Perianth biology in the basal grade of extant angiosperms

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Abstract
Perianth structure and behavior were studied comparatively in representatives of all families of the basalmost extant angiosperms (ANITA grade plus Chloranthaceae). In addition, data from the literature were reviewed. Tepal aestivation is spiral imbricate in Amborella and Austrobaileyales, with broadly overlapping flanks; aestivation is mainly contort within each of the two tepal whorls in Cabomba (but open within each whorl and imbricate only between whorls in Brasenia) and is whorled imbricate in Nymphaeaceae. Tepals are absent in Hydatellaceae, Chloranthaceae (other than Hedyosmum), and Ceratophyllaceae. In two genera of Nymphaeales (Cabomba and Nuphar), nectaries are present on inner tepals. Tepals are caducous during or at the end of anthesis in Austrobaileyales. Preformations of the tepal abscission zone in flowers with caducous tepals include a narrow tepal base, constriction as seen in median longitudinal sections, and small-celled tissue. In contrast, the perianth organs of Amborella, Nymphaeales, and Chloranthaceae are not caducous and are associated with a broad tepal base without indentation and often without small-celled tissue. Only in the latter groups are there genera with basally united tepals (Amborella, Cabomba, and Hedyosmum).
PERIANTH BIOLOGY IN THE BASAL GRADE OF EXTANT ANGIOSPERMS

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Perianth structure and behavior were studied comparatively in representatives of all families of the basalmost extant angiosperms (ANITA grade plus Chloranthaceae). In addition, data from the literature were reviewed. Tepal aestivation is spiral imbricate in Amborella and Austrobaileyales, with broadly overlapping flanks; aestivation is mainly contort within each of the two tepal whorls in Cabomba (but open within each whorl and imbricate only between whorls in Brasenia) and is whorled imbricate in Nymphaeaceae. Tepals are absent in Hydatellaceae, Chloranthaceae (other than Hedyosmum), and Ceratophyllaceae. In two genera of Nymphaeaceae (Cabomba and Nuphar), nectaries are present on inner tepals. Tepals are caducous during or at the end of anthesis in Austrobaileyales. Preformations of the tepal abscission zone in flowers with caducous tepals include a narrow tepal base, constriction as seen in median longitudinal sections, and small-celled tissue. In contrast, the perianth organs of Amborella, Nymphaeaceae, and Chloranthaceae are not caducous and are associated with a broad tepal base without indentation and often without small-celled tissue. Only in the latter groups are there genera with basally united tepals (Amborella, Cabomba, and Hedyosmum).

Keywords: Amborellaceae, Austrobaileyales, basal angiosperms, Chloranthaceae, Nymphaeales, perianth.

Introduction

The basal grade of extant angiosperms, the ANITA grade (Qiu et al. 1999), consists of Amborella, Nymphaeales, and Austrobaileyales. In some phylogenetic analyses, Chloranthaceae and Ceratophyllaceae immediately follow the ANITA grade as the next step, still below the remainder of the angiosperms (Doyle and Endress 2000; Qiu et al. 2005, 2006; Duvall et al. 2006; Mathews 2006; Endress and Doyle 2008). Although the position of Chloranthaceae and Ceratophyllaceae is not yet settled (for other positions, see Jansen et al. 2007; Moore et al. 2007), I also include them in this study.

The perianth is a basic part of the flowers of the crown group of angiosperms (for which the name Angiospermae was proposed; Cantino et al. 2007) and may even be much older (Doyle 2008). The perianth in the basalmost extant angiosperms has diverse functions. It plays a role in the protection of flower buds and, in some cases, also of fruits, often in optical attraction of anhetic flowers, exceptionally in nectar production. To what extent perianth organs, together with other floral organs, are specifically involved in scent production and thermogenicity is largely unexplored (Thien et al. 2000; Yuan et al. 2008).

The flowers of all families of the ANITA grade have a perianth, except Hydatellaceae, a long-neglected family that has been moved from the monocots to Nymphaeales as sister to the remainder of the order (Saarela et al. 2007). The flowers of Hydatellaceae are minute and extremely simple (Hamann 1975, 1976; Rudall et al. 2007), and anthesis is, at least in part, underwater (Edgar 1966). In Chloranthaceae, only the female flowers of Hedyosmum have a perianth. In Ceratophyllaceae, a perianth is lacking if the whorl of phyllomes around a female or male flower is not regarded as a perianth (discussion in Endress 1994b); furthermore, it is not clear whether the male flowers are real flowers or rather inflorescences with unistaminate flowers (Endress 2004)—in the latter case, a perianth would be missing anyway.

Perianth phyllotaxis is diverse (Endress and Doyle 2007): spiral in Amborella (Endress and Igersheim 2000) and Austrobaileyales (Endress 1980b, 1983, 2001; Endress and Sampson 1983; Tucker and Bourland 1994) and largely whorled in Nymphaeaceae (Endress 2001; Schneider et al. 2003). Diverse phyllotaxis patterns commonly appear to be functionally linked with different aestivation patterns in angiosperms. However, aestivation has been little studied in basalmost angiosperms. Therefore, aestivation and potential correlations with phyllotaxis are addressed here.

Perianth abscission, although a topic of much interest in horticulture with regard to the longevity of flowers (e.g., van Doorn 1997, 2001), has been little studied by plant systematists and morphologists interested in the diversity of angiosperms. The perianth of flowers may fall off during or after anthesis, it may stay and even grow further (especially green organs), or it may simply dry out or rot after anthesis without abscising. Interest in the process of abscission or dehiscence of organs in general in plants has also grown, especially with regard to crop plants in agriculture (Addicott 1982; Roberts et al. 2000, 2002; Leslie et al. 2007), with a focus on fruit dehiscence in the model plant Arabidopsis (Gu et al. 1998; Liljegren et al. 2000; Rajani and Sundaresan 2001; Child et al. 2003; Dinneny and Yanošky 2005; Dinneny et al. 2005). However, in these works, floral organ abscission has been tackled less extensively than fruit abscission (Li et al. 2006) or dehiscence (Stenvik et al. 2006). Some of the basalmost angio-
sperm families are characterized by caducous perianth organs (Endress 2004). The genus *Piptocalyx* (Trimeniaceae) even owes its name to this behavior (“falling calyx”). In other groups, tepals are persistent even in fruit. Thus, presence or absence of early or late perianth organ abscission will be explored, studying morphology and histology of the tepal base, especially the site where the tepal abscises from the floral base.

