Morphological Studies in Zygophyllaceae. II. The Floral Development and Vascular Anatomy of Peganum harmala

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Morphological Studies in Zygophyllaceae. II. The Floral Development and Vascular Anatomy of *Peganum Harmala*[1]

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Floral development and vascular anatomy are investigated in *Peganum harmala,* emphasizing its unusual androecium with 15 stamens. Sepals arise successively; petals emerge simultaneously with five antesepalous stamens. The five stamen pairs arise in the space between the petals and the antesepalous stamens. The gynoecium arises from three carpel primordia with evidence of two reduced carpels. Placentae are axile and each bears two double rows of ovules. A weakly developed nectary surrounds the base of the ovary. The antepetalous stamen traces diverge from a common supply to petals and sepal laterals, independent of the antesepalous stamen traces. The androecium of *Peganum* is described as a derived obdiplostemonous form, differing from the complex haplostemonous androecium of *Nitraria.* "Congenital dédoublement" cannot adequately explain the origin of the paired antepetalous stamens; two stamens can arise either by the splitting of a common primordium or independently, and both ways of inception are best understood as extremes of a gradation. The systematic position of *Peganum* is discussed in relation to other Zygophyllaceae using a cladistic analysis with *Ptelea* (Rutaceae) and *Quassia* (Simaroubaceae) as outgroups. The basal division in the Zygophyllaceae is between *Peganum* and the rest of the family.

Key words: androecium; floral development; *Nitraria*; obdiplostemony; phylogeny; *Peganum harmala*; stamen pairs; vascular anatomy; Zygophyllaceae.

The Zygophyllaceae are a family of ≈24 genera and 240 species (Mabberley, 1987), mostly of xerophytic or halophytic habitats. Flowers of Zygophyllaceae have a common "Bauplan," being mostly pentamerous, rarely tetramerous, bisexual, and regular with a calyx and corolla usually present. The androecium has occasionally three or four to five stamens (*Tetradiclis, Seetzenia*), most often eight to ten, arranged in an obdiplostemonous pattern and occasionally 15 stamens (*Nitraria, Peganum*). The gynoecium of five carpels (rarely two or three, and up to 12) has an axile placentation with a single to numerous ovules per locule. Fruit morphology is diverse and related to different dispersal strategies. The taxonomic subdivision of the family into subfamilies is largely based on fruit characters (Engler, 1931).

There are numerous problems in the delimitation of the family. The position of *Nitraria* and *Peganum,* as well as *Balanites* (uninvestigated) is debatable, as some authors prefer a segregation in different families. R. Dahlgren (1980, 1983) and G. Dahlgren (1989) suggested, without explanation, that the Zygophyllaceae should be split into four families, Zygophyllaceae, Nitrariaceae, Peganaceae, and Balanitaceae. However, Takhtajan (1980) kept *Peganum* in the Zygophyllaceae. Goldberg (1986) accepted two families, viz. Zygophyllaceae (including *Peganum*

and *Nitraria*) and Balanitaceae (with *Balanites*). For an overview of the taxonomic treatment of the Zygophyllaceae we refer to Sheahan and Cutler (1993).

The floral development of Zygophyllaceae has not been studied extensively; since earlier works (e.g., Payer, 1857; Beille, 1901) no recent studies have been carried out except the work of Eckert (1966) and our investigation on *Nitraria* (Ronse Decraene and Smets, 1991). The investigation of *Peganum harmala* aims to fill the gap in our knowledge of the family.

Peganum is a genus of five to six species distributed in the Old World from the Mediterranean to Mongolia and in the New World from Texas to Mexico. Differences between species are insignificant, except for size, habit, and fruit morphology. Some authors divide *Peganum* into two genera, *Peganum* and *Malacocarpus* with one species *M. crithmifolius* (Hutchinson, 1967; Sheahan and Cutler, 1993), while other keep *Malacocarpus* as a section of *Peganum* (Engler, 1931). We did not see material of *Malacocarpus* though there is little difference with *Peganum* in vegetative anatomy (Sheahan and Cutler, 1993). However, anatomical differences of *Peganum* and *Malacocarpus* with the other Zygophyllaceae are more important and would justify the separation of Peganaceae (Sheahan and Cutler, 1993).

The androecium of *Peganum* is another controversial point that needs clarification. The androecium of the Zygophyllaceae (Geraniales or Rutales) is currently described as obdiplostemonous with eight to ten stamens (Engler, 1931; Saunders, 1934, 1937; Kumar, 1976; Goldberg, 1986). Two genera, *Nitraria* and *Peganum,* differ in having more than ten (usually 15) stamens. *Peganum harmala* has 15 stamens arranged in five outer pairs opposite the petals and five inner stamens opposite the sepals. In a previous contribution we investigated the floral

ontogeny and anatomy of *Nitraria retusa* in order to understand the configuration of its androecium and to clarify the position of the genus relative to the Zygophyllaceae. The androecium of *Nitraria* is believed to be based on haplostemony, but with antesepalous triplets of stamens (Ronse Decraene and Smets, 1991). Within the Geraniales–Linales alliance, 15 stamens are not restricted to *Peganum* and *Nitraria* of the Zygophyllaceae, but are also occasionally found in other families such as Geraniaceae, Ixonanthaceae, Ctenolophonaceae, and Oxalidaceae.

