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## Preliminary data on microcharacters and chromosome number in *Tornabenea* species (Apiaceae) from Cape Verde Islands

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### Abstract

*Tornabenea* is a small Apiaceae genus that is endemic to the Cape Verde Islands. Its species differentiation is based just on a few macromorphological characters: leaf shape, number and shape of umbel bracts and mericarp ribs. These characters vary within each species and show high plasticity. Thus, in recent taxonomic data of the genus, there are different viewpoints as to the number of species. Here, in order to improve the taxonomy of the genus, microcharacters of the vegetative and reproductive structures of three taxa—*T. insularis*, *T. annua* and *T. tenuissima*—have been examined. The shape and arrangement of hairs on the surface of the mericarps, and the presence and structure of starch grains are the only different microcharacters noted in *T. insularis* and *T. annua*. Chromosome number of the latter two species is  $2n=18$ . Our preliminary results disagree with the existing classifications of the genus *Tornabenea*. In fact, they do not lead to a clear separation between *T. insularis* and *T. annua*. By contrast, it is easy to distinguish between these species and *T. tenuissima*, which possesses more peculiar microcharacters.

**Key words:** *Apiaceae*, *Cape Verde Islands*, *cytology*, *microcharacters*, *Tornabenea*

### Introduction

Man introduced some of the plants in the Macaronesian flora, but a few are endemic to the various archipelagos. In the Cape Verde Islands the Apiaceae Lindl. are represented by about 10 species. The genus *Tornabenea* Parl., 1849, which belongs to the subfamily Apioideae and to the tribe Laserpitieae (Heywood, 1971), is the only endemic one (Schmidt & Lobin, 1999). It includes annual, biennial or short-lived perennial herbs, which are usually found on humid and sub-humid hills between 0 and 1000 m above sea level, as well as in cultivated areas.

Parlatore established the genus in 1849 with a single species: *T. insularis* Parl. ex Webb. Some years later come the descriptions of *T. bishoffii* J. A. Schmidt (1852), *T. hirta* J. A. Schmidt (1852), *T. annua*, Bég. ex A. Chev. (1920), and *T. tenuissima* (A. Chev.) A. Hausen & Sunding (1979).

These species can also be found in the genus *Melanoselinum* Hoffm., which is endemic to Madeira

and the Azores Islands, and both genus names have been used (Press & Dias, 1998). Later, *T. hirta* was reduced to a synonym of *T. insularis* (Schmidt & Lobin, 1999). Recent taxonomic data on the genus still offer little agreement as to the number and delimitation of its species: in the *Cape Verde Flora*, Martins (1996) also considers *T. hirta* and *T. bishoffii* to be synonymous with *T. insularis*, and only mentions three species: *T. insularis*, *T. annua* and *T. tenuissima*. According to Brochman et al. (1997), the *Tornabenea* genus comprises five species: *T. insularis*, *T. annua*, *T. humilis*, *T. bishoffii* and *T. tenuissima*. Subsequently, the new species *T. ribeirensis* Schmidt & Lobin (1999) was established. All these studies on species differentiation are primarily based on leaf shape, and on the number and shape of umbel bracts and mericarp ribs, but it is recognized that these characters vary within each species and show high plasticity (Martins, 1996; Brochman et al. 1997).

Microcharacters are often a useful support although they are not used often as basis for a

classification. They are regarded as a contribution, and rarely are of great value to the identification and delimitation of species (Metcalf & Chalk, 1950; Stace, 1989; Husain et al., 1990; Teixeira & Diniz, 2003). This paper is the first report on a study of microcharacters in *Tornabenea*.

Cytological studies on the genus *Tornabenea* are also still very limited. Brochman et al. (1997) report chromosome counts in *Tornabenea* species, but their results are not significant for some of the species.

