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Article in *Harvard Papers in Botany* · June 2008

DOI: 10.3100/1043-4534(2008)13[165:FATABC]2.0.CO;2

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Source: Harvard Papers in Botany, 13(1):165-170. 2008.

Published By: Harvard University Herbaria

DOI: [http://dx.doi.org/10.3100/1043-4534\(2008\)13\[165:FATABC\]2.0.CO;2](http://dx.doi.org/10.3100/1043-4534(2008)13[165:FATABC]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.3100/1043-4534%282008%2913%5B165%3AFATABC%5D2.0.CO%3B2)

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FIVE ADDITIONAL TRIBES (APHRAGMEAE, BISCUTELLEAE, CALEPINEAE, CONRINGIEAE, AND ERYSIMAEAE) IN THE BRASSICACEAE (CRUCIFERAE)

DMITRY A. GERMAN¹ AND IHSAN A. AL-SHEHBAZ²

Abstract. The tribes Aphragmeae and Conringieae are proposed as new, and the tribes Biscutelleae, Calepineae, and Erysimeae (Brassicaceae; Cruciferae) are re-established. The unigeneric Aphragmeae, Biscutelleae, and Erysimeae include the genera *Aphragmus*, *Biscutella*, and *Erysimum*, respectively. The Conringieae comprises *Conringia* and *Zuvanda*, whereas the Calepineae includes *Calepina*, *Goldbachia*, and *Spirorrhynchus*. The prior tribal assignments of these genera, total number of species, and geographic distribution of all five tribes are listed.

Keywords: Brassicaceae, Cruciferae, tribal classification

Extensive molecular studies (for leads, see Koch et al., 2003; Mitchell-Olds et al., 2005; Al-Shehbaz et al., 2006; Beilstein et al., 2006; Bailey et al., 2006; Koch et al., 2007; and Warwick et al., 2007) were conducted during the past dozen years on the phylogeny and evolution of Brassicaceae (Cruciferae). As a result, tribal classifications of the family based strictly on morphology, such as the systems of de Candolle (1821), Prantl (1891), Hayek (1911), Schulz (1936), and Dorofeyev (2004), as well as the modifications of Schulz's system by Janchen (1942) and Al-Shehbaz (1984), were shown to be highly artificial. Although the boundaries of only a few tribes (e.g., Brassiceae DC., Heliophileae DC.) remained largely unaltered, circumscription of almost all of the remaining tribes needed re-adjustments.

The first attempt to achieve a tribal classification of the family based on molecular studies and re-examination of morphology was made by Al-Shehbaz et al. (2006). In that study, 25 tribes (including six new) were recognized. However, further adjustments at the tribal level, including

placements of several smaller genera not previously studied or with unresolved positions on the phylogenetic trees (see Bailey et al., 2006; Warwick et al., 2007) or super network (Koch et al., 2007), became immediately evident. As a result, the tribes Dontostemoneae Al-Shehbaz & Warwick, and Malcomieae Al-Shehbaz & Warwick were described as new, and the tribe Buniadeae DC. was re-established (Al-Shehbaz and Warwick, 2007).

Based on molecular studies by German et al. (in prep.), the present paper deals with the tribal assignments of nine, predominantly Old World, genera (*Aphragmus* Andr. ex DC., *Biscutella* L., *Calepina* Adans., *Conringia* Heist. ex Fabr., *Erysimum* L., *Goldbachia* DC., *Megadenia* Maxim., *Spirorrhynchus* Kar. & Kir., and *Zuvanda* (Dvořák) R. K. Askerova), either inadequately studied or with no previous molecular studies. They are placed in five tribes, of which two (Aphragmeae and Conringieae) are described as new, and three (Biscutelleae, Calepineae, and Erysimeae) are re-established.

APHRAGMUS

This genus previously included about four species (Ebel, 1998), but has recently been expanded by the discovery of new species and by its union with the Himalayan *Staintoniella* H. Hara and *Lignariella* Baehni (Al-Shehbaz,

2000, 2002, 2003; Warwick et al., 2006a). As presently delimited (Warwick et al., 2006b), the genus includes 11 species, centered primarily in the Himalayas and adjacent central Asia, with one species, *Aphragmus eschscholtzianus* Andr.

We are grateful to Gustavo A. Romero-González and Donna Tremonte for their editorial advice and help. We thank Steve L. O'Kane, Jr. and an anonymous reviewer for their remarks on the manuscript.