In the present study, floral morphology, particularly of the androecium, of *Peganum harmala* is described and compared with earlier descriptions of *Nitraria* and other Zygophyllaceae. The androecial configuration of *Peganum* has been interpreted variously in the past. To some authors (e.g., Payer, 1857; Eichler, 1878) the unusual stamen number is caused by the "congenital" dédoublement of the antepetalous stamens. For others (e.g., Corner, 1946) the outer stamen pairs represent a stepwise reduction from an original multistaminate androecium with centrifugal development ("centrifugal obdiplostemony"); this would be an ancestral condition of the obdiplostemonous stamen configuration commonly found in other Geraniales.

Our study of the floral ontogeny and floral anatomy should reveal (1) whether the floral development of *Peganum* is comparable to that of *Nitraria* and other Zygophyllaceae, and (2) whether the androecial configuration of *Peganum* has the same origin as in *Nitraria,* and (3) whether a separation of *Peganum* from the Zygophyllaceae is justified. This research also contributes to the interpretation of the stamen pairs and the circumscription of obdiplostemony in general.

MATERIALS AND METHODS

Flower buds of *Peganum harmala* L. were collected in the South of Tunisia (Ksar Ouled Debbab) and on Jerba (Borj el Kébir) by the first author in April 1988. Plants of different sites did not differ morphologically. Pickled material (Ronse Decraene 303 L$_t$) as well as herbarium specimens (Ronse Decraene 932 and 956) are kept at the Laboratory of Systematics of the Katholieke Universiteit Leuven (LV). For fixation and preparation for the scanning electron microscope (SEM) and light microscopy (LM) we refer to Ronse Decraene and Smets (1991). Line drawings were made using a camera lucida installed on a Wild M12 microscope.

In order to determine the position of *Peganum* and *Nitraria* relative to the other Zygophyllaceae, we constructed a data set for cladistic analysis. This data set (Tables 1, 2) contains 43 macromorphological, anatomical, embryological, and biochemical characters. Within the Zygophyllaceae, eight genera were taken from six of the seven subfamilies of Engler (1931), viz. *Peganum* (Peganoideae), *Morkillia* (Chitonioideae or Morkillioideae), *Augea* (Augeoideae), *Tribulus, Zygophyllum,* and *Fagonia* (Zygophylloideae), *Nitraria* (Nitrarioideae), and *Balanites* (Balanitoideae). Following Takhtajan (1980, 1983), we added one genus of Rutaceae (*Ptelea*) and one genus of Simaroubaceae (*Quassia*) as outgroups. The data for *Peganum, Nitraria, Tribulus, Fagonia,* and *Zygophyllum* were partly obtained from our own observations of pickled or herbarium material (Ronse Decraene, personal observations; Ronse Decraene and Smets, 1991) and partly from literature. The data for the other genera are compiled from literature (mainly Engler, 1931; Hegnauer, 1973; Corner, 1976; Ronse Decraene and Smets, 1991; Vijayalakshmi Sarma and Raja Shanmukha Rao, 1991; Sheahan and Cutler, 1993).

TABLE 1. Characters and character states used in the cladistic analysis of the Zygophyllaceae.