The aim of this preliminary study was to contribute to the improvement of our knowledge about *Tornabenea* by presenting a comparison of the microcharacters, concerning vegetative and reproductive structures, for *T. insularis*, *T. annua* and *T. tenuissima*, and of chromosome numbers for *T. insularis* and *T. annua*.

These results are part of a larger project in which phytochemical and molecular approaches are also considered, along with seedling development.

## Material and methods

### Plant material

This study on *Tornabenea* species was performed with dry specimens housed at the Herbarium of the Centro de Botânica (LISC, Botanic Centre), Instituto de Investigação Científica Tropical, Lisboa (Institute of Tropical Scientific Research) (Table I). We only considered flower and fruit-bearing specimens.

Table I. *Tornabenea* herbarium specimens included in this study.

Taxa	Herbarium voucher number	Island
<i>T. insularis</i>	Matos 6498	S. Vicente
<i>T. insularis</i>	Martins, Gonçalves and Gomes 457	Santiago
<i>T. insularis</i>	Martins, Gonçalves and Gomes 477	Fogo
<i>T. insularis</i>	Martins, Gonçalves and Gomes 533	Brava
<i>T. insularis</i>	Barbosa 6687	S. Vicente
<i>T. insularis</i>	Barbosa 7090	Santo Antão
<i>T. insularis</i>	Barbosa 7231	S. Nicolau
<i>T. insularis</i>	Barbosa 13970	Fogo
<i>T. insularis</i>	Gomes D72A	Santiago
<i>T. insularis</i>	Gomes 90B	Santo Antão
<i>T. annua</i>	Martins 1703	Santiago
<i>T. annua</i>	Barbosa, Matos and Silva 14256	Santiago
<i>T. annua</i>	Barbosa, Matos and Silva 14292	Santiago
<i>T. annua</i>	Barbosa, Matos and Silva 14263	Santiago
<i>T. annua</i>	Gomes D72	Santiago
<i>T. annua</i>	Matos 5923	Fogo
<i>T. annua</i>	Matos and Moreira 6104	Fogo
<i>T. tenuissima</i>	Barbosa 6272	Fogo
<i>T. tenuissima</i>	Barbosa 6882	Santo Antão
<i>T. tenuissima</i>	Barbosa 7087	Santo Antão
<i>T. tenuissima</i>	Barbosa 9311	Santo Antão
<i>T. tenuissima</i>	Matos 5856	Fogo

### Morphological studies

**Light microscopy (LM).** Dried material was previously hydrated and fixed in a 2.5% glutaraldehyde solution (Hayat, 1981). Cross-sections were hand-cut, clarified with sodium hypochlorite and washed in distilled water (Evans 2002).

Observations were carried out using a Nikon Labophot 2 microscope. Images were obtained with a Nikon FX-35W camera equipped with a semi-automatic Nikon PFX adapter.

Qualitative and quantitative characters are the average of ten different observations per specimen. Stoma classification followed Stace (1989) and the stomatal index was estimated according to Salisbury (1927).

**Scanning electron microscopy (SEM).** Plant material was fixed as above, critical-point dried and coated with gold in a Jeol JFC-1200. Observations were carried out at 15 kV with a Jeol JSM-5220 LV scanning electron microscope equipped with a direct image acquisition system. Measurements and counts were obtained by computer-assisted image analysis.

### Chromosome number

Chromosome number was only established for *T. insularis* and *T. annua*. Seeds of both species were germinated on moist filter paper in the dark at room temperature for 5–8 days. Root tips were treated for 3 h with 0.002 M 8-hydroxyquinoline, fixed for 24 h in ethanol:glacial acetic acid (3:1, V/V), and digested in a mixture of 5% cellulase and 5% pectinase for 30 min at 37°C. The cell suspension was filtered, treated with 75 mM KCl, re-fixed in ethanol:glacial acetic acid (3:1) and stained with Feulgen reagent.