In basal angiosperms, nectaries, if present, are on perianth organs (Nymphaeales and Magnoliidae) or on stamens and staminodes (Laurales). In the basalmost extant angiosperms, floral nectaries are known from only two genera of Nymphaeales (*Cabomba* and *Nuphar*; Bernardello 2007). They are located on perianth organs. However, they were found to be different histologically and were therefore interpreted as non-homologous (Vogel 1998). More comparative studies are necessary.

A long-standing question is whether outer sepaloid organs and inner petaloid organs in basalmost (and also in other basal) angiosperms are homologous with sepals and petals in eudicots. This question will not be addressed here in any detail. The neutral term “tepals” will be used for all perianth organs. This article integrates new results and current knowledge on the perianth structure and behavior of basalmost angiosperms.

**Material and Methods**

The following species and collections were studied (abbreviations: BGZ = cultivated, Botanical Garden of the University of Zurich; PKE = collected by Peter K. Endress).

**Amborellaceae**

*Amborella trichopoda* Baill.; male flowers, Hugh S. McKee 38907, New Caledonia (figs. 1A, 2A, 3A, 5C; fig. 7A, 7B); female flowers, Hugh S. McKee 38909, New Caledonia (figs. 3B, 5D; fig. 7C, 7D); male flowers, raised from seeds received from Hugh S. McKee, BGZ (fig. 5A, 5B); female flowers, cultivated, Santa Cruz Botanical Garden (received by Hiroshi Tobe; fig. 5E).

**Cabombaceae**

*Brasenia schreberi* J.F. Gmel.; Rolf Rutishauser, s.n., July 2001, Ontario, Canada (fig. 3D; fig. 7G, 7H).

*Cabomba caroliniana* A. Gray; PKE 9841, BGZ (fig. 7E, 7F; fig. 9B, 9C); PKE s.n., cultivated, Botanic Garden, University of Basel (figs. 1G, 9A); PKE 07-02, cultivated, Botanic Garden, University of Basel (fig. 2B); PKE 06-05, cultivated, Botanic Garden, University of Basel (figs. 3C, 9D).

*Cabomba furcata* Schult. & Schult. f.; PKE 00-58, cultivated, Zurich (commercial plants; fig. 1B).

**Nymphaeaceae**

*Euryale ferox* Salisb.; PKE, s.n., BGZ (fig. 1D).

*Nuphar advena* Aiton; PKE 07-07, BGZ (fig. 9B, 9C).

*Nuphar pumila* (Timm) DC.; PKE 07-14, BGZ (figs. 3E, 9D).

*Nymphaea tetragona* Georgi; PKE 96-45, BGZ (fig. 2C); PKE 01-16, BGZ (fig. 7F, 7J); PKE 07-31, BGZ (fig. 3F).

*Victoria cruziana* A.D. Orb.; PKE, s.n., BGZ (fig. 1E).

**Austrobaileyaceae**

*Austrobaileya scandens* C.T. White; PKE 4218, Boonjee, Northern Queensland, Australia (fig. 4A); PKE 4265, Boonjee, Northern Queensland, Australia (figs. 1F, 2D; fig. 8A, 8B); raised from seed of PKE 9083, Mt. Lewis, Northern Queensland, Australia, BGZ (fig. 5F–5K).

**Trimeniaceae**

*Piptocalyx moorei* Oliv.; PKE 4005, New South Wales, Australia (figs. 4C, 8F–8H); PKE 4367, New South Wales, Australia (fig. 5L–5N).

*Trimenia neocaledonica* Baker f.; PKE 6316, New Caledonia (fig. 5O).

*Trimenia papuana* Ridl.; PKE 4066, Papua New Guinea (figs. 2E, 8C–8E); John S. Womersley s.n., September 1970 (received by F. Bruce Sampson; fig. 4B).

**Schisandraceae**

*Kadsura japonica* Benth.; PKE s.n., BGZ (figs. 1G, 4E); PKE 4530, BGZ (fig. 2F).

*Schisandra chinensis* Baill.; PKE 99-29, BGZ (fig. 8I–8K); PKE 99-32, BGZ (fig. 4D).

*Schisandra grandiflora* Hook.f. & Thomson; male flowers, PKE 7331, BGZ (not figured).

**Illiciaceae**

*Illicium anisatum* L.; PKE, s.n., cultivated, Isole di Brissago, Switzerland (fig. 1H); PKE 930, cultivated, Isole di Brissago, Switzerland (figs. 2G, 4F, 8L–8N).

**Chloranthaceae**

*Hedyosmum bonplandianum* Humb., Bonpl. & Kunth; PKE 97-103, Costa Rica (fig. 6A, 6B).

*Hedyosmum costaricense* W.C. Burger; PKE 97-106, Costa Rica (fig. 6C).

*Hedyosmum cf. racemosum* (Ruiz & Pav.) G. Don; female flowers, Jürg Schönberger 482, Bolivia (fig. 4G).

Flowering material, fixed in 70% ethanol or FAA, was used for LM and SEM studies. For serial microtome sectioning, the material was embedded in Kulzer’s Technovit 7100 (2-hydroxyethyl methacrylate) and sectioned at 5–10 μm thick. The sections were stained with ruthenium red (Trimeniaceae) even owes critical-point dried, sputter-coated with gold, and studied at 20 kV with a Hitachi S-4000 scanning electron microscope.

**Results and Comparative Analysis**

Tepal Aestivation and Differential Size in Bud (Figs. 1–5)

Amborella. Tepal aestivation in bud is imbricate, following a Fibonacci spiral phyllotaxis pattern. The overlapping parts of the tepals are broad. The margins are two cell layers thick...
for a short distance. The size of the tepals increases from the outer to the inner ones. Thus, only the inner tepals are efficient protective organs in advanced buds (figs. 1A, 2A, 5B).

