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The movement of involucral bracts of *Syngonanthus elegans* (Eriocaulaceae-Poales): Anatomical and ecological aspects

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Abstract

Syngonanthus elegans flowers are distributed in capitula whose involucral bracts open and close in a diurnal rhythm. The anatomy of these bracts was studied to understand how such movements occur and how it influences reproductive ecology of the species. The involucral bracts have a single layered epidermis composed of thick-walled cells on the abaxial surface, which are responsible for the movement. Since they are hygroscopic, these cells swell when they absorb water from the surrounding environment, causing the bracts to bend and the capitula to close. In natural conditions, the capitula open by day, when temperature increases and the relative air humidity decreases, and close at night, when temperature decreases and the relative air humidity increases. The involucral bracts may thus protect the flowers from abiotic factors, exposing them only at the time of the day when temperature is higher and insects are more active, favoring pollination by small insects. The closed capitula do not only protect the flowers, but they also function as a shelter for floral visitors as *Brachiacantha australe* (Coccinellidae) and Eumolpini sp. (Chrysomelidae). These small Coleoptera pollinate the flowers of *S. elegans* during the day and remain within the closed capitula during the night, in a possible mutualistic relationship.
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Introduction

Eriocaulaceae comprise 11 genera and about 1200 pantropically distributed species (Giulietti and Hensold, 1990; Sano, 2004). Most of this family occur in Brazilian "campos rupestres" (rocky outcrops) (Giulietti et al., 1987) found at altitudes above 900 m and characterized by herb–shrub vegetation, shallow and poor soils, high light intensity, and temperature and humidity that vary greatly throughout the day.

Eriocaulaceae are easily recognized by their capituliform inflorescences that differentiate them from the other monocotyledons (Eichler, 1875). Since these paleaceous, long-lasting inflorescences are collected and commercialized for decorative purposes, many endemic species of this family, *Syngonanthus elegans* (Bong.) Ruhland included, are at the risk of extinction (Giulietti et al., 1988; Mendonça and Lins, 2000).

The high commercial value of *S. elegans* is primarily due to the beauty of its capitula whose involucral bracts

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are longer than the flowers. Field observations showed that these involucral bracts present a daily movement that results in the capitulum opening and closing and probably influences the pollination mechanisms. Hensold (1988) has already reported such movement in involucral bracts of some species of *Paepalanthus* subgen. *Xeractis*. According to this author, it occurs because the cell walls of the abaxial epidermis are hygroscopic, causing the bracts to close over the capitulum in wet weather. Stützel (1998) has also claimed that the bracts of *Paepalanthus* subgen. *Xeractis* and *Syngonanthus* sect. *Eulepis*, that includes *S. elegans*, are hygroscopic. Nevertheless, no study on the anatomy of these bracts or the way they function has yet been carried out.

As it is intensely harvested, *S. elegans* is one of the most studied species of Eriocaulaceae. In addition to its phytochemical (Bonfim, 1993), phenological (Scatena et al., 1997), taxonomic (Parra, 1998, 2000) and anatomical aspects (Scatena and Menezes, 1995, 1996a, b; Scatena et al., 2004), seed germination and post-seminal development have also been studied (Oliveira and Garcia, 2005; Scatena et al., 1996). Recent data on the pollination biology of *S. elegans* indicate that this species is an insect-generalist, and is mainly pollinated by small insects of Coleoptera, Diptera, Hemiptera and Hymenoptera (Oriani et al., UNESP, Brazil, unpubl. res.).

The present work is an anatomical study of the involucral bracts of *S. elegans* that aims to elucidate the opening and closing movement of the capitula and its relation to the reproductive aspects of this species.

Materials and methods

This study was conducted at Parque Nacional da Serra do Cipó, Santana do Riacho district, Minas Gerais State, Brazil. The Parque Nacional da Serra do Cipó is characterized by "campos rupestres" vegetation and shelters a great number of Eriocaulaceae species (Coelho et al., 2008; Giulietti et al., 1987), including *S. elegans* that has a restricted distribution on some mountains of Minas Gerais State.

S. elegans flowers from February to June, with a peak in April (Scatena et al., 1997). Monthly scientific expeditions to the study area were conducted in the period from April to June/2005 and from February to June/2006.

In the field, the movement of *S. elegans* involucral bracts was monitored and the capitulum opening and closing times were recorded. The observations were documented with photographs taken with a digital camera (Coolpix 8700, Nikon). The variation in the frequency of flower visitors was also monitored during three non-consecutive days, in April, for two years (2005 and 2006). The number of insect visits to the capitula was recorded from 0900 to 1800 h, during 30 min per hour, by simultaneously observing two different *S. elegans* individuals each hour (Dafni, 1992). The temperature and relative air humidity were also measured once an hour with a thermohygrometer (Thermo-Hygro, ESMO). Meteorological data, recorded daily at 0900, 1500 and 2100 h, were provided by the Meteorological Station of the Parque Nacional da Serra do Cipó.

