy Bull. Jard. Bot. Nat. Belg.); B, C and F from Schotsman 1988 (Courtesy Birkhäuser Verlag AG); D from Schotsman 1984 (Courtesy Bull. Mus. Natl. Hist. Nat.).

variation in pollination systems. It is, however, obvious that “taxonomic and logistic difficulties have dissuaded people from working in the Callitrichaceae” (Philbrick & Anderson 1992: 282).

Those difficulties have resulted in a rather meagre amount of herbarium material of African *Callitriche* available, a fact that became strikingly obvious to the senior author at an early stage in his work. Realizing the need for more material of the genus from tropical Africa he consequently put particular attention to it during his field-work, also collecting root tips for chromosome studies. This resulted in what appears to be the first chromosome studies in African *Callitriche* (Hedberg & Hedberg 1977) and yielded very interesting results: no less than three different somatic chromosome numbers were found in the collections.

Differences in ploidy between different populations have long been considered taxonomically important, and differences in basic chromosome number are usually deemed even more significant. Originally all indigenous Tropical East African material was classified as *Callitriche stagnalis* (*cp. e.g.* Hedberg 1957: 127), but Schotsman's studies of morphological differences, supported by our chromosome counts, made her describe six new species from Tropical Africa, viz. *Callitriche favargerii*, *C. oreophila*, *C. vulcanicola*, *C. anisoptera*, *C. hedbergiorum* and *C. keniensis* (Schotsman 1984, 1985, 1988). The distinctions between these species were not entirely apparent, however, and in order to prepare accounts for the Flora of Ethiopia and Eritrea and Flora of Tropical East Africa, we found it necessary to revise the material in greater detail. For this revision the following features were used: leaf and fruit morphology, chromosome numbers, and pollen morphology. The latter character was shown by Martinsson (1993) to provide useful distinctions in Scandinavian material of *Callitriche*.

## Gross morphology

As to leaf morphology the shape of the lamina varies from lanceolate to spatulate, and the size is very variable. Shape and size are therefore difficult to use for taxonomic distinction, also because the infraspecific variation is considerable (Fig. 2), but the total length and the width of the leaves may sometimes be useful. Thus in *C. keniensis* the larger leaves are considerably longer than in all the other species, and in *C. favargerii* the leaves are narrower than in its closest relatives. The number of veins in the petiole, which is normally 1 or 3, seems to be the most reliable leaf feature.

A more rewarding set of characters is found in the fruits, separating at maturity into four mericarps (Fig. 3). In two of the species the mericarps are distinctly winged, symmetrically so in *Callitriche oreophila* (Fig. 3A) and asymmetrically in *C. anisoptera* (Fig. 3B). In three other species (*C. keniensis* (Fig. 3C), *C. favargerii* (Fig. 3D), and *C. vulcanicola* (Fig. 3E)) the mericarps are edged, and in the sixth one, *C. hedbergiorum* (Fig. 3F) they are evenly rounded.

## Chromosome numbers

Counts in material from Europe (Schotsman 1967; Schotsman & Andreas 1980) and North America (Philbrick 1994) revealed considerable variation in chromosome numbers within *Callitriche*, with somatic numbers between 6 and 40 (*cp.* Table 1). The numbers obtained by the authors for three tropical African species fall well within the same range of variation. Thus  $2n=10$  was found in *C. favargerii*,  $2n=18$  in *C. vulcanicola* and  $2n=10$  or  $20$  in *C. hedbergiorum*. In this connection it is interesting to note that the African *C. hedbergiorum* displays the same type of infraspecific polyploidy as *C. heterophylla* in North America.

