Morphology of *Heliotropium* (Boraginaceae) Dispersal Units[1]

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Abstract

In flowers of *Heliotropium* s.l. the primary carpel tips are overtopped by commissural outgrowths. Therefore the stylar cleft mimics a lateral orientation of the carpels. In species in which the fruit splits into four diaspores the separation tissues run through both the median and the transverse fruit planes. In species where only two two-seeded nutlets are developed the fruit splits within the false septa and each half is composed of parts of both carpels ("syn-mericarpids").

Key words

Heliotropium, Boraginaceae, flower, fruit, mericarpid, ontogeny.

Introduction

The genus *Heliotropium* L. s.l. (Boraginaceae-Heliotropioideae, including "*Ceballosia*") is mainly classified according to the number of diaspores (dispersal units or partial fruits) developed in each flower. The typical *Heliotropium* s. str. fruit divides into four uniform mericarpids ("Klausen", "eremocarps"), each composed of one carpel half and containing a single seed. The fruits of other groups are characterized either by disymmetry or by the formation of only two mostly two-seeded nutlets, respectively. Members of the latter groups were separated as distinct genera, e.g. *Tiaridium* Lehm. (Lehmann, 1818), *Heliophytum* (Cham.) DC. (De Candolle, 1845), *Cochranea* Miers (Miers, 1868), or "*Ceballosia* Kunkel" (Kunkel, 1980) but most of these taxa are now again included at sectional rank in *Heliotropium*.

In the Boraginaceae the two carpels arise in the median plane of the flower. In the Boraginoideae the tips of the carpel primordia grow out into stigmatic rims or lobes (Hilger, 1984, 1985) on top of the style. The stylar cleft is directed in the same way as the septal plane and the lobes are parallel with the inflorescence axis (*Eritrichum canum* [Benth.] Kitam., Eritricheae, Fig. 1).

In flowers of *Heliotropium* the upper part of the style is thickened into a globose or conical stigmatic head, often tapering into two more-or-less long free tips. In this terminal part stylus and stylar cleft do not have the function of a transmission tissue because the receptive surface is a circular secondary papillate outgrowth at the lower edge of the stigmatic head. Thus, only in this lower part does the inner epidermis of the stylar cleft function as transmission tissue.

In species of Boraginoideae and Heliotropioideae with four nutlets, the ovary splits in both the transverse (septum) and median (false septum) plane. Each diaspore is a mericarpid. If there are only two nutlets in Boraginoideae (as in *Rochelia* Reichenb. of tribe Eritricheae), they develop from a single carpel (Hilger, 1984). "Double nutlets", the typical diaspores in the genus *Cerinthe* L. (Lithospermeae), correspond with true carpids and are generated by a transverse cleft of the gynoecium (Hilger, 1985). To date, authors who have investigated flower and fruit morphology of Heliotropioideae (e.g. Rosanoff, 1866; Lawrence, 1937; Sharma, 1954; Di Fulvio, 1978; Khaleel, 1978; and Hilger, 1987, 1989) have assumed that this developmental sequence is the same in *Heliotropium*. During carpological investigations of *Heliotropium* species with two diaspores it has now become apparent that the position of the stylar cleft (Fig. 2) is not in accordance with this assumption.

Thereupon, in addition to the species under current investigation, the slides of *Heliotropium supinum* (Hilger, 1987) and "*Ceballosia fruticosa*" (Hilger, 1989) were re-examined to complete possibly inadvertent descriptions, and some *Heliotropium* species with four nutlets were screened to ascertain the morphological homogeneity within the genus.

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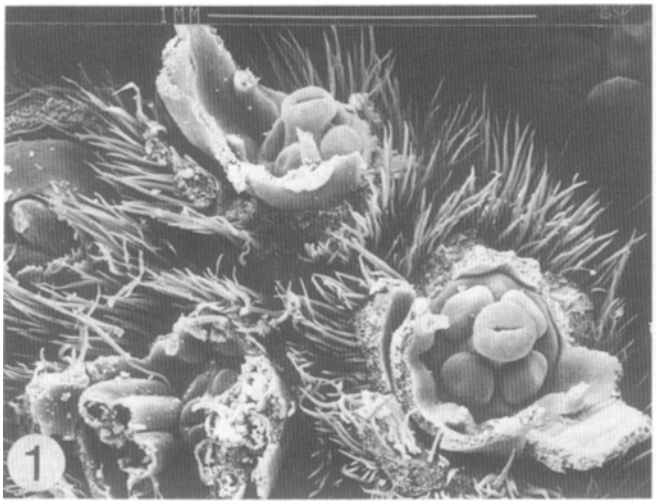
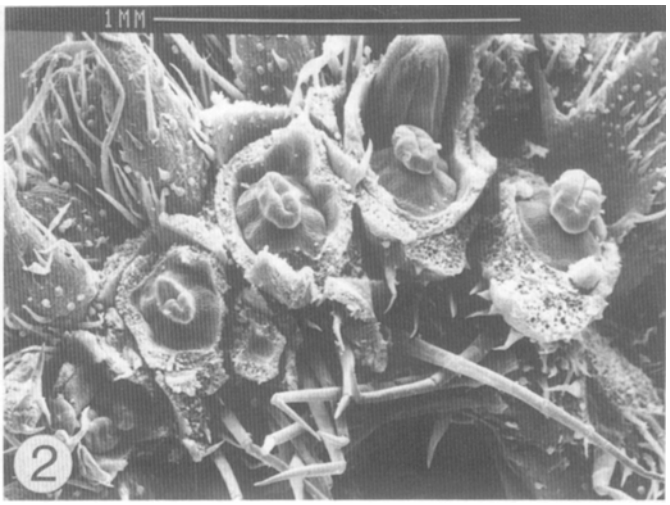
[1] Carpological investigations in the Heliotropioideae. III. (I: Hilger, 1987, II: Hilger, 1989).