For the anatomical study, *S. elegans* inflorescences were fixed in FAA 50 (1 formalin:1 glacial acetic acid:18 50% ethanol v/v) (Johansen, 1940) and stored in 70% ethanol with a few drops of glycerin added. Vouchers were deposited in the Herbarium Rioclarense (HRCB) of the Universidade Estadual Paulista, Rio Claro (HRCB 45959).

Once fixed, capitula and detached involucral bracts were dehydrated through a normal-butyl alcohol series under vacuum (Feder and O'Brien, 1968), embedded in (2-hydroxyethyl)-methacrylate (Leica Historesin Embedding Kit), and sectioned at 4–8 μm on a microtome (Model 2040, Reichert-Jung) using disposable microtome blades. The cross sections were stained with periodic acid-Schiff's reagent (PAS reaction) and toluidine blue (Feder and O'Brien, 1968), and mounted on permanent slides using Entellan (Merck). Longitudinal sections were stained with toluidine blue (Feder and O'Brien, 1968).

Dissociation of the involucral bract epidermis was performed in a solution of glacial acetic acid and hydrogen peroxide (1:1) (Franklin, 1945). Together with some trichomes detached from the capitula, this material was stained with fuchsin and astra blue (Roeser, 1972) and mounted on semi-permanent slides with glycerin jelly. The results were documented with photomicrographs made with a photomicroscope (BX 40, Olympus) equipped with a photographic device (PM-20, Olympus).

Whole involucral bracts detached from the capitula and stained with fuchsin and astra blue (Roeser, 1972) were photographed with a stereomicroscope (MZ 125, Leica) equipped with a photographic device (MPS 30, Leica). The same equipment was used to monitor and photograph the torsion process of the capitulum trichomes.

To determine the influence of humidity on the involucral bract movement, capitula were exposed to different continuums of relative humidity in the laboratory. These capitula were placed in closed 35 ml-snapcap vials with 10 ml of a sulfuric acid solution at concentrations ranging from 5% to 60%, which resulted in different relative humidities in each vial (International Standard, 1988). The same test was repeated at different temperatures, ranging from 5 to 50 °C (International
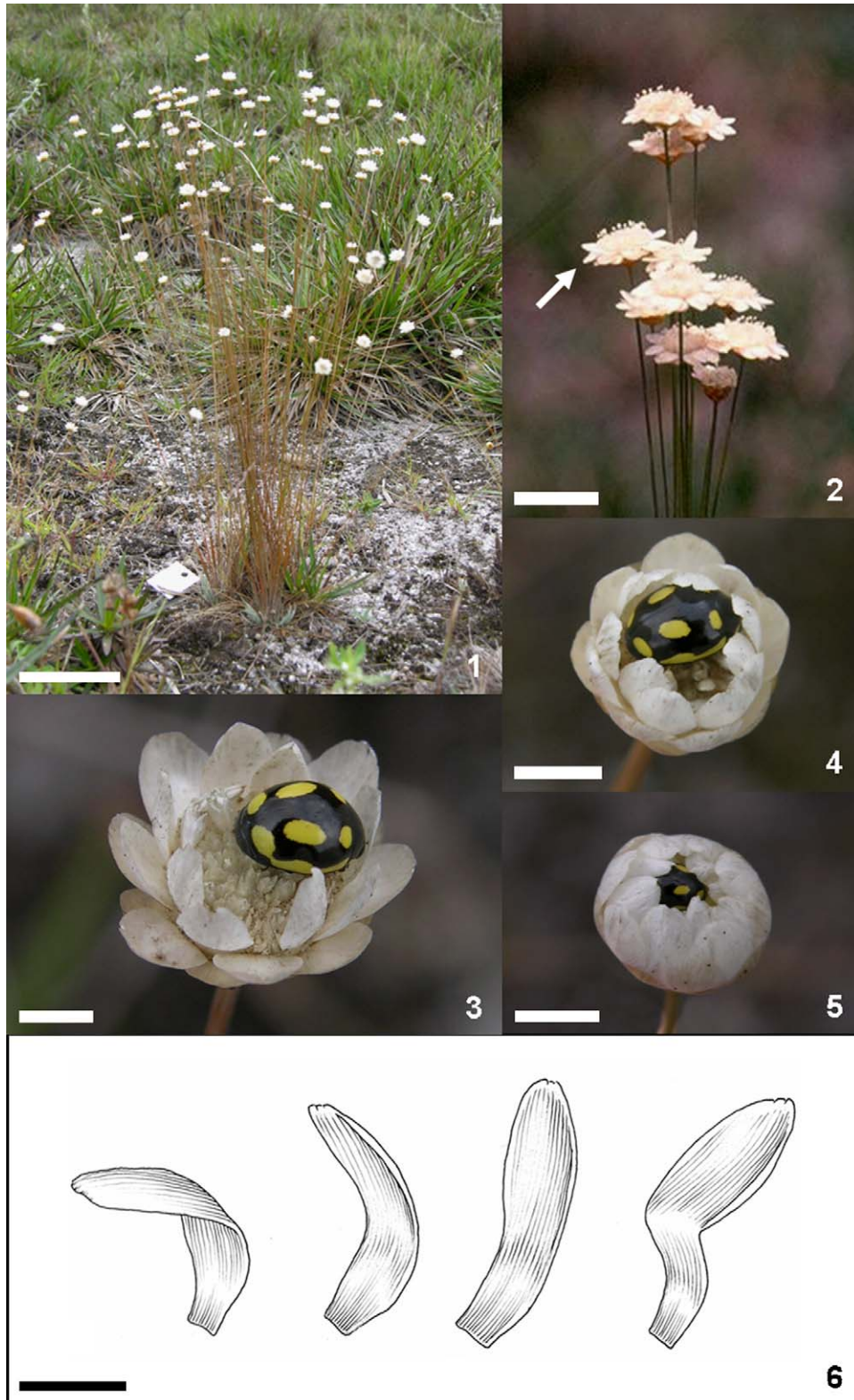
Figs. 1–6. (1) Habit of *Syngonanthus elegans*. (2) Detail of the capitulum. The arrow indicates the involucral bracts. (3–5) Closing movement of the capitulum, making a shelter for a *Brachiacantha australe* (Coccinellidae, Coleoptera) specimen. (6) Schematic representation of the movement of an involucral bract detached from the capitulum. Scale bars = (1) 7 cm; (2) 13 mm; (3–5) 3 mm; (6) 2 mm.

