A REVIEW OF THE TRIBE ECHINOPHOREAE (UMBELLIFERAE)

I. C. HEDGE & J. M. LAMOND

ABSTRACT. A taxonomic review is given of the tribe Echinophoreae (Umbelliferae). Six genera, *Pycnocycla*, *Dicyclophora*, *Ergocarpon*, *Anisosciadium*, *Echinophora* and *Thecocarpus*, are recognized in the tribe which is characterized by a very distinctive type of fruiting umbellule in which occurs both sexual differentiation of the flowers and varying degrees of fusion and induration involving bracteoles, pedicels and fruit. Keys are given to the genera and species; available taxonomic characters are discussed as are aspects of fruit dispersal and evolutionary trends.

INTRODUCTION

Because of the remarkable structure of the fruiting umbellules (fig. 1), the Echinophoreae is one of the relatively few distinct and apparently homogeneous tribes in the whole of the Umbelliferae. It was first recognized and described by Bentham & Hooker in Genera Plantarum (1: 865, 1867) who included in it *Echinophora* L. and *Pycnocycla* Lindl.; *Anisosciadium* DC. and *Dicyclophora* Boiss. were regarded as hardly different from the former and the latter respectively. The tribe was originally described as having female flowers solitary and sessile in the umbellules, surrounded in fruit by the indurated pedicels of the male flowers, and by the unicarpellate subterete fruit (the other carpel of the flower aborting). Boissier, a few years later in 1872 (Fl. Orient. 2: 917), gave a similar definition of the tribe but added that the albumen was deeply sulcate with involute margins. He recognized *Anisosciadium* and *Dicyclophora* as independent genera. Drude in 1897 (Pflanzenfam. 3.8: 146) transferred *Thecocarpus* Boiss. from the tribe Seselineae, where it had been placed by its author on account of the more or less flat albumen, to the Echinophoreae. Drude modified the tribal description to cover the characteristic 2-carpellate and fused fruits of the new generic addition. Recently *Ergocarpon* C.C. Townsend was described, based on *Exoacantha cryptantha* Rech. fil., and added to the tribe thus bringing the total of genera in the Echinophoreae to six.

The purpose of this short paper is to give an up to date review of the tribe, to describe the range of variation in the infructescence, to discuss the available taxonomic characters and to make some general comments about the sexual differentiation, fruit structure and dispersal.

DEFINITION OF THE TRIBE

Although Townsend (1964) recently gave a formal description of the tribe, a few emendations are needed, some of which were pointed out to us by Dr S. Tamamschian, Leningrad. There are also some additional features worthy of mention and accordingly a full fresh description is given.

Umbels compound; flowers polygamous. Bracts and bracteoles present, persistent, often foliaceous or indurated in fruit. Central flower of umbellule

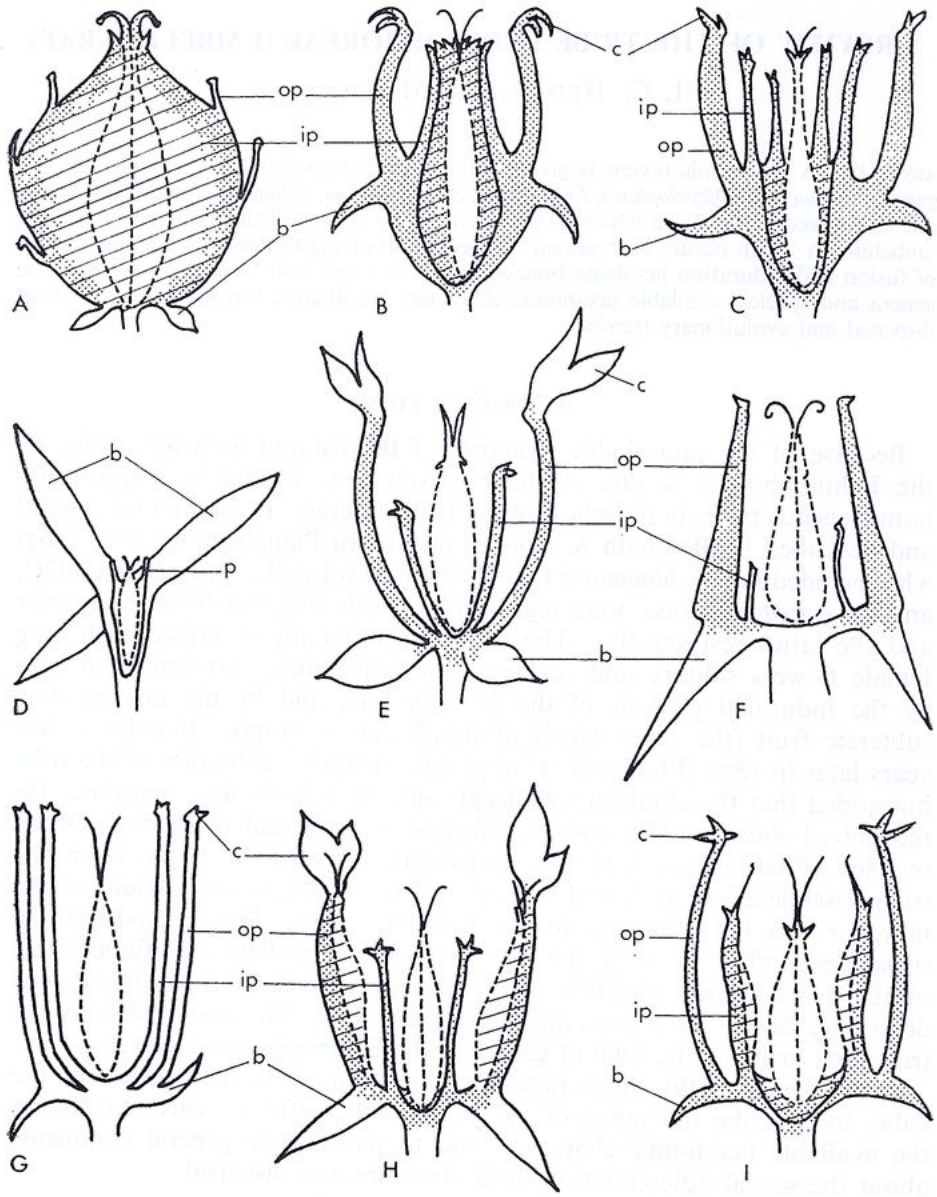

FIG. 1. Diagrammatic L.S. of fruiting umbellules of Echinophoreae. The central sessile fruit of the umbellule is surrounded by pedicels of male flowers and bracteoles which may indurate and/or fuse in a variety of ways. b, bracteoles; c, calyx lobe; p, pedicel (i, inner; o, outer); ----- position of fertile mericarp; hatching indicates fused parts; shading indicates indurated parts. A, *Thecocarpus carvifolius*; B, *Echinophora trichophylla*; C, *E. tournefortii*; D, *Ergocarpon cryptantha*; E, *Echinophora chrysantha*; F, *Dicyclophora persica*; G, *Pycnocycla spinosa*; H, *Anisosciadium orientale*; I, *Anisosciadium lanatum*.

hermaphrodite, sessile, bilocular, biovulate; outer flowers male (no stylopodium present) and/or female sterile (with anthers and stylopodium but no styles) or a few outer also hermaphrodite. Calyx lobes present or absent, often varying among different flowers within the umbellules. Petals white or yellow, sometimes pinkish, with an inflexed tip with or without side lobes. Outer pedicels after anthesis usually elongated, often indurated, often concrescent and forming a cage or shell around the central fruit, seldom fused with it forming a false nut. Fruit oblong-pyramidal, ± terete, bicarpellate or monocarpellate through abortion of second carpel, sessile, free on the receptacle or immersed in it; primary ribs inconspicuous, secondary absent; pericarp parenchymatous, not lignified; styles usually elongate, often hardened below, seldom very short. Stylopodium shortly conical, flat or hollowed. Carpophore, if present, bifid. Albumen on commissural face deeply sulcate, seldom ± flat or concave.

Annual to perennial herbs or shrubs, glabrous or with an indumentum, sometimes spiny, with variously pinnatisect, pinnate, palmate or rarely entire leaves. Mostly in SW Asia but extending in the southwest to Guinea in W Africa.

6 genera; *Anisosciadium* DC., *Dicyclophora* Boiss., *Echinophora* L. (type genus of the tribe), *Ergocarpon* C. C. Townsend, *Pycnocycla* Lindl. and *Thecocarpus* Boiss.