Figs. 1 and **2** SEM pictures of Boraginaceae inflorescence tips, showing different arrangement of the stylar clefts referring to the inflorescence axis (from left to right).

Fig. **1**: *Eritrichum canum* (Boraginoideae); Fig. **2**: *Heliotropium indicum* (Heliotropioideae).

Materials and Methods

Flowering and fruiting material of the following *Heliotropium* s.l. taxa was investigated, comprising 8 or 9 sections:

Species with fruits separating at once into 4 nutlets (Fig. 3)

Sect. *Gottliebia* Verdc.: *Heliotropium zeylanicum* (Burm. f.) Lam. (Kenya, leg. Hilger and Schultka, 1986 s. n.).

Sect. *Catimas* DC.: *Heliotropium digynum* (Forssk.) Aschers. ex C. Christ. (Saudi Arabia, leg. Frey and Kürschner, 81–44).

Sect. *Catoxys* Bunge: *Heliotropium maris-mortui* Zohary (Israel, leg. Hilger 1981 s.n.).

Sect. *Heliothamnus* I. M. Johnston: *Heliotropium arborescens* L. (= *H. peruvianum* L.) (cult. Bot. Gard. Berlin-Dahlem).

Species with 4 nutlets, first cohering in pairs, then separating completely (Fig. 4)

Sect. *Tiaridium* (Lehm.) Griseb.: *Heliotropium indicum* L. (Sri Lanka, Peradenya Bot. Gard. leg. Nowak, 1981 s.n.).

Taxa with 2 diaspores (Fig. 5)

Heliotropium messerschmidioides Kuntze (≡ *Ceballosia fruticosa*[2] [Lam.] Kunkel) (Spain, Canary Islands, Tenerife, leg. Hilger, TEN, 86/2);

Sect. *Coeloma* (DC.) I. M. Johnston: *Heliotropium pectinatum* Vaupel (Kenya, leg. Hilger, 1985 s.n.).

Sect. *Pterotropium* (DC.) Bunge[3]: *Heliotropium erosum* Lehm. (Spain, Canary Islands, Tenerife, leg. Hilger, 1986 s.n.).

Species with 1-seeded fruit (in European populations, Verdcourt 1991) not breaking into nutlets

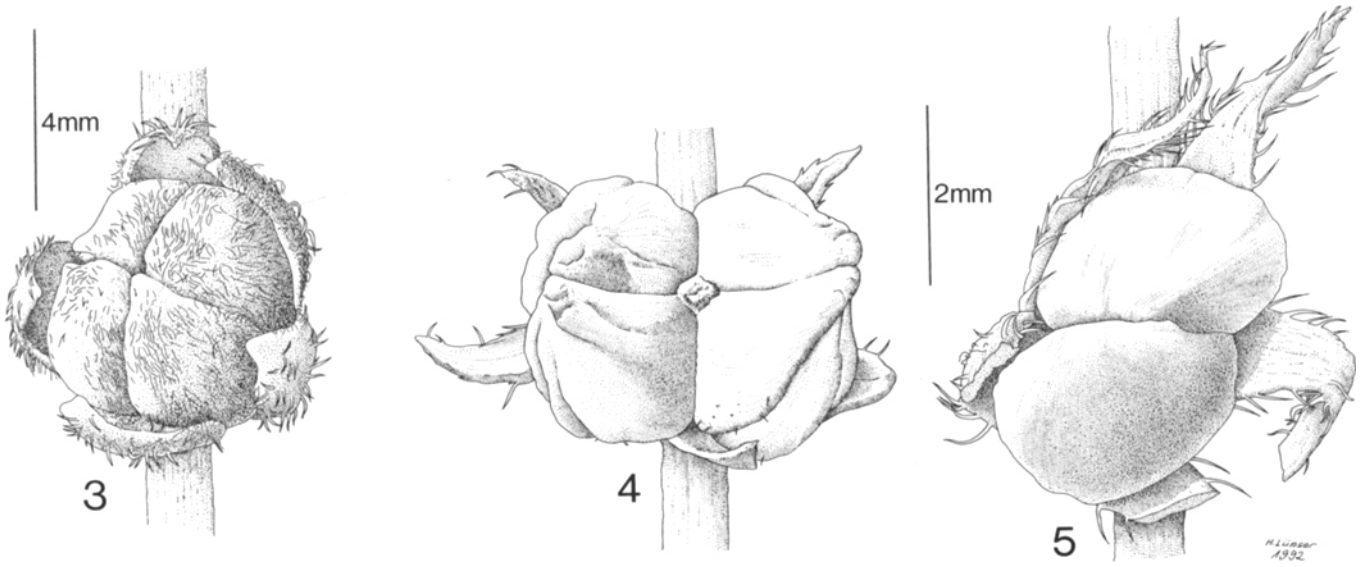
Subgen. *Piptoclainia* (G. Don) H. Riedl sect. *Piptoclainia: Heliotropium supinum* L. (Italy, Sicily, leg. Hilger, 1984 s.n.).

