

BORAGINACEAE

CODONOIDEAE, A NEW SUBFAMILY BASED ON *CODON*

The genus *Codon* was formally established by Carl Linnaeus (1767) in the second volume of the 12th edition of his *Systema naturae*. He placed the genus in his Class X: Decandria, Monogynia. The generic name is derived from the Greek word *kodon*, a bell (although the flowers do not hang down), and alludes to the shape of the flowers of *C. royenii* L., which are deeply cup-shaped. *Codon* comprises two described species, *C. royenii* and *C. schenckii* Schinz, both endemic to Namibia and South Africa. A possible undescribed third species is found in the southern part of Namibia and is currently under investigation.

It was in France that a move towards more 'natural' groupings of plants was first made. It is clear from his writings that Linnaeus recognized natural affinities, but that ease of classification and identification were his main objectives (Gunn & Codd 1981). Michel Adanson's *Familles des plantes* (1763–64) can be regarded as the

first 'logically and philosophically sound basis for a classification of plants' (Stafleu & Cowan 1976). In 1789 Antoine-Laurent de Jussieu followed with his *Genera plantarum*. He published the description of 'Borragineae' as one of 100 orders (i.e. families). Many of his families are still maintained in modern classifications. De Jussieu based 'Borragineae' on the genus *Borago* L. He divided 28 genera into three different groups using fruit morphology as a distinguishing character: 1, berry-like fruits; 2, one- or two-locular capsules; and 3, four separate nutlets. He regarded *Codon* as a genus of uncertain position.

Of the five genera of Hydrophyllaceae known to him, De Jussieu (1789) assigned *Hydrophyllum* L., *Phacelia* Juss. and *Ellisia* L. to 'Borragineae' and *Nama* L. and *Hydrolea* L. to 'Convolvuli'. R. Brown separated the former trio of genera as the natural order Hydrophyllae in 1810, and the latter two as the natural order 'Hydroleae' in 1818. Choisy (1833) treated the Hydroleae in a mono-

graph, recognizing the genera *Hydrolea*, *Nama*, *Wigandia* Kunth and *Romanzoffia* Cham.; to these he added *Eriodictyon* Benth. in 1846, and at the same time vigorously defended the distinctness of the Hydroleae. De Candolle (1846: 589) was the first to place *Codon* in the family Hydrophyllaceae. Gray (1875) united all the genera mentioned in the family Hydrophyllaceae, which he divided into four tribes. Baillon (1890) merged Hydrophyllaceae under Boraginaceae, but his view was not followed at the time. Hydrophyllaceae was restored by Brand (1913) in a monograph of the family.

Until recently, most authors accepted the Hydrophyllaceae as a separate family. A comparison between Hydrophyllaceae and Boraginaceae in southern Africa based on pollen and macromorphological characters, however, shows a strong overlap of features. The surface structure of pyrenes of *Ehretia* P.Browne shows similarity with the seeds of *Nama* (compare Retief & Van Wyk 2001: 15 and Chance & Bacon 1984: 832), although this may not be meaningful, as the outer surfaces in these two structures are obviously not homologous. Of more significance is the likeness between pollen grains of *Wellstedtia* Balf.f. and those of *Eriodictyon*, *Nama* and *Phacelia* (compare Constance & Chuang 1982 and Retief & Van Wyk 2005); tapetal orbicules or Ubisch bodies—sporopollenin particles usually lining the inner tangential tapetal cell walls of secretory tapetums—of *Wellstedtia* and *Codon* show similarity in morphology (Retief *et al.* 2001). The broad family concept of Baillon (1890) is followed here, and we agree with the Angiosperm Phylogenetic Group (APG) (1998, 2003) and Långström & Chase (2002) who regard Hydrophyllaceae and Lennoaceae as synonyms of Boraginaceae *s.l.*

Modern views on the delimitation of Boraginaceae differ, for example, 1, segregating a separate family, Heliotropiaceae (Diane *et al.* 2002) from Boraginaceae *s.l.*; or 2, recognizing several segregate families: Boraginaceae *s. str.*, Cordiaceae, Ehretiaceae, Heliotropiaceae, Hydrophyllaceae, Lennoaceae and Wellstedtiaceae (Lebrun & Stork 1997; Gottschling *et al.* 2001; Gottschling 2003). However, in neither of these two approaches has the position of *Codon* been considered.