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ex DC., distributed in the northern Russian Far East, northwestern Canada, and Alaska.

Aphragmus was placed in the tribes Arabideae DC. and Sisymbrieae DC. by Hayek (1911) and Schulz (1936), respectively. It was not assigned to a tribe by Al-Shehbaz et al. (2006) because none of its species were included in previous molecular studies. Although Warwick et al. (2006a) clarified the generic limits of *Aphragmus* (8 spp.) and showed that it is unrelated to *Braya* Sternb. & Hoppe (tribe Euclidieae DC.), they did not address its tribal position. Warwick et al. (2006a) showed that *Aphragmus* formed a distinct, well-supported clade separate from the other tribal groups (Arabideae, Eutremeae, and Euclidieae) included in the analysis. Koch et al. (2007) included only *A. oxycarpus* (Hook.f. & Thomson) Jafri and showed it to form a weakly supported clade with a species of *Heliophila* L.

in a basal polytomy of the family-wide tree. That relationship was not confirmed in the ITS-based phylogeny (German et al., in prep.), in which both *A. eschscholtzianus* and *A. involu-cratus* (Bunge) O. E. Schulz formed a well-supported clade (100% bootstrap [BS]) distinct from the other existing tribes.

Aphragmus is characterized by an indumentum of minute simple and forked trichomes, entire or 3–7-lobed leaves, bracteate inflorescences, usually eseptate fruits, and often minutely papillate seeds on long filiform funicles often longer than seeds (except for four species previously assigned to *Lignariella*). This character combination is not found in other genera of the family and, together with its molecular distinctness (German et al., in prep.), support the placement of *Aphragmus* in an independent, unigeneric tribe, Aphragmeae.

BISCUTELLA AND MEGADENIA

Biscutella (53 spp.; Warwick et al., 2006b), is a primarily Mediterranean genus placed by de Candolle (1821) in the tribe Thlaspideae DC., and by Hayek (1911) and Schulz (1936) in the tribe Lepidieae DC. Such placements were based primarily on having angustiseptate silicles characteristic of all three taxa. Molecular phylogenetic studies by Beilstein et al. (2006) included only one species of *Biscutella*, whose position was not resolved in the tree and, as a result, the genus was not assigned to any tribe by Al-Shehbaz et al. (2006).

The monospecific genus *Megadenia* includes *M. pygmaea* Maxim., a species distributed in S. Siberia, S. Russian Far East, and C. China (E. Xizang, S. Gansu, Qinghai, and W. Sichuan). The first molecular study of the genus by German et al. (in prep.) demonstrated that it forms a moderately supported clade (71% BS)

with *Biscutella*. Both genera have didymous silicles that split at maturity into two one-seeded mericarps. Although this fruit type has evolved independently in *Lepidium* L. (Lepidieae), *Heliophila* L. (Heliophileae DC.), *Megacarpaea* DC. and *Cremolobus* DC. (both unassigned to tribes), *Physaria* (Physarieae), and *Physoptychis* (Alysseae), the clade containing *Biscutella* and *Megadenia* was not related to any of them. Therefore, *Biscutella* and *Megadenia* are assigned herein in the re-established tribe Biscutelleae Dumort. Dorofeyev (2004) recently placed all genera of the family with didymous fruits in the tribe Cremolobae. In doing this, he ignored all the morphological, cytological, palynological, and molecular data that clearly support the independent origin of didymous fruits at least five times in the family (Al-Shehbaz et al., 2006).

CONRINGIA AND ZUVANDA

Conringia, a Eurasian genus of six species centered primarily in Turkey and adjacent Iran, was placed by Hayek (1911), Schulz (1923, 1936), and Al-Shehbaz (1985) in the tribe Brassiceae. Its tribal assignment was based primarily on having in one species, *C. planisiliqua* Fisch. & C. A. Mey., subconduplicate cotyledons, a feature characteristic of most members of the Brassiceae. The tribe was subjected to a number of phylogenetic studies (see Warwick

and Sauder, 2005, and references therein), but the placement of *Conringia* remained unresolved after its exclusion from the Brassiceae (Lysak et al., 2005; Al-Shehbaz et al., 2006). *Conringia* showed strong alliance (92 to 100% BS) to the tribe Noccaeeae Al-Shehbaz, Beilstein & E. A. Kellogg in the *ndhF* (Beilstein et al., 2006) and ITS studies (Bailey et al., 2006; German et al., in prep.), and similar support (90% BS) in the *trnL-F* phylogeny of Koch et al. (2007).

