

# The floral development of *Neurada procumbens* L. (Neuradaceae)

L. P. RONSE DECRAENE and E. F. SMETS

*Laboratory of Plant Systematics, Botanical Institute, Katholieke Universiteit Leuven,  
Kardinaal Mercierlaan 92, B-3001 Heverlee, Belgium*

## SUMMARY

The floral ontogeny of *Neurada procumbens* L. has been investigated to clarify the position of the family Neuradaceae and to elucidate a number of morphological problems, such as the nature of the epicalyx and the 10-carpellate gynoecium. Morphological and ontogenetic evidence suggests a close affinity with the Rosaceae, contrary to reports of *rbcL* sequence data. There is a strong gynoecial resemblance with Maloideae, but other characteristics suggest that the affinities of Neuradaceae lie at the base of the Rosaceae.

*Key-words:* floral ontogeny, epicalyx, gynoecium, *Neurada procumbens*, Neuradaceae, Rosaceae.

## INTRODUCTION

The Neuradaceae consists of the three small genera: *Grielum* L. (five to six species), *Neurada* L. (one species) and *Neuradopsis* Bremek. & Obermey. (three species) (Melchior 1964; Hutchinson 1964; Cronquist 1981; Mabberley 1987). Most authors agree that the family is closely related to the Rosaceae in which it has sometimes been placed as a subfamily or tribe (e.g. Focke 1894; Murbeck 1916, 1941; Lawrence 1951; Hutchinson 1964, 1973; Rowley 1978; Thorne 1983). The Neuradaceae differ from the Rosaceae by a few conspicuous characters, such as their unique pollen morphology, unusual zygomorphic gynoecium, habit, seed morphology and embryology (see Murbeck 1916; Melchior 1964; Corner 1976; Cronquist 1981). However, these differences are usually considered as merely phyletic advances compared with the gross of the Rosaceae (cf. Cronquist 1981). Willis (1966) takes an exceptional position in pointing to similarities with the Malvaceae in the leaf shape, vertically inserted carpels and similar colour changes of the corolla upon drying. The Neuradaceae have also been compared with the Chrysobalanaceae or the Geraniaceae (see Murbeck 1916). Recently, Morgan *et al.* (1994) suggested that the *rbcL* sequence data of *Neurada* are not congruent with a close relationship with the Rosaceae; instead, *Neurada* is the sister group of *Gossypium* (Malvaceae) on their *rbcL* tree, in line with the opinion of Willis (1966).

The only detailed morphological study of the group has been carried out by Murbeck (1916) who gave a detailed account of the genera *Neurada* and *Grielum*. *Neurada* is highly unusual in its habit and flower morphology. It is a low spreading annual herb growing in an area ranging from the Southern Mediterranean coasts to Indian deserts. The flowers and fruits are flattened, strongly epigynous saucer-shaped mounds covered with spines and a thick indumentum. The petals and hardening styles emerge on top of

the mound enclosed by the small sepals. Fertilized seeds remain within the hardened flower structures, which are dispersed as a whole.

The gynoecium differs in essential details from the current state known in the Rosaceae and shows a number of specific morphological characteristics. At maturity one side of the gynoecium is normally developed, while the other aborts. This leads to a zygomorphic gynoecium while the flower remains regular in its other organs. There are 10 carpels that are generally believed to have arisen by *dédoublément* of an original set of five. This enabled earlier authors to link *Neurada* with Rosaceae having five antesepalous carpels, as was done by Murbeck (1916) on the basis of the orientation of the ovules. However, this assumption has never been checked ontogenetically.

Uncertainty also reigns on the number of ovules per carpel, as some authors accept a single pendulous ovule per locule (e.g. Focke 1894; Willis 1966; Cronquist 1981) or one to two ovules (e.g. Murbeck 1916; Melchior 1964; Goldberg 1986). For Murbeck, two ovules are originally superposed within each locule and the basal one becomes aborted. The presence of floral spines in *Neurada* represents an interesting character for comparison with the Rosaceae where similar structures are found in some genera (e.g. *Agrimonia*). Murbeck (1916) believed the spines of *Neurada* to be secondary emergences and not an epicalyx. Hutchinson (1964) and Willis (1966) refer to an epicalyx of five bracteoles. *Grielum* bears no spines but has short knobs and *Neuradopsis* has spines but not the five bracteoles, which Hutchinson (1964) takes as a diagnostic character to distinguish *Neurada* from the other genera. Little is known about the morphology of the nectary. Murbeck (1916) mentions a weak intrastaminal 'Ringwulst' covered with hairs in *Neurada*. In *Grielum* these emergences may be scale-like ('Schuppen').

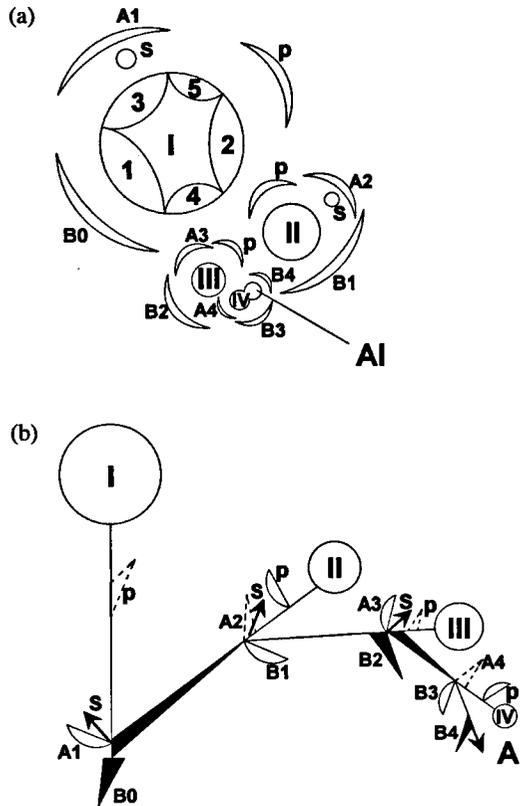
The above-mentioned morphological problems, as well as the fact that evidence from molecular data does not fit with the morphological evidence justifies a renewed investigation of *Neurada*. More data can provide a stronger basis for discussing the relationships of the group in relation to the Rosaceae.