As the above description indicates, there is a considerable degree of sexual differentiation within the umbellule and much variation in the form of the fruiting umbellule. There are no precise botanical terms to cover the infructescence structures but rather than coining new terms we use the following for the three main types:

(i) 'cage'—where the fruit is not or only slightly sunk in the receptacle and is surrounded by a more or less circular cage of which the bars are the indurated but not concrescent pedicels (fig. 1, E–I; fig. 4);

(ii) 'shell'—where the fruit is sunk within the receptacle and surrounded by a shell formed by the indurated and partly or wholly concrescent pedicels, but stands more or less free within the shell (fig. 1, B–C);

(iii) 'false nut'—where the fruit is completely fused with the surrounding concrescent pedicels forming a false nut, indurated without and somewhat spongy within (fig. 1A).

Key to Genera

1. Bracteoles ± hiding the flowers of the umbellule, lanceolate-triangular with prominent white margins; fruit not surrounded by a cage, shell or false-nut . . . . . 3. *Ergocarpon*
+ Bracteoles never hiding the flowers of the umbellule, rarely with white margins; fruiting umbellules with a cage, shell or false-nut structure 2
2. Fruiting pedicels and mericarps completely fused together to form a false nut; albumen ± flat . . . . 6. *Thecocarpus*
+ Fruiting pedicels forming a shell or cage around fruits but not fused with them; albumen inrolled to sulcate . . . 3

3. Umbellules with some outer monocarpellate fruits in addition to the central bicarpellate fruit; annuals . . 4. *Anisosciadium*
+ Umbellules with only central fruit developing, usually monocarpellate; perennials, biennials or annuals . . . 4
4. Fruiting umbellule shell- or cage-like, bracteoles fused with pedicel bases or rarely free and elliptic to orbicular; dorsal vittae 4; often much branched rather bushy plants with shortly pedunculate umbels, occasionally peduncles long . 5. *Echinophora*
+ Fruiting umbellule cage-like, bracteoles free, lanceolate-triangular to linear-lanceolate; dorsal vittae 9 to several; often stiffly erect plants with somewhat capitate umbels, clearly pedunculate 5
5. Pedicels of inner flowers not enlarging at fruiting time, outer glabrous, thickened; annuals with a sterile central umbellule forming a black cone . . . . . 2. *Dicyclophora*
+ Pedicels all lengthening at fruiting time, ±equal, not or scarcely thickening, hirsute; perennials with all umbellules similar 1. *Pycnocycla*

Genera and species

1. Pycnocycla Lindl. in Royle, Ill. Bot. Himal. 232 (1835); Boiss., Fl. Or. 2: 951–954 (1872). Figs. 1G; 2.

Perennials, glabrous or pubescent, often rigid and shrubby. Stems terete, grooved. Leaves 1–4-pinnate, subpalmately divided or entire and palmately veined, often spinose. Umbels condensed usually on long peduncles. Bracts often spinose. Rays few to several, short and subequal. Bracteoles often spine-tipped, in fruit neither indurated nor becoming part of cage. Umbellule with central flower only hermaphrodite. Calyx lobes usually present on all flowers. Petals long, narrow, white, sometimes flushed pink, pubescent on incurved tip, with a prominent oil canal, outer radiant or not. Anthers with an oil globule present or not. Pedicels of outer flowers indurated or not after anthesis, always lengthening and forming a cage, hirsute. Fruit bi- or mono-carpellate, sessile, not immersed in receptacle. Dorsal and commissural vittae several. Albumen sulcate.

c. 8 species; type of genus *P. glauca* Lindl.

In Boissier's time, seven fairly distinct species of *Pycnocycla* were recognized. Since then five others have been described; most of them are known only from the type gatherings and their status is uncertain until a wider range of material is at hand. Accordingly in the key given below closely related species are grouped together and not dealt with individually. When the account of the genus is prepared for Rechinger's Flora Iranica, we hope to have further material available so that a more definitive list of species can be given for this area.

The dense, more or less capitate heads of the flowering umbels are superficially similar in appearance to the inflorescences of some species of *Scabiosa* in the Dipsacaceae.

1. Plant not spiny; leaves pinnate 2
+ Plant spiny; leaves entire or trifidly or palmately divided or veined 4
2. Segments of leaves ovate-lanceolate, ±dentate sometimes deeply so; Sinai . . . . . 3. *P. tomentosa*
+ Segments of leaves linear or filiform, entire-margined; India, Arabia, Africa 3
3. Bracts 5-9, 4-8 mm; stems with few leaves, up to 75 cm high 1. *P. glauca*
+ Bracts c. 12, 10–13 mm; stems leafy, up to 1.5 m 2. *P. ledermannii*
4. Basal leaves trifidly or palmately divided to base, segments acicular 5
+ Basal leaves entire or palmately divided up to c. ¾ length . . 7
5. Umbels shortly pedunculate, 0–4 cm, axillary . . . 5. *P. nodiflora*, 5a. *P. caespitosa*
+ Umbels clearly pedunculate (4-) 9–50 cm, axillary or terminal . 6
6. Stem much branched, ±leafy; upper leaves entire or with abbreviated (1–8 cm) lateral lobes; calyx lobes ± absent 4. *P. spinosa*, 4a. *P. aitchisonii*
+ Stem branched below, leafy at base; upper leaves never entire, lateral lobes to 55 cm; calyx lobes present . . 6. *P. aucheriana*
7. Bracts ± shorter than rays; longest spines of leaf less than breadth of blade . . . 8. *P. flabellifolia*, 8a. *P. cephalantha*
+ Bracts exceeding umbellules; shortest spines of leaf equal to or more than breadth of blade 7. *P. acanthorhipsis*, 7a. *P. mesomorpha*

1. P. glauca Lindl. in Royle, Ill. Bot. Himal. 232 (January 1835).
Syn.: *P. abyssinica* Hochst. ex A. Rich., Tent. Fl. Abyss. 1: 333 (1848).
Ic.: Royle, Ill. Bot. Himal., t.51 (1835).
Type. India, banks of the Sutlej.
Abyssinia, Yemen, N and C India; c. 2400 m; fl. Sept.

2. P. ledermannii Wolff in Engl. Bot. Jahrb. 57: 220 (May 1921).
Syn.: *P. occidentalis* Hutch. in Kew Bull. 1921: 374 (Dec. 1921).
Syntypes. Cameroon: Adamau, Ngauma Sese, *Edlinger*, Niger-Benu-Chad Expedition 9 (B†); between Mashita and Kontscha, 750 m, *Ledermann* 5351 (B†); Gendero Mts, Dodo, *Ledermann* 3002 (B†).
Guinea, N Nigeria, Cameroon, Central African Republic; fl. March-Nov.

Jacques-Félix (1970) suggests that this should perhaps be thought of as a W African vicariad of the more eastern and north-eastern *P. glauca*.

3. P. tomentosa Dcne. in Ann. Sc. Nat. ser. 2, 3: 258 (May 1835).
Ic.: Jaub. & Spach, Ill. Pl. Or. 3: t.242 (1848).
Type. Sinai, Teyen or Beyen, *Bové* 122 (P).
Sinai; wadis; fl. May–June.

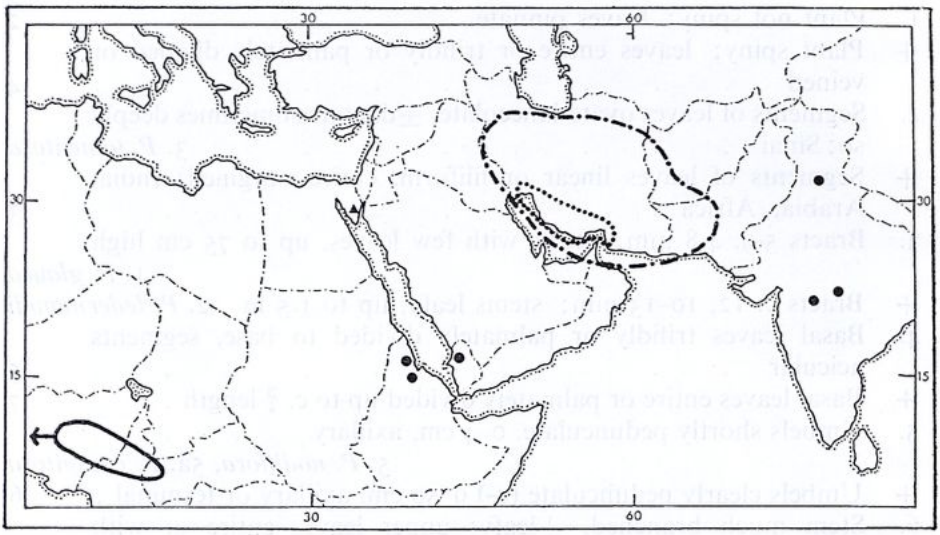

FIG. 2. Distribution of ● *Pycnocycla glauca*, ▲ *P. tomentosa*, —— *P. ledermannii* (records from Guinea not shown), —·—·— nine closely related spiny species of *Pycnocycla*, ···· *Dicyclophora persica*.