Standard, 1988), and in a desiccator whose relative humidity and temperature were monitored with the thermohygrometer. After 24 h, results were photographed.

Results

S. elegans is a small terrestrial herbaceous plant (Fig. 1). Fig. 2 shows details of its capitula surrounded by involucral bracts (arrow). These bracts present a daily movement, thus the capitula open in the morning (Fig. 3) and close at the end of the afternoon (Figs. 4 and 5). Details of the movement of a bract detached from the capitulum are shown in Fig. 6 with evidence that the movement occurs in the median region of the bract. This can be verified by applying water to different regions of the bract: the median region takes up water most readily and causes a response.

Fig. 7 shows the regions where the anatomical sections of the bracts were made (Figs. 8–12). In cross sections, these bracts are characterized by the presence of epidermis, parenchyma and reduced vascularization (Figs. 8–12).

The epidermis is single layered and the cells of the abaxial surface have thickened walls composed of cellulose and lignin while those of the adaxial surface have thin walls constituted of cellulose only (Figs. 8–12). The thick-walled cells of the abaxial surface present a great quantity of cellulose, mainly in the innermost layers of the secondary wall (Fig. 16). In the median region of the bracts, where movement occurs, these cells contain more cellulose in the walls than the other epidermal cells (Figs. 10, 16 and 22 – arrow). Differential staining with periodic acid-Schiff (PAS) reagent and toluidine blue (pink for cellulose and blue for lignin) confirmed the constitution of these cells (Fig. 16). Fuchsin and astra blue (blue for cellulose and pink for lignin) corroborated these results (Fig. 22).

In frontal view, the thick-walled cells of the median region of the bract (Fig. 20) also differ from the other cells of the abaxial epidermis (Fig. 17); they are shorter, wider and have a higher number of pits in their walls, what can be observed in longitudinal sections as well (Figs. 13–15). The longitudinal sections show that these cells exhibit thicker outer periclinal walls and many pits, compared to their inner periclinal walls, and swell with hydration (Figs. 14 and 15). They are also shorter, wider and thicker when compared to the cells of the adaxial epidermis (Figs. 14 and 15).

From the median to the apical region of the bract (Fig. 7, arrow), which is broader, the adaxial epidermis presents a papillate aspect in cross sections, because its cells lose their content and the outer periclinal walls become concave and collapse with the inner periclinal wall (Figs. 8–10). Details of these cells are shown in the Fig. 18. Fig. 19 shows the adaxial epidermis in the basal region of the bract, where the epidermal cell walls do not collapse.

In the mesophyll, both the number of layers of parenchymatic cells and the number of cells that constitute the vascular bundle decrease from the base to the apex of the bracts (Figs. 8–12). In the basal region of the bract, the mesophyll cells subjacent to the abaxial epidermis become thickened (Fig. 12).

Located in the capitulum receptacle and in the flower pedicels, the trichomes also contribute to the capitulum opening because they are sensitive to changes in the air humidity and curl when they lose water (Fig. 21 – arrow). These trichomes are uniseriate, multicellular and their cell walls have non-uniform thickenings in the longitudinal direction as more thickened regions alternate with less thickened regions (Fig. 23).