## Results

### Leaf microcharacters

The main leaf microcharacters are presented in Table II. Both *T. insularis* and *T. annua* have alternate, 2- to 3-pinnatisect leaves with lobed final segments. Upper and lower leaf surfaces are covered with long unicellular, non-glandular hairs. *T. tenuissima* has 3- to 4-pinnatisect leaves with oblong or linear final segments no more than 1.5 mm wide. This species is glabrous.

Leaf surfaces in *T. insularis* and *T. annua* present differently outlined epidermal cells. In the lower epidermis they are more sinuous than in the upper one. In *T. tenuissima* they are polygonal with straight walls. In the upper surface and in the lower epidermis there are sinuous anticlinal walls. The three species show cuticular grooves on the epidermal cell walls.

Table II. Main leaf microcharacters used in the study of *Tornabenea* species.

Taxa	Leaf shape	Leaf indumentum	Trichome length ( $\mu\text{m}$ )	Adaxial epidermis cell shape	Abaxial epidermis cell shape	Stoma type	Stoma length/width ( $\mu\text{m}$ )	Stomatatal index	Major vein	Mesophyll	Calcium oxalate crystals
<i>T. insularis</i>	2–3-pinnatisect	Long unicellular	138.0 $\pm$ 34.0 244.1 $\pm$ 110.1	Irregular, sinuous	Irregular, more sinuous	Diacytic (++++)	25.7 $\pm$ 2.1 17.5 $\pm$ 2.3	21.9	Abaxially prominent	Bifacial	Prismatic
<i>T. annua</i>	2–3-pinnatisect	Long unicellular	138.0 $\pm$ 34.0 244.1 $\pm$ 110.1	Irregular, sinuous	Irregular, more sinuous	Diacytic (++++)	24.8 $\pm$ 2.7 14.0 $\pm$ 2.9	20.5	Abaxially prominent	Bifacial	Prismatic
<i>T. tenuissima</i>	3–4-pinnatisect	Glabrous	–	Polygonal	Irregular, sinuous	Diacytic (++++)	24.6 $\pm$ 3.7 16.2 $\pm$ 4.7	14.5	Not abaxially prominent	Mono-facial	Prismatic

Stomata are more abundant on the lower face, evenly distributed, superficial but sometimes slightly raised. Diacytic stomata are more frequent. *T. insularis* and *T. annua* present the highest stomatal index values (Table II).

In cross-section, *T. insularis* and *T. annua* leaves have a lamina thickness of  $117 \pm 5.7 \mu\text{m}$ , a bifacial mesophyll composed of two layers of palisade cells with more than half the width of the whole lamina, and two layers of spongy cells that are not very loose, a midrib abaxially convex and adaxially flat or slightly convex,  $220.8 \pm 4.9 \mu\text{m}$  thick; a subepidermal collenchyma can be seen both abaxially and adaxially. In *T. tenuissima* major veins are not prominent, the midrib is abaxially slightly convex and adaxially flat, lamina thickness is  $138.8 \pm 2.1 \mu\text{m}$ , and the midrib is  $150 \pm 1.8 \mu\text{m}$  thick. In the mesophyll only palisade cells are present.

As for as secretory tissues are concerned, *Tornabenea* species present oil ducts—canals that are also called *vittae*—implanted near the vascular bundles. In the midrib *T. insularis* and *T. annua* show similar round *vittae* surrounded by 6–8 cells. *T. tenuissima* also has round *vittae* near the upper surface, surrounded by 9 cells, while and on the lower face the canal is oval, and surrounded by 11 cells.

All the observed specimens have prismatic calcium oxalate crystals inside epidermal cell vacuoles.