**Nymphaeales.** Tepal aestivation is imbricate based on a whorled phyllotaxis. The outermost organs are the largest in bud and cover all the subsequent ones (fig. 1B–1E; fig. 2B, 2C). Among Cabombaceae, in *Brasenia*, the three tepals of the outer whorl and the three tepals of the inner whorl have an open aestivation, but the tepals of the outer whorl partly cover those of the inner whorl; only the median parts of the tepals of the inner whorl remain uncovered (fig. 3D). All uncovered areas of the six tepals have a dense carpet of mucilage-producing hairs, so the bud is completely surrounded by mucilage (fig. 3D). In *Cabomba*, both whorls of tepals are

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imbricate. They are either contort or with one organ inside and one outside. A cover of hairs is present in young buds (fig. 1B) but later is no longer obvious (fig. 3C). However, this may also be different from species to species (Warner et al. 2008). The tepals of the inner whorl are conspicuously delayed in bud (fig. 1B). Although the tepals are thin in both genera, the flanks do not flare out into two-cell-layered margins. Among Nymphaeaceae, in Nymphaea, the outer four tepals are imbricate, and in the region where they overlap, they are postgenitally connected so that they provide a firmly closed envelope for the inner floral organs (fig. 3F). The mechanism of coherence of the contiguous surfaces of neighboring tepals is not by cellular or cuticular interdentation, but they appear to be glued together by secretion. Also, the surfaces of the subsequent four tepals are stuck to the outer four to some degree. In Nuphar, the flanks of the outer tepals are at least appressed to each other (fig. 3E). In Victoria (and Nymphaea), at the time the perianth organs are initiated, the flower is more developed on the abaxial side than on the adaxial side and thus is somewhat incurved. Thus, the outer (abaxial) tepal appears first and, as a result, later covers the other four. The outer four tepals can be interpreted as forming one whorl of four or two whorls of two tepals each but with a unidirectional development. In the following, they will be described as forming one whorl.

**Austrobaileyales.** Tepal aestivation is imbricate, following a Fibonacci spiral phyllotaxis pattern. The tepals have very wide overlapping areas (figs. 1F, 4A). They are not stuck together by their surfaces. The size of the tepals increases from the outer to the inner ones. In Austrobaileya, the outermost ones are very small and bractlike (fig. 1F). The broad flanks of the inner ones are only two cell layers thick. In Trimenia, the outermost tepals are bractlike (fig. 5L, 5O) and are formed pronouncedly earlier than the inner organs; they are smaller than the inner ones (fig. 4C). In Schisandraceae and Illiciaceae, the outer tepals are also smaller than the inner ones. In both families, the inner tepals may have thin margins (two cell layers thick). Thus, in Austrobaileyales, only the middle or the inner tepals are efficient protective organs in later floral bud stages.

**Chloranthaceae.** In Hedyosmum female flowers, the three tepals are small, and aestivation is more or less valvate (figs. 4G, 6A–6C). At the flanks, they are more than two cell layers thick.
Amborella. The perianth is inconspicuous (whitish-cream). In male flowers, the nine to 11 tepals soon become reflexed and are more or less covered by the spreading stamens so that they are not easily visible from above (fig. 5A–5C). In female flowers, the seven or eight tepals are more exposed because the carpels are more upright (and there are fewer carpels than there are stamens in the male flowers; fig. 5D, 5E); the inner five tepals appear in series (Endress 2001). The upper surface of the inner tepals is irregularly papillate, and this layer is full of tannins in bud (fig. 7B, 7D).

Nymphaeales. In Cabombaceae, there are two trimerous whorls (rarely dimerous in Cabomba) of spreading white, yellow, or purple tepals, all six of similar size (fig. 1C). Histology of the outer and inner tepals is similar (except for the nectariferous area of the inner ones in Cabomba; fig. 3C). In Cabomba, the upper surface of the thin tepals is papillate (but not the lower). In Brasenia, instead of having a simple papillate epidermis, the upper surface is covered with spherical (roundish) tricellular hairs. In Nymphaeaceae, the tepals are in several commonly tetramerous whorls (rarely trimerous or pentamerous whorls; Conard 1905; Schneider et al. 2003); tepal number of the inner whorls is increased by double positions (Endress 2001) and is from four to eight in forms of Ondinea, up to more than 50 in Nymphaea, and more than 70 in Victoria (Schneider and Williamson 1993). They are spreading (upright in Nuphar). The tepals of the outermost whorl are commonly green, and all other ones are white, yellow, pink, red, blue, or purple. In bud, the outermost tepals cover all the inner ones. In Nuphar, the tepal areas exposed in bud are green, and the covered areas are yellow (Warner et al. 2008). In some Hydatellaceae, at first sight, the reproductive organs

Fig. 3 Transverse sections of perianth in bud (Amborella, Nymphaeales). A, Amborella trichopoda, male flower. B, Amborella trichopoda, female flower. C, Cabomba caroliniana. D, Brasenia schreberi. E, Nuphar pumila. F, Nymphaea tetragona. Scale bars = 0.5 mm.
look like flowers with a dimerous perianth in two whorls. However, these are inflorescences with four bracts; in some species, there is only one pair, or there are more than two pairs of bracts (Cooke 1987). A perianth is missing. The bracts cover the flowers in bud, although they grow to their full length relatively late (Rudall et al. 2007).

**Austrobaileyales.** Austrobaileyaceae have the largest flowers of all families in the order (fig. 5F–5K). The 19–24 tepals are greenish-yellowish, sometimes with brown spots. The outermost organs are green, small, and decussate. They gradually change to colored and larger and spiral toward the inside (Endress 1980b; fig. 1F). The inner tepals have a papillate epidermis on both sides, with the papillae unexpectedly more developed on the lower surface; the outer tepals are not papillate. Trimeniaceae have very small flowers with an inconspicuous perianth of two to 38 brownish tepals (Endress and Sampson 1983; fig. 5L, 5O); the optically attractive organs are mainly the stamens. The outer tepals are smaller than the inner ones (Endress and Sampson 1983). The inner tepals are slightly papillate on the upper surface. Illiciaceae flowers have relatively large tepals of various shape, number (seven to 33), and color (white, cream, pink, red, or purplish; Saunders 1995; fig. 1H). The outer tepals are smaller than the inner ones. In the inner tepals, the epidermis of the upper surface is papillate. In Schisandraceae, tepal number and shape vary somewhat less than in Illiciaceae. The five to 20 tepals are commonly white, cream, or red (Saunders 1998, 2000, 2001; fig. 1G). The outer tepals are smaller than the inner ones. The inner tepals have shallow papillae on both surfaces and the outer tepals slightly on the upper surface (*Schisandra grandiflora*), or the inner tepals have papillae only on the upper surface (*Kadsura japonica*). In some species of Schisandraceae and Illiciaceae, the small, outermost tepals are permanently green.