## MATERIALS AND METHODS

Flowering material of *Neurada procumbens* L. was collected by the first author during a field trip on Jerba (Tunisia). Flower buds of *Agrimonia eupatoria* L. (Rosaceae) were gathered on Mont Panisel near Mons (Belgium). Reference material (pickled: Ronse Decraene 310 L<sub>t</sub> and 198 L<sub>o</sub>) and a herbarium specimen (Ronse Decraene 968) are kept at the Botanical Institute of the Katholieke Universiteit Leuven (LV). For methods of preparation we refer to earlier reports (Ronse Decraene 1990; Ronse Decraene & Smets 1991). Observations were made with a Philips 501.B (Meise) and a Jeol JSM.6400 scanning electron microscope (Leuven).

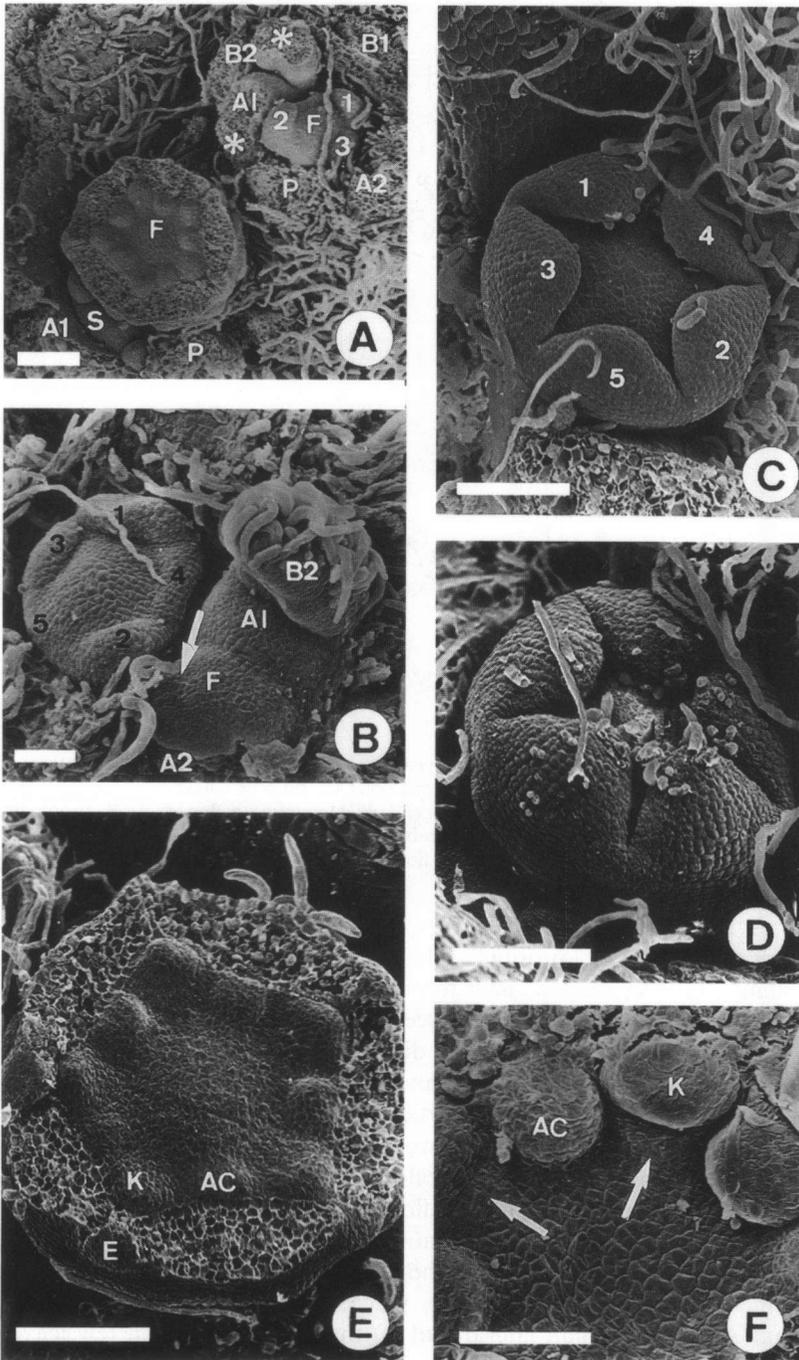
## RESULTS

Flowers arise sequentially alongside a continuously growing apical meristem (Figs 1a,b, 2A). Inception starts with the unequal division of an elliptical primordium which arises between two leaflike prophylls (A1 and B1). One part of this division gives rise to a first flower primordium, while the other produces a new pair of prophylls (A2 and B2) and repeats the process. By unequal division, a lanceolate bract-like structure (p) is detached from each flower primordium (Fig. 2B). The growth of this appendage is limited and it appears as a small ligule-like structure below the pedicel of the mature flower. The two



**Fig. 1.** *Neurada procumbens*. (a) Diagrammatic representation of part of inflorescence apex from above (with successive development of four flower buds). Next to flower IV, no p or s have yet been formed. (b) Lateral view of the same. Abbreviations: P, bract-like appendage subtending a flower; A, B, prophylls A and B; AI, inflorescence apex; S, small lateral shoot. Arabic numbers indicate order of inception of the sepals and prophylls; roman numbers indicate successive flower buds.

