COMPARATIVE MORPHOLOGY OF THE CAPITULUM OF ENCELOPSIS (ASTERACEAE: HELIANTHEAE)

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ABSTRACT

Features of the capitula of all four species of Encelopsis were examined with light and scanning electron microscopy, measured, and subjected to univariate analysis. Differences were found in the complement, distribution, and density of trichomes, the size of the receptacle, ray ligule, and disk corolla tube, and the size and shape of the phyllaries, paleae, disk corolla throats, and achenes. Morphology of trichomes, phyllaries, and achenes, as well as other vegetative characteristics, show that E. nudicaulis, E. covillei and E. argophylla form a group separate from E. nutans. Features of the achene suggest affinity of the former group with Geraea, whereas features of the trichomes and achene of E. nutans support affinity with Encelia. Characters of the receptacle, paleae, ray and disk corollas, and achene clearly show that E. nudicaulis, E. covillei, and E. argophylla are distinct.

ENCELOPSIS, a genus of four species, inhabits the Colorado Plateau and Great Basin, including canyons of the peripheral mountains. The genus was first established by Nelson (1909) and last treated as a whole by Blake (1913). It is allied with Encelia and Geraea (Robinson, 1981; Clark and Sanders, 1986). Previous taxonomic works have been based primarily on herbarium specimens and have left unclear the relationships within the genus and even the number of taxa. Even though an understanding of the morphology is critical to clarification of these taxonomic and evolutionary problems, there have been no detailed morphological studies of the genus. The purpose of this study is to explore the morphology of the capitulum.

MATERIALS AND METHODS—This study includes materials from 26 collections representing all four species (Table 1). (Encelopsis nudicaulis (A. Gray) A. Nelson var. corrugata Cronquist is included within E. nudicaulis—no consistent differences were found between these taxa in the features studied.) Capsules were taken from material collected and preserved in the field or from cultivated plants grown from achenes collected in the field.

Cultivated plants were started in the greenhouse and then grown in 8 inch pots outside at California State Polytechnic University, Pomona. The soil consisted of 8 parts pumice, 4 parts commercial container soil, and 1 part gypsum.

Materials for the scanning electron microscope were prepared and photographed by the methods of Clark, Sanders and Charest (1986) and Charest-Clark (1984).

Measurements were made of flower heads in 70% ethanol and mature dry achenes using a vernier caliper and a dissecting microscope at 10× magnification. Eighty-three capitula were examined, and from each, the following were measured: each receptacle, one of each type of mature floret present, one of each type of palea, and one phyllary from each rank. Disk florets and associated paleae were chosen in anthesis with the stigmatic surfaces exposed.

In order to confirm perceived differences, univariate statistical analyses were performed: one-way ANOVA and correlation coefficient with MINITAB and two-sample t test with Bonferroni distribution with BMDP, both located on the California State University Central Cyber computer.

RESULTS—The capitulum (Fig. 1), borne on a scapose peduncle which occasionally also supports one or more small, linear bracts, is nodding in fruit and is usually nodding briefly in early bud. Additionally in E. nutans, the slender peduncle bends at its base and arches until the maturing head rests on the ground.

Phyllaries—Within a taxon, phyllaries do not vary significantly in length (Fig. 2); however, throughout the genus the middle ranks tend to be longer. The outer two ranks (one in E. nutans) are wider than the inner two. The mean width of phyllaries does not differ significantly.

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Fig. 1. *Enceliopsis covillei* (234; accession numbers refer to Table 1). ×1.8. Median longitudinal section (MLS) of capitulum showing convex receptacle, recurved phyllaries, and disk florets.

![Image of *Enceliopsis covillei* capitulum](image)

Fig. 2. Length and width (at widest point) of *Enceliopsis* phyllaries by ranks. In this and subsequent bar plots, thick bars represent 95% confidence interval of the mean as derived from analysis of variance. (In this case applied independently to the data from each species and to the combined data of all species.) Thin lines represent the range. Significant differences suggested by graphed confidence intervals of the mean are confirmed by pairwise two-sample *t* tests using the Bonferroni distribution except as noted.
for *E. covillei* and *E. argophylla*. While the combined data indicate that the mean widths of all other taxa and the mean lengths of all taxa are distinct, there is a great deal of overlap in the range of sizes.