**Chloranthaceae.** In the wind-pollinated *Hedyosmum*, the minute tepals are green and inconspicuous (fig. 6A).
Behavior of the Tepals through Anthesis: Persistence and Caducousness of Tepals (Figs. 5, 6)

Amborella. The tepals are basally united and tear apart when the flower opens. Anthesis takes 4–5 d in male flowers (Thien et al. 2003). Tepals do not abscise during anthesis or at the end of anthesis. Male flowers fall off as a whole after anthesis (see also Thien et al. 2003). In female specimens, the tepals may persist up to the fruiting stage, as found in herbarium specimens (although Thien et al. [2003] state that they abscise 1–2.8 d after anthesis). The perianth is inconspicuous, and it simply dries out after anthesis. The tepals have a broad base, and during anthesis, they successively recurve, so they cannot be seen in their full extent when the flowers are viewed from above (fig. 5A–5E).

Nymphaeales. The perianth parts have a broad base. In many species, they make movements during anthesis. They open, close again, and reopen in a diurnal rhythm. At the end of anthesis, they finally close (fig. 1C). Among Cabombaceae, in Brasenia, the flowers last 2 d. They withdraw underwater after the female phase to reappear the following morning when the pollen is shed, and finally, they are withdrawn again (Tokura 1937; Osborn and Schneider 1988). In Cabomba, all tepals are united at the base. The same imbibition pattern they had in bud is attained again when the flower closes. In Cabomba caroliniana, the flowers last 2 d. They close in the afternoon on both days (Schneider and Jeter 1982). Closed flowers lie close beneath the surface of the water, the bud being elevated 1–4 cm above the surface just before anthesis. Among Nymphaeaceae, Nuphar has mostly five or six thick tepals (Nuphar polysepala nine to 12; Padgett 2007). The area that was exposed in bud is green; the area that was covered in bud is yellow (studied in detail by Warner et al. [2008]). In Nuphar lutea, the flowers close at night (Heslop-Harrison 1955a); the tepals are persistent. In Nymphaea, there are day-flowering species, in which flowers close at night and during unfavorable weather (Heslop-Harrison 1955b; Meeuse and Schneider 1980; P. K. Endress, personal observation). Some tropical Nymphaea species are night flowering, and they are open at night and closed during the day during two to four consecutive days (Schmucker 1932; Prance and Anderson 1977). Tepals are more or less persistent and enclose the developing fruit (Heslop-Harrison 1955b; P. K. Endress, personal observation). Fruit ripening takes place below water (Wood 1959), where tepals become entirely or partially putrescent, leaving transverse scars of attachment on the fruit walls when shed (Heslop-Harrison 1955b). The same pattern of diversity, day flowering and night flowering, is also exhibited by the closely related Euryale and Victoria. Euryale flowers are open during the day and closed at night over 2 d or, more often, are cleistogamous (Kadono and Schneider 1987). In Victoria, a flower emerges and opens in the evening and closes later on the same night during two consecutive nights, and after anthesis, it becomes submerged again (Gessner 1960; Valla and Cirino 1972; Prance and Arias 1975). In general, the fruits of most Nymphaeaceae appear to develop underwater, covered by the persistent perianth. There, the perianth parts and stamens slowly rot. Exceptions are at least some of the species of Nuphar, in which the fruits develop above water and the perianth parts slowly become dry (Heslop-Harrison 1955a). However, in Nuphar pumila, the flowers go back underwater after anthesis (P. K. Endress, personal observation).

Austrobaileyales. In Austrobaileyaceae, the perianth organs, stamens, and staminodes remain for the duration of

Fig. 6 Female structures of Hedyosmum (Chloranthaceae). A, Hedyosmum bonplandianum, female inflorescence. B, Hedyosmum bonplandianum, young fruit with persistent tepals. C, Hedyosmum costaricense, young fruit with persistent tepals. Scale bars = 0.5 mm.
anthesis and then fall off. On days 1 and 2, the flower is in the female phase: the yellow gynoecium in the center is presented. Later, in the male phase, the gynoecium is covered by the brown inner staminodes, and pollen is presented. On day 10 (or earlier), perianth and androecium have fallen. However, the smallest, outermost green tepals are persistent (fig. 5F–5K). The base of the tepals is very narrow, except for the persistent outermost tepals. Among Trimeniaceae, in *Trimena*, the perianth organs fall off when the flower opens or during anthesis (fig. 5L–5O). The stamens fall off right after anthesis. The attachment area of the tepals is narrow and thin. Thus, anthetic flowers commonly do not retain their tepals (or at least not all of them). In *Piptocalyx moorei*, in bisexual flowers, the female phase lasts 3–5 d, and the tepals fall off in the subsequent male phase (Bernhardt et al. 2003). Because the tepals are present only in the floral buds and the female phase of anthesis and are absent in the male phase, their role in floral attraction is lacking or minor. Tepals and stamens in SEM micrographs of early anthetic flowers of Trimeniaceae typically appear overexposed because of charging as the abscission process has already started and the organs are only loosely attached at this stage (fig. 5M, 5N). In contrast to *Austrobaileya*, the outermost organs also have a very narrow attachment region, and they fall off. In Illiciaceae and in the female flowers of Schisandraceae, the tepals fall off after anthesis, whereas male flowers of Schisandraceae fall off in their entirety. If the outermost tepals are very small (this is the case in certain species of both families), they may also persist longer,

as in Austrobaileyaceae. The tepal base in both Schisandraceae and Illiciaceae is also narrow.

**Chloranthaceae.** Tepals are present only in female flowers of *Hedyosmum*. They cover the large developing stigma in bud. They are basally united and form a short tube, which at anthesis surrounds the style or base of the stigma. After anthesis, the stigma breaks off. The three tepals are persistent (fig. 6B, 6C; Endress 1971; Todzia 1988). The persistent floral bracts become fleshy and attractive for animal dispersal (Todzia 1988). It is uncertain whether parts derived from the tepals may also have a similar function in some species (Endress 1973). In some fossil Early Cretaceous fruits of *Hedyosmum*, the three tepals are still present (Friis et al. 1994, 2000, 2006).