Herbarium specimens and/or fixed material are deposited in the Herbarium of the Institut für Systematische Botanik und Pflanzengeographie der Freien Universität Berlin (BSB).

For light microscopy (LM) the AFE-fixed (acetic acid-formalin-ethanol) material was dehydrated with an ethanol/tertiary butanol series and embedded in Paraplast (Sherwood). The photographs of safranine-astra blue stained serial sections (10–15 µm, Reichert-Jung Supercut 2050) were taken with a Leitz Ortholux II microscope and a Leitz Vario-Orthomat camera. For scanning electron microscopy (SEM), the FDA-dehydrated material (formaldehyde dimethyl acetal, Gerstberger and Leins, 1978) was critical point dried with CO_2 in a Polaron E 3000 and coated with gold in a Balzers sputter coater. The SEM micrographs were prepared with a Cambridge S100.

[2] This taxon, endemic to Macaronesia, is distinguished by a character set not found in other *Heliotropium* species. But, to my knowledge, the genus has still not yet been validly published by Kunkel (without Latin description). If the taxon is included in *Heliotropium*, it belongs to sect. *Messerschmidia* (DC.), Gürke (Gürke, 1893).

[3] This combination, already made by Bunge (1870: 330), seems to have been overlooked by Riedl (1967).



Figs. 3–5 Mature *Heliotropium* fruits.
Fig. **3**: *H. digynum*: 4 symmetrical mericarpids. Fig. **4**: *H. indicum*: 2 + 2 mericarpids. Fig. **5**: *H. pectinatum*: 2 two-seeded synmericarpids.

Results

SEM investigation of gynoecial development: Ontogeny and torsion of stylar lobes and clefts

As in Boraginoideae, the carpels of *Heliotropium* are initiated parallel to the inflorescence axis. Their upper rims soon become horse-shoe-shaped and are curved outwards (Fig. **6**, *H. indicum*) with the median parts still longer than the lateral ones, thereby indicating the original course of the stylar cleft. Accelerated growth not only fills up the gaps between the stylar tips, yielding a short globose head as in *H. indicum* (Fig. **7**), but in many species the commissural parts by far overtop the morphological apices and mimic a twisted position perpendicular to the original one as in *H. erosum* (Figs. **8, 9**). Sometimes more than two stylar tips could be found in e.g. *H. erosum* and *H. arborescens*.

After the initiation of the stigmatic head, but prior to style elongation, the nectariferous disc begins to grow at the base of the gynoecium (Fig. **7**). Normally, it has two median and two lateral depressions. In most species the median indentations are as deep as or deeper than the lateral ones (Fig. **9**) and support the impression of two halves in lateral position.

The ontogeny of the gynoecium and the altered position of the stylar cleft described above were found in all species that were investigated.