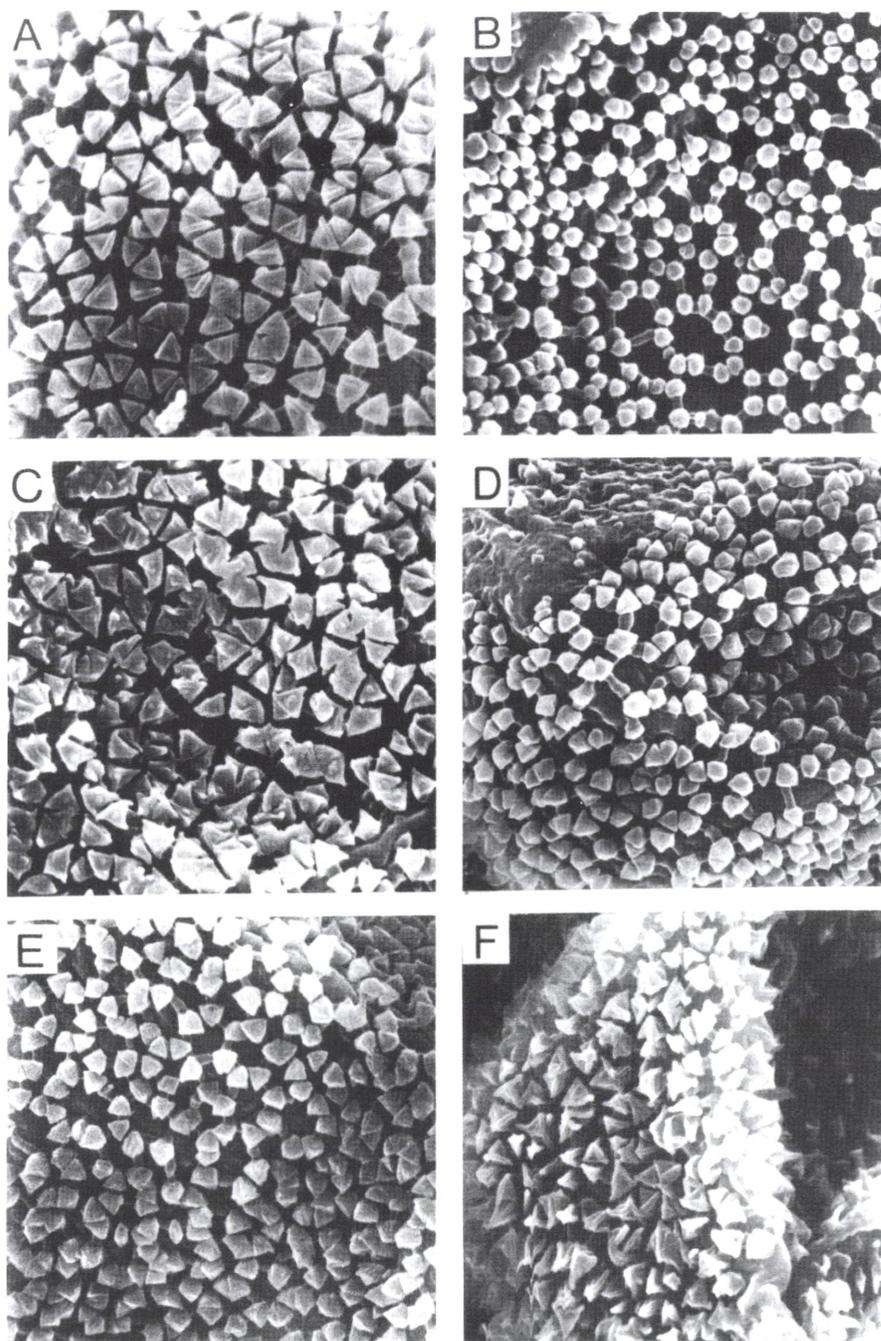
**Table 1.** Somatic chromosome numbers in *Callitriche* L.

Taxon	2n	Origin	References
<i>C. brutia</i>	28	Europe	Schotsman 1967
<i>C. cophocarpa</i>	10	Europe	Schotsman 1967
<i>C. favargerii</i>	10	E. trop. Africa	Schotsman 1984
<i>C. hamulata</i>	38	Europe	Schotsman 1967
<i>C. hedbergiorum</i>	10, 20	E. trop. Africa	Schotsman 1988
<i>C. hermafroditica</i>	6	U.S.A.	Philbrick 1994
<i>C. heterophylla</i> var. <i>heterophylla</i>	20, 40	U.S.A.	Philbrick 1994
<i>C. heterophylla</i> var. <i>bolanderi</i>	20	Canada	Philbrick 1994
<i>C. lusitanica</i>	8	Europe	Schotsman 1967
<i>C. marginata</i>	20	Canada	Philbrick 1994
<i>C. nuttallii</i>	20	U.S.A.	Philbrick 1994
<i>C. obtusangulata</i>	10	Europe	Schotsman 1967
<i>C. peploides</i>	10	U.S.A.	Philbrick 1994
<i>C. platycarpa</i>	20	Europe	Schotsman 1967
<i>C. pulchra</i>	8	Europe	Martinsson 1991
<i>C. stagnalis</i>	10	Europe U.S.A.	Schotsman 1967 Philbrick 1994
<i>C. terrestris</i>	10	U.S.A.	Philbrick 1994
<i>C. trochlearis</i>	40	U.S.A.	Philbrick 1994
<i>C. truncata</i> subsp. <i>truncata</i>	6	Europe	Martinsson 1991
<i>C. truncata</i> subsp. <i>occidentalis</i>	6	Europe	Schotsman 1967
<i>C. verna</i>	20	Canada	Philbrick 1994
<i>C. vulcanicola</i>	18	Kenya	Unpublished, counted in Hedberg 5485