prophylls grow unequally; prophyll B1 becomes displaced along the horizontally growing stem, while A1 remains next to the first flower that it originally enclosed. B1 encloses the growing point of the inflorescence that produces the two next prophyll A2 and B2. This process is repeated with a displacement of B2 to a higher level and the insertion of B1 next to the second flower and A2, and so on. As a result, each node bears a flower, a small appendage (p) and two leaves of unequal size (A1–B0, A2–B1, A3–B2, etc.). Prophyll B is always larger than prophyll A and has been shifted from a lower level; prophyll A stands on the side of the flower primordium with an angle of 90° to the bract-like appendage p subtending the flower (Fig. 1a). B is always situated at the underside in relation to the main stem and flower on opposite sides of p, while A is inserted in an upper lateral position. The inflorescence is monochasial and could be termed a cincinnus with a terminal flower placed at each node. Prophylls also differ in the fact that A covers a small lateral bud (s) that only develops a few leaves in later stages (Figs 1a,b, 2A), while B has no small lateral bud but encloses the main growing stem in its axil. The result of this unequal growth is that B and p behave as prophylls in relation to the terminal flower, while A and B behave as prophylls to the flower and



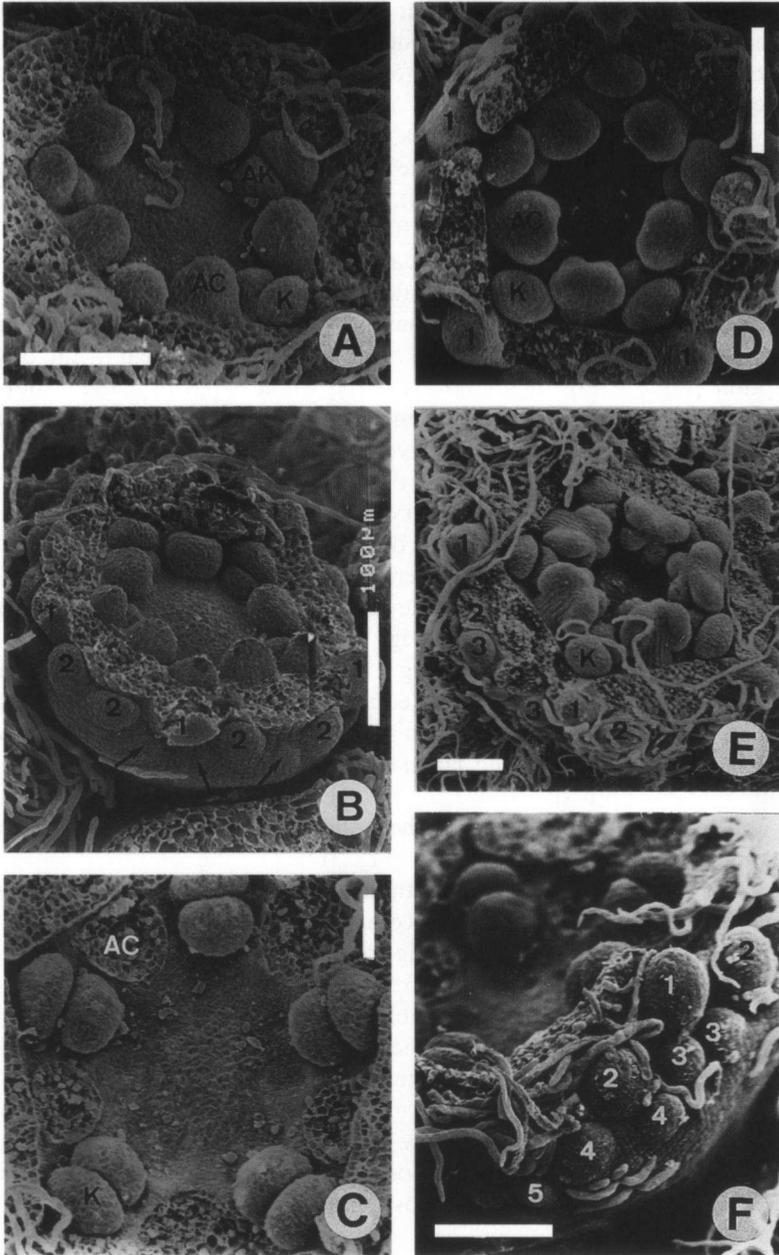
inflorescence apex. Each subsequent flower is oriented at an angle of 90° in relation to an older flower, concomitant with the position of B.

Calyx inception is successive along a 2/5 sequence (Figs 1a, 2A–C). Sepals arise as hemispherical primordia on the periphery of a flattened floral apex. The first sepal is oriented towards prophyll B (B3 of Fig. 1a,b; B1 of Fig. 2A) and arises simultaneously with sepals number 2 (oriented towards the inflorescence apex) and 3 (oriented towards prophyll A; A4 on Fig. 1a,b, A2 on Fig. 2A). In some cases a fourth and fifth sepal follow immediately or the fifth lags in time. The fifth sepal is situated against p (Figs. 1a,b, 2A). Sepal primordia rapidly become almost equal in size as they progressively cover the floral apex. Sepal shape is triangular with rounded apices; sepals touch each other laterally without fusing and finally cover the bud completely in a valvate aestivation (Fig. 2 C,D). At that time unicellular hairs are initiated basipetally on each sepal in the order of the calyx inception (Fig. 2C,D), finally covering the whole sepal in a thick indumentum. Sepals are persistent but they do not grow much from this stage on. The basal part of the flower increases dramatically in size and becomes a broad platform on which the sepal lobes are inserted. Removing the sepals at this stage reveals a flattened pentagonal apex with a girdle of primordia on the periphery (Fig. 2E). Petals and antesepalous stamen primordia arise simultaneously and do not differ in size and morphology (no stages were seen with only petals and without stamens). Antepetalous stamen primordia follow rapidly as small hemispheres (Fig. 2F). They do not always arise simultaneously, as can be seen by the slight differences in size (Fig. 3A). As a result of this, three alternating whorls can be readily observed surrounding a flattened floral apex. Antepetalous stamen primordia and petal primordia remain of equal size for a long time, as petal growth is very slow. Size differences between the two stamen whorls are expressed very early with the antesepalous stamens remaining largest (Fig. 3B,D,E); peripheral growth lifts the antesepalous stamens on a rim above the antepetalous stamens (Figs 3D, 4D, 5A,B). Filaments appear simultaneously with anther differentiation at the time the central area becomes invaginated by peripheral growth (Fig. 3D). The stamens are slightly bent over the floral apex with the antesepalous stamens overlapping the lower antepetalous stamens in a manner characteristic for Rosaceae. Four pollen sacs develop on each anther; the dorsals are larger and diverging from the ventrals, which converge towards each other (Figs 3E, 4D, 5A,B). Anthers are basifixed at anthesis and filaments have an inflated base. Petal growth lags considerably behind that of the stamens. Only before anthesis do the small ligulate primordia increase in size and overtop the stamens (Fig. 5B). They cover the floral bud in a contorted aestivation. Petals drop off rapidly.