4. P. spinosa Dcne. ex Boiss. in Ann. Sc. Nat. ser. 3, 2: 87 (1844).
Ic.: Jaub. & Spach, Ill. Pl. Or. 3: t.243 (1848).
Syntypes. Iran: 'in Persiae aridis', *Aucher* 3714 (W!P); near Tehran, *Aucher* 4558 (W!P).
C, S Iran, W Afghanistan (?); dry sandy desert, 1500–2000 m; fl. June-Sept.

4a. P. aitchisonii Rech. f. & Riedl in Biol. Skr. 13, 4: 117 (1963).
Ic.: l.c. f. 80, 81.
Type. Iran: Khorassan, Malkat, 2 ix 1885, *Aitchison* 817 (holo C!; iso W).

Only known from the single gathering and recognized as a separate species on account of the very long bracts. Undoubtedly very near to *P. spinosa* and possibly further material will show that they cannot be separated.

5. P. nodiflora Dcne. ex Boiss. in Ann. Sc. Nat. ser. 3, 2: 88 (1844).
Type. Iran: "in Persia", *Aucher* 4561 (P,W!).
E, S Iran, W Afghanistan (?); fl. April-May (-Sept.).

5a. P. caespitosa Boiss. & Hausskn. ex Boiss., Fl. Or. 2: 953 (1872).
Type. Iran, SW: near Teng Tokab and Kuh Gelu, 910 m, *Haussknecht* (W!)
SW Iran: fl. June.

6. P. aucheriana Dcne. ex Boiss. in Ann. Sc. Nat. ser. 3, 2: 88 (1844).
Ic.: Flora of W Pakistan, ed. E. Nasir & S. Ali, No 20, fig 5 (1972).
Syntypes. Iran: S Persian desert, *Aucher* 4559 (W! P,G). Muscat and Oman: Chebek mts, *Aucher* s.n. (G).
Baluchistan, SE Iran and W Pakistan, E Arabia; gravel plains, sandy wadis, 250–900 m; fl. April-May.

7. P. acanthorhipsis Rech f., Aell. & Esfand. in Anz. math.-naturw. Kl. Oesterr. Akad. Wiss. 1952: 195 (1952).
Ic.: Biol. Skr. 13, 4: f. 78, 79 (1963).
Type. Iran: Baluchistan, between Khwash and Iranshahr, Karvandar mts, c. 1600 m, 17 v 1948, *Rechinger f., Aellen & Esfandiari* 4038 (W!E!).
SE Iran.

7a. P. mesomorpha Rech. f., Aell. & Esfand. in Anz. math.-naturw. Kl. Oesterr. Akad. Wiss. 1952: 196 (1952).
Ic.: Biol. Skr. 13, 4: f. 83 (1963).
Type. Iran: Baluchistan, SE limit of Lut desert, near Nasratabad, between Bam and Zahedan, c. 1400 m, 11 v 1948, *Rechinger f., Aellen & Esfandiari* 3921 (W! E!).

This and the previous species are known only from the type gatherings in SE Iran. The authors separated them from each other on the character of the very long leaf spines on *P. mesormorpha* but with the material at hand they seem to be scarcely specifically separate and very closely related to *P. aucheriana*.

8. P. flabellifolia (Boiss.) Boiss. in Diagn. ser. 2, 2: 105 (1856).
Syn.: *Echinophora? flabellifolia* Boiss. in Ann. Sc. Nat. ser. 3, 2: 92 (1844).
Type. Iran: *Aucher* 3761 (G).
E Iraq, W Iran; fl. June-August.

8a. P. cephalantha Rech. f. & Riedl in Biol. Skr. 13, 4: 117 (1963).
Ic.: l.c. f. 82.
Type: SW Afghanistan: Kouh Bachtou near Farah, 970 m, 25 iv 1958, *Lindberg* 303 (W!)

Known only from the single type gathering, *P. cephalantha* may prove to be conspecific with *P. flabellifolia*, when more material of that species is available for examination. Although *P. cephalantha* was said in the type description to seem to have all flowers fertile it is only the central flower of the umbellule that possesses styles, the outer are male with stylopodia.

2. Dicyclophora Boiss. in Ann. Sc. Nat. ser 3, 2: 89 (1844); Boiss., Fl. Or. 2: 951 (1872). Figs. 1F; 2.

Annual with ± striate grooved erect stem and a short asperulous indumentum. Leaves 2–3 pinnatisect with ultimate segments ovate to oblong, dentate to deeply dissected, petiole slightly winged at base. Umbels with very long peduncles. Bracts long narrow acuminate. Rays several, outer longer than inner. Bracteoles scarcely indurated after anthesis. Central umbellule sterile, clavate, purplish black. Outer umbellules with central flowers only hermaphrodite. Calyx absent. Petals white (drying yellowish), outer prominently radiant, glabrous or with ciliate margins. Anthers with a conspicuous oil globule. Pedicels of outer flowers indurated after anthesis and forming a cage; those of inner flowers very small. Fruit free, not sunk in receptacle, often bicarpellate, ± terete, pyriform; dorsal vittae 9, commissural 2. Albumen sulcate.

Monotypic.

D. persica Boiss. in Ann. Sc. Nat. ser. 3, 2: 91 (1844).
Type. Iran: 'in Persia australis', *Aucher* 4556A (G,W!).
SW Iran; sandy deserts, hillsides, 60–1900 m; fl. April-May.

A very distinctive species easily recognized by the tall annual habit, the thickened rather flattened rays, the showy outer petals (to 20 mm), the sterile purplish black central umbellule and the scarcely indurated bracteoles. It differs from all other genera in the tribe in the character of the inner ring of pedicels remaining ± capillary after anthesis.

Its nearest ally is probably *Pycnocycla* with which it shares the cage fruit structure, the central fruit not sunk in the receptacle, the several dorsal vittae and the frequent presence of oil globules in the anthers of the outer umbellules.

Boissier's generic name refers to the outer stalked flowers which are arranged concentrically in two ranks. However this is slightly misleading in that a comparable arrangement appears to occur in some *Pycnocycla* species and in *Anisosciadium*. Although Boissier said that the outer flowers were sterile, in fact they do have stamens which, however, as in many species in the tribe, are soon shed.

3. Ergocarpon C. C. Townsend in Kew Bull. 17: 437 (1964). Fig. 1D; 3.

Annual, glabrous, branched from base; stems striate, ridged. Leaves pinnate, herbaceous, soon withering. Umbels clearly pedunculate. Bracts triangular-lanceolate. Rays few. Bracteoles with prominent white margins, stiff, much longer than the umbellules and hiding the flowers, not hardened in fruit. Umbellules few-flowered; central flower and occasionally an outer flower hermaphrodite. Calyx lobes absent. Anthers without an oil globule. Fruit at centre of umbellule deeply sunk in receptacle, bi- or monocarpellate. Pedicels minute, not indurated nor enlarging in fruit. Dorsal vittae 5, slender. Albumen sulcate.

Monotypic.

E. cryptanthum (Rech. f.) C. C. Townsend, l.c. 438.
Syn.: *Exoacantha cryptantha* Rech. f. in Anz. math.-naturw. Klasse Oesterr. Akad. Wiss. 1952: 201 (1952).
Type. Iran: Baktiari, Siachal, *Koelz* 15253 (W, BPI).
E Iraq, SW Persia; hillsides, rocks and cliffs.

This is an extremely distinct species recognized by the whitish stems, the stiffly erect habit, the white-margined prominent bracts and bracteoles and the central fruit of the umbellule deeply sunk in the receptacle.