The results of the humidity tests are shown in Figs. 24–26. These tests confirm that water is the abiotic factor responsible for the bract movement, since the capitula open as relative humidity diminishes within the vials, irrespective of temperature (Figs. 24–26). The results also show that the hygroscopic movement occurs over a range of relative humidities and the opening of the capitula is proportional to the decrease in the humidity (Figs. 24–26). The same results were obtained with capitula placed in a desiccator where the relative humidity and temperature were controlled with a thermohygrometer.

The graphical representation of the temperature and relative air humidity mean, at different times of the day in the study area, shows that these factors varied greatly throughout the day (Fig. 29). During the five months of *S. elegans* flowering (February to June), the temperature was lower in the morning, increased during the day and diminished again by the end of the afternoon (Fig. 29a) while the relative air humidity was high in the morning, diminished during the day and increased again by the end of the afternoon (Fig. 29b), establishing a daily pattern.

In the field, accordingly to this daily variation of the relative air humidity, the capitula began to open around 0930 h and were completely open after 1030 h. They then started to close around 1800 h and were totally closed after 1900 h. Individuals of two Coleoptera species – *Brachiacantha australe* (Coccinellidae) (Figs. 3–5) and Eumolpini sp. (Chrysomelidae) (Figs. 27 and 28) – spent the night within the closed capitula.