As early as stamen and petal inception, globular primordia become apparent outside the saucerlike floral primordium just below the sepal insertion. These primordia initiate the epicalyx and are situated in antepetalous position (Figs 2E, 3D); each one is rapidly followed by two adjacent primordia opposite the sepals (Fig. 3B,E,F). A third whorl

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**Fig. 2.** *Neurada procumbens*. (A) View of inflorescence apex showing two flowers and a growing point (most prophylls removed). Asterisks represent the youngest prophylls related to the inflorescence apex. (B) View of inflorescence apex and an older bud with the inception of the sepals; one prophyll removed. Note the separation of the bract-like appendage from the young flower bud (arrow). (C) Older stage of young flower with initiation of trichomes on sepals 1 and 2. (D) Older flower bud; the sepals enclose the bud in a valvate aestivation. (E) Initiation of the epicalyx, antesepalous stamens and petals; sepals removed. (F) Detail of petal and stamen primordia at the earliest inception of the antepetalous stamens (arrows). Bars = 100 µm, except (B) and (F) = 50 µm. Abbreviations: AI, inflorescence apex; AC, antesepalous stamen primordium; F, flower bud; E, epicalyx primordium; K, petal primordium; P, bract-like appendage; PA, PB, prophylls A and B; S, lateral shoot. Numbers indicate order of inception of sepals.



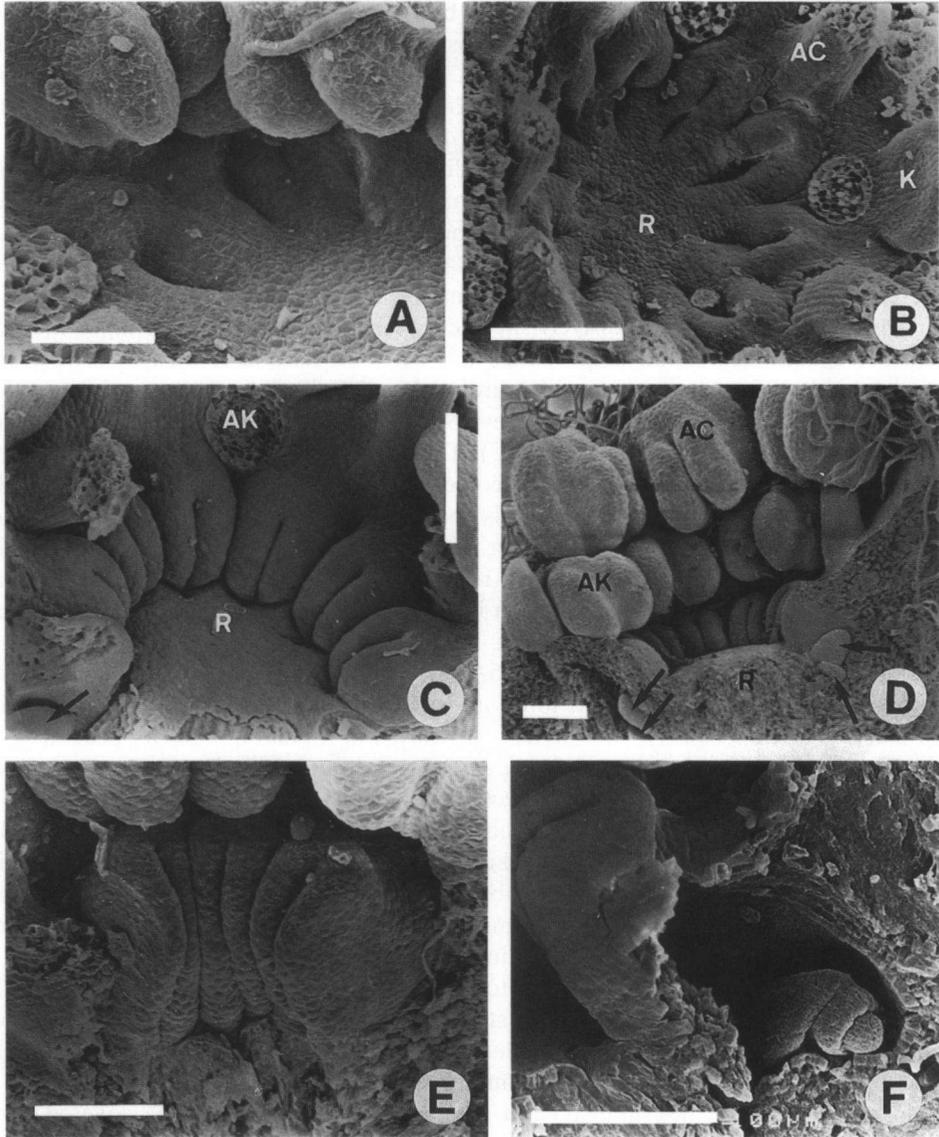
**Fig. 3.** *Neurada procumbens* (sepals removed in all cases). (A) Lateral view showing initiation of petals and androecium. (B) Lateral view of the same showing the basipetal inception of the epicalyx primordia. Arrows point to the inception of the third whorl. (C) Apical view; antesealous stamens removed. Formation of slight depressions on the flat apex. (D) Slightly older bud showing the beginning of the curvature of the stamens and anther initiation. (E) Lateral view of older bud with epicalyx members. (F) Lateral view similar to (C) with epicalyx development. Bars=100 µm, except (C)=50 µm. Abbreviations: AC, antesealous stamen; AK, antepetalous stamen; K, petal. Numbers indicate order of inception of epicalyx members.

arises with two antepetalous primordia just below the first, together with another one between two adjacent pairs in antesepalous position (Fig. 3B). A fourth whorl arises in the spaces formed by the second and third whorl. Murbeck (1916) confounded the third and fourth whorls on his floral diagram (p.7; Fig. 2A). He mentioned only a single primordium opposite the first whorl; we saw two of these. More primordia may appear basipetally in alternation with previous ones. It remained difficult to identify their exact numbers and positions due to the abundant indumentum. Primordia grow into spines, which are largest on top of the flower. At maturity the upper spines have strongly inflated bases.