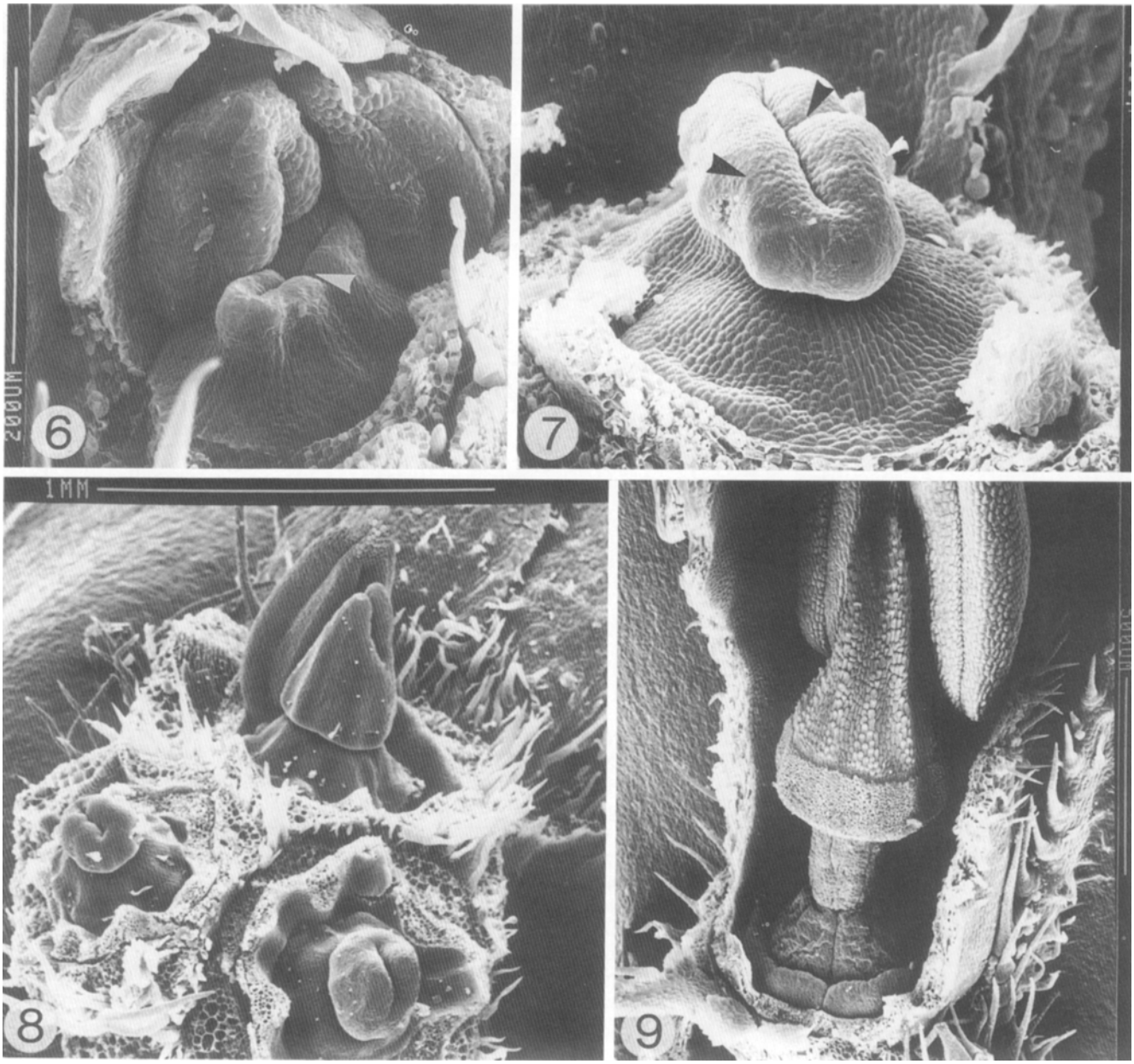
LM investigations

General gynoecial morphology and placentation in *Heliotropium*

The four ovules are inserted on placentae in the symplicate region of the gynoecium. The placentae are rectangular outgrowths of the transverse septa which are often pressed together (Figs. **16, 22**). At that level, funicles or ovules of the same carpel are separated by a short median false septum (Figs. **12, 16, 19, 22**). Following ovule inception the gynoecium grows mainly in its basal parts and the ovules hang down into the four separate chambers formed by basal septa (terminology follows Hilger, 1985). These basal septa can be interpreted as connections between false and true septa. They separate the seeds in their secondary locules from the primary gynoecial cavity. The basal septa are separated by a slit, which is the continuation of the primary gynoecial cavity. Distinct apical septa (which separate the nutlet cavity from the stylar transmission tissue) are developed only in *H. arborescens* (Fig. **23**).

The position of the carpels can only be determined unequivocally when looking at the place of attachment of the funicles and the free false septa, i.e., in the symplicate region (Figs. **12, 16, 19, 22**). It can lead to misinterpretations to assume that the extension of the slits in the synascidiate part corresponds with the septal plane. This erroneous assumption led to the wrong description and arrangement in Hilger (1989, Fig. **4 b, e** and Fig. **6**). From the comparison of e.g. Figs. **15/16** or **18/19** it is possible to deduce the position of the carpels even in the synascidiate zone: the adjacent vascular bundles leading to the funicles on each side of the central slit belong to the same carpel. Sometimes the space between the funicles is filled by a tuft of hairs that may be either outgrowths of the apical septa and/or the appressed placentae. The hairs may serve as an obturator guiding the pollen tubes into the funicular canals.

If one follows sections up through an anthetic gynoecium from the basis to the style (Figs. **10–14**), one sees that the prolongations of the septa, but not those of the false septa, end in the free stylar tips.