Fig. 30 presents the variation in the frequency of flower visitors throughout the day and its relationship with temperature and relative air humidity. It shows that the number of insect visits to the capitula was higher when temperature was higher and relative air humidity was lower and that it diminished as temperature diminished and relative air humidity increased. The
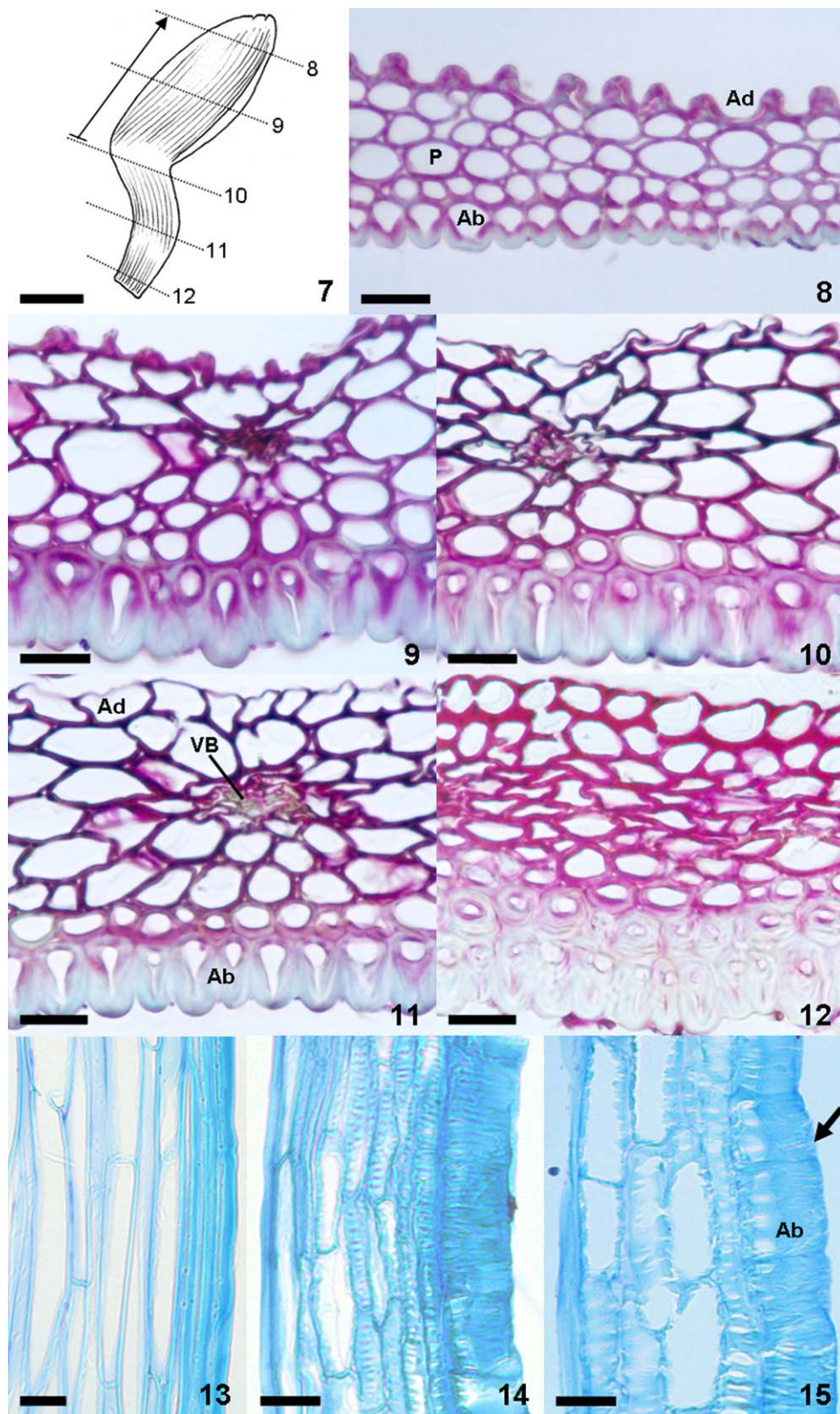
Figs. 7–15. (7) Diagram of the *Syngonanthus elegans* involucral bract showing the regions where the anatomical sections were made. The arrow indicates the broader portion of the bract, where the adaxial epidermis presents a papillary aspect in cross section. (8–12) Cross sections from the apex to the base of the bract. (13) Longitudinal section of the basal region of the bract. (14) Longitudinal section of the median region of a dried bract. (15) Longitudinal section of the median region of a wet bract. The arrow indicates the pit in the outer periclinal wall of the cell. Scale bars = (7) 1 mm; (8–15) 20 μm. Abbreviations and labels: Ab = abaxial epidermis; Ad = adaxial epidermis; P = parenchyma; VB = vascular bundle.
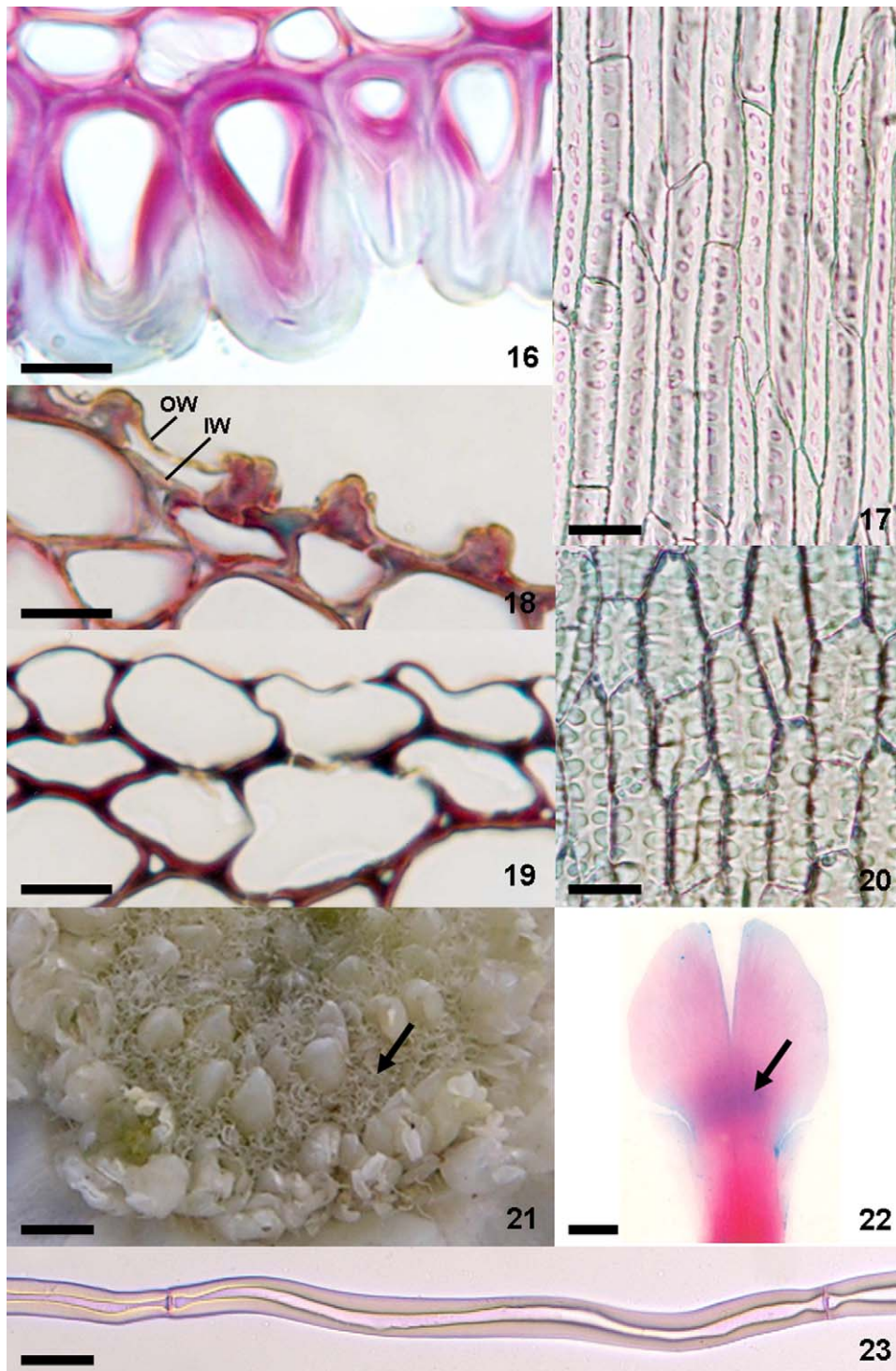