When the periphery of the flower starts to be lifted up, ten depressions become apparent on the flattened central area in alternation with the stamen primordia (Fig. 3C). The depressions become progressively slit-like by the appearance of arc-shaped margins overarched each depression (Fig. 4A,B); adaxially no margin is formed. These arcs appear laterally joined into a sinusoidal girdle taking up the space between the insertion of the stamen whorls (Fig. 4A,B), but they soon become detached by their pronounced growth into U-shaped primordia (Fig. 4C). The slits extend in size towards the central flattened area of the flower, while they become elevated in an almost vertical position by peripheral growth. At that time the carpels appear as flattened wings or curtains as they are fully ascidiate (Fig. 4D,E). The lower part of the gynoecium appears congenitally fused and is completely embedded in the receptacular tissue (Fig. 4D,E). The ascidiate structure, which was originally seen as an individual carpel, now curves with the apical part pointing towards the stamens and is lifted up by the formation of a stalk with a longitudinally running groove (Figs 4F, 5A–C). The result is a fairly long style with a broad stigmatic area showing two lobes and a slit turned towards the stamens (Figs 5C,D, 6A). The upper part of the style, just below the stigmatic papillae, bears a large number of stomata. Ovule primordia arise just above the congenitally fused area between the curtain-like margins. They are connected with the carpel margins on opposite sides and arise singly or as an unequal pair within each locule (Fig. 4C,D). One ovule is smaller and readily aborts. In some cases a small cavity is seen below the remaining ovule (Fig. 6A, arrow), corroborating Murbeck's observations. The remaining ovule curves outwards and becomes enclosed by two integuments (Figs 4F, 5A). During ovule maturation the area of the flower between the ovule insertion and the sepals extends horizontally in considerable proportions. Ovules tend to be pressed into sinuous bodies within the limited space (Figs 5C,D, 6A). They are strongly anatropous and can be detached from their massive funiculus. Only at a very late stage of development does one side of the gynoecium stop growing, giving it a zygomorphic appearance.

The area between the stamens and gynoecium becomes densely covered with unicellular hairs during the development of the style (Fig. 5B–D). Close inspection of the stamen bases after partial removal of the hairs reveals some sunken stomata which may indicate the presence of nectariferous tissue. However, at maturity there are no obvious traces of a nectary. To our knowledge, no information is available about pollination of the flower. After anthesis, petals and stamens drop, but the sepals and erect styles remain on top of the spiny fruit.

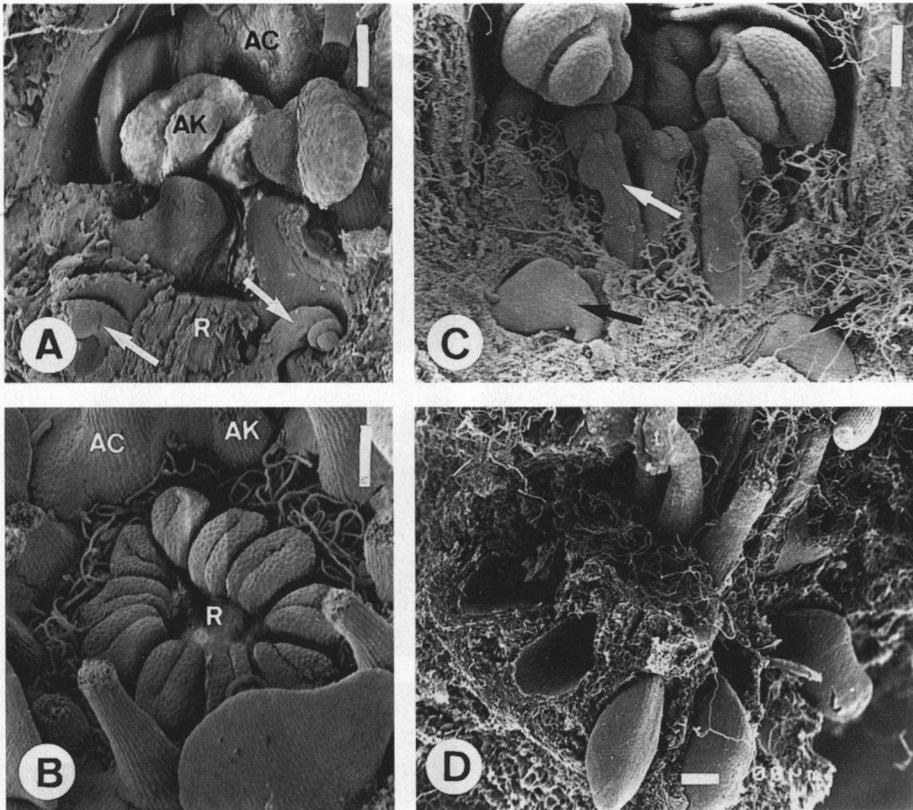
For comparison, a few floral buds of *Agrimonia eupatoria* (Rosaceae) were also observed with special emphasis on the epicalyx development (Fig. 6B–E). Flowers are essentially diplostemonous with an often incomplete antepetalous whorl (Fig. 6E). The epicalyx consists of long bristles that arise in a centrifugal fashion similar to *Neurada*. The first primordia appear in alternation with the calyx lobes (Fig. 6B,C) and rapidly fill the space around the base of the flower bud (Fig. 6D).