The southwest Asian *Zuvanda* (3 spp.) was segregated from *Malcolmia* W. T. Aiton by Askerova (1985) based on its lack of branched trichomes and presence of auriculate leaves. *Malcolmia* was placed by de Candolle (1821), Hayek (1911), and Schulz (1936) in the tribes Sisymbrieae, Alysseae DC., and Hesperideae DC., respectively. More recently, Dorofeyev (2002) transferred all species of *Zuvanda* and *Conringia perfoliata* (C. A. Mey.) N. Busch to *Moricandia* DC., but that transfer was not followed by Appel and Al-Shehbaz (2003) and Al-Shehbaz et al. (2006) because *Moricandia*, like other members of Brassiceae, has conduplicate cotyledons (vs. incumbent cotyledons in *Zuvanda*). As shown by Lysak et al. (2005) and Warwick and Sauder (2005), *Moricandia* is a member of Brassiceae unrelated to *Conringia*.

Warwick et al. (2007) demonstrated that *Zuvanda crenulata* (DC.) R. K. Askerova, *Z. exacoides* (DC.) R. K. Askerova, and *Goldbachia laevigata* (M. Bieb.) DC., formed a separate, but loosely supported (< 50% BS)

clade, unrelated to *Malcolmia*, and the other 13 tribes included in their study; but they did not assign the three species to a tribe. Although they did not include any member of the Brassiceae in their study, *Zuvanda* was unrelated to the Sisymbrieae, a tribe most closely related to the Brassiceae (Al-Shehbaz et al., 2006). German et al. (in prep.) showed that *Conringia perfoliata* and *Z. crenulata* formed a clade related to, but distinct from, the Noccaeeae.

Both *Conringia* and *Zuvanda* resemble members of the Noccaeeae in being glaucous and glabrous or with only simple trichomes, and in having entire or dentate, sessile, mostly amplexicaul, cauline leaves. However, they differ by having terete, latiseptate, or 4-angled (vs. angustiseptate) and linear siliques (vs. oblong, elliptic, obcordate, obovate, or obdeltoid silicles), many (vs. few) seeds per fruit, and often decurrent (vs. entire) stigmas. These significant differences justify the placement of *Conringia* and *Zuvanda* in a tribe separate from the Noccaeeae and recognized herein as Conringieae.

CALEPINA, GOLDBACHIA, AND SPIORRRHYNCHUS

Calepina, a monospecific southwest Asian genus, was placed by de Candolle (1821) in the tribe Zilleae and by Hayek (1911), Schulz (1919, 1936), and Al-Shehbaz (1984) in the tribe Brassiceae because of having slightly conduplicate cotyledons with involute margins. Gómez-Campo (1980) suggested the removal of *Calepina* from the Brassiceae, but he later (Gómez-Campo, 1999) retained it in that tribe. Recent molecular studies (Lysak et al., 2005; Warwick and Sauder, 2005) clearly supported the exclusion of *Calepina* from the Brassiceae, a position followed by Al-Shehbaz et al. (2006), but no tribal placement was suggested.

Goldbachia, a Eurasian genus of six species, was placed by de Candolle (1821) in the tribe Anthonieae DC.; by Hayek (1911) in the tribe Arabideae; and by Schulz (1936) in the tribe Hesperideae. Recent molecular studies by Beilstein et al. (2006) revealed a weak relationship between *Goldbachia* and the tribe Thlaspideae. Both *Goldbachia* and *Zuvanda* showed no affinity to any of the 13 tribes included in the analysis (Warwick et al., 2007).

Goldbachia was not assigned to a tribe by Al-Shehbaz et al. (2006).

The Asian monospecific *Spirorrhynchus* was placed by Hayek (1911) in the tribe Arabideae and by Schulz (1936) in the tribe Euclidieae. The genus was not included in previous molecular studies, though Al-Shehbaz et al. (2006) suspected affinity to the tribe Isatideae.

Molecular studies by German et al. (in prep.) showed that *Calepina*, *Goldbachia*, and *Spirorrhynchus* formed a clade (58–67% BS) not closely related to any of the tribes. They are placed herein in the re-established Calepineae Horan., a tribe characterized by several characters given below.