#### Bract and flower microcharacters

The three species present a similar number of bracts per umbel (6–10, or up to 14 in *T. insularis*) and a similar number of bracteoles on the partial umbels, but with different shapes. *T. insularis* has 3-lobate to 5-sect bracts, while *T. annua* has entire linear-oblongate bracts; both have two layers of hairs that are inserted along the margin and leaning towards the apex. Diacytic and some anomocytic stomata are distributed on the upper surface, without any orientation. *T. tenuissima* has linear involucral bracts, with two layers of hairs along the margins, oriented towards the bract apex. A large number of diacytic and a few anisocytic stomata are mostly distributed on the upper surface, with a clear longitudinal orientation.

In all three species, the flowers are hermaphrodite and pentamerous, with whitish–yellowish glabrous petals with bent tips. Pollen morphology is also similar: grains are tricolpate, of an oval type, with long ectoapertures, and a rugulose or cerebroid exine surface. Pollen grain measures (equatorial axis  $\times$  polar axis) are very similar, except the equatorial axis (Table III).

#### Mericalp microcharacters

The genus *Tornabenea* has dry bilocular fruits that split at maturity into two oblong elliptical

Table III. Main bract, flower and mericarp microcharacters used in the study of *Tomabeneza* species.

Taxa	Bract shape	Number of bracts per umbel	Pollen exine surface	Pollen equatorial axis × polar axis (µm)	Mericarp marginal ribs	Mericarp length/width ratio	Mericarp hairs	Mericarp starch grains description/ diameter (µm)	Calcium oxalate crystals
<i>T. insularis</i>	3-lobate to 5-sect	up to 14	Cerebroid	10.2 ± 1.6 24.4 ± 1.3	Slightly winged and serrated	1.8	Hairs with dense covering of wax arranged in warty blobs with no basal cells	Isolated and compound/ 8.13 ± 2.25	Druses
<i>T. annua</i>	Entire linear oblanceolate	6–10	Cerebroid	9.9 ± 0.5 25.2 ± 2.4	Large, clearly winged and serrated	2.1	Simple hairs surrounded by cells	Isolated/ 6.15 ± 1.14	Druses
<i>T. tenuissima</i>	Linear involucrel	6–10	Cerebroid	14.0 ± 1.4 24.8 ± 1.1	Neither winged nor serrated	1.5	Glabrous	Compound/ 8.42 ± 1.69	None

homomorphic mericarps, which are slightly compressed dorsally. The mericarp coats are lignified, indehiscent and fused with the seed coat. These mericarp coats present 5 inconspicuous primary ribs (1 dorsal, 2 lateral and 2 commissural) and 4 secondary narrowly winged ones, all running longitudinally from the base to the end of the fruit. In cross-section, they possess 6 *vittae*: 2 dorsal, 2 lateral and 2 ventral.

*T. insularis* mericarps present a length/width ratio of 1:8, with slightly winged and serrated marginal ribs; they have hairs, in and between the dorsal ribs, and a dense covering of wax arranged in warty blobs with no additional basal epidermal cells (Figure 1). *T. annua* mericarp marginal ribs are usually large, clearly winged and serrated, with a length/width ratio of 2:1, and show simple hairs very similar to those found on their leaves and bracts. These hairs are spread sideways in relation to the secondary ribs and lean towards the apex. At the base of each hair there are some cells surrounding it (Figure 2). In *T. tenuissima* mericarps the marginal ribs are neither winged nor serrated, no hairs are to be seen over or between the ribs, and the length/width ratio is 1:5.

*T. annua* is characterized by the presence of isolated starch grains and druses inside some endosperm cells (Figure 3), while *T. insularis* possesses isolated and compound starch grains and