**Fig. 4.** *Neurada procumbens*. (A) Partial view of the central area of the flower showing gynoecial slits. (B) Apical view of a slightly older bud; stamens removed. (C) Older stage showing the ascidiate form of the carpel primordia around the receptacular residue. Note the ovule primordium on the flank of a carpel (arrow). (D) Longisection through flower bud at about the same stage as (C), showing position of stamens and ovules (arrows). (E) Detail of curtain-like carpellary folds. (F) Section through one carpel showing one ovule and developing style. Bars = 100  $\mu\text{m}$ , except (A) = 50  $\mu\text{m}$ . Abbreviations: AC, antesepalous stamen; AK, antepetalous stamen; K, petal; R, receptacular residue.

## DISCUSSION

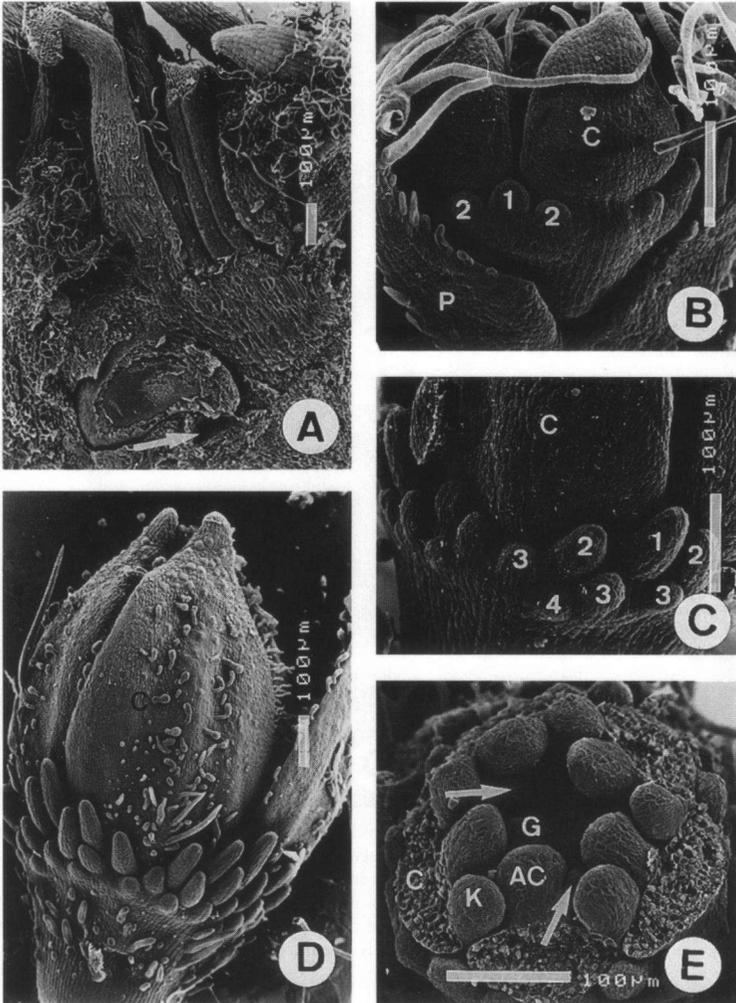
*Neurada* resembles the Rosaceae in several aspects of its floral development, such as the formation of a hypanthium with stamens inserted at two levels, the curved stamens with the outer in an upper position, the early dropping petals with retarded growth and small



**Fig. 5.** *Neurada procumbens*. (A) Longisection with developing style and two ovules (arrows). (B) Partial view of flower prior to anthesis. Note the indumentum between stamens and carpels and young styles; anthers removed. (C) Longisection through flower showing the erect styles with extrorse stigmas and two ovules (black arrows). Note the groove running through the middle of the style (white arrow). (D) Lateral view of section of the central part of the flower showing the ovules and parts of the locules. All bars=100  $\mu$ m. Abbreviations: AC, antesepalous stamen; AK, antepetalous stamen; K, petal; R, central residue of the apex.

insertion base; sepals arise in an almost identical manner as small persistent lobes on a broad platform; the spines are reminiscent of similar structures; an inferior ovary with persistent styles and few axile ovules is also characteristic.

Murbeck (1916) described the complex sympodial inflorescence of *Neurada* and also provided a drawing. Our observations agree with his description in that the flowers stand in a terminal position between two unequal prophylls ('Vorblättern'). Also, the larger prophyll (Fig. 1: B) encloses the bud that continues the inflorescences and ends with the next flower, while the smaller (Fig. 1: A) bears a short stem in its axil. Each larger prophyll is believed to have been shifted to a higher level (next to a younger flower), a fact that we could also observe. Murbeck interpreted the small appendage (p) as a small ligular stipule belonging to prophyll A. He believed the other stipule of the pair to be lost due to the horizontal growth of the stem. However, the position of p is opposite each flower and is in no way linked with the smaller prophyll (Figs 1a, 2A,B). Moreover, it arises independently of the prophylls and is initially larger. As indicated by Murbeck, the horizontal growth form may well be responsible for the displacement of flowers and bracts and the unusual construction of the inflorescence.



**Fig. 6.** (A). *Neurada procumbens*. Longisect of gynoecium with young ovule and styles. Note the small locular space below the ovule (arrow). (B)–(E) *Agrimonia eupatoria*. (B) Early stage of the initiation of the epicalyx. (C) Lateral view of older bud showing the centrifugal inception of epicalyx primordia. (D) Idem, nearly mature stage. (E) Lateral view of young flower bud showing petals, antesepalous stamens and two antepetalous stamens (arrows); sepals removed. All bars=100 µm. Abbreviations: C, sepal; P, prophyll; K, petal; AC, antesepalous stamen; G, carpel primordium.