*E. nutans* also differs from the other members of the genus in phyllary shape, trichome complement and trichome density. The phyllaries of the outer ranks of all members of the genus except *E. nutans* are triangular to broadly falcate, often with a broadened ovate base. Moving centrally, members of each rank become more like the lanceolate phyllaries of the innermost rank (Fig. 3–5, 7–9). Phyllaries of inner ranks are recurved a minimum of one half of their lengths, while those of outer ranks are recurved as much as full length (Fig. 1). A dense pubescence covers all exposed surfaces (Fig. 3–5). The outermost phyllaries of *E. nutans* (Fig. 6) sometimes have an ovate base, but normally they are lanceolate with only the distal 1–2 mm recurved. Phyllaries are in 2–3 series in *E. nutans*, while the *E. nudicaulis* they are in 3–4 series, and *E. argophylla* and *E. covillei* are similar in having phyllaries in 4–6 series (most commonly five).

The pubescence of the exposed areas of the phyllaries of *E. covillei* (Fig. 7), *E. argophylla* (Fig. 8) and *E. nudicaulis* (Fig. 9) consists of uniseriate hairs usually of four or five cells. The shorter basal cells and the longer distal cells are all of about the same diameter. Biseriate glandular trichomes are common on phyllaries of *E. nudicaulis*, and are sometimes present on those of *E. covillei* and *E. argophylla*. When present, they are most abundant on the bases of the abaxial surface and margins, sometimes only on the inner phyllaries.

The densely hispid appearance of the abaxial surface and recurved portion of the adaxial surface in *E. nutans* (Fig. 10) is produced by uniseriate hairs that are very different from those of the other three species. They are larger, and the shorter basal cells have much larger diameters than the more distal cells. The longer cells are abruptly constricted past their unions with cells of larger diameter, giving the appearance of having swollen joints. Biseriate glandular trichomes have not been observed on the phyllaries of *E. nutans*.

Receptacle—In all species the florets are borne on a convex receptacle (Fig. 1). In fruit the receptacle swells as the capitulum nods. The receptacles of *E. covillei* and *E. argophylla* have nearly equal diameters and are the broadest (Fig. 11). While *E. nutans* and *E. nudicaulis* have receptacles with similar mean diameters, the latter has a greater range. The receptacle of *E. nudicaulis* also occasionally supports hairs arising at the bases of the paleae.

Palaee—The caducous paleae subtending each disk floret are of two types in all taxa (ray florets, where present, are subtended by phyllaries). Characteristic of the central paleae is a narrow densely pubescent terminal appendage which partially covers the corolla in bud (Fig. 12–15). It is much reduced or absent in the peripheral palea of each parastichy not ending with a ray floret or phyllary (Fig. 16–19). This appendage becomes slightly longer in the more centrally located paleae. Central paleae of *E. argophylla* and *E. nutans* have much longer appendages than do the others (Fig. 16–20).

In all taxa the appressed parts of the paleae (primarily the margins and the base) are scarious, the exposed areas (tip and in outer members the keel) being green. In the rayless *E. nutans*, outer paleae may easily be mistaken...
for phyllaries (Fig. 6, 19). *Enceliopsis covillei* paleae tend to be somewhat more cartilaginous than those of the others. The uniseriate hairs that cover the chlorenchymatous areas and form a tuft at the tip are similar to those of the phyllaries except that the hairs of *E. covillei* (Fig. 12) tend to be shorter than those of other species (Fig. 13–15). Biseriate glandular trichomes are present on all taxa (sparsely on the central paleae of *E. nutans* and rarely on *E. covillei*). Glandular trichomes tend to be concentrated about the keel, but in *E. nudicaulis* the entire chlorenchymatous area and the upper margins are often densely glandular, particularly on the outer paleae.

Excluding the tip, paleae have varying shapes: those of *E. nutans* (Fig. 19) are oblong; in all the other species (Fig. 16–18), they are more likely to be lanceolate or sublunate-lanceolate to nearly elliptic.