Figs. 16–23. (16) Cross section detail of the thick-walled cells of the abaxial epidermis of *Syngonanthus elegans* bracts stained with periodic acid-Schiff's reagent and toluidine blue (cellulose stained more intensely). (17) Frontal view of the abaxial epidermis (region that corresponds to number 9 in Fig. 7). (18) Cross section detail of the adaxial epidermis in the apical region of the bract. (19) Cross section detail of the adaxial epidermis in the basal region of the bract. (20) Frontal view of the abaxial epidermis (region that corresponds to number 10 in Fig. 7). (21) Detail of the capitulum. The arrow indicates the dried curled trichomes. (22) Bract detached from the capitulum stained with fuchsin and astra blue. The arrow indicates the region with higher cellulose concentration, responsible for the movement (cellulose stained more intensely). (23) Trichome detail showing the differential thickening of the cell wall. Scale bars = (16, 18–19) 10 μm; (17, 20) 20 μm; (21) 500 μm; (22) 400 μm; (23) 50 μm. Abbreviations and labels: IW = inner periclinal wall; OW = outer periclinal wall.
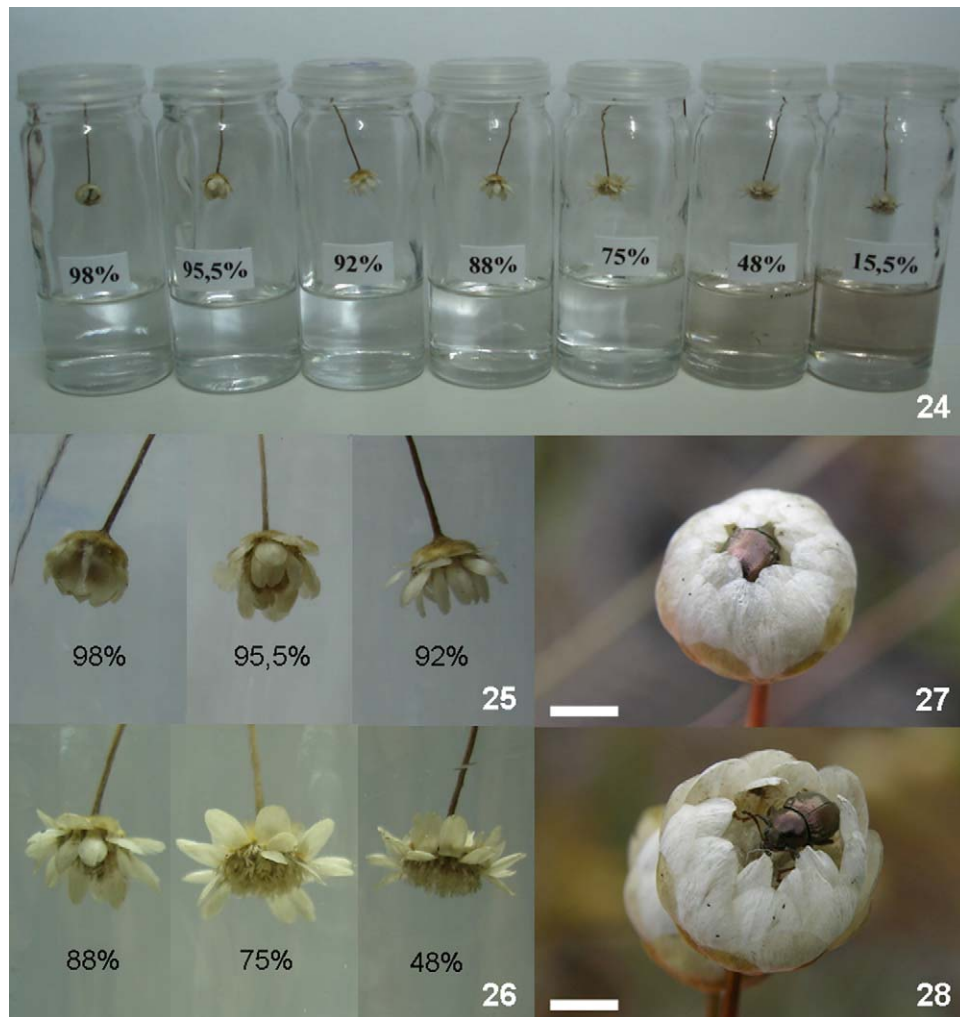
Figs. 24–28. (24–26) Effect of relative air humidity on the movement of *Syngonanthus elegans* involucral bracts. (27–28) Capitulum closing with a specimen of Eumolpini sp. (Chrysomelidae, Coleoptera). Scale bars = 3 mm.