**Morphology and Histology of Tepal Base in Relation to Caducousness or Persistence (Figs. 7, 8)**

Amborella. In *Amborella*, outer and inner tepals of both male and female flowers do not have a specially differentiated base. There is no basal indentation and no small-celled abscission tissue (fig. 7A–7D).

**Nymphaeales.** Cabombaceae and Nymphaeaceae studied here do not have any special morphological or histological differentiation at the base of the tepals (fig. 7E–7F). There is no indentation and no especially small-celled tissue.

**Austrobaileyales.** In Austrobaileyales, which all have abscising tepals, the situation is different. In *Austrobaileyia*, the tepals have morphologically a medianly constricted base and histologically smaller-celled tissue. In the outermost tepals, which do not abscise after anthesis, this differentiation is not present (fig. 8A, 8B). In Trimeniaceae, with their early caducous tepals, the differentiation of the tepal base is most conspicuous. The tepals have a long dorsal projection ("spur"), and the abscission tissue is very small-celled. This dorsal spur may expedite the abscission process, when the flower opens and the tepals spread. The spur is more developed on the outer tepals than on the inner tepals (fig. 8C–8H). In Illiciaceae, there is also a constriction of the tepal base, and the abscission tissue is also small-celled (fig. 8L–8N). In Schisandraceae, with its unisexual flowers, a constriction is present in female flowers (fig. 8I–8K). However, in male flowers of *K. japonica*, a constriction is lacking. This is not surprising because the male flowers fall off as a whole after anthesis.

**Chloranthaceae.** In Chloranthaceae, in which only the female flowers of *Hedyosmum* have a perianth and the three tepals are persistent in extant species, there is no articulation at the base of the tepals. A false impression of articulation may occur in paramedian sections, in which the area of the peculiar windows on the inferior ovary is sectioned (for an analysis of the windows, see Endress 1971).

**Presence of Nectaries on Tepals (Fig. 9)**

Among the ANITA grade, floral nectaries are known from only two genera in Nymphaeales, *Cabomba* (Cabombaceae) and *Nuphar* (Nymphaeaceae). In *Cabomba*, the tepals of the inner whorl differ from the outer ones in having nectaries on a curved appendage on both sides of the base of the blade (fig. 9A, 9B). The nectariferous area is further conspicuous by its yellow coloration. The nectaries are formed by cytoplasm-rich mesophyll and special short hairs through which nectar appears to be released (fig. 9C, 9D). The hairs are multicellular but have extremely short basal cells that look like a stack of coins. This type of hair is common in Nymphaeales (Chifflet 1902) and other members of the ANITA grade (Endress 2001) and is very versatile in its position and function. Such hairs are also present and prominently developed in the family Hydatellaceae (Hamann 1975; Rudall et al. 2007), both in the vegetative region, where they can produce mucilage, and on carpels, where they function as stigmatic hairs (Hamann 1975; Rudall et al. 2007).

In *Nuphar*, the nectaries are situated on inner tepals that have sometimes been called "petals" (Hiepko 1965). These organs are small, about the size of stamens, and spathulate. The nectaries form a dark yellow round area in the middle of each organ on the dorsal side (fig. 9E, 9F; Heslop-Harrison 1953). The organs are thick, and the mesophyll and epidermis are rich in cytoplasm. The epidermis of the nectary consists of tall cells, as in an epithelium. In contrast to that of *Cabomba*, the nectary is devoid of hairs but has conspicuous nectar pores (fig. 9G–9I). It would be interesting to know whether nectar is produced only by the mesophyll and released through the nectar pores or whether it is also secreted by the epithelial epidermis.

**Discussion**

**Tepal Phyllotaxis**

Floral phyllotaxis in basalmost angiosperms was comparatively studied and discussed by Endress (2001) and Endress and Doyle (2007). Here some additional aspects on tepal phyllotaxis will be brought into the discussion.

Tepal phyllotaxis in *Amborella* is spiral (Endress and Igersheim 2000; Endress 2001). Buzgo et al. (2004, p. 943) consider "the difference between spiral and whorled phyllotaxy in *Amborella* to be gradual." In all angiosperms, the spiral and whorled patterns are two distinct, clear-cut patterns. What is flexible, however, is that the two patterns can switch between each other relatively easily in some clades (but not in *Amborella*, where floral phyllotaxis is always clearly spiral; Endress and Igersheim 2000). In *Amborella*, in a lateral flower of an inflorescence (which is a botryoid or double botryoid, often with accessory flowers; Endress and Igersheim 2000; Poslusnzy and Tomlinson 2003), the first two organs are transverse and in normal prophyll position, and the following organs adjust into a Fibonacci spiral. This is the most common pattern in spiral angiosperm flowers and also in the calyx of lateral pentamers. Core eudicot flowers; in core eudicots flowers have a spiral onset in the calyx, but otherwise, they are whorled (e.g., Breindl 1934; Endress 1987b). Thus, *Amborella* behaves in no way differently from less "basal angiosperms" in the phyllotaxis of the outermost floral organs. In a terminal flower of a botryoid of *Amborella*, tepal phyllotaxis is spiral, beginning with the outermost perianth organs, which continue the spiral of the bracts on the inflorescence axis.

Phyllotaxis of perianth organs in Nymphaeales is basically whorled (Endress 2001; Schneider et al. 2003). In *Nuphar*, the onset of tepal initiation may be in a spiral sequence. However, if there are six tepals, the final position of the tepals, i.e., their
divergence angles, follows a whorled pattern (Endress 2001). Initiation of the tepals in Nuphar and Nymphaea was described in several studies (Cutter 1957, 1961, 1966; Chassat 1962; Grob et al. 2006).

Floral phyllotaxis in Austrobaileyales is spiral throughout (Endress 2001). In contrast to Amborella, in Austrobaileyaceae and Trimeniaceae, the vegetative phyllotaxis is not spiral but decussate (i.e., forming dimerous whorls). At the onset of a terminal flower, the outermost, smallest organs (bracts) are decussate, with a short transition zone to spiral (Austrobailey [fig. 3; Endress 1980b], Trimenia [fig. 7; Endress and Sampson 1983]). However, this does not mean that there is a gradual difference between whorled and spiral phyllotaxis. It means only that there is a short transitional zone where they switch between each other and that the two patterns are completely distinct. A similar switch was shown in detail in flowers of Calycanthaceae (eumagnoliids, Laurales; Staedler et al. 2007). The distribution of perianth organ phyllotaxis patterns in the component clades of basal extant angiosperms makes the basal state for the crown group equivocal (Endress and Doyle 2007).