In Ferguson's (1999) phylogenetic analysis of evolutionary relationships within the Hydrophyllaceae, it is concluded that the family is nested within a paraphyletic Boraginaceae *s.l.*, excluding *Codon* and *Hydrolea*. *Hydrolea* is placed in a family of its own (APG II 2003). *Codon* is included in Boraginaceae *s.l.* in a treatment of this family for the Cape flora (Retief & Buys 2000: 374, 706). The genus *Codon* has traditionally been assigned to the Hydrophyllaceae, where it seems to be unusual geographically, as the family is otherwise largely restricted to the New World. Similarities between *Codon* and other members of Boraginaceae indicate that *Codon* should be placed in a subfamily of its own within Boraginaceae *s.l.* A new subfamily, Codonoideae, is established here to accommodate this southern African genus within Boraginaceae *s.l.*, the other local subfamilies being Wellstedioideae, Ehretioideae, Cordioideae, Heliotropioideae and Boraginoideae (Retief 2000: 179; Retief & Van Wyk 2001). The precise classification of the other, mainly New World genera (see Brand 1913) of Hydrophyllaceae *s. str.* within Boraginaceae *s.l.* has not yet been addressed

but they would most probably also require placement in one or more additional subfamilies.

Phytogeographically the restriction of *Codon* to the arid southwestern corner of Africa is of special interest. Its nearest relatives appear to be those members of Boraginaceae *s.l.* previously placed in Hydrophyllaceae *s. str.*, found mainly in North America, but with members of both *Nama* and *Phacelia* also occurring in South America (Deginani 1999). Among plants, African-New World distributions are rather unusual, but for southern Africa, involve as many as seven families and many more genera (Goldblatt 1978). It is intriguing that several other plant groups with a distribution pattern comparable to that of *Codon*, namely with a disjunct presence in southwestern and in northeastern Africa, show links with taxa in the New World. Among these are the boraginaceous genus *Wellstedtia* as well as members of *Calliandra*, *Caesalpinia*, *Haematoxylon*, *Hoffmannseggia*, *Parkinsonia*, *Xerocladia* (all Fabaceae), *Nicotiana* (Solanaceae), *Thamnosma* (Rutaceae) and *Turnera* (Turneraceae) (Van Wyk & Smith 2001). These African-New World disjuncts may have been established in different ways, but one possible explanation is based on the proximity of Africa and South America during Gondwana times and for quite some time after the break-up of the supercontinent.

Members of the new subfamily Codonoideae, established here, show the strongest affinity with the subfamilies Wellstedioideae and Ehretioideae in Boraginaceae *s.l.*—in similar pollen, inflorescence and trichome morphology. However, the Codonoideae differ from Wellstedioideae in the 10 or 12 (not 4) corolla lobes and in the seed which is subglobose and glabrous (not truncate and pubescent). They differ from Ehretioideae in habit in that they are annual or short-lived perennial herbs (not shrubs or trees) and in the fruit which is a capsule (not a drupe).

Codonoideae Retief & A.E. van Wyk, subfam. nov.

Type: *Codon royenii* L.

Herbae annuae vel breviter perennes, patentes ad erectae, interdum basi lignescentes. Partes vegetativae aculeato-pubescentes trichomatibus spiniformibus, et setis trichomatibusque multicellularibus non ramosis. *Folia* petiolata. *Flores* cymis scorpioides, ebracteati. *Calyx* profunde lobatus, lobi lineares. *Corolla* 10- vel 12-lobata, tubus cylindricus vel campanulatus, fauce glabra. *Stylus* terminalis, linearis, paene ad medium fissus, persistens; stigma capitatum. *Fructus* capsula multiseptata. *Semina* globosa vel irregulariter angulosa, ornata.

Spreading to erect, annual or short-lived perennial herbs, sometimes woody at base. All vegetative parts prickly pubescent with spine-like trichomes, also with setae and unbranched, multicellular trichomes. *Leaves* petiolate. *Inflorescence* scorpioid. *Calyx* deeply lobed, lobes linear. *Corolla* 10- or 12-lobed, tube cylindric or campanulate, throat naked. *Style* terminal, linear, cleft to almost halfway, persistent; stigma capitate. *Fruit* a capsule, many-seeded. *Seeds* globose or irregularly angled, ornamented.

Genus: *Codon* L.

ACKNOWLEDGEMENT

We wish to thank Dr O.A. Leistner for translating the subfamily description into Latin.

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MS. received: 2004-06-30.