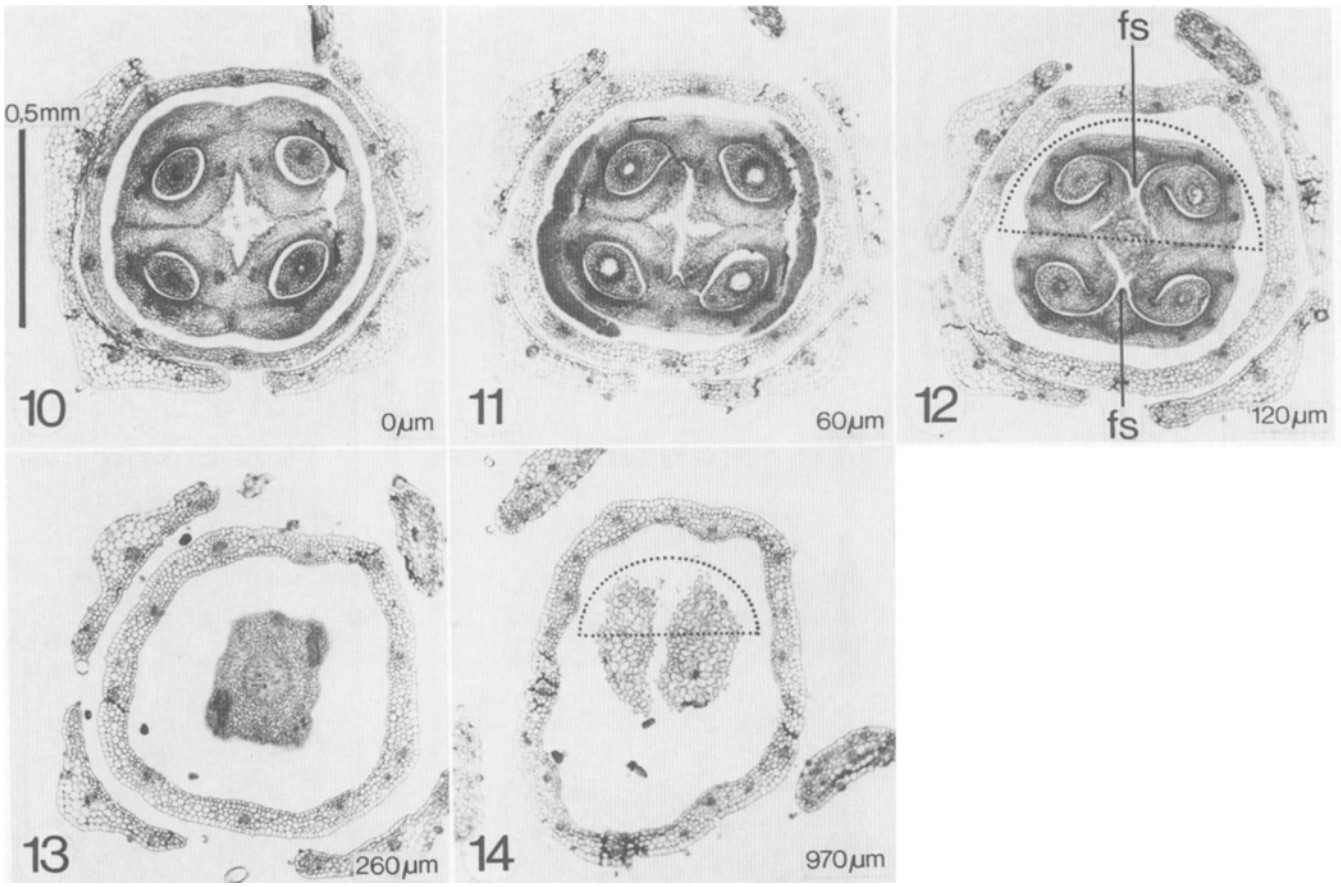


Figs. 6–9 SEM pictures of gynoecium development in *Heliotropium*. Figs. **6** and **7**: *H. indicum*, details of Fig. **2**. Fig. **6**. The carpel tips are horse-shoe shaped (arrow = carpel boundary). Fig. **7**: Commissural rims (arrows) overtop the primary carpel tips. Figs. **8** and **9**: *H. erosum*, Fig. **8**: Growth of the stigmatic head. Fig. **9**: Preanthetic gynoecium with lobed basal nectariferous disc and papillous stigmatic ring.

The extension of separation layers

The cells of the future separation layers are very small and are already discernible as dark lines before or at anthesis, even in *H. supinum* (Fig. **21**), where they disappear later on. In some cases the median plane ruptures earlier than the lateral one. Except in *H. arborescens*, a central columella does not develop.