The upper half of the margins are usually finely toothed, and may also be symmetrically or asymmetrically notched at the base of the appendage (Fig. 12–15). Those of *E. covillei* tend to be shallowly notched and more commonly symmetrical. Venation, although more obvious in *E. covillei*, is so inconsistent and varying in clarity as to make its usefulness as a character unlikely.

*Ray florets*—Where present, ray florets of

![Fig. 20. Length of terminal appendages of central paleae of *Enceliopsis.*](image)

*Enceliopsis* are neutral, yellow (tending toward orange in *E. argophylla*) and absorb ultraviolet (370 nm) radiation (Clark and Sanders, 1986). The ray florets of *E. covillei* are larger than those of *E. argophylla* and *E. nudicaulis* which

![Fig. 21. Scatterplot of length vs. width of the *Enceliopsis* ray corolla ligule. In this and subsequent scatter plots, bars represent 95% confidence interval of the mean as derived from analysis of variance. Width is significantly correlated with length only in *E. nudicaulis.*](image)
are similar in size (Fig. 21). *E. nutans* is the only ericoid taxon.

The corollas of all species tend to be narrowly spatulate (narrowly oblong-collate in some *E. argophylla*) and deeply to obscurely threetoothed at the tip. In some individuals the separation between corolla and rudimentary ovary is indistinguishable.

The adaxial surfaces are papillose (Clark and Sanders, 1986). Uniseriate, usually swollen hairs are present on the throat and the veins of the abaxial surface of the ligule in all three species (Fig. 22–24). They also occur between the veins in *E. covillei* and *E. nudicaulis*. The hairs are noticeably shorter in *E. covillei*. Glan-
dular trichomes are lacking in *E. covillei* (Fig. 22), sometimes present in *E. argophylla* (Fig. 23), and always present in *E. nudicaulis* (Fig. 24), sometimes densely so and extending to the tip of the ligule.

**Disk florets**—All are bisexual, yellow (toward orange in *E. argophylla*), and ultraviolet-absorptive (Clark and Sanders, 1986) with differences among the taxa including the length of the tube and throat, the shape of the throat, and the distribution and morphology of the trichomes.

The tube is shorter in *E. nudicaulis* than in the other taxa, and the throat is shorter in *E.*
covillei and E. argophylla (Fig. 16–19, 34). The throat of E. covillei is strongly bulbous at the base (Fig. 30); that of E. argophylla is amphiate (Fig. 31); and the throat in the other two taxa is more narrowly cylindrical to slightly bulbous (Fig. 32, 33). Occasionally individual heads of E. nudicaulis are composed of disk corollas so strongly bulbous as to be indistinguishable from E. covillei in this respect.

Uniseriate hairs occur on the abaxial surface of the limb in all species (Fig. 26–29). Although shorter, they are similar in shape and density to those on the phyllaries (Fig. 7–10). In E. nutans (Fig. 10, 29), they are less stout, but

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Fig. 34. Scatterplot of tube length vs. throat length of Enceliopsis disk corollas. The tube and throat lengths are significantly correlated in E. argophylla, E. nudicaulis, and E. nutans. The significant difference between the tube lengths of E. argophylla and E. nutans suggested by the confidence interval is not confirmed by the two-sample t test using the Bonferroni distribution.
TABLE 1. Range of each species and collections used in the study. Collections, arranged within each species by accession number, are from the field unless otherwise indicated

EncelOPSIS argophylla (D. C. Eaton) A. Nelson: Virgin River and Colorado River canyons of Clark Co., Nevada and Mohave Co., Arizona. The type specimen is reported to have been collected "near St. George," Utah, but it was more likely from Nevada (Sanders and Clark, unpublished).

219—Nevada. Clark Co.: 0.6 mi S of NV Hwy 167 on road to Callville Bay. Roadside, E of road on cut, 28 May 1983, Sanders 3 (achenes only).

220—Nevada. Clark Co.: Gypsum Wash at junction of NV Hwys 167 and 147, 28 May 1983, Sanders 4 (capitula only).