Calepina differs from both *Goldbachia* and *Spirorrhynchus* in having spreading, non-saccate sepals, somewhat zygomorphic petals, basally non-articulate pedicels, and subconduplicate cotyledons (Appel and Al-Shehbaz, 2003). The three genera, however, resemble each other in habit, indumentum, cauline leaves, and fruits (see below).

ERYSIMUM

Erysimum comprises some 223 species (Warwick et al., in prep.) distributed primarily in Eurasia, with 8 species native to North Africa

and Macaronesia, and 16 to North America (authors' compilation). Many authors recognized *Cheiranthus* L. and *Erysimum* as distinct

genera distinguished by the presence of median nectaries (vs. their absence), terete or 4-angled (vs. latiseptate) fruits, and incumbent (vs. accumbent) cotyledons. These differences were considered by some to be significant at the tribal level. Indeed, de Candolle (1821) placed *Erysimum* and *Cheiranthus* in the tribe Sisymbrieae and Arabideae, respectively, whereas Hayek (1911) placed *Erysimum* in the Arabideae and *Cheiranthus* in the Alysseae; Schulz (1936) maintained both genera in the Hesperideae.

Al-Shehbaz et al. (2006) assigned *Erysimum* (including *Cheiranthus*) to the broadly circumscribed tribe Camelinae DC., a position that

was later maintained by Warwick et al. (2007). The genus *Erysimum* formed a distinct monophyletic group in several ITS-based studies (e.g., Heenan et al., 2002; Warwick et al. 2007). Molecular studies by German et al. (in prep.) demonstrated that the Camelinae sensu Al-Shehbaz et al. (2006) is polyphyletic, and *Erysimum* (3 spp.) formed a separate, well-resolved clade from other members of the Camelinae, that merits the recognition at the tribal level, herein Erysimeae Dumort. In their comprehensive ITS phylogeny of the Brassicaceae, Bailey et al. (2006) also showed *Erysimum* to form a well-resolved clade with 100% bootstrap support.

TAXONOMIC CONSIDERATIONS

Based on the above discussions, the following five tribes are recognized. The number of species in a given genus follows Warwick et al. (2006b). Listing of the genera under each tribe is based on molecular studies that are either published or in preparation.

Tribe Aphragmeae D. German & Al-Shehbaz, *trib. nov.* Type genus: *Aphragmus* Andr. ex DC., *Prodr.* 1: 209. 1824.

Herbae perennes vel annuae, pilis minutis simplicibus vel furcatis; folia basalia integra vel 3–7-partita; folia caulina petiolata vel sessilia, basi cuneata nonauriculata; racemi bracteati; petala alba, rosea, azurea vel purpurea; ovula numerosa; fructus siliculae vel siliquae, glabri vel pubescentes, tereti vel latiseptati; stigma integra; semina uni- vel biseriata, rarius solitaria; cotyledones incumbentes.

Annual or perennial herbs; *trichomes* minute, simple or forked; *basal leaves* entire or palmately 3–7-lobed; *cauline leaves* petiolate or sessile, cuneate, non-auriculate at base; *racemes* bracteate; *petals* white, rose, deep-blue, or purple; *ovules* numerous; *fruits* siliques or silicles, glabrous or pubescent, terete or latiseptate; *stigma* entire; *seeds* uni- or biseriata, rarely solitary; *cotyledons* incumbent.

This unigeneric tribe includes 11 species distributed primarily in the high mountains of central Asia and Himalaya, and only *Aphragmus eschscholtzianus* grows in the arctic (see above). The tribe is distinguished from other tribes by a combination of bracteate racemes, minute trichomes, numerous ovules, entire stigmas, and incumbent cotyledons.

Tribe Biscutelleae Dumort., *Fl. Belg.*: 118. 1827. Type genus: *Biscutella* L., *Sp. Pl.* 2: 653. 1753.

Annual or perennial herbs; *trichomes* simple or absent; *basal leaves* entire, dentate, or lobed; *cauline leaves* sessile, often non-auriculate at base, sometimes absent; *racemes* bracteate or not; *petals* white or yellow; *ovules* 2; *fruits* silicles, didymous, glabrous or pubescent, angustiseptate; *stigma* entire; *seeds* flattened; *cotyledons* accumbent.