H. indicum has a disymmetrical fruit. The nutlets originating from each carpel terminate in short beaks which lie against one another (Fig. **4**). They first break in the transverse plane. This sort of disymmetry is not uncommon in *Heliotropium* fruits. Besides sect. *Tiaridium*, according to Verdcourt (1991), extra-European populations of *H. supinum* often have plants with two to four nutlets per flower (then provided with the name *H. supinum* var. *malabaricum* [Retz.] A. DC. & DC.) which may also be arranged two by two. I found no clues as to their method of splitting. Though the plants I investigated (Hilger, 1987) developed only one seed when mature (*H. supinum* proper), a broad rupture along the median plane is already visible in the anthetic gynoecium (Fig. **21**). The asymmetrical shape of the diaspore (Fig. **26**) develops after anthesis.



Figs. 10–14 Cross-section series through preanthetic gynoecium of *H. indicum*, adaxial carpel on top.
Fig. **10**: Basal synascidiate zone, Fig. **11**: Transition to symplicate zone, transverse lobes of nectariferous disc longer than median ones, Fig. **12**: Symplicate zone with placentae (fs = false septum), Fig. **13**: Top of ovary, Fig. **14**: Tips of stigmatic head. In Figs. **12** and **14**: the adaxial carpel is marked with straight line indicating septal plane. Numbers to the right indicate distance (µm) from start of series.

The separation layer in two-seeded diaspores

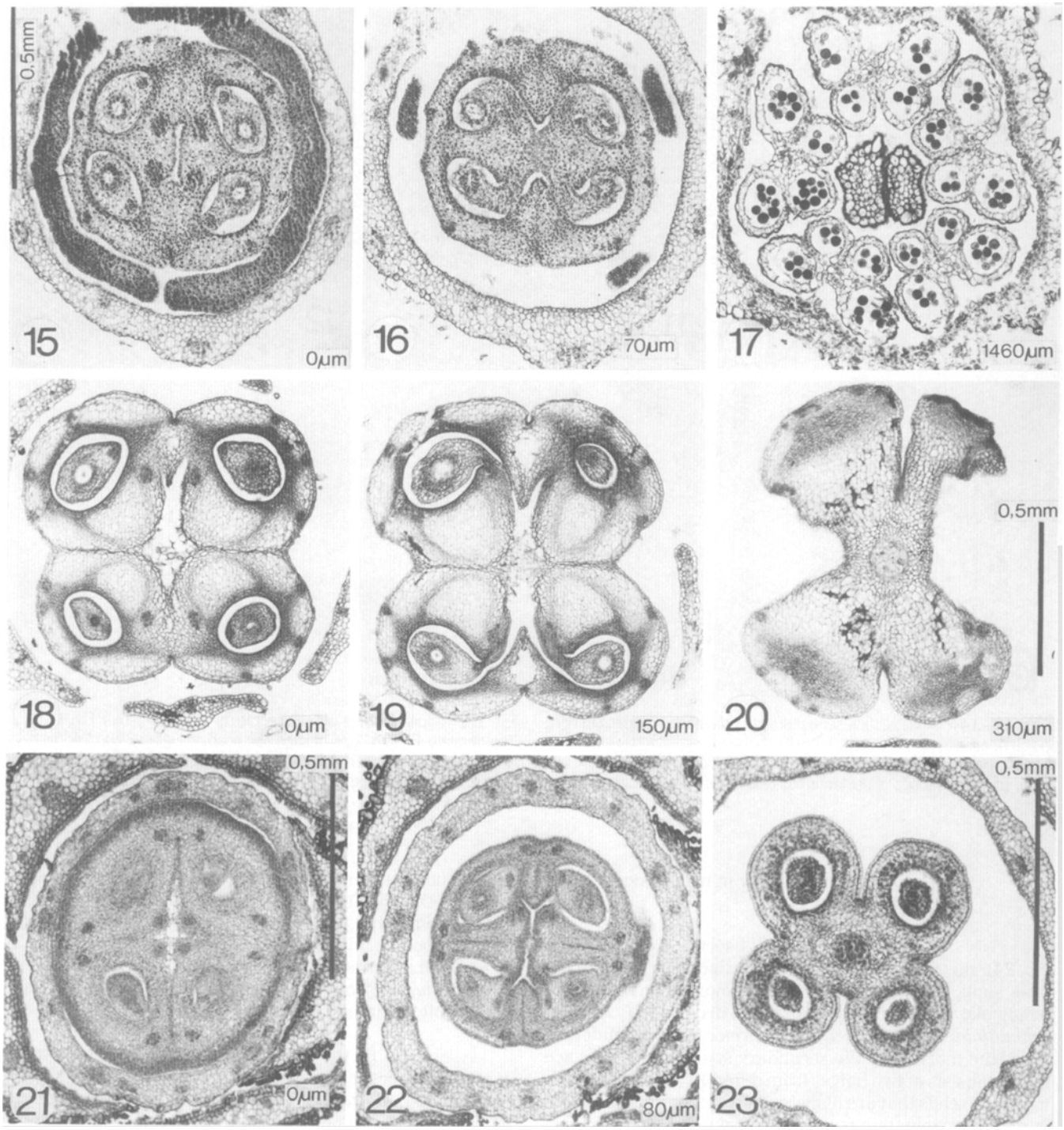
As visible in cross-sections (*H. erosum*, Fig. **24**), the ovary splits along a line that runs through the false septa and their downward prolongations, i.e. perpendicular to the carpels. Also, the fruits of *H. messerschmidioides* and *H. pectinatum* break into two nutlets in the plane marked by the secondary stylar slit. Thus, each nutlet consists of two halves from different carpels and contains two seeds that are dispersed together and remain united until germination (synaptospermy). The close connection of the two halves from different carpels is strengthened by dark staining lateral sclerenchyma bridges (Fig. **24**) which are developed less or not at all in the median plane.