When Rechinger originally described this species he was dealing with a non-fruiting specimen and consequently was uncertain of the correct genus to which it should be assigned. It was only when Townsend had additional fruiting material from Iraq that he was able to show that it had nothing to do with *Exoacantha*, except in superficial appearance, and that it merited separate generic rank in the Echinophoreae. In his discussion of *Ergocarpon*, Townsend stated that it differed from all other members of the tribe in that the outer pedicels do not harden in fruit and in the character of the short non-indurated horny styles. However, in *Pycnocycla*, the pedicels

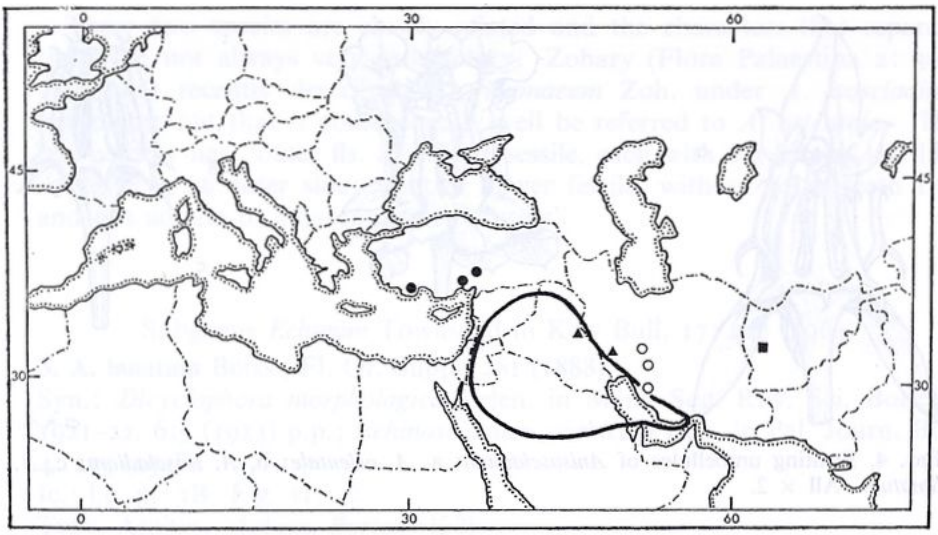

FIG. 3. Distribution of ●*Thecocarpus carvifolius*, ○*T. meifolius*, ■ —— *Anisosciadium* (3 species), ▲*Ergocarpon*.

do not always harden (though they do lengthen) and in some species of *Echinophora*, the styles, although much longer than those of *Ergocarpon*, only harden at the base. Despite these points, however, *Ergocarpon* seems to occupy quite an isolated position in the tribe, sharing in particular characters some points of similarity with *Dicyclophora* (such as the ring of non-enlarging inner pedicels and the long narrow acuminate ± white margined bracteoles) but quite distinct from it.

4. Anisosciadium DC., Mem. Omb. 63 (1829); DC., Prodr. 4: 234 (1830); Boiss., Fl. Or. 2: 950–951 (1892); Townsend in Kew Bull. 17: 427 (1964). Figs. 1 H,I; 3; 4.

Syn.: *Echinosciadium* Zohary in Pal. Journ. Bot. 4: 174 (1948).

Annuals, glabrescent or pubescent, ± prostrate and diffusely branched; stems terete, smooth or grooved. Leaves 2 × pinnate, ultimate segments oblong-ovate, 2-3-fid. Umbels sessile to pedunculate. Bracts narrow oblong, acuminate, later reflexed. Rays few to several, eventually ± flattened. Bracteoles foliaceous or spinescent, recurved. Umbellule with central flower and some outer flowers hermaphrodite. Calyx lobes present or absent on central flower, present on outer with two often prominent foliaceous outer lobes. Petals white, glabrous, radiant or not. Anthers with or without an oil globule. Pedicels of outer flowers indurated after anthesis and forming a cage. Fruit of central flower bicarpellate, outer monocarpellate, slightly immersed in receptacle. Dorsal vittae 9 or 4, commissural vittae 2. Albumen sulcate.

3 species; type of genus *A. orientale* DC.

The three species grow in deserts and in flower are superficially similar to *Scandix* spp. Frequently among plants of *Anisosciadium*, a sessile umbel is borne at soil level in the centre of the leaves.

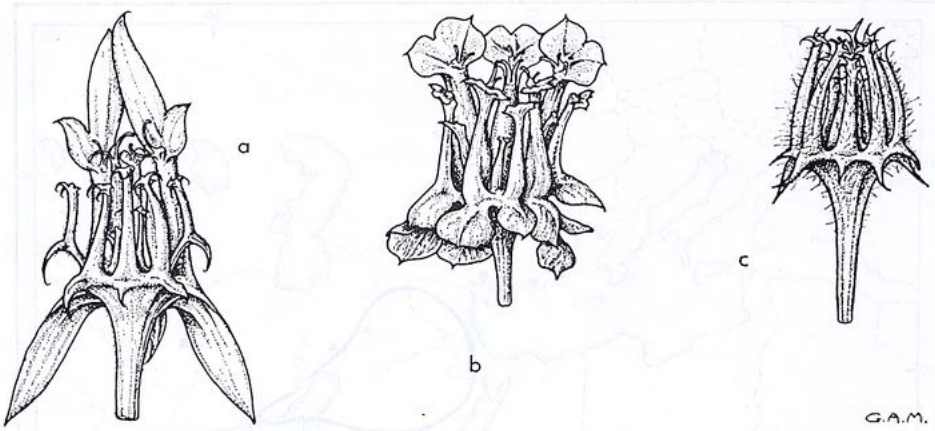

FIG. 4. Fruiting umbellules of *Anisosciadium*: a, *A. orientale*; b, *A. isosciadium*; c, *A. lanatum*. All × 2.

1. Bracteoles and calyx lobes of outer flowers not foliaceous, hard and spiny in fruit; monocarpellate fruits developing from the innermost row of flowers; central flower with calyx lobes; dorsal vittae 4 . . . . . 3. *A. lanatum*

\+ Bracteoles and outer calyx lobes of outer flowers foliaceous, scarcely hardening after anthesis; monocarpellate fruits developing from outermost row of flowers; central flower without calyx lobes; dorsal vittae 9 2

2. Outer petals conspicuously radiant; outer pairs of calyx lobes clearly unequal, the larger oblong-lanceolate; leaves glabrous or nearly so . . . . . 1. *A. orientale*

\+ Outer petals scarcely radiant; outer pairs of calyx lobes almost equal, ovate lanceolate to orbicular; leaves with stiff white hairs . . . . . 2. *A. isosciadium*

Subgenus *Anisosciadium*

1. A. orientale DC., Mem. Omb. 63, pl. 15 (1829); DC., Prodr. 4: 234 (1830).
Syn.: *Dicyclophora morphologica* Velen. in Mém. Soc. Roy. Sci. Bohême 1921–22, 6:5(1923) p.p.!; K. H. Rechinger in Bot. Not. 115: 43 (1962).
Ic.: DC., Mem. Omb. pl. 15 (1829); Fig. 4a.
Type. Iraq: between Baghdad and Aleppo, *Olivier & Bruguière* (P).
C Syria, E Iraq, W & S Iran, SW Afghanistan; desert, steppe, riverbanks, 60–1200 m; fl. March-May.

2. A. isosciadium Bornm. in Fedde Rep. Sp. Nov. 10:468 (1912).
Syn.: *Dicyclophora caucaloides* Velen. in Mém. Soc. Roy. Sci. Bohême 1921–22, 6:5 (1923)!; *A. lanatum* sensu Rech. f., Fl. Lowland Iraq 452 (1964) non Boiss.
Ic.: Zohary, Fl. Palaestina 2, plate 561 (1972); Fig. 1H; 4b.
Type. Syria: near Palmyra, v 1900, *G. Post* (BEI?)
Syria, Jordan, W & S Iraq; deserts, 200–1600m; fl. April-June.

These two species are closely related and the characters that separate them are not always very satisfactory. Zohary (Flora Palaestina 2: 368, 1972) has recently described var. *idumaeum* Zoh. under *A. isosciadium* but points out that it could equally well be referred to *A. orientale*. The new variety has "outer fls. all fertile, sessile, each with 2-3 broad, leaf-like calyx teeth at outer side; central flower fertile, without calyx teeth free and not adnate to adjacent sterile flowers".