_Tepal Aestivation and Floral Bud Protection with Regard to Phyllotaxis_

Protection of the young floral organs in bud is different in flowers with spiral and whorled perianth phyllotaxis among basalmost extant angiosperms. In Amborella and all Austrobaileyales with spiral perianth phyllotaxis, the outer tepals are smaller than the inner ones and become gradually larger (Endress 2004; fig. 3). This results in a staggered disposition of the tepals in bud, and the periphery of the advanced floral bud is formed by a larger number of tepals. The smaller the outer ones, the higher their number. In early development, the outermost tepals cover the floral apex, but because they do not grow much, this function gradually is taken over by larger inner tepals.

In contrast, in Nymphaeales, which have whorled perianth phyllotaxis, the outer tepals are the largest ones, and they completely cover all inner ones in bud. Thus, the periphery of the bud is made up by only the tepals of the outermost whorl (fig. 1D, 1E; Meusel and 1965; Endress 2001, 2004). In Nymphaeales, the floral buds develop underwater, emerging from the water only shortly before anthesis. In the female flowers of Hedysomum (Chloranthaceae), the short perianth covers the stigma in bud, and the young flowers are protected by the subtending bract. In the other three genera of Chloranthaceae, the youngest stages of the perianthless flowers are completely covered by their subtending bract, which forms a kind of sheath around each flower (Endress 1987a; von Balthazar and Endress 1999). Male flowers of Hedysomum lack not only a perianth but also a subtending bract. The naked stamens protect each other in bud with their shieldlike, sterile apical portion (Endress 2008).

_**Interpretation of Floral Fossils**_

The results of this study have implications for the interpretation of floral fossils. An example is Microvictoria from the Upper Cretaceous, which was placed in a clade with Victoria, Euryale, and Nymphaea (Gandolfo et al. 2004; reconstruction in Crepet et al. 2004). (1) The phyllotaxis of the androecium is spiral in the fossil, which is not the case in extant Nymphaeales (it is whorled, as in the perianth, or may become irregular in the inner whorls when there is a large number of stamens, which is not the case in the fossil; Endress 2001; Schneider et al. 2003), and (2) the position of the tepals is staggered, as in those ANITA-grade plants with spiral phyllotaxis and not as in Nymphaeales. In some Nymphaeaceae (Nymphaea), the attachment areas of the rotten tepals may become staggered in fruit by the growth of the inferior ovary, but they are closer together in flower (see figures in Conard 1905). However, the described fossil of Microvictoria does not represent a fruit but a flower bud because there are no developing seeds apparent. In Nymphaeales (Cabombaceae and Nymphaeaceae), even if not all perianth organs are inserted at the same level, the outermost organs are always the longest and enclose all upper ones in bud. This is the case even in Barclaya, in which the outermost tepals are inserted at the base of the flower (Winter 1993; Williamson and Schneider 1994).

Further, the nature of the less well-preserved center of the flower as a gynoecium or a sterile structure not homologous with a gynoecium (the latter favored by Gandolfo et al. [2004]) is unclear but would be important for an interpretation of the flower. According to the interpretation of Gandolfo et al. (2004), the ovary is inferior. However, an inferior ovary is not visible, and from the shape of the flower bud, which is tapering downward in the attachment zone of the floral organs (in contrast to extant Nymphaeaceae; fig. 1E), the presence of an inferior ovary is unlikely.

These features indicate that the position of Microvictoria is most likely not with Nymphaea and related genera (Victoria, together with Euryale, appears to be nested in Nymphaea or at least sister to Nymphaea; Borsch et al. 2007; Löhne et al. 2007) and not even with Nymphaeales. Another argument for a different position of Microvictoria is that the split between Victoria/Euryale and Nymphaea was calculated at 19.6–11.5 million years ago (Yoo et al. 2005), which is much more recent than the Turonian (90 million years old) Microvictoria. Thus, a structural reevaluation of Microvictoria will be necessary for a new cladistic analysis.

In general, the perianth is sometimes the most difficult part to reconstruct in fossil flowers because it often is the least well-preserved part (Schönenberger 2005) or is not preserved at all. If scars of outer organs are still present, then at least the phyllotaxis can be reconstructed, such as in the Early Cretaceous Nymphaeales flower described by Friis et al. (2001).

Certainly, interpretations of fossils based on extant plants should be made with caution. However, comparisons between extant plants and fossil plants are necessary and should be carried out in as much detail as possible (see also Friis and Endress 1990; Friis et al. 2006).

_Movements of Tepals (and Other Floral Organs) during Anthesis_

Whereas in Cabombaceae and Nymphaeaceae the tepals commonly open and close, sometimes more than once, in Amborella and Austrobaileyales, the perianth does not close again after anthesis, and thus the only conspicuous movement is opening when anthesis begins. This closure and reopening in Nymphaeales is associated with its aquatic habitat and
Fig. 9  Tepals with nectaries (Nymphaeales).  A–D, Cabomba caroliniana.  A, Flower in female phase of anthesis, with paired nectaries on inner tepals (arrow).  B, Close-up of nectariferous appendage, nectary (arrow).  C, Nectariferous hairs.  D, Transverse section of tepal, showing
flowering above the water surface. In most taxa of Nymphaeales, the flowers are submerged before and after anthesis and sometimes even rhythmically for certain periods during anthesis. Most publications deal with the behavior of single species at a specific place. From these studies, overarching patterns emerge. However, a comparative study on a larger number of taxa is missing.

The only other movements known so far in bisexual flowers among Austrobaileya are in Austrobaileya, in which the staminodes close over the gynoecium at the transition from the female to the male phase of anthesis (Endress 1980b; 2001; this article; fig. 5G, 5H), and in Illicium, in which the carpels close together, forming a cone at the transition from the female to the male stage of anthesis. In Trimeniaceae, in contrast to Amborella, the tepals do not reflex during anthesis. They just spread and then fall off.