The nature of the epicalyx is controversial in the Rosaceae and in the Neuradaceae alike. Hutchinson (1964) probably confused the upper spines of *Neurada* (which alternate with the calyx lobes) with bracteoles, as each upper spine is connected with more appendages arising basipetally. Kania (1973) interpreted the epicalyx of the Rosaceae as emergences, because he could not find any ontogenetic evidence for a stipular nature (the classical view, cf. Eichler 1878). This interpretation was refuted by Trimbacher (1989) who presented a morphological sequence starting from the simple appendages of *Rhodotypos* to the complex epicalyx of *Agrimonia*. In *Rhodotypos* the epicalyx primordia arise as marginal appendages of the outer sepals and recall stipules. All other taxa of the Rosaceae as well as *Neurada* have their epicalyx primordia arising

independently and outside the sepal whorl. They arise simultaneously except in *Comarum palustre* L., where the epicalyx primordia continue the spiral sequence of the sepals, indicating their stipular nature. Trimbacher concluded that the whorled arrangement is induced by the isolation and displacement of the stipules. *Neurada* closely resembles *Agrimonia* in the inception of its epicalyx (Fig. 6B–D). There is a similar centrifugal increase of appendages recalling the secondary increase of stamens. Also the floral development of *Agrimonia* bears similarities with *Neurada* (Fig. 6E).

The androecium of *Neurada* is a typical illustration of diplostemony and is characterized by the absence of interactions (in time and space) between petals and stamens (such as stamen–petal complexes) (see also Ronse Decraene & Smets 1995). *Neurada* shares a diplostemonous androecium with taxa of the Rosoideae (e.g. *Stephanandra*, *Agrimonia*: Fig. 6E) and the Quillajae (e.g. *Quillaja*) of the Rosaceae. Endress & Stumpf (1991) also observed the stamens of *Neurada procumbens*. The anther shape with larger dorsal pollen sacs agrees with the Rosaceae. Their observations also agree with ours except for their report of hairy filaments. A thick indumentum is found at the base of the filaments, but it is inserted on the hypanthium, not on the filament (Fig. 5B,C).

Murbeck (1916) placed a link with Maloideae where an inferior gynoecium of five carpels is characteristic. Indeed, the gynoecial development of *Amelanchier* and other Maloideae resembles *Neurada* in several points (compare with Steeves *et al.* 1991).

1. The gynoecial primordia contribute little to the development of the ovary; instead, they develop almost exclusively into the style and stigmatic area but they also contribute to the initiation of the ovules that appear laterally on the carpellary flanks (Fig. 4C,D). The fact that a wholly ascidiate carpel develops as a stigmatic structure is not common in the dicots. The entire carpel develops as a stalk which is the continuation of the septa. Carpellary tissue hardly participates in the development of the ovary. Processes of development occur deep in the receptacular tissue and the limits between carpellary and receptacular tissue are not discernable below the insertion of the style (Figs 4E, 5C,D, 6A).

2 The deepening of the hypanthium induces the carpel primordia to extend vertically inside the continuous cylinder of meristematic tissue (Figs 4D,E, 5A).

3 The basal region of the floral cup between ovule insertion and periphery expands horizontally during ontogeny and forms the roof of the ovary (Figs 4F, 5C,D, 6A).

4 The gynoecial development of Rosaceae with an inferior ovary and that of *Neurada* is not strictly epigynous (in comparison with the development in, e.g. Asteraceae or Dipsacaceae). Indeed, the epigynous appearance is enhanced by strong hypanthial growth lifting perianth and the androecium above the free gynoecial parts. The receptacle remains flattened (Figs 4C,D, 5A–C) or forms a dome on which ascidiate primordia arise (e.g. Rosoideae: van Heel 1981, 1983). Carpels do not fuse as such with the receptacular tissue; only their basal parts become connected with receptacular tissue.

The difference between the five-carpellate condition of most Maloideae and the 10 carpels of *Neurada* is important. Ten carpels develop in *Neurada*, with a position intermediate between the two stamen whorls. It would be tempting to accept an original dédoublement of five carpels as is done by most authors. However, there is absolutely no ontogenetic evidence for this. Carpels arise independently and remain so during the whole development of the flower. However, this does not exclude the fact that five carpels were present in a condition ancestral to the Neuradaceae. As for stamens, paired

structures may arise by the division of a complex primordium, or they may arise independently and be at the same time connected (see Ronse Decraene & Smets 1993). In *Grietum* there are 5–10 carpels (Focke 1894). The suggestion of a partition of the locules by false septa seems more plausible than the idea of dédoublement, as certain genera of Maloideae show false septa which partially divide the locules (e.g. *Amelanchier*, *Malacomeles*, *Peraphyllum* (Murbeck 1916; Steeves *et al.* 1991; Rohrer *et al.* 1994). In *Neurada* this invagination is believed to be complete and accompanies the shift of the placental area to a central position (Murbeck 1916). In this case one would expect that only one ovule would remain within a locule (as they tend to be paired in Maloideae). As suggested by Murbeck (1916), the orientation of the ovules in *Neurada* indicates an original arrangement in pairs. Indeed, the ovules are inserted on one lateral flank of a carpel (Fig. 4C,D) and not in a strictly median position.

On the other hand, the presence of a supernumerary sterile ovule tends to disagree with this assumption as the second ovule is laterally inserted on the other carpel flank and not strictly below the fertile ovule. There is occasionally a hollow space below the fertile ovule, where the lost ovule should have been nestled (Fig. 6A, compare with Murbeck 1916). Moreover, there is no difference between the real and false septa. Most Maloideae have two collateral ovules per carpel; in *Cretaegus* and *Mespilus* they are superposed and only one develops into a seed as the fruit matures. *Neurada* shows the independent inception of 10 carpels without sufficient evidence for a pairing or the building of false septa. However, the similar arrangement of all locules in *Neurada* does not exclude that possibility *per se*.