flower visitors belonged to Coleoptera, Diptera, Hemiptera and Hymenoptera.

Discussion

The movement of the involucral bracts of *S. elegans* is influenced by air humidity due to the presence of hygroscopic cells on the bract abaxial epidermis. The thickened walls swell when they absorb environmental humidity, causing the bracts to bend. The differentiation in water-absorbing power between the abaxial and adaxial epidermis of the bracts is thus the cause of the movement.

Thick-walled cells with a great capacity to absorb water have been observed in the epidermis of reproductive structures such as bracts, sepals and pericarps (fruits), in which they are associated with seed dispersal by the imbibition mechanism (Fahn and Werker, 1972). When the walls of these cells imbibe or lose water, they, respectively, swell or shrink, which results in a bending or torsion movement of the organ. Such imbibition mechanism is also responsible for the involucral bract movement of some species of Asteraceae that grow in arid conditions (Fahn, 1947; Fahn and Werker, 1972; Gutterman and Ginott, 1994; Uphof, 1924).

In *Asteriscus pygmaeus* (Asteraceae), for instance, the heads only open when they are wet and close when dry (Fahn, 1947). This species flowers in the most humid season (winter), when the heads are open (Gutterman and Ginott, 1994). According to Gutterman and Ginott (1994), the movement of *A. pygmaeus* involucral bracts is due to the presence of a specialized tissue in the bract adaxial epidermis. In wet conditions, this tissue absorbs water and consequently swells, inducing the heads to open, while its shrinkage in dry conditions makes them close. It is the opposite of what happens to *S. elegans* and can be explained by the position of the hygroscopic cells: on the adaxial epidermis of *A. pygmaeus* bracts and on the abaxial epidermis of *S. elegans* bracts.

(a)

(b)
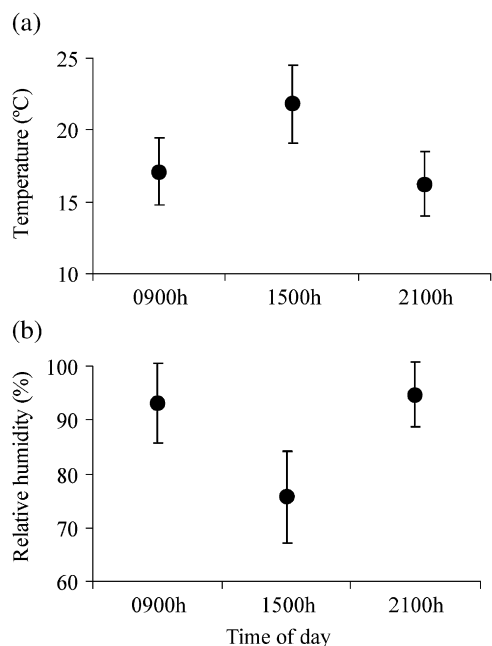
Fig. 29. Means and standard deviation of the (a) temperature and (b) relative air humidity, registered daily in the study area at 0900, 1500 and 2100 h, from February to June/2005 (data obtained by the Meteorological Station of the Parque Nacional da Serra do Cipó).

□ Insect visits   ●– Temperature (°C)   △– Relative humidity (%)
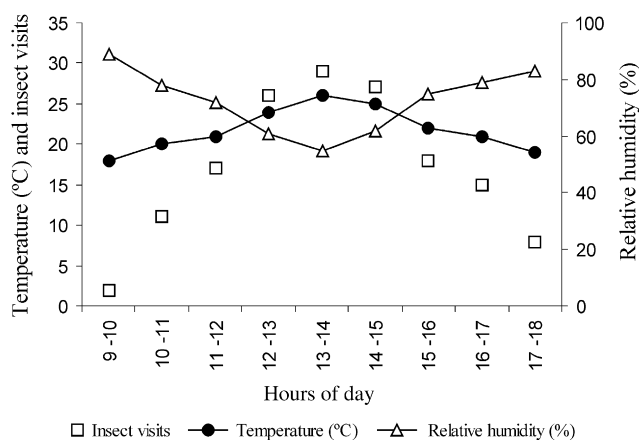
Fig. 30. Means of the temperature, relative air humidity and number of insect visits to the capitula, registered from 0900 to 1800 h along three non-consecutive days, in April, during two years (2005 and 2006).

In *S. elegans*, the frontal view of the abaxial epidermis shows that the thick-walled cells of the median region of the bract, which is responsible for the movement, are shorter, wider and have more pits in their walls than the other epidermal cells. This structural difference is probably related to their motor function.