Subgenus *Echinum* Townsend in Kew Bull. 17: 427 (1964)

3. A. lanatum Boiss., Fl. Or. Suppl. 261 (1888).
Syn.: *Dicyclophora morphologica* Velen. in Mém. Soc. Roy. Sci. Bohême 1921–22, 6:5 (1923) p.p.; *Echinosciadium arabicum* Zoh. in Pal. Journ. Bot. 4: 175 (1948).
Ic.: l.c. pl. 3B; Fig. 11; 4c.
Type. Arabia: Midian, *Burton* (K?).
C Arabia, S Iraq, Kuwait; desert, 100–400 m; fl. Feb.-April.

Clearly differing from the two preceding species in the stiff spiny bracteoles and calyx lobes at fruiting stage.

5. Echinophora L., Gen. Pl. 3 (1754); Boiss., Fl. Or. 2: 947–950 (1872); Davis, Fl. Turkey 4: 306–310 (1972). Figs. 1B, C, E; 5; 6.

Perennials or biennials, pubescent, often much branched, spiny or unarmed; stems terete, smooth, striate or grooved, sturdy. Leaves 1-2-pinnate or 3-ternate with ovate, triangular or filiform segments; petioles often trigonous, winged at base or not. Umbels with long or short peduncles. Bracts conspicuous or not. Rays few to several, equal or unequal. Bracteoles indurated in fruit or not. Umbellules few- to several-flowered; usually only central flower hermaphrodite; rarely central umbellule sterile, forming a black cone. Calyx lobes present or absent, foliaceous or not. Petals white or yellow, glabrous or pubescent, seldom radiant. Anthers without an oil globule. Pedicels hard, spiny and concrescent in fruit forming, usually with the bracteoles, a cage or shell enclosing the fruit. Fruit usually monocarpellate, sunk in receptacle or scarcely so. Dorsal vittae 4, commissural 2. Albumen sulcate.

9 species; type of genus *E. spinosa* L.

1. Outer flowers of umbellules with conspicuous foliaceous calyx lobes; bracteoles not hardening in fruit; indurated pedicels forming a cage around fruit . . . . . 9. *E. chrysantha*
\+ Outer flowers of umbellules with or without small calyx lobes, never foliaceous; indurated pedicels and bracteoles forming a shell, or a cage, around fruit 2
2. Umbels with long peduncles; leaves with filiform herbaceous segments 3
\+ Umbels with short or very short peduncles; leaves with triangular, lanceolate or ovate segments, spiny or not 4

3. Central umbellule sterile, forming a conspicuous black cone; rays 10–25; bracts 8–14 . . . . . 5. *E. trichophylla*
+ Central umbellule not forming a black cone; rays 4–14; bracts 3–8 . . . . . 4. *E. orientalis*
4. Flowers white or pinkish; leaves spiny 5
+ Flowers yellowish; leaves not spiny 7
5. Bracts remaining ± membranous, pilose at least on margin 1. *E. spinosa*
+ Bracts hardening in fruit, ± trigonous, minutely puberulous to glabrate 6
6. Segments of lower leaves triangular-lanceolate; rays 4–8 2. *E. tournefortii*
+ Segments of lower leaves broad triangular; rays 2–3 (–5) 3. *E. platyloba*
7. Rays broadened at base, purplish, ± horizontally spreading; pedicels at fruiting stage concrescent well above middle 8. *E. scabra*
+ Rays scarcely broadened at base, green, ± erect; pedicels at fruiting stage concrescent only in lower half 8
8. Calyx lobes on female flowers prominent; fruit enclosed in a shell . . . . . 6. *E. tenuifolia*
+ Calyx lobes on female flowers ± absent; fruit enclosed in a cage . . . . . 7. *E. sibthorpiana*

Echinophora can readily be divided into four distinct taxa which are here given subgeneric rank. Two had previously been recognised at sectional level.

Subgenus *Echinophora*

Leaves spiny. Umbels usually with very short peduncles. Calyx lobes not foliaceous. Petals white. Pedicels and bracteoles after anthesis indurate, concrescent, forming a shell. Fruit sunk in receptacle.

1. E. spinosa L., Sp. Pl. 239 (1753).
Syn.: *E. maritima* Gouan, Fl. Monspel. 284 (1765).
Ic.: DC., Mem. Omb. pl. 16 (1829); Reichenb., Ic. Germ. 21, t. 190 (1867).
Described from Mediterranean shores.
Mediterranean except east; maritime sands; fl. July-Sept.

Three varieties have been described: var. *pubescens* Guss., var. *orientalis* Griseb. and var. *angustifolia* Pécout.

2. E. tournefortii Jaub. & Spach, Ill. Pl. Or. 3: t. 241 (1848).
Syn.: *E. anatolica* Boiss. & Heldr. in Boiss., Diagn. ser. 1, 10: 56 (1849).
Ic.: Jaub. & Spach, l.c.
Isotypes. Turkey: Galatia, *Tournefort* (P); Black Sea shores, *Aucher* 3809 (G).
W C Anatolia; chalk or salt steppe, arable or fallow fields, 500–1750 m; fl. July-September.

The species has been recorded from Mount Alwand in W Iran (Parsa, Fl. Iran 2: 779, 1948). No details are given and it may be a misidentification of *E. platyloba*.

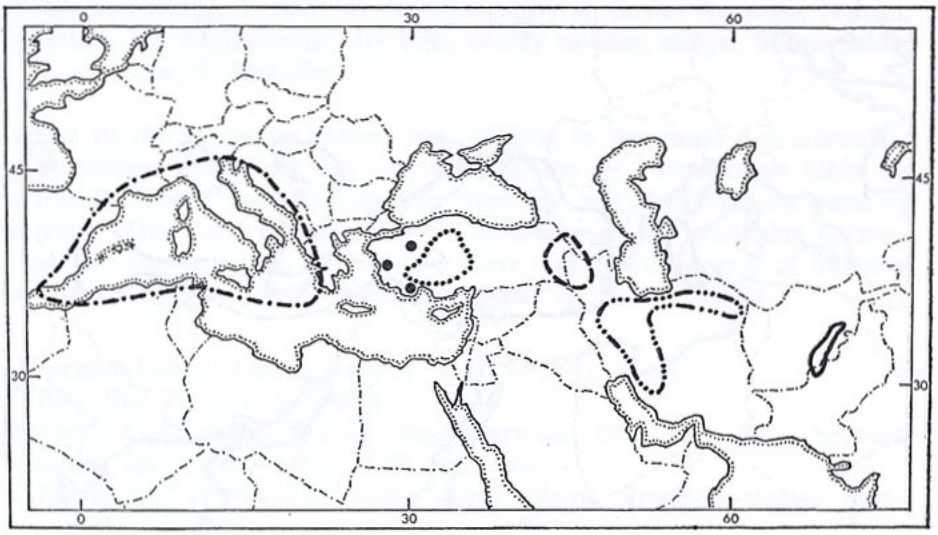

FIG. 5. Distribution of *Echinophora*: ● *E. trichophylla*; ——*E. scabra*; —·——·— *E. spinosa*; — — — *E. orientalis*; —···— *E. platyloba*; ····· *E. tournefortii*.

3. E. platyloba DC., Prodr. 4: 235 (1830).
Ic.: Jaub. & Spach, Ill. Pl. Or. t. 240 (1848).
Type. Iran: near Tehran, *Olivier & Bruguière* (P).
W & NE Iran; fields, desert, 1200–2260 m; fl. Aug–Oct.

Closely allied to the preceding species.

Subgenus **Trichophora** Hedge & Lamond, **subgen. nov.**

Folia non spinosa segmentis filiformibus. Umbellae pedunculis longis. Lobi calycis non foliacei. Pedicelli et bracteolae post anthesin indurati, concreti, putamen formantes. Fructus in receptaculo immersus. Typus subgeneris, *E. trichophylla* J. E. Smith.

Leaves not spiny, with filiform segments. Umbels with long peduncles. Calyx lobes not foliaceous. Petals white. Pedicels and bracteoles after anthesis indurated and concrescent, forming a shell. Fruit sunk in receptacle.

4. E. orientalis Hedge & Lamond in Notes R.B.G. Edinb. 31: 78 (1971).
Syn.: *E. trichophylla* auct. non J. E. Smith (1809).
Ic.: Jaub. & Spach, Ill. Pl. Or. 3: t. 239 (1848) sub *E. trichophylla*.
Type. Turkey: Kars, Ağri Da. (Ararat), *Szovits* 564b (G-DC photo! LE?).
E Anatolia, Soviet Armenia, NW Iran; dry gravelly, often saline hills, sandy steppe, fallow fields, 1100–2000 m; fl. July-Sept.