Abscission and Caducousness of Tepals (Sepals)

Tepal persistence or caducousness characterizes larger clades in basalmost angiosperms. Austrobaileya have caducous tepals, and Amborella, Nymphaeaeae, and Chloranthaceae (Hedyosmum) have persistent tepals. Caducous tepals are associated with a narrow and thin attachment zone (indented in median direction) with small-celled tissue. Persistent tepals have a broad and thick attachment zone (streamlined in median direction), often without especially small-celled tissue. In addition, only in taxa with persistent tepals does syntepaly occur, as is found in Amborella, Cabomba (Nymphaeales), and Hedyosmum (Chloranthaceae).

Early abscission or caducousness of tepals (or sepals in eudicots), although conspicuous in Austrobaileya among the basalmost angiosperms, is not so common in other groups of angiosperms. It is also prominent in Papaveraceae and Berberidaceae (Ranunculales, basal eudicots). In Berberidaceae, as in Austrobaileya, it co-occurs with the presence of a relatively large number of sepals and an increasing size of the sepals from the periphery toward the center of the flowers. In Papaveraceae, there are only a few sepals, and they may be smaller or larger than the petals. However, in contrast to Austrobaileya, Berberidaceae and Papaveraceae have a whorled, not spiral, sepal phyllotaxis (Eichler 1878; Hiepko 1965; Endress 1995).

Also in other flowering plants, organ abscission occurs in small-celled tissue in the narrow and constricted base of the tepals. I did not study the process of abscission at the cytological level, which was done for other groups (Addicott 1982; Bleeker and Patterson 1997; Leslie et al. 2007).

Presence or Absence and Elaboration of Tepals

Most of the basalmost extant angiosperms are characterized by flowers with tepals. However, there are several tepalless taxa that have been transferred to the basalmost angiosperms only recently. Hydatellaceae were transferred from Poales (monocots) to Nymphaeaeae (Saarela et al. 2007). Chloranthaceae (tepallless, except for female flowers of Hedyosmum and Ceratophyllaceae, which were of uncertain position in basal angiosperms for a long time, now also tend to come to the grade of basalmost angiosperms (Doyle and Endress 2000; Qiu et al. 2005, 2006; Mathews 2006). Also, tepalless fossils that may belong to the basalmost angiosperms have recently been described from the Early Cretaceous (Archaefructus, Sun et al. 2002; Friis et al. 2003; Ji et al. 2004).

The flowers of extant tepallless taxa have been studied developmentally, and in all of them, tepals are not even initiated; thus, no cryptic perianth was found (Hydatellaceae [Rudall et al. 2007], Chloranthaceae [Endress 1987a; Kong et al. 2002], Ceratophyllaceae [Endress 1994b; Iwamoto et al. 2003]). Developmental genetic studies in Chloranthus (Chloranthaceae) showed that although there is no perianth, genes related to class A, B, and E genes, which are generally involved in perianth development, are present (Li et al. 2005).

An equally interesting feature is that some of these perianthless plants are water plants that appear to flower underwater (Hydatellaceae, Ceratophyllaceae, and Archaeofructaceae). Another potentially aquatic fossil from the Early Cretaceous with apparently minute, simple, but poorly preserved flowers, Montsechia, may also be an angiosperm (Gomez et al. 2006). To what extent the aquatic habitat, submerged flowering, and tepalllessness may be functionally connected and the evolutionary interpretation of tepalllessness (Friis et al. 2003; Endress and Doyle 2008) will not be followed up on here.

Morphological elaborations are not present in tepals of basalmost angiosperms, perhaps with the exception of Cabomba, in which the inner tepals have curved appendages with nectaries at the base of their blades. This is in contrast to more advanced clades of angiosperms, in which the inner perianth organs (petals) have evolved various elaborations (Endress and Matthews 2006).

Tepals with Nectaries

Distinct floral nectaries are known only from tepals of Cabomba and Nuphar (Nymphaeales) among the ANITA grade (Bernardello 2007). In both genera, these nectaries are associated with dark yellow areas (nectar guides; fig. 9A, 9E). However, the nectaries of Cabomba and Nuphar are at different sites, and even more important, they are histologically different. This different structure and position indicate that the nectaries are probably not directly homologous but rather have arisen by convergent evolution within Nymphaeales (see also Schneider and Jeter 1982; Vogel 1998). Histologically, Cabomba exhibits trichome-type nectaries, and Nuphar appears to conform to a combination of the mesophyll type and the epidermal type (sensu Vogel 1977). Small quantities of nectar, produced at the base of tepals and stamens, were also reported from Illicium of Austrobaileya (Thien et al. 2000).

Among other basal angiosperms, nectaries are present on inner tepals in Asimina triloba (epidermal type; Endress 1994a)

hairs (arrows), E–H, Nuphar advena. E, Flower in female phase of anthesis, with nectary on inner tepals (arrow). F, Inner tepal from dorsal side; lower border of nectary indicated with arrows. G, H, Close-up of nectary, showing nectar pore. I, Nuphar pumila, transverse section of inner tepal with nectary; nectar pore indicated with arrow. Scale bars: B = 0.25 mm; C = 0.05 mm; D, I = 0.1 mm; F = 0.5 mm; G, H = 5 μm.
and some other Annonaceae (Magnoliales). Laurales are characteristic for their nectaries on stamens and staminodes (Endress 1980a; Endress and Lorenz 2004; Chanderbali et al. 2006; Buzgo et al. 2007). It is noteworthy that nectaries in some basal angiosperms are not single massive tissues, as usually found in more derived groups, but associations of many small nectariferous areas, termed “nectaroïdes” by Vogel (1998), such as on the tepals of Chimonanthus (Calycanthaceae, Laurales) and Aristolochia (Aristolochiaceae, Piperales) and on the floral subtending bracts of the tepalless Peperomia (Piperaceae, Piperales; see also Vogel 1998).

The diverse structure, rare occurrence, and scattered distribution of nectaries indicate convergent evolution not only in Cabomba and Nuphar but also in other basal angiosperms. It may also indicate that in early angiosperms, nectar was not a major floral reward (see also Thien et al. 2003).