Similar wide, short epidermal cells with many pits in frontal view are present in the leaves of *Syngonanthus* sect. *Thysanocephalus* (Scatena and Menezes, 1993) and are related to the plant response to water stress.

According to Scatena and Menezes (1993), pits are more numerous in the epidermal cells of species whose leaves curl when they lose water and less numerous in leaves that do not lose water and curl. Numerous pits favor intense water movements between cells (Scatena and Menezes, 1993), as occurs in the bracts of *S. elegans*.

According to Zimmermann (mentioned by Haberlandt, 1914), the hygroscopic movement in a cell can be explained by the orientation of cellulose microfibrils in the cell wall: the absorption of water causes the cell to enlarge in a direction perpendicular to the predominant axis of the microfibrils. In *Daucus carota* (Apiaceae), whose primary rays of umbels also present hygroscopic movement, the net microfibril orientation of the thick-walled parenchyma cells is perpendicular to the long axis of the cell; when the relative humidity rises, these parenchyma cells elongate (Lacey et al., 1983). The same is thus expected in the thick-walled cells of bracts of *S. elegans*. Nevertheless, further studies are necessary concerning their ultrastructure.

Another anatomical characteristic that supports the movement of *S. elegans* involucral bracts is the presence of cells with folded outer periclinal walls on the adaxial epidermis. The formation of wall foldings is particularly rare in plant cells and, when it occurs, it is usually associated with movement and shows the existence of particular elastic properties of the wall (Fleurat-Lessard, 1988), as is the case of *S. elegans*.

Distributed between the flowers, the trichomes also contribute to the opening and closing of *S. elegans* capitula. These trichomes are also equipped with an imbibition apparatus and are sensitive to slight humidity changes. Since their cells present heterogeneous thickening on their walls, the trichomes curl when they lose water, pushing the flowers and the involucral bracts outwards, which favors capitulum opening.

Hygroscopic movement influences seed dispersal in a number of plants (Friedman et al., 1978; Gutterman et al., 1967; Lacey, 1980). In *A. pygmaeus*, which grows in desert regions, the involucral bracts protect the fruits (achenes) against granivorous animals during the dry season and, during the rainy season, the heads open, guaranteeing that the seeds are dispersed in conditions that allow germination (Gutterman and Ginott, 1994).

As in *A. pygmaeus*, the opening and closing movement of the capitula of *S. elegans* has an ecological meaning, because the involucral bracts protect the flowers from abiotic factors and only expose them in conditions that favor pollination.

During the flowering of *S. elegans*, the capitula only open around 0930 h and close around 1800 h. Since this movement occurs daily, according to the variation of the relative air humidity, the flowers are thus protected by the involucral bracts during the night and are exposed to visitors during the day. The period when the capitula are open, that is, when the relative air humidity diminishes,

coincides with increased temperature, which is when the insects are more active so that the number of visits to the capitula is higher. This favors pollination by insects, which agrees with the data obtained in the study on the pollination biology of *S. elegans,* for which Oriani et al. (unpubl. res.), through field observations and selective exposure tests, demonstrated that pollination by diverse small insects contributes most effectively to the reproductive success of this species. In *Metrodorea stipularis* (Rutaceae), Pombal and Morellato (2000) observed a significant positive correlation between the air temperature and the number of visitors, and a significant negative correlation between the air humidity and the number of visitors, which corroborates our results.

In *S. elegans,* the movement of involucral bracts does not only influence the pollination, but the closed capitula also serve as shelter for small Coleoptera, such as *Brachiacantha australe* (Coccinellidae) and Eumolpini sp. (Chrysomelidae), which are pollinators of *S. elegans* (Oriani et al., UNESP, Brazil, unpubl. res.). During the day, they use the capitula as landing bases, copulation sites and sources of pollen and nectar. While they walk over the flowers, feed on pollen and nectar, or copulate, pollen grains become attached to the ventral region of their abdomen and to their legs, and are then left on the stigmas when they visit capitula with pistillate flowers at anthesis (Oriani et al., UNESP, Brazil, unpubl. res.). At the end of the afternoon, these Coleoptera stay on the flowers until the capitula close. Insects which stay inside flowers or inflorescences may get an energetic gain because these structures are warmer than the ambient temperature (Dafni, 2005). Since temperature diminishes drastically during the night in the study area, the closed capitula probably protect the Coleoptera against the cold. *B. australe* and Eumolpini sp. thus pollinate *S. elegans* during the day and remain protected within its capitula during the night, in a probable mutualistic relationship.

Because *S. elegans* has been intensely harvested from the wild since the 1980s, resulting in its current extinction risk, the data obtained in this work not only contribute to a better understanding of its reproductive ecology, but also highlight the importance of its management and conservation. Extinction of *S. elegans* would put at risk other species related to it through ecological interaction, such as *B. australe* and Eumolpini sp.

Acknowledgements

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