On the basis of the morphological evidence, we may confidently suggest that *Neurada* belongs to the vicinity of the Rosaceae. However, Morgan *et al.* (1994) indicate that *rbcL* data do not support a close relationship between *Neurada* and the Rosaceae. Instead, a group composed of Rhamnaceae, Moraceae and Ulmaceae should be considered as the sister groups to the Rosaceae. These results are incongruent with the morphological and ontogenetic information that has been assembled during more than a century. As with all characters used in taxonomy, one must be careful in deciding about the impact of different approaches. This seems to be the case where molecular data are in conflict with morphological evidence. More characters from other sources would be also helpful for clarifying this incongruence. Zhang (1992), for example, mentions the lack of information on the wood anatomy of the Neuradaceae.

A relationship with Malvaceae (as suggested by Willis 1966) on the superficial resemblance of the flower is difficult to support against the wealth of evidence of a rosoid affinity. Affinities with specific taxa of the Rosaceae are difficult to determine. Apart from strong resemblances in the gynoecial morphology, a relationship with the Maloideae tends to be excluded by the basic chromosome number of *Neurada* ( $x=7$ ), which does not resemble Maloideae ( $x=17$ ) but corresponds to the basic number of the Rosaceae as found in the Rosoideae (Morgan *et al.* 1994). Also, certain embryological characters tend to be different from the Maloideae, such as absence of an obturator and endosperm (Murbeck 1916). In certain characters *Neurada* resembles taxa of the Rosoideae (e.g. chromosome number, diplostemony, epicalyx) while other, especially gynoecial characters point to the Maloideae. In the latter case we may suggest the possibility of convergent evolution linked with an extreme epigynous condition. Neuradaceae are probably an early offsprung of the bulk of the ancestral Rosaceae and should be treated as such.

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## REFERENCES

- Corner, E.J.H. (1976): *The Seeds of Dicotyledons*. Cambridge University Press, Cambridge.
- Cronquist, A. (1981): *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York.
- Eichler, W.A. (1878): *Blüthendiagramme II*. Engelmann, Leipzig.
- Endress, P.K. & Stumpf, S. (1991): The diversity of stamen structures in 'lower' Rosidae (Rosales, Fabales, Proteales, Sapindales). *Bot. J. Linn. Soc.* **107**: 217–293.
- Focke, W.O. (1984): Rosaceae. In: Engler, A. & Prantl, K. (eds): *Die natürlichen Pflanzenfamilien III*, 3. 1–61. Engelmann, Leipzig.
- Goldberg, A. (1986): Classification, evolution and phylogeny of the families of Dicotyledons. *Smithson. Contr. Bot.* **58**: 1–314.
- Heel, W.A. van (1981): A SEM-investigation on the development of free carpels. *Blumea* **27**: 499–522.
- Heel, W.A. van (1983): The ascidiform early development of free carpels, a SEM-investigation. *Blumea* **28**: 231–270.
- Hutchinson, J. (1964): *The Genera of Flowering Plants*. Vol. 1. Clarendon Press, Oxford.
- Hutchinson, J. (1973): *The Families of Flowering Plants*, 3rd edn. Clarendon Press, Oxford.
- Kania, W. (1973): Entwicklungsgeschichtliche Untersuchungen an Rosaceenblüten. *Bot. Jahrb. Syst.* **93**: 175–246.
- Lawrence, G.H.M. (1951): *Taxonomy of Vascular Plants*. MacMillan, New York.
- Mabberley, D.J. (1987): *The Plant-Book. A Portable Dictionary of the Higher Plants*. Cambridge University Press, Cambridge.
- Melchior, H. (1964): *Engler's Syllabus der Pflanzenfamilien*, 12th edn. Borntraeger, Berlin.
- Morgan, D.R., Soltis, D.E. & Robertson, K.R. (1994): Systematic and evolutionary implications of *rbcL* sequence variation in Rosaceae. *Am. J. Bot.* **81**: 890–903.
- Murbeck, S. (1916): Über die organisation, Biologie und Verwandtschaftlichen Beziehungen der Neuradoideen. *Lund Univ. Årsskr.* **212**: 1–29.
- Murbeck, S. (1941): Untersuchungen über das Androeceum der Rosaceen. *Lund Univ. Årsskr.* **37**, 7: 1–56.
- Rohrer, J.R., Robertson, K.R. & Phipps, J.B. (1994): Floral morphology of Maloideae (Rosaceae) and its systematic relevance. *Am. J. Bot.* **81**: 574–581.
- Ronse Decraene, L.P. (1990): Morphological studies in Tamaricales. I. Floral ontogeny and anatomy of *Reaumuria vermiculata* L. *Beitr. Biol. Pflanz.* **65**: 181–203.
- Ronse Decraene, L.P. & Smets, E.F. (1991): Androeceum and floral nectaries of *Harungana madagascariensis* (Clusiaceae). *Pl. Syst. Evol.* **178**: 179–194.
- Ronse Decraene, L.P. & Smets, E.F. (1993): Dédoulement revisited: towards a renewed interpretation of the androeceum of the Magnoliophytina. *Bot. J. Linn. Soc.* **113**: 103–124.
- Ronse Decraene, L.P. & Smets, E.F. (1995): The distribution and systematic relevance of the androeceal character oligomery. *Bot. J. Linn. Soc.* **118**.
- Rowley, G.D. (1978): Rosaceae. In Heywood, V.H. (ed.) *Flowering Plants of the World*. 141–144. Oxford University Press, Oxford.
- Steeves, T.A., Steeves, M.W. & Randall Olson, A. (1991): Flower development in *Amelanchier alnifolia* (Maloideae). *Can. J. Bot.* **69**: 844–857.
- Thorne, R.F. (1983): Proposed new realignments in the Angiosperms. *Nord. J. Bot.* **3**: 85–117.
- Trimbacher, C. (1989): Der Aussenkelch der Rosaceen. In: Weber, A., Vitek, E. & Kiehn, M. (eds) *9. Symposium Morphologie, Anatomie und Systematik, Zusammenfassungen der Vorträge*. 66. Wien.
- Willis, J.C. (1966): *A Dictionary of the Flowering Plants and Ferns*, 8th edn. Cambridge University Press, Cambridge.
- Zhang, Shu-Yin (1992): Systematic wood anatomy of the Rosaceae. *Blumea* **37**: 81–158.