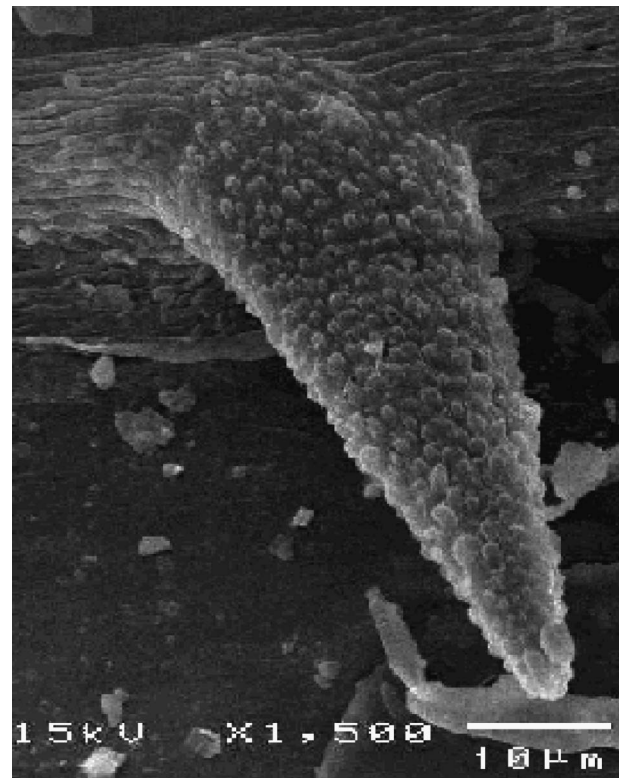


Figure 1. *T. insularis* mericarp dorsal view over the ribs showing a hair with a dense covering of wax arranged in warty blobs, and with no basal cells (SEM, ×1500).



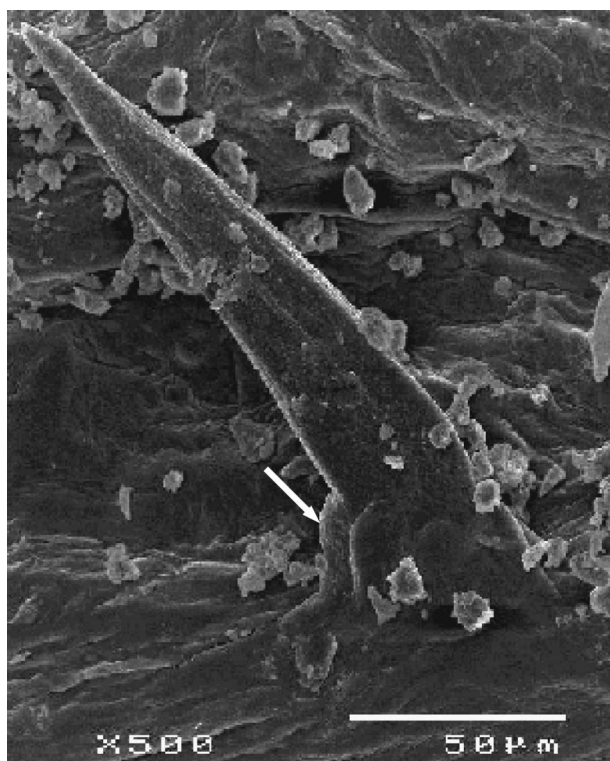


Figure 2. *T. annua* mericarp dorsal view showing a simple hair, with cells surrounding the base (arrow) (SEM, ×500).

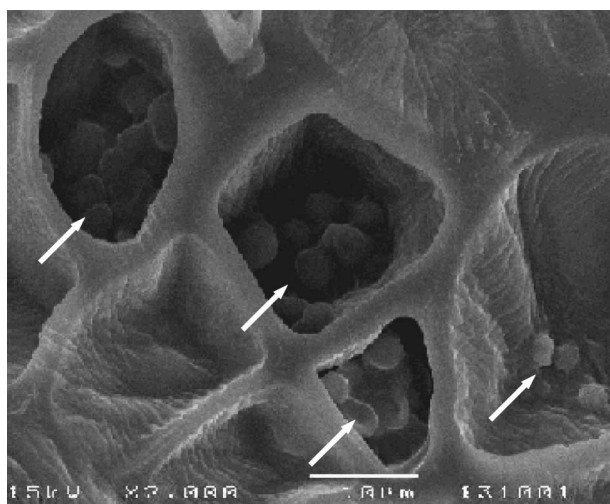


Figure 3. *T. annua*: isolated starch grains inside endosperm cells (arrows), (SEM, ×2000).

druses (Figure 4). In *T. tenuissima* no calcium oxalate crystals are to be seen and starch grains are mostly compound (Figure 5). The starch grain measures and the main mericarp microcharacters are also presented in Table III.