221—Nevada. Clark Co.: NV Hwy 167, 14.7 mi S of Echo Bay turnoff, 29 May 1983, Sanders 5 (achenes only).

222—Nevada. Clark Co.: NV Hwy 167, 8.9 mi N of Echo Bay turnoff, 29 May 1983, Sanders 6 (field achenes and field and cultivated capitula).


253—Nevada. Clark Co.: NV Hwy 167, 8 mi S of Overton, 19 Apr 1984, Sanders 18 (capitula only).

292—Nevada. Clark Co.: NV Hwy 167, 10.4 mi S of Echo Bay turnoff, 4 Aug 1984, Sanders 34 (achenes only).

Encelopsis coviLelli (A. Nelson) S. F. Blake: five canyons of the western side of the Panamint Mountains of Inyo Co., California.


234—California. Inyo Co.: Trona-Wildrose Rd., 1.8 mi S of Wildrose Campground, 3 Jul 1983, Clark 609 (field achenes and capitula from cultivated plants).


256—California. Inyo Co.: Jail Canyon, 4.5 mi up canyon from junction with Indian Ranch Road, near mine, 20 Apr 1984, Sanders 21 (capitula only).

257—California. Inyo Co.: Surprise Canyon, 3.7 mi up canyon from junction with Indian Ranch Road, 20 Apr 1984, Sanders 22 (capitula and achenes).

Encelopsis nudicaulis (A. Gray) A. Nelson: scattered populations throughout most of Utah and Nevada, extending into southern Idaho, northern Arizona, and eastern California.


223—Utah. Emery Co.: Interstate 70, 0.9 mi W of Castle Valley View Point, 9 mi E of Sevier Co. line, 4 Jun 1983, Sanders 8 (capitula only).

236—Idaho. Owyhee Co.: off ID Hwy 78, about 7 mi E of Bruneau, 11 Jul 1983, Sanders 10 (capitula and achenes).


TABLE 1. Continued


261—Utah. Wayne Co.: UT Hwy 24 at Hanksville, junction of UT Hwys 24 and 95, 19 May 1984, Sanders 27 (capitula only).


294—Nevada. Nye Co.: Nevada Nuclear Test Site, Eagle Roost Canyon, about 0.4 mi E of Mercury Road on jeep trail, then about 20 meters up first tributary from S, 20 May 1985, Sanders 33 (achenes only).

Encelopsis nutans (A. Eastwood) A. Nelson: eastern Utah and the valley of the Colorado River in extreme western Colorado.

258—Utah. Emery Co.: near town of Green River, 0.9 mi S of railroad tracks on Airport Rd, 19 May 1984, Sanders 24 (capitula and achenes).

259—Utah. Grand Co.: UT Hwy 128, 5.9 mi S of I-70, 19 May 1984, Sanders 25 (capitula only).

262—Utah. Emery Co.: near UT Hwy 28, 17 mi N of I-70, 1 mi W on gravel to old US 6-50, 0.5 mi S on old 6-50 to gravel road to Huntington, 0.7 mi NW on Huntington Rd, 20 May 1984, Sanders 28 (capitula only).


otherwise identical to those on the phyllaries. The hairs of E. coviLelli (Fig. 26) have obtuse tips, while those of E. nudicaulis (Fig. 28) and sometimes E. argophylla have acute tips (Fig. 27). Hairs may be slightly longer in E. argophylla and slightly shorter in E. coviLelli. The cells are usually swollen, particularly in E. nudicaulis (Fig. 28).

Glands occur on the abaxial surface of the limb in E. argophylla (but may be hidden by the longer hairs as in Fig. 27) and in E. nudicaulis (Fig. 28).

There are usually no trichomes on the throat (Fig. 30—33), but with the exception of E. nutans, hairs may extend down the throat in lines below or between the corolla lobes. In E. nudicaulis (Fig. 32) tube trichomes may extend to the base of the throat.