5. E. trichophylla J. E. Smith in Rees, Cyclop. 12 (1809).
Syn.. *E. radians* Boiss. in Ann. Sc. Nat. ser. 3, 2: 92 (1844).
Ic.: Davis, Fl. Turkey 4: fig 5, 10, p. 273 (1972).
Described from the Orient (Hb. Linn. in herb. J. E. Smith!)
Mainly W & SW Anatolia; stony hillsides, ditches and fields; fl. June-July.

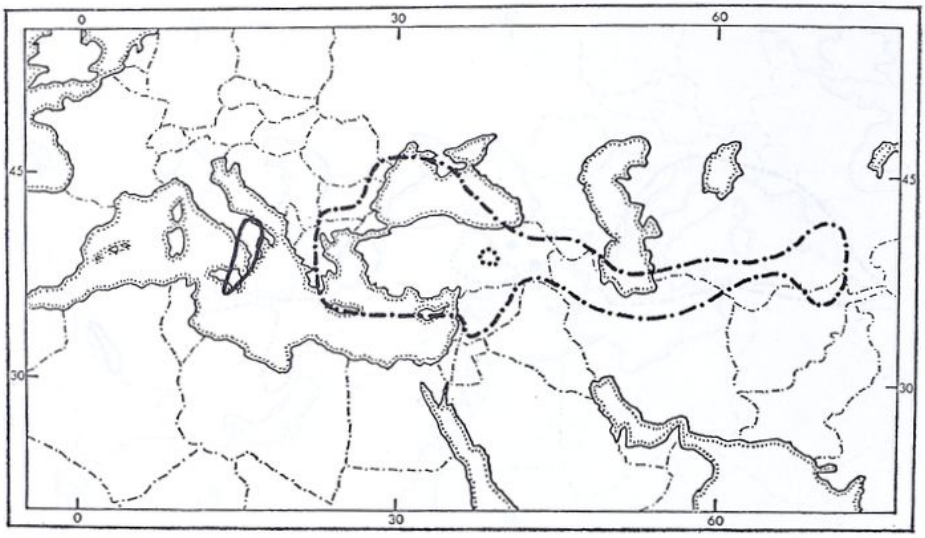

FIG. 6. Distribution of *Echinophora*:——*E. tenuifolia*; ····*E. chrysantha*; —·—·—*E. sibthorpiana*.

This and the preceding species differ markedly from all other species in the genus on account of the filiform leaf segments and the long peduncles. They are related but can be readily distinguished on the characters given in the key; in addition the outer petals of *E. trichophylla* are clearly radiant (6 mm not 1.5–3.5 mm), its basal leaves are less elongated (15–25 cm not 25–40 cm), and its fruiting shell is occasionally hirsute. Both species are said to abound with gum.

Subgenus **Chrysophora** (DC.) Hedge & Lamond, **stat. nov.**

Syn.: *Echinophora* sect. *Chrysophora* DC., Prodr. 4: 235 (1830); *Chrysosciadium* Tamamsch.—*nomen invalidum* in Grossh., Fl. Kavk. 7: 24 (1967).

Leaves not spiny. Umbels pedunculate, peduncles often very short. Calyx lobes not foliaceous. Petals yellow? Pedicels and bracteoles after anthesis indurated, concrescent forming a shell or accrescent forming a cage. Fruit ± sunk in receptacle or scarcely so.

6. E. tenuifolia L., Sp. Pl. 239 (1753).
Ic.: Fiori & Paol., Ic. Fl. An. Ital. t. 2419 (1901).
Described from Italy, Apulia (LINN-photo!).
S Italy, Sicily; field margins; fl. July-Sept.

7. E. sibthorpiana Guss., Suppl. Fl. Sic. Prodr. 69 (1832).
Syn.: *E. tenuifolia* L. var. *sibthorpiana* (Guss.) Fiori & Paol., Fl. An. Ital. 2: 210 (1900); *E. tenuifolia* L. subsp. *sibthorpiana* (Guss.) Tutin in Feddes Rep. Sp. Nov. 74: 31 (1967); *Chrysosciadium sibthorpianum* (Guss.) Tamamsch. in Grossh., Fl. Kavk. 7: 24 (1967)—*nomen invalidum*.
Ic.: Sibth. & Sm., Fl. Graec. 3: t. 266 (1821)—as *E. tenuifolia*.
Type not indicated.

E Balkans, Crimea, Turkey, Crete, Cyprus, Syria, Soviet Armenia, N Iran, Turkestan, NE Afghanistan; dry hills, chalky ravines, steppe, fallow fields; ± s.l.—1300 m; fl. Aug.-Sept.

Close to the preceding species but differing in the ovate not lanceolate leaf segments, the striate not sulcate stem, the ± absent calyx lobes on the female flowers and the cage-like structure, not shell-like, surrounding the fruit. There also appears to be a difference in the branching systems of the two species; in *E. sibthorpiana* there is a greater degree of intricate branching. One varietv has been recognised: var. *incisa* Griseb.

8. E. scabra Gilli in Feddes Rep. Sp. Nov. 61: 193 (1959).
Ic.: Biol. Skr. 13, 4: f. 20 (1963).
Syntypes. Afghanistan: Kabul, Sher Darwasa, *Gilli* 2011 (W); between Tschardeh and Logar valley, *Gilli* 2010 (W).
E Afghanistan, W Pakistan; rocky slopes, plains, *Artemisia*-steppe, 1830–2400 m; fl. July-Aug.

Careful observations on flower colour are desirable to show whether the 'yellow' of some collectors' field notes refers to petals or stylopodium. In the dry state the petals can appear almost red.

Subgenus **Lamprosciadium** Hedge & Lamond, **subgen. nov.**

Folia non spinosa. Umbellae pedunculatae. Lobi exteriores calycis florum exteriorum foliacei, lutei, lucidi. Petala lutea? Pedicelli post anthesin indurati, accrescentes, caveam formantes. Bracteolae liberae, plusminusve foliaceae. Fructus liber, vix in receptaculo immersus. Typus subgeneris, *E. chrysantha* Freyn & Sint.

Leaves not spiny. Umbels pedunculate. Outer calyx lobes of outer flowers foliaceous, yellow, shining. Petals yellow? Pedicels after anthesis indurated, accrescent forming a cage. Bracteoles free, ± leafy. Fruit free, scarcely sunk in receptacle.

9. E. chrysantha Freyn & Sint. in Oest. Bot. Zeit. 42: 121 (1892).
Type. Turkey: Erzincan, Sipikor Da., *Sintenis* 1890: 3348 (LD!)
C Anatolia; igneous slopes, 1100–1700 m; fl. Aug.

A very distinct species on account of the large yellow shining calyx lobes of the outer flowers, the non-indurated free, ± leafy bracteoles and the fruit not or scarcely immersed in the receptacle.

Fruit structure within Echinophora

The type of fruit structure within the genus varies from a complete shell as in subgenus *Trichophora* where the fruit is sunk in the receptacle and enclosed by the indurated, concrescent pedicels and bracteoles, only the styles emerging at the top, to the cage of subgenus *Lamprosciadium* with the fruit scarcely sunk in the receptacle and enclosed by indurated but never concrescent pedicels, the bracteoles remaining leafy. Between these

two extremes lies a complete range with the inner pedicels concrescent from well above their middle forming shells, as in *E. platyloba* and *E. scabra*, to the cage of *E. sibthorpiana* where the pedicels are scarcely concrescent and the fruit scarcely sunk in the receptacle.

6. Thecocarpus Boiss. in Ann. Sc. Nat. ser. 3, 2: 93 (1844); Boiss., Fl. Or. 2: 954 (1872). Figs. 1A; 3.
Syn.: *Echinophora* L. sect. *Sphaerocarpaea* Boiss., Fl. Or. 2: 950 (1872).