#### Chromosome number

Mitotic metaphases in the root tips of both *T. insularis* and *T. annua* revealed a chromosome

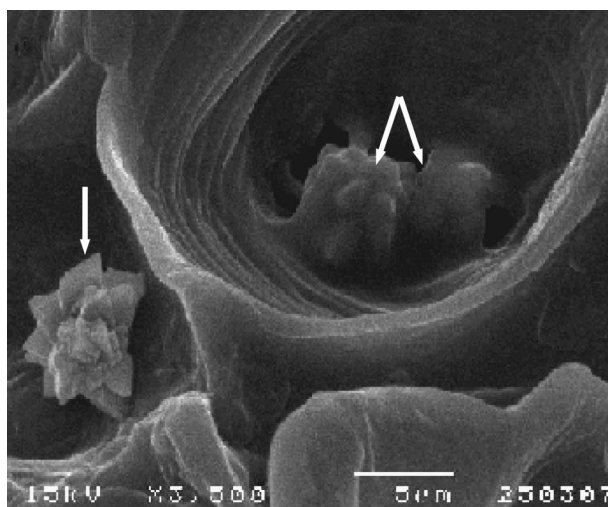


Figure 4. *T. insularis*: compound starch grains (double arrow) and druses (single arrow) inside endosperm cells (SEM, ×3500).

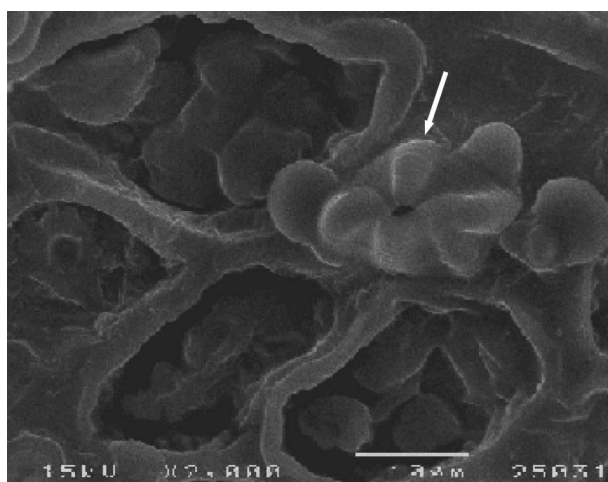


Figure 5. *T. tenuissima*: compound starch grains stored in endosperm cells (arrow), (SEM, ×2000).

number of  $2n=18$ . Chromosomes are small in size, with an average length of  $1.1 \pm 0.2 \mu\text{m}$ .

#### Discussion

The classification of the Apiaceae at the generic level and above is traditionally largely based on the general form and arrangement of hairs and ribs on the mericarps, and to a lesser extent on details having to do with inflorescence, floral and vegetative structures. These may be complemented by additional characters such as pollen and stomata (Heywood & Dakshini, 1971). Given that different stomatal types reveal different evolutionary tendencies, Guyot (1971) attributes to the stomatal type of the Apiaceae a systematic and phylogenetic value comparable to that of pollen grains. This

author studied more than 150 species of Apiaceae and noticed that the simple observation of the mature epidermis makes it possible to distinguish two general epidermal types: (i) epidermis with stomata belonging to one well-known type (anomocytic, anisocytic, diacytic and paracytic); and (ii) epidermis with stomata belonging to more than one type. Both these situations are frequent in nearly every genus of the Apiaceae (Guyot, 1971). *Tornabenea* also seems to follow this rule: despite the dominance of the diacytic type, the leaves and the bracts of the examined species presented more than one type of stomata.