Encelopsis coviLelli (Fig. 35) lacks trichomes on the tube, and E. nutans (Fig. 38) has only glands. E. argophylla (Fig. 36) and E. nudicaulis (Fig. 37) may have hairs and glands, glands only, or neither on the tube. When hairs occur on the tube, they are similar to those found on other organs of E. nutans or occasionally biseriate like those of all achenes. In all taxa on which they occur, tube trichomes vary greatly in density from floret to floret.

Individual anther appendages may lack tri-

Trichomes in all species. Anthers of **E. covillei** (Fig. 39) are without trichomes or with one to four short hairs; **E. nutans** anthers (Fig. 42) lack hairs, but usually are densely glandular; **E. nudicaulis** anthers (Fig. 41) usually are densely glandular, but rarely have hairs; **E. argophylla** anthers (Fig. 40) vary, some resembling **E. nudicaulis** and some **E. covillei**.

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Fig. 35–42. Scanning electron micrographs of **Enceliopsis** disk corolla tubes and anthers. Fig. 35–38. Corolla tubes (all of equal magnification). **35. E. covillei** (256). **36. E. argophylla** (249). **37. E. nudicaulis** (260). **38. E. nutans** (258). Fig. 39–42. Anthers (all of equal magnification). **39. E. covillei** (256). **40. E. argophylla** (253). **41. E. nudicaulis** (254). **42. E. nutans** (258).
Enceliopsis stigmas (Fig. 25) are alike in shape and in having the stigmatic surface fused (Robinson, 1981). The lobes tend to be a little longer in *E. argophylla* and *E. covillei*; they may curl to form a circle of one and one-half loops at maturity.

**Achene**—In all taxa the mature achene (Fig. 43–46) is flattened and consists of a darkly pigmented, double convex body surrounded by an ivory to yellow thickened margin. In all taxa except *E. nutans*, the margin widens and thickens at the apex to form a broad crown which when viewed from above encloses an elliptic depression containing a central corolla and style scar. One or both ridges above the depression are topped by a thin line of squamellae which are most obvious (to 0.6 mm high) in *E. nudicaulis* and reduced to a low thin ridge in *E. covillei*.

The crown may form the widest dimension, giving the achene an obtriangular shape, or it may be medially indented and laterally rounded producing an obcordate shape. In *E. argophylla* the darkly pigmented surface occasionally also extends in a narrow band through the crown dividing it medially. *E. covillei* achenes (Fig. 43, 49) tend to be shorter, wider, and more obcordate, while those of *E. nudicaulis* and *E. argophylla* (Fig. 44, 45, 49) are longer in proportion to their widths and tend to be more narrowly deltoid. The ivory margin is most pronounced in *E. covillei* (Fig. 43). In *E. argophylla* (Fig. 45) it is usually reduced to a thin lateral line giving the appearance of being absent.

Two subulate awns, one of which may be reduced or absent, arise from the crown at the points of the depression. Those of *E. covillei* are always very short and lunulate (Fig. 43) while in other taxa they vary from short and lunulate to long and acicular (Fig. 44).

At the basal tip of the achene, the margin becomes thickened into a bilobed, asymmetrical callus or carpopodium (Robinson, 1981) the growth of which forces the mature achene from the receptacle. The carpopodium is most obvious in *E. argophylla* (Fig. 45).

Setiform biseriate trichomes (*zwillings-haare*) cover the body and the margin, usually leaving a band between them in which the hairs are either shorter or lacking. Body hairs do not extend much beyond the crown, and marginal hairs do not extend beyond the awns. In *E. covillei* (Fig. 43) the hairs are minute, giving a silvery sheen to the achene, or occasionally they are nearly absent.

The achenes of *E. nutans* (Fig. 46) differ from those of all others in shape and trichome characteristics. The achene lacks the broad crown and squamellae, and the nearly white margin uniformly surrounds the body. The apical depression is reduced to a notch only large enough to provide for corolla and style attachment. Rarely, two short stout awns, from which tufts of long hairs extend, may arise from the margin beside the notch. The trichomes are more sericeous and long enough to obscure the corolla tube.