Bracts and Tepals, Sepaloid and Petaloid Tepals, and Sepals and Petals

It has often been reported that in some basal angiosperms there is a gradual transformation from (smaller) bracts to (larger) tepals and from (green) sepaloid tepals to (colored) petaloid tepals. This is especially obvious in spiral flowers with a relatively high number of organs and relatively long and equal plastochrons between the initiation of subsequent organs, in which the transformation occurs in equal steps. In Amborella and Austrobaileyales, in which the outermost tepals are smaller than the inner ones and bractlike, this is especially obvious (Amborella [Endress and Igersheim 2000; Poslusny and Tomlinson 2003; Buzgo et al. 2004], Austrobaileyya [Endress 1980b, 1983], Trimeniaceae [Endress and Sampson 1983]). Among other basal angiosperms, it is present in Calycanthaceae of Laurales (Staedler et al. 2007). However, the phenomenon is not restricted to basal angiosperms. It also occurs rarely in eudicots (e.g., Camellia, Tutechera, Theaceae, Ericales; Eichler 1878; Melchior 1925; Tsou 1998).

Developmentally, instead of a one-step change from bracts to tepals (sepal) or from sepal to petals, as is common in whorled flowers with very short plastochrons between the organs of a whorl but a very long plastochron between two whorls, the change occurs in several smaller steps. A “fading border” model has been proposed to explain this pattern at the genetic level (Buzgo et al. 2004; Soltis et al. 2007a, 2007b). It appears easier to apply this model to describe the development of flowers with an increased (evolutionarily derived) number of perianth organs in spiral arrangement rather than to see it as an expression of a primitively multistep gradation from an outer to an inner morph of tepals or from sepal to petals. The multistep gradation per se may not be basal in angiosperms, but it could easily evolve at this level and less easily in more derived groups. This should be further explored.

Perianth Organ Origin and Evolutionary Differentiation

In earlier publications, the delay in development of the inner tepals in Cabomba, which, together with the presence of nectaries on them, resembles the petals of some eudicots (especially Ranunculales), was emphasized (Endress 2001, 2002). This was similarly discussed for Nuphar (Hiepko 1965). However, a more inclusive view, including additional structural aspects, makes the situation more complicated. In Cabomba, apart from developmental delay and nectar production, there is no obvious difference between the outer tepals and the inner tepals. Both have the same size and color, both are relatively thin, both have intercellular spaces, and both have a papillate epidermis. In other groups, the outer and inner tepals are much more different in these features but may not have the developmental delay in the inner tepals.

A concept for the understanding of perianth evolution and the use of sensible terms for the perianth organs in different clades of angiosperms is still to be worked out. How much will the use of the existing terms “tepals,” “sepals,” and “petals” need to be modified in the future? As an important step toward a resolution, it would be useful to know more about the development, anatomy, histology, and behavior of the perianth organs across all groups of basal angiosperms (not only the basalmost clades). Also, the fossil record should be evaluated. The currently oldest-known fossils with preserved tepals are related to Hedyosmum (Eklund et al. 2004; Friis et al. 2005, 2006). Such a comparative structural study is still lacking, and it would need a big effort. For eudicots, such an approach has been attempted (Ronse De Craene 2007, 2008). As a further step, the evolution of the diversity of these features should be analyzed on the basis of the currently available phylogenetic studies of angiosperms; there are some initial attempts of such studies (Doyle and Endress 2000; Ronse De Craene et al. 2003; Zanis et al. 2003; Endress and Doyle 2007, 2008). Likewise, the genetic program for perianth development and its origin and evolution in angiosperms should also be further elucidated (Jaramillo and Kramer 2004, 2007a, 2007b; Stellari et al. 2004; Kim et al. 2005; Baum and Hileman 2006; Irish 2006; Kramer and Zimmer 2006; Soltis et al. 2006, 2007a, 2007b; Litt 2007). Both the structural and the developmental genetic approach would be important to evaluate homologies (Wagner 2007). The evolutionary understanding

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Fig. 10. Cladogram of basalmost angiosperms (topology combined from Qiu et al. 1999, 2005, 2006; Renner 1999; Doyle and Endress 2000; Duvall et al. 2006; Mathews 2006; Saarela et al. 2007). Blue, taxa with persistent tepals; red, taxa with caducous tepals; green, taxa without tepals.
of sepsals and petals is so difficult because specific functional and developmental constraints similar to those of male- and female-producing parts in stamens and carpels are not present, and thus, more evolutionary flexibility may be expected (see also Endress 1994a, 2006; Stuessy 2004).

Conclusions

Austrobaileyales are distinctive among the basalmost angiosperms in having tepals that fall off during or at the end of anthesis (fig. 10). The site of abscission is preformed structurally by narrowness and constriction of the tepal base, associated commonly with small-celled tissue. In contrast, in Amborella, Nymphaeales, and Hedyosmum (Chloranthaceae), tepals are persistent. Their base is broad, not constricted (streamlined in median longitudinal section) and commonly not especially small-celled. Amborella and Austrobaileyales are distinctive in their spiral perianth phyllotaxis, combined with the staggered placement of tepals, with the smallest being outside and becoming gradually larger toward the inside of the flower. In contrast, in Nymphaeales, perianth phyllotaxis is whorled and not staggered, with the largest tepals outside, covering all the inner ones in bud. In the basal grade of extant angiosperms, complete lack of a perianth is more common than in more derived groups because it occurs in Hydatellaceae, Chloranthaceae (except for female flowers of Hedyosmum), and Ceratophyllaceae as well as the fossil Archaefructaceae (see also Endress and Doyle 2008).

Some of these differential features of the perianth are comparatively largely unexplored in other basal extant angiosperms (i.e., magnoliids). It would be of interest to shed light on the diversity in behavior of the perianth in a large range of basal angiosperms, also in comparison with monocots and eudicots, to contribute to the elucidation of perianth evolution in angiosperms.

Acknowledgments

I thank Thomas Denk and Jürg Schönberger for the invitation to participate in the international paleobotanical symposium “In Search of the Earliest Flowers” in honor of Professor Else Marie Friis, held in Stockholm in June 2007, and to contribute to this special issue of the International Journal of Plant Sciences. In the early 1980s, Else Marie Friis pioneered studies of three-dimensionally preserved Cretaceous flowers that became important for our understanding of early flower evolution. She is a leader in the field, and her research has been a model for many colleagues and students. I thank Bernie Hyland for support in the field in Northern Queensland, Alex Floyd in New South Wales, and Gordon McPherson in New Caledonia. Further, I thank F. Bruce Sampson, Jürg Schönberger, and Hiroshi Tobe, who provided fixed material. I am grateful to Rosemarie Siegrist for microtome sections, Urs Jauch for support with the SEM, and Alex Bernhardt for artwork. Three anonymous reviewers are thanked for valuable comments on the manuscript.

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