Discussion

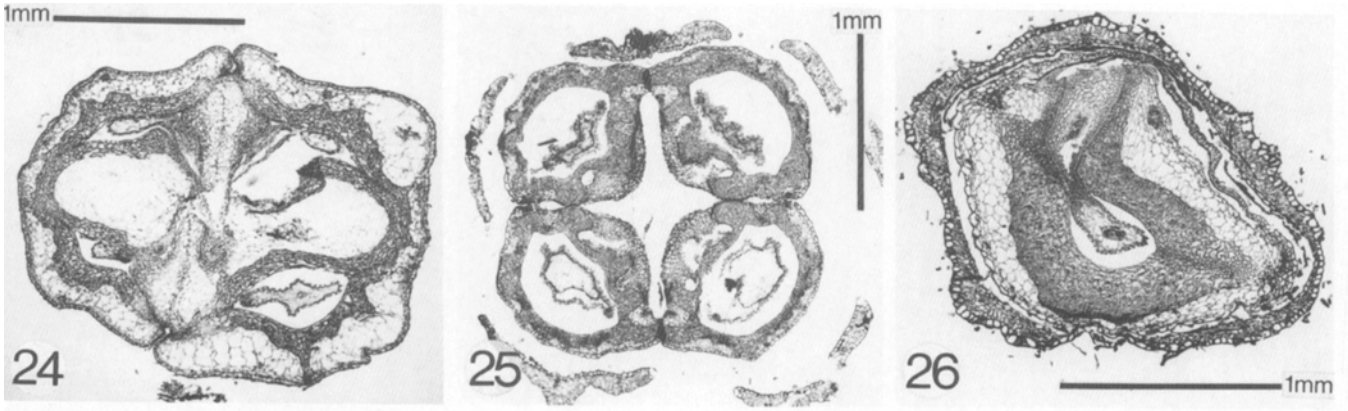
To my knowledge no complete ontogenetical series of flowers or fruits exists for species of the Heliotropioideae to discern the spatial position of carpels, placentae, stylar tips, diaspores, or separation planes. In their illustrations, Lawrence (*H. peruvianum*, 1934), Sharma (*H. indicum*, 1954), and Di Fulvio (1978, who investigated *Ixorhea tschudiana* Fenzl) orient the carpels in a horizontal position, which (today) traditionally means laterally. Only Di Fulvio (1978) draws the stylar tips, which end in the median position. Following her description, the fruit first breaks into carpids and then into the nutlets, as in *H. indicum*. Sharma (1954) describes the floral anatomy of *H. indicum*, but only from one stage and nothing is said about fruit formation.

In the subfamily Boraginoideae, in most cases, the nutlets are arranged crosswise. Disymmetry occurs e.g. in *Asperugo* L. and *Sclerocaryopsis* Brand of the Eritricheae where neighbouring mericarpids of different carpels face each other (Hilger, 1985). In *Asperugo* they are shed into the persistent calyx and dispersed separately. In *Sclerocaryopsis* they are not released and the whole plant is synaptospermous. Hitherto, the formation of diaspores that consist of coherent carpel halves ("synmericarpids") has been unknown in the Boraginaceae.

The section *Heliothamnus*, to which *H. arborescens* belongs, is, among other characters, distinguished by nutlets separating from a persistent(?) gynoecial columella with a cicatrix typical for the Boraginoideae-Eritricheae and – Cynoglosseae (Johnston, 1928). Distinct apical septa are developed which are lacking in the other



Figs. 15–23 Cross-sections through *Heliotropium* gynoecia. All figures are arranged identically with the adaxial carpel on top.
Figs. **15–17**: *H. erosum*, preanthetic gynoecium. Fig. **15**: Synascidiate zone with surrounding dark-staining nectariferous disc. Fig. **16**: Symplicate zone with placentae, Fig. **17**: Transversally orientated tips of stigmatic head.
Figs. **18–20**: *H. indicum*, postanthetic gynoecium. Fig. **18**: Synascidiate zone, Fig. **19**: Symplicate zone with placentae, Fig. **20**: Solid pericarp of the beak region.
Figs. **21** and **22**: *H. supinum*, preanthetic, still symmetric gynoecium. Fig. **21**: Synascidiate zone, Fig. **22**: Symplicate zone with placentae.
Fig. **23**: *H. arborescens*, zone of apical septa.
Numbers to the right indicate distance (µm) from start of each series. Magnification is constant within each series (15–17, 18–20, 21–22).