## Pollen morphology

One of the most useful taxonomic characters is provided by the pollen. Studies of pollen morphology in *Callitriche* have earlier been published by Erdtman (1952), Martinsson (1993) and Osborn & Philbrick (1994). The exine surface displays a structure for which Erdtman (1952: 169, 173) coined the term *Croton* pattern: a reticulate pattern with processes (clavae) at the intersections of the walls (muri). This pattern was reported by Martinsson (1993) from three Swedish species and

occurs in all the six species described from Tropical Africa. In the latter the differences between the species are large enough to be used for species discrimination (Fig. 4). The shape of the clava tops forms a series from *Callitriche anisoptera* over *C. favargerii* and *C. vulcanicola* to *C. oreophila*, *C. keniensis* and *C. hedbergiorum*. In *C. anisoptera* (Fig. 4B) the top of the clava is regularly rounded. In *C. favargerii* (Fig. 4D) the top has distinct angles but a more or less flat and smooth surface. In *C. vulcanicola* (Fig. 4E) the top has distinct angles and a flat



**Fig. 4.** Exine surface of pollen grains in Tropical East African *Callitriche*. **A:** *C. oreophila*. **B:** *C. anisoptera*. **C:** *C. keniensis*. **D:** *C. favargeri*. **E:** *C. vulcanicola*. **F:** *C. hedbergiorum*. Scale in A-E  $\times 10,000$ ; in F  $\times 13,000$ . Voucher specimens for A: Eriksson 623 (UPS), for B: Hedberg 398 (type, UPS), for C: Paolo 997 (isotype K), for D: Friis *et al.* 5631 (C), for E: Hedberg 4403 (UPS), for F: Hedberg & Aweke 5485 (UPS).

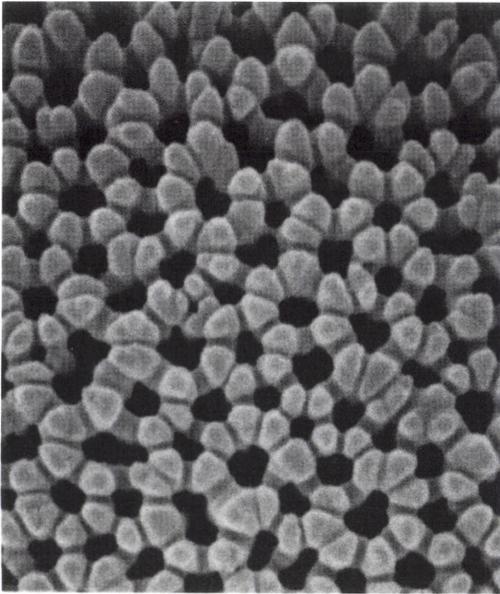


Fig. 5. *Croton* pattern in exine surface of pollen in *Bartsia longiflora* subsp. *macrophylla*. SEM photo x 10,000. (From O. Hedberg *et al.* 1979).

and scabrid surface. In *C. oreophila* (Fig. 4A) most tops are regularly triangular with broken surface. In *C. keniensis* (Fig. 4C) the top is irregularly triangular with a central papilla. In *C. hedbergiorum* finally (Fig. 4F), most tops are irregularly triangular without a central papilla.

A *Croton* pattern, resembling that in *Callitriche favargerii*, was described for *C. marginata* and *C. stagnalis* in Osborn & Philbrick (1994: 262) as well as in Philbrick & Osborn (1994: Figs. 4 and 10). The virtual absence of an exine in the perennial form of the hypohydrophilous *C. hermaphroditica* was also described in both papers.

The width of the reticulum meshes furnishes an additional character for species delimitation. In *C. anisoptera* they are much wider than the clavae, in *C. favargerii* equal, and in the other species narrower than the clavae.

### Systematics and evolution

Because of its strongly reduced flowers *Callitricheaceae* has not been easy to connect to other taxonomic groups. In earlier taxonomic

literature the family has, for instance, been placed either near Haloragaceae or Euphorbiaceae and Verbenaceae (*cp. e.g.* Melchior 1964), or Plantaginaceae (Cronquist 1981).