Biennial or perennial, glabrous, with terete, striate to grooved stems. Basal leaves 1-2 pinnate with pinnae deeply divided into short ± linear segments; petioles winged. Umbels clearly pedunculate. Rays several, unequal. Bracteoles not indurated. Central flower of umbellule hermaphrodite (occasionally, in lowermost umbel, a few outer flowers also hermaphrodite). Calyx present on central flower of umbellule, absent or present on outer. Petals white, glabrous. Anthers without an oil globule. Pedicels of all outer flowers indurated at fruiting stage and concrescent with each other and with pericarp of central fruit forming an ovoid to globose somewhat angular bi-locular false nut, bi- or monocarpellate, outermost pedicels persistent as spreading protrusions; bracteoles fused at base. Vittae several, slender. Albumen ± flat to slightly concave.

2 species; type of genus *T. meifolius* Boiss.

1. Umbellules of all umbels with only one hermaphrodite flower; upper leaves ovate in outline, 1–2 × ternate with linear ultimate segments to 5mm . . . . . 2. *T. carvifolius*
\+ Umbellules of lowermost umbel with several hermaphrodite flowers; upper leaves linear-oblong in outline, 1 × pinnate with ovate pinnae deeply divided into linear segments to 2 mm 1. *T. meifolius*

1. T. meifolius Boiss. in Ann. Sc. Nat. Ser. 3, 2: 94 (1844).
Isotypes. Iran: Isfahan, *Aucher* 4552, 4559 (G).
W Iran, c. 3200 m; fl. June.

The illustration of the 'false nut' in Baillon, Hist. Pl. 7: 113 f. 112 (1881) gives a rather exaggerated view of the hardening of the outermost pedicels of this species.

2. T. carvifolius (Boiss.) Hedge & Lamond, **comb. nov.**
Syn.: *Echinophora carvifolia* Boiss., Diagn. ser. 2, 5: 104 (1856); Davis, Fl. Turkey 4: 307 (1972).
Type. Turkey: Içel, Kechlik near Mersin, *Balansa* 624 (G!).
S Turkey, c. 600 m, woodland; fl. May-June.

Although originally described by Boissier in *Echinophora* there seems no doubt that the species should be transferred to *Thecocarpus* on account of the false nut type of fruiting umbellule where the concrescent pedicels fuse with the pericarp of the fruit and also on account of the ± flat or slightly concave commissural face of the albumen.

Superficially a flowering specimen bears a distinct resemblance in habit, leaf and petiole characters to *Carum carvi* L.

Boissier originally described *Thecocarpus* in the Echinophoreae but in Flora Orientalis (1872) he transferred it to the tribe Seselineae on the basis of the ± flat, i.e. not incurved, albumen. However, the characters of fused and indurate pedicels enclosing a fertile solitary fruit ally the two species more closely with those of the Echinophoreae.

The fruiting umbellules of the genus show the greatest amount of fusion of parts within the tribe, the concrescent inner pedicels and pericarp forming a region of spongy tissue. However the bracteoles form no part of this structure remaining ± herbaceous.

Taxonomic Characters

Habit. Several of the genera or species groups within the genera of the Echinophoreae can be easily recognized in the vegetative state and are unlikely to be confused with other genera. For instance, the entire spiny-leaved species of *Pycnocycla* are unmistakable at least among the SW Asiatic genera. Likewise in *Echinophora* the subgenus *Echinophora* with its spiny leaves, thick stems and much branched habit is distinctive. It is of interest to note that in both *Pycnocycla* and *Echinophora*, there are spiny and non-spiny species and in both genera these two habit groups are very different in appearance from each other and it is only when they are in flower and fruit that their similarities are obvious. *Ergocarpon* is another genus, albeit monotypic, that is very distinct in facies. The stiffly erect annual habit, the white stems and in flower the prominent white-margined bracts and bracteoles are very characteristic. The genus does however have some superficial resemblance to the unrelated SW Asiatic *Exoacantha* Lab.

In contrast to the previously mentioned examples, *Thecocarpus* and *Anisosciadium* are much less distinctive in habit. In leaf shape and habit, *Thecocarpus carvifolius* is quite similar to *Carum carvi* and the three species of *Anisosciadium* look very like *Scandix* spp.

Floral characters. Although the basic floral arrangement in the tribe, as in the family, is very uniform there is some variation in the form and occasionally the numbers of floral parts. For example, calyx lobes, basically five in number, may be present on all the flowers of the umbellule (*Pycnocycla* spp.); quite absent (*Dicyclophora*, *Ergocarpon*); absent on the central flower and present on the outer flowers with two often very prominent foliaceous lobes (*Anisosciadium* spp); or present or absent on all the flowers (*Echinophora* spp.).

The petals are fairly similar throughout the tribe, usually with side lobes and always with an entire or lacerated inflexed tip. They are white or yellow, sometimes pinkish, glabrous (*Thecocarpus*, *Anisosciadium*) or pilose on the dorsal surface (*Echinophora* spp.) or only pilose on the incurved tip (*Pycnocycla*). In *Dicyclophora* the outer petals are very prominently radiant; in some other genera (*Echinophora*, *Anisosciadium*) they may be somewhat radiant or not. *Pycnocycla* has longer narrower petals than the other genera of the tribe and also has prominent oil canals.

Although the anthers normally do not provide any characters, in *Pycnocycla* and *Dicyclophora* there are prominent oil glands at the anther bases. These are apparently absent in the other genera.

The stylopodium of the outer male flowers varies from more or less conical in *Dicyclophora* through almost flat, as in most genera, to basin-shaped in *Echinophora orientalis*.

Fruit characters. The shape of the fruit varies little throughout the tribe; the mericarps are more or less pyriform, occasionally almost beaked above, terete and scarcely compressed so that it is not possible to indicate either lateral or dorsal compression. Those fruits that are enclosed in shell-like structures are glabrous while those within a cage have an indumentum either short or quite long and dense (*Pycnocycla* spp.).

A bifid carpophore appears to be present in most species. It is often adnate to the mericarps and more or less membranous, never rigid.

The pericarp is not hard and the three layers of the exocarp, mesocarp and endocarp are usually easily separable. The portion of the fruit immersed within the receptacle of some species has an even thinner covering than the non-immersed part. Frequently a membranous frill of parenchymatous tissue surrounds the protruding section of the fruit where it emerges from the receptacle.

Dorsal and lateral ridges, often a conspicuous and important taxonomic character in the family are scarcely developed in the tribe and their position, at least in *Echinophora*, is only obvious because of the conspicuous vittae lying between them.

With regard to vittae, their number and position seem to vary appreciably between the different genera and are of little use as a tribal character. In *Echinophora* a single distinct dorsal oil canal lies between the ridges and two are present on the commissural surface. In *Pycnocycla* many vittae surround the mericarp lying both within and between the ridges. Two *Anisosciadium* species have a slender oil canal within each ridge and a conspicuous one between them. In all cases the vittae are septate and can often be completely dissected out of the pericarp. Their precise position within the pericarp will require more detailed anatomical investigation. It appears in some cases that the vittae lie between the exocarp and the mesocarp; sometimes they come away with the one, sometimes the other. In *Thecocarpus* there are very slender vittae which appear to lie in the testa of the seed.

Although the general form of the albumen is deeply sulcate on the commissural face, often with inrolled margins, in *Thecocarpus* the albumen is more or less flat.

As this short review of characters indicates, there are a reasonable number of habit, floral and fruit characters available but very few that are of constant taxonomic usefulness above species level. In fact in the tribe, as in the family as a whole, one has to fall back on fruit characters but in the Echinophoreae it is not just the fruit that provides characters—in fact the fruit itself is relatively unimportant taxonomically—but the whole aspect of the infructescence including bracteoles, the outer and inner pedicels, their varying degrees of fusion and induration, and the position of the fruit. These are the important characters.

Geography

As the four distribution maps show (figs, 2, 3, 5, 6), the greatest concentration of species and genera in the tribe is in Turkey, Iraq and Iran although the total range extends considerably beyond these countries. *Echinophora* has a wide and almost continuous distribution from the shores of the W Mediterranean eastwards as far as Afghanistan and Soviet Central Asia. *Pycnocycla* on the other hand has several disjunctions in its range (fig. 2): *P. glauca* is in India, Arabia and Ethiopia; its ally and possible western vicariad *P. ledermannii* grows in western Africa; *P. tomentosa* is endemic to Sinai; the remaining nine closely related species are in Iran, W Pakistan and Afghanistan.

With the possible exception of *P. ledermannii*, most of the species of the tribe grow in more or less xerophytic habitats. The three annual species of *Anisosciadium* are desert plants and grow in the most extreme conditions of aridity.