**DISCUSSION**—This study provides evidence supporting 1) existing species boundaries within *Enceliopsis*, 2) kinship among the species of *Enceliopsis*, and 3) affinities among the genera of the *Encelia* alliance. While this discussion will emphasize unique homologies (synapomorphies), the phylogenetic analysis necessarily will include more than the capitulum and will be considered elsewhere.

Although *E. argophylla* and *E. covillei* have most often been treated as distinct species (Blake, 1913, 1931; Jaeger, 1940; McDougall, 1973; Munz, 1974; Abrams and Farris, 1960), they have also been considered varieties of one species (Jepson, 1925; Munz and Keck, 1959). In addition it has been suggested by Kearney and Peebles (1960) and Thorne, Prigge and
Henrickson (1981) that *E. argophylla* and *E. nudicaulis* may not be distinct. The morphology of the capitulum provides supporting evidence of three distinct species. Table 2 shows 10 differences between *E. nudicaulis* and *E. argophylla*, 15 between *E. nudicaulis* and *E. covillei*, and 15 between *E. argophylla* and *E. covillei*.

Evidence that *E. nudicaulis*, *E. argophylla* and *E. covillei* form a natural group can be seen in their similarity of habit, trichome complement (which forms a white pubescent covering on the leaves and peduncle), and stout scapose peduncle. For the purposes of this discussion, we shall refer to these three species (excluding *E. nutans*) as *Enceliopsis* sensu stricto. The morphology of the capitulum provides additional supporting evidence for this grouping. The density and type of uniseriate hair is reasonably uniform throughout the capitulum; however, the presence or absence of trichomes in a particular location on the organs of the capitulum may be variable and often does not appear to be a useful character. In this respect, the members of this group are very similar, but differ significantly from *E. nutans*. The phyllaries are similar in size, shape, and degree of recurvature. Additionally, biseriate glands may occur on the phyllaries, while none have been observed on those of *E. nutans*. The large disk florets—one character shared with *E. nutans*—contrast sharply with the smaller florets in *Encelia*. The density and type of hairs on the abaxial surface of the disk corolla lobes is consistent within *Enceliopsis* sensu stricto.

All species of both *Enceliopsis* and *Geraea* are more or less herbaceous. In addition the morphology of the achene suggests an affinity of *Enceliopsis* sensu stricto with *Geraea*. Both have achenes in which the white margin becomes broad and thick at the apex to form a crown which in all except *G. canescens* supports a more or less conspicuous fringe of squamellae (Fig. 43–45, 47).

The uniqueness of *E. nutans* has long been recognized. Originally, it was described as an *Encelia* (Eastwood, 1891). A few pages later in the same publication, Marcus E. Jones (1891), in order to avoid erecting “a new genus upon it,” described it as *Verbesina scaposa*, noting that “this curious plant differs widely from any known species of *Verbesina.*” Probably the most compelling reasons for its placement in *Enceliopsis* involved its basal leaves, scapose peduncle and desert habitat. However, these apparent similarities are generally only superficial, obscuring real differences. *E. nutans* has no vegetative stem above the ground, and all herbaceous parts arise from a swollen root six to ten centimeters underground. All above-ground parts are much less densely trichomed and exist for less than two months (April and May).

Although the capitula of *E. nutans* do not show many quantitative differences from the

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other species, it is difficult to find qualitative similarities which support its placement in *Enceliopsis*. The phyllaries differ from those of the other species in size, shape and degree to which they are recurved. The achene (Fig. 46) with its notched apex that lacks squamellae and only rarely supports awns suggests an affinity with the genus *Ecelia* (Fig. 48). The hairs of the achene are unlike those of *Enceliopsis* sensu stricto in that they are more flexible, and are long enough to obscure the tube of the disk corolla. In addition, the hairs covering the leaves and peduncle and occurring throughout the capitulum are more similar to those found on some species of *Ecelia*.

This study of *Enceliopsis* capitulum morphology is an essential contribution to an eventual cladistic analysis of the genus (Sanders and Clark, in preparation). In addition it will provide a comparative foundation for similar studies of *Ecelia* and *Geraea* and thus add to our understanding of relationships among all three genera.

**LITERATURE CITED**