According to a cladistic study performed by Olmstead & Reeves (1995) *Callitriche* and *Hippuris* form a strongly supported clade. These two together with *Antirrhinum*, *Digitalis*, *Veronica* and *Plantago* form a larger, equally well-supported, clade. On the base of these results the APG (1998) tentatively included *Callitriche* and *Hippuris* in the Plantaginaceae. However, the possibility to delimit an extended Plantaginaceae by morphological criteria remains to be tested. And the same *Croton* pattern, which is found in the pollen of *Callitricheaceae* occurs not only in *Bartsia* of the *Scrophulariaceae* (Fig. 5, *cp.* Hedberg *et al.* 1979, Fig. 3) but also in *Euphorbiaceae*.

Philbrick & Jansen (1991) conducted a detailed phylogenetic study of North American *Callitriche*, utilizing chloroplast DNA restriction fragment analysis, combined with several morphological characters. Their task was mared by

difficulties to find a functional outgroup and they finally selected species from the families Verbenaceae and Lamiaceae. They found *Callitriche hermaphroditica* basal to all other North American taxa, which formed two opposing clades. One Wagner parsimony analysis resulted in 5 equally parsimonious trees (of 78), and Doko analysis generated 8 trees. From these was derived a strict consensus tree which the authors suggest reflects the evolution within the group. Their result may obviously be useful for further studies, the results of which, however, may not necessarily confirm the clade structure presented.

Also because of the various types of pollination found within the family, Callitrichaceae offers very interesting evolutionary aspects. According to Philbrick & Andersson (1992: 282) *Callitriche* is outstanding in this respect, since it is the only genus in which aerial, water surface, and subsurface pollination systems have been recorded. They therefore consider that the Callitrichaceae could serve as a model system for understanding the nature of changes that occur during the evolution from aerial pollination systems to hydrophily. They made a good start by investigating in detail taxa occurring in North America north of Mexico. Of particular interest was the unique mode of self-fertilization developed in *C. palustris*, where the pollen germinates already within the anthers, with the pollen tubes growing through vegetative tissue and entering the ovary (internal geitonogamy, Philbrick 1984). The occurrence of underwater cross-pollination (hypohydrophily) in *C. hermaphroditica* has been assumed by several authors, but evidence for this has been rather circumstantial. Strong supporting evidence was, however, supplied by Philbrick (1993) through paternity exclusion analysis using random amplified polymorphic DNA markers.

For the African species little is known about the pollination, but according to Schotsman (1984) "pollination in *C. favageri* is accom-

plished by contact between stigma and anther and seems to be mainly aerial". Further detailed pollination studies in African material would obviously be highly desirable.

Additional understanding of the breeding system in *Callitriche* might be obtained through studies of the pattern of intra- and interpopulational allozyme variation. Such analyses were, according to Philbrick & Anderson (1992) currently under way in 1992. We have, however, not been able to find a reference to any results from those studies.

## Distribution

The *Callitriche* species of Tropical Africa are mainly concentrated to mountain areas. Two of them, *C. oreophila* and *C. vulcanicola* are rather widespread, whereas the four others have a very restricted distribution. For details, see below (Taxonomic synopsis).

## Conclusion

From this short survey it is obvious that *Callitriche* offers some difficulties in species delimitation because of its very reduced flowers and the considerable variation in the vegetative parts. At the same time it offers extremely interesting problems from an evolutionary point of view, and should therefore be subjected to in-dept studies, preferably comprising the whole genus.

## Taxonomic synopsis

*Callitriche* L. (1753). Type: *C. palustris* L.

*Key to Tropical African species based on gross morphology*

- |  |                        |
|--|------------------------|
| 1. Fruits distinctly winged  | 2                      |
| – Fruits not winged  | 3                      |
| 2. Wings symmetrical around the mericarp;<br>petiole mostly 3-veined | 1. <i>C. oreophila</i> |

- Wings asymmetric; petioles at base 1-veined 2. *C. anisoptera*
- 3. Larger leaves at least 10 mm long, 5(-8)-veined 3. *C. keniensis*
- Larger leaves less than 10 mm long; usually 3-veined 4
- 4. Mericarps evenly rounded 4. *C. hedbergiorum*
- Mericarps edged 5
- 5. Leaves lanceolate, up to 2 mm wide 5. *C. favargerii*
- Leaves spatulate, at least 2.5 mm wide 6. *C. vulcanicola*