The Apiaceae show a wide variety of pollen shapes, which, according to Cerceau-Larrival (1971), have a polar axis size ranging from 15 to 70  $\mu\text{m}$ , and may be grouped into five clearly distinguishable basic types: subrhomboidal, subcircular, oval, subrectangular, and equatorially constricted. All the studied *Tornabenea* pollen grains belong to the oval type, are small-sized ( $25 \mu\text{m} < P \leq 35 \mu\text{m}$ ) and present a third-order symmetry, long ectoapertures and a rugulose or cerebroid exine (Table III).

As mentioned earlier, mericarps are considered to be basic characters for the Apiaceae. Although very little is known about their functional or adaptive value, their general shape, the presence/absence of wings, the form and arrangement of hairs and ribs, and their anatomical features are very important for characterizing genera and separating species (Heywood & Dakshini, 1971). The general morphology of all the mericarps studied is similar. However, in *T. tenuissima* the mericarps are not winged or serrated, but they are in *T. insularis* and *T. annua*, although this is more evident in the latter species. As regards the surfaces of the mericarps, our studies showed that surface ornamentation is poor and simple in all three species. In *T. tenuissima* it is almost inexistent because there are no hairs. There are some significant differences between the other two species in this respect. They both have hairy mericarps, but *T. insularis* presents a few hairs with a dense covering of wax arranged in warty blobs over and between the secondary ribs, while *T. annua* has simple hairs spread sideways in relation to the secondary ribs, with basal cells that surround them.

About 14 different types of starch grains can be recognized among the angiosperms and these are used to delimit taxa based on their form, appearance and measurements (Stace, 1989; Evans, 1996). In *Tornabenea* they might be considered a useful microcharacter. In fact, each species presents particular starch grains (Table III).

Calcium oxalate crystals have also been considered to be important characters and to be particularly valuable as taxonomic evidence and much work has been done in angiosperms (Stace, 1989; Evans,

1996; Prychid & Rudall, 1999; Ilarslan et al., 2001; Nakata, 2003). However, studies on crystal distribution in Apiaceae are scarce and, according to Kljuykov et al. (2004), calcium oxalate crystals are considered to be relatively rare in the Apioideae, except in basal groups such as some woody African genera. In *Tornabenea* their presence was noted both in leaves and seeds (Tables II and III) but, as far as could see, with no taxonomic value.

Chromosome counts for both *T. insularis* and *T. annua* showed  $2n = 18$ . Brochman et al. (1997) reported the same number of chromosomes for these two species, with some reservations in relation to *T. insularis*. We also found that *Tornabenea* chromosomes are rather small. A more detailed analysis has been started to collect further cytotoxic information.

Chromosome studies on the Apiaceae have shown that members of the Hydrocotoyloideae and Saniculoideae subfamilies are likely to have  $n = 8$ , while members of the Apioideae (such as *Tornabenea*) most frequently have  $n = 11$  (Moore, 1971). Indeed, *Melanoselinum decipiens* (Schrad & Wendl.) Hoffm. (also an Apioideae) has  $n = 11$  (Press & Dias, 1998). It is commonly accepted that sometimes chromosomes can be used for taxonomic discrimination, in our research results justified the separation of *Tornabenea* in the Laserpitiae, as well as the *Tornabenea/Melanoselinum* separation.

## Conclusion

In short, our contribution on *Tornabenea* species represents a preliminary study, but we can already assume that *T. insularis* and *T. annua* show many similar microcharacters in their vegetative and sexual reproductive features, albeit differences in a very few characters concerning their mericarps (Table III). Thus, our results are in disagreement with the existing classifications of *Tornabenea*. In fact, the separation between *T. insularis* and *T. annua* is not very certain, unlike that between these two species and *T. tenuissima*, which has more peculiar microcharacters.