A bigeneric tribe consisting of the primarily Mediterranean *Biscutella* (53 spp.) and the monospecific *Megadenia*. Schulz (1936) placed both genera in the tribe Lepidieae subtr. Iberidineae, but this subtribe included a heterogeneous assemblage of genera assigned by Al-Shehbaz et al. (2006) to at least four tribes. It is distinguished from other tribes by the didymous, angustiseptate silicles, 2-ovuled ovaries, entire stigmas, and accumbent cotyledons.

Tribe Calepineae Horan., *Char. Ess. Fam.*: 169. 1847. Type genus: *Calepina* Adans., *Fam.* 2: 423. 1763.

Annual or biennial herbs; *trichomes* simple or absent; *basal leaves* rosulate or not, dentate or pinnatifid to pinnatisect; *cauline leaves* petiolate or sessile and auriculate to amplexicaul; *racemes* bracteate or not; *petals* white, pink, purple, or yellowish; *ovules* 1–3; *fruits* silicles or siliques, indehiscent, woody, often glabrous, terete, or slightly flattened; *style* short or beak-like; *stigma* entire; *seeds* aseriata; *cotyledons* incumbent, rarely subconduplicate.

The tribe consists of eight Asian species, of which six belong to *Goldbachia* and one each to *Calepina* and *Spirorrhynchus*. It is distinguished from other tribes by the indehiscent, woody fruits, 1–3-ovuled ovaries, simple or no trichomes, and entire stigmas.

Tribe Conringieae D. German & Al-Shehbaz, *trib. nov.* Type genus: *Conringia* Heist. ex Fabr., Enum.: 160. 1759.

Herbae annuae vel biennes, pilis simplicibus vel nullis; folia basalia integra vel dentata; folia caulina integra vel dentata, sessilia, basi cordata, sagittata vel auriculata; racemi ebracteati; petala alba, lutea, rosea, vel purpurea; ovula numerosa; fructus siliquae, glabri, tereti, latiseptati, vel angulari; stigma capitata vel conica, biloba, decurrentis, rarissimi integra; semina uniseriata, cotyledones incumbentes vel rarissimi subconduplicati.

Annual or biennial herbs; *trichomes* simple or absent; *basal leaves* rosulate or not, entire or dentate; *cauline leaves* entire or dentate, sessile, cordate or sagittate to auriculate at base; *racemes* ebracteate; *petals* white, yellow, rose, or purple; *ovules* numerous; *fruits* siliques, glabrous, terete, latiseptate, or angled; *stigma* capitata or conical, 2-lobed, decurrent, rarely entire; *seeds* uniseriate; *cotyledons* incumbent or rarely subconduplicate.

The tribe includes *Conringia* (6 spp.) and *Zuvanda* (3 spp.). All species grow in southwest Asia, but the range of one, *C. planisiliqua*, extends into the Himalayas, whereas *C. orien-*

talis (L.) Dumort. is a naturalized weed outside its native Eurasian range. The tribe Conringieae is distinguished from other tribes by being primarily glabrous or with simple trichomes only and by having sessile, cordate, auriculate or sagittate cauline leaves, linear fruits, capitata or conical and decurrent stigmas, and incumbent or rarely subconduplicate cotyledons.

Tribe Erysimeae Dumort., Fl. Belg. 123. 1827. Type genus: *Erysimum* L., Sp. Pl. 2: 660. 1753.

Annual or perennial herbs, sometimes shrubs or subshrubs; *trichomes* sessile, malpighiaceae or stellate; *basal leaves* rosulate, entire or dentate, rarely pinnately lobed; *cauline leaves* entire or dentate, petiolate or sessile, non-auriculate or very rarely auriculate at base; *racemes* often ebracteate; petals white, yellow, rose, or purple; *ovules* numerous; *fruits* siliques, often pubescent, terete, latiseptate, or angled; *stigma* capitata, 2-lobed or subentire; *seeds* uniseriate or rarely biseriata; *cotyledons* incumbent or accumbent.

This unigenic tribe consists of 223 species in *Erysimum*. It is distinguished from the other tribes by the predominantly malpighiaceae and stellate trichomes with unbranched rays, many-seeded siliques, and predominantly yellow flowers. Both *Erysimum* and *Cheiranthus* were simultaneously published by Linnaeus (Sp. Pl. 2: 660, 661. 1753). Wettstein (1889) was the first to unite the two genera under *Erysimum* and, therefore, this generic name has priority (McNeill et al., 2006: Article 11.5).

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