*Key to species based on pollen morphology*

- 1. Clavae tops regularly rounded, without angles 2. *C. anisoptera*
  - Clavae tops with distinct angles 2
- 2. Clavae tops with more or less flat surface 3
  - Clavae tops with uneven surface 4
- 3. Clavae tops with smooth surface 5. *C. favargerii*
  - Clavae tops with scabrid surface 6. *C. vulcanicola*
- 4. Most clavae tops regularly triangular 1. *C. oreophila*
  - Most clavae tops irregularly triangular 5
- 5. Clavae tops often with central papilla 3. *C. keniensis*
  - Clavae tops without central papilla 4. *C. hedbergiorum*

1. *C. oreophila* Schotsman (1985).

Type: Rwanda, Gitovu, *Becquet* 780 (BR holotype).

*C. stagnalis* auct. non Scop. 1772

Stems 10-35 cm in water, or 3-20 cm on mud. All leaves with elliptic to spatulate, 3-7-veined blade and 3-veined petiole, up to 11 x 5 mm, but often much smaller. Flowers solitary, in the axiles of both submerged and floating or aerial leaves, bracteoles 2, falcate. Stamen at dehiscence 1-2 mm long, after dehiscence up to 7

mm; anther 0.5-0.6 mm. Style-lobes up to 2 mm long, erect or spreading. Fruit suborbicular, *c.* 1.6-1.8 x 1.6-2 mm, with distinctly winged mericarps. Reticulum meshes of the pollen surface not as wide as the clavae; the latter irregularly triangular with broken top surface. Chromosome number unknown. Evidently anemophilous. – Figs 1A, 2A, 3A, 4A.

On moist ground along streams and ponds, sometimes submerged, and in forest; 1150-3200 m. Ethiopia, Uganda, Kenya, Tanzania, Burundi and Cameroon.

2. *C. anisoptera* Schotsman (1988).

Type: Uganda, Ruwenzori, Bujuki valley near Bigo camp, *Hedberg* 398 (BR holotype; BM, EA, K, UPS isotypes).

*C. stagnalis* auct. non Scop. 1772

Stem prostrate, mat-forming. Leaves spatulate with elliptic, 3-5-veined blade *c.* 4-6 x 2-2.5 mm and 1-veined petiole. Flowers solitary, the male ones with 2 narrow bracteoles, the female without or with 2 bracteoles. Stamen 2-6 mm long; anther *c.* 0.5 mm long. Style-lobes 1.5-3.5 mm. Fruit *c.* 1.3-1.5 x 1.6-1.8 mm, unequally and variously winged with better developed wing in the terminal part. Some reticulum meshes of the pollen grain surface more than twice as wide as the clavae; the latter with globular top. Chromosome number unknown. – Figs 1B, 2B, 3B, 4B.

On moist ground along streams or in bogs; 3450-4000 m. Uganda and Zaire: Ruwenzori.

3. *C. keniensis* Schotsman (1988).

Type: Kenya, Murua Nysigar, *Paulo* 977 (BR holotype; EA, K, PRE isotypes).

*C. stagnalis* auct. non Scop. 1772: *Hedberg* 1957: 127, p.p.

Robust aquatic plant; stems 30-40 cm long, 0.8-0.9 mm in diam., with sparse hairs. Leaf rosettes with 6-8(-10) leaves; rosette leaves

spathulate, with elliptic, 3-7-veined blade, 15-20 x 4-6 mm; petiole of the same length as blade or shorter, with a single vein. Flowers solitary, or staminate and pistillate forming an axillary pair, usually the opposite axils with a solitary flower and a pair of flowers; bracteoles 2, 1.5-2 x 0.6 mm. Staminate flower with erect stamen, at dehiscence *c.* 4 mm long; extending to 6.5 mm after dehiscence, occasionally recurving; anther 0.7-0.9 mm long. Pistillate flower subsessile, with erect or patent style-lobes, 2-3 mm long, persistent. Fruit subsessile, ellipsoid or rarely subglobose, 1.6-1.8 x 1.3-1.5 x 0.8-1 mm, with style remnants to 1 mm long, splits between mericarps shallow, mericarps obtuse, edged but not winged. Reticulum meshes of pollen surface not as wide as the clavae, the latter irregularly triangular with sharp angles and often carrying a central papilla. Chromosome number unknown. – Figs 1C, 2C, 3C, 4C.