Figs. 24–26 Cross sections through almost ripe *Heliotropium* fruits. Fig. **24**: *H. erosum*, fruit prior to breaking into two transverse synmericarpids. Fig. **25**: *H. zeylanicum*, fruit prior to breaking into four mericarpids. Fig. **26**: *H. supinum*, fruit with only one seed developed, region of funicular canal.

species. In the specimen investigated the stigmatic head terminates in four tips. The ovules reach into both the upper and lower part of the mericarpidial cavity and the funicles are attached near the middle of the ovules. The shape is campylotropous rather than anatropous. Taking into account the distinguishing characters of other infrageneric taxa of *Heliotropium*, the gynoecial and fruit morphology of *Heliothamnus* indicates a higher than sectional rank in the genus.

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References

Bunge, A. von – Über die Heliotropien der mittelländischen orientalischen Flor. Bull. Soc. Imp. Naturalistes Moscou 42 (1870), 279–332.

De Candolle, A. – Prodromus systematis naturalis regni vegetabilis IX. p. 566. Masson, Paris, 1845.

Di Fulvio, T. E. – Sobre la vasculatura floral, embriología y chromosomas de *Ixorhea tschudiana* (Heliotropiaceae). Kurtziana 11 (1978), 75–105.

Gerstberger, P. and Leins, P. – Rasterelektronenmikroskopische Untersuchungen an Blütenknospen von *Physalis philadelphica* (Solanaceae). Ber. Deutsch. Bot. Ges. 91 (1978), 381–387.

Gürke, M. – Borraginaceae (Asperifoliaceae). In: Engler, A. and Prantl, K., eds., Die natürlichen Pflanzenfamilien 4, Abt. 3a, pp. 71–131. Engelmann, Leipzig, 1893.

Hilger, H. H. – Wachstum und Ausbildungsformen des Gynoeceums von *Rochelia* (Boraginaceae). Pl. Syst. Evol. 146 (1984), 123–139.

Hilger, H. H. – Ontogenie, Morphologie und systematische Bedeutung geflügelter und glochidientragender Cynoglosseae- und Eritrichеae-Früchte (Boraginaceae). Bot. Jahrb. Syst. 105 (1985), 323–378.

Hilger, H. H. – Fruchtbiologische Untersuchungen an Heliotropioideae (Boraginaceae). I. Die Ontogenie der monospermen Früchte von *Heliotropium supinum* L. Flora 179 (1987), 291–303.

Hilger, H. H. – Flower and fruit development in the Macaronesian endemic *Ceballosia fruticosa* (syn. *Messerschmidia fruticosa*, Boraginaceae, Heliotropioideae). Pl. Syst. Evol. 166 (1989), 119–129.

Johnston, I. M. – Studies in the Boraginaceae. VII. Contr. Gray Herb. 81 (1928), 3–83.

Khaleel, T. F. – Embryology of *Heliotropium scabrum* and *H. strigosum* (Boraginaceae). Pl. Syst. Evol. 129 (1978), 45–62.

Kunkel, G. – Die Kanarischen Inseln und ihre Pflanzenwelt. 1. Aufl., p. 185. Fischer, Stuttgart, New York, 1980.

Lawrence, J. R. – A correlation of the taxonomy and the floral anatomy of certain of the Boraginaceae. Amer. J. Bot. 24 (1937), 433–444.

Lehmann, J. C. G. – Plantae e Familia Asperifoliarum nuciferae. p. 478. Dümmler, Berolini, 1818.

Miers, J. – Observations on some of the Heliotropieae. Ann. Mag. Nat. Hist. 2 (1868), 121–133.

Riedl, H. – Boraginaceae. In: Rechinger, K.-H., ed., Flora Iranica Lfg. 48. p. 281. Akademische Druck- und Verlagsanstalt, Graz, 1967.

Rosanoff, S. – Morphologisch-embryologische Studien. Jahrb. Wiss. Bot. 5 (1866), 72–81.

Sharma, R. – Floral anatomy of *Heliotropium indicum* L. Agra Univ. J. Res. Sci. 3 (1954), 349–357.

Verdcourt, B. – Boraginaceae. In: Polhill, R. M., ed., Flora of Tropical East Africa. p. 124. Balkema, Rotterdam, 1991.

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