In altitude, the species range from sea level (*Echinophora spinosa* from maritime sands) to about 3200 m (*Thecocarpus meifolius*).

Fruit dispersal

There is little definite information about the mechanics of fruit dispersal in the tribe. Some of the species of *Echinophora*, particularly the bushy ones, are apparently tumbleweeds but in this genus, as in most of the others, field observations are needed to determine what are the units of dispersal. Apparently the most highly evolved type of dispersal is that of *Anisosciadium*. Here the fruiting umbellules break off readily when ripe together with their stalk (fig. 2) and form single units of dispersal. These are presumably wind-blown and one can assume that the various projections of calyx lobes, bracteoles and stylar arms help both to roll the unit along and to collect particles of soil eventually anchoring it. Murbeck (1920, 1943) used the term synaptospermy to cover instances where several seeds were kept together until germination; he found it to be quite a common phenomenon in arid regions of N Africa, particularly amongst annuals. So at least *Anisosciadium*, with several seeds in each umbellule, provides another instance of synaptospermy. In *Echinophora chrysantha*, the dispersal unit also appears to be the individual cage-like umbellule. That is the same as *Anisosciadium* but with only one fertile fruit, containing one seed.

In the remaining genera of the tribe it is very difficult to judge from herbarium specimens, of which there are relatively few in full fruit, what the dispersal units are. In *Thecocarpus* it also appears to be the individual umbellule and this may be the general pattern throughout.

Evolutionary trends

As mentioned in the introduction the differentiation that occurs in the umbellules of Echinophoreae is unique in the family. It is, however, not just the sexual differentiation that is unique. In fact, there are probably relatively few genera of the Umbelliferae in which there is not sexual separation of one kind or another. This ranges from a simple type of male sterility of the outer flowers of an umbel through that of the central fertile and lateral sterile umbels of *Ferula* and *Ferulago* to the extreme case of some

Trinia species where dioecism occurs. In Echinophoreae it is the sexual differentiation combined with the varying degrees of fusion and induration of pedicels and bracteoles that makes the tribe so distinct.

Fig. 1 illustrates the various evolutionary trends that can be observed within the fruiting umbellule. If one considers degree of fusion and immersion of the fruit as the yardsticks of evolutionary progress, *Pycnocycla* and *Dicyclophora* are the least advanced. In these two genera there is no fusion of parts and the fertile mericarps are free on the receptacle (fig. 1F, G). *Echinophora*, with its four distinct subgenera, shows considerable variation from that of the relatively simple structure of *E. chrysantha* (fig. 1E) to that of *E. trichophylla* (fig. 1B) where there is much fusion of parts and immersion of the fertile mericarp in the receptacle. In *Thecocarpus carvifolius* (fig. 1A) there is the greatest degree of fusion and induration in the tribe and at least from this point of view it is the most highly evolved genus.

The evolution of these rather intricate infructescences must be viewed from the point of view of fruit dispersal. It also seems likely that they have evolved in a climate of aridity and desiccation. How biologically successful they are today is doubtful. Several species of *Echinophora* are quite widespread and common within their ranges but many of the other species in the tribe have limited ranges, are known from few gatherings and seem to be isolated relics.

In looking at the umbellule of those Echinophoreae with a single hermaphrodite flower it is impossible to avoid comparison with the cyathium of *Euphorbia*. In *Euphorbia* a cup-like involucre of fused bracts, often provided with glands and appendages at the top, has a central female flower surrounded by a number of male flowers each reduced to a single stamen. In Echinophoreae the central flower remains hermaphrodite, but it is the only flower that is functionally female, and the male flowers are much less reduced than in *Euphorbia*. Nevertheless there is a basic structural similarity, and indeed in *Echinophora chrysantha* there is some parallel between the shining calyx lobes of the outer flowers and the involucral glands of the cyathium. However, there is no evidence that the structures owe their existence to similar evolutionary pressures. Venkata Rao (1971) has put forward a theory of the origin of the cyathium, deriving it by concentration from a catkin of male flowers with a terminal female one, such as is found in the living *Acalypha indica*. It is not unreasonable to link the morphological sequence traced by Venkata Rao to changes in pollination mechanisms. This particular step would be from the wind-pollination of unisexual flowers to the recovery by the hermaphrodite pseudanthium (cyathium) of insect-pollination, which he envisaged as the more primitive state in the family e.g. in *Jatropha*. In Echinophoreae, on the other hand, the evolution of the specialized umbels seems to be linked not to any pollination mechanism, but to the biology of the fruit (see p. 185).*

The sexual differentiation within the umbellules of Echinophoreae invites comparison with that so often found in the capitulum of Compositae. Here, however, there is one fundamental difference. In Compositae differentiation always takes the form of female flowers at the periphery, males in the centre. In Echinophoreae (and in the cyathium of *Euphorbia*) the male flowers are peripheral, the hermaphrodite seed-bearing flower central.

* We are grateful to Mr B. L. Burtt for providing this paragraph.

Taxonomic conclusions

One can only speculate on the questions of inter-relationships of the genera within the tribe and their relatives outwith it. The information at hand is too meagre. However, on the available morphological evidence, the tribe does seem to form a natural unit characterized by the distinctive umbellules and none of its component genera is particularly anomalous within it. Likewise, there are no genera from other tribes that are possible candidates for inclusion within it.

Dicyclophora and *Pycnocycla* are clearly quite closely related to each other, particularly with regard to their infructescence structure; *Echinophora*, the least homogeneous of the genera, has links with *Anisosciadium* particularly through the similar fruiting umbellules of *Echinophora chrysantha*; *Thecocarpus* and *Ergocarpon* have fewer links both to other genera in the tribe and to each other. *Thecocarpus* is the only genus in the tribe with more or less flat albumen.

Although links among the component genera of Echinophoreae are not hard to find, links with genera outwith the tribe are considerably more difficult to recognize. But among the tribes and subtribes of the Apioideae of which we have some knowledge, the subtribe Scandicinae is a possible candidate and does share a few points of similarity with the Echinophoreae. In both cases sulcate albumen is the general rule (though there are exceptions to this), the fruits are to at least some degree beaked and in some genera a comparable sexual differentiation occurs. For instance, in *Rhabdosciadium* Boiss., a small SW Asiatic genus, the central flower of the umbellule is sessile and hermaphrodite and the outer flowers are male and pedicellate; in *Scandix australis* L. the central fruit of the umbellule is often sessile and often shorter and broader than the outer fruits. In general facies there is little resemblance between any of the perennial species of the two tribes but among the annuals, as has already been remarked, there is a marked superficial resemblance between flowering species of *Anisosciadium* and *Scandix*.

Unfortunately there is little evidence available from other botanical disciplines to give hints of internal and external relationships. Evidence from stomatal patterns, chemistry, chromosome counts and anatomy is either very sparse or lacking. However on the basis of comparative pollen studies Cerceau-Larrival (in Heywood, 1971, p. 134) suggested that the Echinophoreae is a highly advanced tribe (although it appears that she studied only a few species) with similar pollen to such genera of the tribe Dauceae as *Orlaya*, *Lisaea* and *Turgenia*. It is interesting to note in this respect that similar variations within the flowering umbels of Dauceae and Echinophoreae can be observed in certain genera. For example, in *Artedia* L. and *Daucus* L. the central umbellules are often sterile and reduced to conspicuous purple or blackish tufts; the same reduction occurs in *Echinophora trichophylla* and *Dicyclophora*. Radiant outer petals occur in the last two genera and are also found in *Artedia* and *Orlaya* Hoffm.; nodal umbels occur in *Pycnocycla nodiflora* and in *Torilis nodosa* (L.) Gaertner; numerous rayed umbels occur in *Pycnocycla tomentosa* and *Astrodaucus* Drude, few rayed umbels in *Echinophora platyloba* and *Turgenia* Hoffm.

However, too much emphasis should not be laid either on the rather slender links between the Echinophoreae and Scandicinae or the apparently

parallel evolutionary trends in the flowering umbels of the Dauceae. Rather, the overall impression should be that Echinophoreae is a very distinct, probably old and highly evolved tribe.

Undoubtedly there are many other lines of enquiry that can be investigated. Extremely little is known about the general biology of the plants, their pollinators, methods of dispersal and germination. Chemical investigations and comparative anatomical and developmental studies of the flowers and fruit might well yield worthwhile information about their inter-relationships and their antecedents.

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