Further cytological, phytochemical and molecular studies are underway to collect certain taxonomic information about the genus *Tornabenea*.

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## References

- Brochman C, Rustan OH, Lobin W, Kilian N. 1997. Apiaceae—*Tornabenea*. In: University of Oslo, editors. Botanical garden and museum. The endemic vascular plants of the Cape Verde Islands, W Africa. *Sommerfeltia* 24: 77–91.
- Cerceau-Larrival MT. 1971. Morphologie et correlations chez les Umbellifères. In: Heywood VH, editor. The biology and chemistry of the Umbeliferæ. *Bot J Linn Soc* 64(Suppl. 1):109–155.
- Evans WC. 2002. Trease and Evans pharmacognosy. 15th ed. London: Saunders Company Ltd.
- Guyot M. 1971. Phylogenetic and systematic value of stomata of the Umbelliferae. In: Heywood VH, editor. The biology and chemistry of the Umbeliferæ. *Bot J Linn Soc* 64(Suppl. 1):199–214.
- Hayat M. 1981. Principles and techniques of electron microscopy. In: Biological applications. 2nd ed. London: Edward Arnold.
- Heywood VH. 1971. Systematic survey of the old world Umbelliferae. In: Heywood VH, editor. The biology and chemistry of the Umbeliferæ. *Bot J Linn Soc* 64(Suppl. 1):31–41.
- Heywood VH, Dakshini KM. 1971. Fruit structure in the Umbelliferae–Caucalideae. In: Heywood VH, editor. The biology and chemistry of the Umbeliferæ. *Bot J Linn Soc* 64(Suppl. 1):215–232.
- Husain SZ, Marin P, Silic C, Qaiser M, Petcovic B. 1990. A micromorphological study of some representative genera in the tribe Satureja (Lamiaceae). *Bot J Linn Soc* 103:59–80.
- Ilarslan H, Palmer R, Horner H. 2001. Calcium oxalate crystals in developing seeds of soybean. *Ann Bot* 88:243–257.
- Kljuykov EV, Liu M, Ostroumova TA, Pimenov MG, Tilney PM, van Wyk B-E. 2004. Towards a standardised terminology for taxonomically important morphological characters in the Umbelliferae. *S Afr J Bot* 70:488–496.
- Martins ES. 1996. Flora de Cabo Verde: Plantas vasculares. 67. Apiaceae. Lisboa: IICT, Praia: INIDA.
- Metcalfe C, Chalk L. 1950. Anatomy of dicotyledons, Vol I. Oxford: Clarendon Press.
- Moore DM. 1971. Chromosome studies in the Umbelliferae. In: Heywood VH, editor. The biology and chemistry of the Umbeliferæ. *Bot J Linn Soc* 64(Suppl. 1):234–250.
- Nakata P. 2003. Advances in our understanding of calcium oxalate crystal formation and function in plants. *Plant Sci* 164:901–909.
- Press JR, Dias E. 1998. The genera *Melanoselinum* Hoffm. and *Angelica* (Umbelliferae) in Macaronesia. *Arquipélago* 164:1–9.
- Prychid C, Rudall P. 1999. Calcium oxalate crystals in monocotyledons: A review of their structure and systematics. *Ann Bot* 84:725–739.
- Salisbury EJ. 1927. On the causes and ecological significance of stomatal frequency with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London* 216B:1–65.
- Schmidt K, Lobin W. 1999. *Tornabenea ribeirensis* (Apiaceae)—a new species from São Nicolau, Cape Verde Islands (West Africa). *Feddes Repert* 110:7–11.
- Stace C. 1989. Plant taxonomy and biosystematics. 2nd ed. London: Edward Arnold.
- Teixeira G, Diniz MA. 2003. Contribution of micromorphology to the taxonomy of *Abrus* (Leguminosae). *Blumea* 48:153–162.