In streams, ponds and bogs; 2150-4300 m. Endemic to Kenya (Elgon, Mt Kenya, Murua Nysigar Peak) and known from 6 collections only.

4. *C. hedbergiorum* Schotsman (1988).

Type: Ethiopia, Gonder, Simien, *O. Hedberg* & *Getachew Aweke* 5485 (UPS holotype).

*C. stagnalis* auct. non Scop. 1772; I. & O. Hedberg 1977: 5,6, 16, p.p.

Stems 5-25 cm. All leaves with elliptic, 3-5 veined blade, 4-6 x 2-3 mm, and 1-2 (rarely 3)-veined petiole. Flowers solitary, bracteoles absent or 1-2, falcate. Stamen at dehiscence *c.* 1 mm long, after dehiscence up to 10 mm; anther 0.5-0.8 mm. Style-lobes up to 3 mm, first erect, later spreading. Fruit suborbicular, *c.* 1.3 x 1.6 mm, with rounded mericarps. Reticulum meshes of pollen not as wide as the clavae; the latter with triangular irregularly pyramidal top with broken surface. Chromosome number 2n=10 (*Hedberg* 5485); 2n=20 (*Hedberg* 5574). Probably anemophilous.

– Figs 1F, 2F, 3F, 4F.

More or less submerged in small streams; 3650-3950 m. Endemic to Ethiopia (Gonder and Bale regions) and known only from 2 collections.

5. *C. favargerii* Schotsman (1984).

Type: Ethiopia, Arsi, *Hedberg* 4234 (UPS holotype; ETH, K isotypes).

*C. stagnalis* auct. non Scop. 1772; I. & O. Hedberg, 1977: 5, 6, 16, p.p.

Stems to 35 cm long, submerged or terrestrial. Submerged leaves linear, up to 9 x 0.5-1 mm, 1-3-veined; aerial leaves lanceolate, up to 6.5 x 2 mm, 1-3-veined; petioles always 1-veined. Flowers on both submerged and aerial shoots, without bracteoles; most often one male flower in one leaf axil and one female – or one male and one female – in the opposite axil. Stamen short, *c.* 0.5 mm long before, and up to 1.3 mm after dehiscence; anther 0.3-0.4 mm. Style-lobes 1-1.5 mm. Fruit *c.* 1 mm long and 1.3 mm wide, with slightly edged mericarps. Reticulum meshes of pollen surface rarely as wide as the clavae; the latter with triangular, irregularly pyramidal top with smooth surface. Chromosome number 2n=10 (type collection). The species appears to be persistently autogamous. – Figs 1D, 2D, 3D, 4D.

In small streams and ponds in the afroalpine belt, 3800-4050 m. Ethiopia, Arsi and Bale Regions. Known only from 6 collections.

6. *C. vulcanicola* Schotsman (1985).

Type: Kenya, Mt Kenya, Burguret track, *Hedberg* 4403 (UPS holotype; BR, EA, K isotypes).

*C. stagnalis* auct. non Scop. 1772; Hedberg 1957: 127, p.p.; I. & O. Hedberg 1977: 5, 6, 16, p.p.; Robyns 1958: 350.

Amphibious. Rosette leaves spathulate, 5-12 x 2-5 mm, blade elliptic-rhomboid, with 3-5 main veins; petiole 1-veined, shorter than the blade. Flowers solitary, the male ones with 1 or 2 bracteoles, 1-1.3 x 0.1-0.2 mm. Ripe stamen

erect, 2-3 mm long, after flowering increasing up to 8 mm; anther 0.7-1 mm long. Female flowers usually without bracteoles; style-lobes at first erect, 1.5-2 mm long. Fruit wider than long, 1.2-1.5 x 1.6-2.2 mm. Mericarps keeled. Some reticulum meshes of the pollen surface as wide as the clavae, which are obtusely triangular, almost flat, with scabrid surface. Chromosome number  $2n=18$ . – Figs 1E, 2E, 3E, 4E.

In pools, on moist ground along streams, and in flushed grassland; 3000-4000 m. Uganda, Kenya, Rwanda and Zaire.

## Note

One collection from East Africa of a seventh species, *C. deflexa* A. Br. ex Hegelm., was found in the Kew Herbarium (Tanzania, Kilimanjaro Coffee Research Station, Lyamungu, 22.7. 1967, *Bigger* 1236). This is, however, an introduction of a South African species occurring as a weed also in Portugal, Morocco and the Azores, and it has no close relation to the Tropical African species treated here.

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