0 habit: shrubs (or trees) (0) herbs (1)
1 thorns homologous to stems: absent (0) present (1)
2 leaves: simple (0) compound with odd number of leaflets (1) compound with even number of leaflets (2)
3 insertion of leaves: opposite (0) alternate (1)
4 stipules: absent (0) present (1)
5 multicellular trichomes: absent (0) present (1)
6 unicellular trichomes: absent (0) present (1)
7 inflorescence: racemose (0) cymose (1) flowers solitary (2)
8 sepal aestivation: contorted (0) valvate (1)
9 sepals: not small in bud (0) small in bud (1)
10 sepal lateral traces fused with petal traces: no (0) yes (1)
11 calyx: deciduous (0) persistent (1)
12 petal aestivation: valvate (0) contorted (1)
13 petals: not cucullate (0) cucullate (1)
14 petals: not clawed (0) clawed (1)
15 petals: not retarded in growth (0) retarded in growth (1)
16 antepetalous stamen traces fused with petal traces: no (0) yes (1)
17 stamen configuration: haplostemony (0) obdiplostemony (1)
18 filaments: not basally fused (0) basally fused (1)
19 staminal appendages at base of filament: absent (0) present (1)
20 nectaries: absent (0) receptacular, disc-like (1) receptacular, not disc-like (2)
21 gynoecium: tricarpellate (0) tetracarpellate (1) pentacarpellate (decacarpellate in *Augea*) (2)
22 ovary semi-immersed in disk: no (0) yes (1)
23 ovary shape: pyriform (0) globose (1)
24 style: not very short (0) very short (1)
25 stigma: confined to top of style (0) spreading along fused margins (1)
26 ventral bundles in gynoecium: not paired (0) paired (1)
27 dorsal traces in gynoecium: 1–2 per carpel (0) >2 per carpel (1)
28 ovules per carpel: one (0) >1, in two series (1) >1, not in two series (2)
29 ovule insertion on axile placenta: basal (0) median (1) apical (2)
30 ovule curvature: syntropous (0) antitropous (1) (see Endress, 1994)
31 fruit: drupaceous (0) capsular (loculicidal dehiscence) (1) schizocarp with mericarps (2)
32 embryo: straight (0) curved (1)
33 endosperm: absent (0) present (1)
34 cotyledons: thin (0) thick (1)
35 crystal cells in testa: absent (0) present (1)
36 lignified cells in endotegmen: absent (0) present (1)
37 leaf epidermal cell shape: rectangular-elongated (0) polygonal (1) irregular (2)
38 brachysklereids: absent (0) present (1)
39 axial parenchyma: absent (0) present (1)
40 rays: absent (0) uniseriate (1–3 cells wide) (1) multiseriate (>3 cells wide) (2)
41 saponins: absent (0) present (1)
42 quercetin: absent (0) present (1)

In a first step, a standard parsimony analysis with equal weighting of all characters was carried out using NONA (Goloboff, 1993b). In a second analysis, the characters were weighted by means of implied weights (Goloboff, 1993a, c), a technique in which characters are non-iteratively weighted during tree search according to their homoplasy. This was carried out with the computer program Pee-Wee (Goloboff, 1993c). In both cases multistate characters were treated as unordered (Hauser, 1992). Apart from this, all other default settings were retained. Polymorphisms are treated as such in both computer programs (subset coding). The most parsimonious cladograms were obtained using the instruction MULT*25. This instruction carries out 25 replications of randomizing the taxa, creating a Wagner tree and submitting it to branch-swapping by means of tree-bissection reconnection.

TABLE 2.   Data matrix. The numbers of the characters and the character states refer to Table 1. Polymorphisms are indicated between square brackets; "?" indicate missing values and inapplicable characters.

	0	12	3	4567	11 8901	11111111 23456789	22 01	22 23	2222 4567	22333333333344 89012345678901	4 2
Quassia	0	01	1	0110	0101	10010101	12	01	0011	01120010001110	0
Ptelea	0	01	[01]	0??0	0101	1001?000	10	01	1010	101201000??1?1	1
Nitraria	0	10	1	1011	1111	01000000	20	00	1101	0210000??10110	0
Peganum	1	00	1	1101	0111	10001100	10	11	0011	12111100100000	?
Balanites	0	12	1	1011	0000	10000100	12	10	1011	02100010011121	1
Tribulus	1	02	[01]	1011	000[01]	1001011[01]	12	01	1110	1001000112111[01]	1
Fagonia	[01]	0[01]	0	1012	000[01]	10111110	02	0[01]	0011	10010101011111	[01]
Zygophyllum	[01]	0[02]	0	1012	0010	10111111	1[12]	01	001[01]	1011010101111[01]	1
Morkillia	0	01	[01]	1012	00?0	100??100	?1	00	00??	21?1110??21110	?
Augea	1	00	0	000[12]	0001	000?1101	12	00	1000	2111?011?10111	?

RESULTS

Initiation of the flower bud and sepals—Flowers appear in dichasia that are grouped in thyrses. Floral buds arise laterally on the main inflorescence axis between a bract (pherophyll) and two bracteoles (prophylls) (Figs. 1, 2). A hemispherical primordium emerges opposite each bract primordium (Figs. 1, 2). From this primordium two lateral bracteoles arise successively (Figs. 1–3). They enclose a floral bud laterally and are pressed against the main inflorescence axis by the larger bract. In the axil of each bracteole a younger secondary flower bud develops successively (Figs. 3, 4). Each lateral flower is also enclosed by two secondary bracteoles, which arise sequentially (Fig. 3). The process of floral initiation is thus repeated in a basipetal sequence. The sepal primordia arise rapidly in a regular spiral (2/5) sequence (Figs. 3, 4). The first primordium arises in an adaxial position. The next primordium emerges on the abaxial side in a lateral position. The third primordium arises next to the first. These initial primordia rapidly increase in size and start overgrowing the floral apex by the time the last sepal primordia form. It was difficult to distinguish between sepal primordia and bract primordia; that is, the separation of inflorescence and flower inception is not clear. All sepals develop as narrow, free, laciniate primordia, which overgrow the floral apex and enclose the bud completely in an imbricate aestivation. The sepals rapidly become almost equal in size and envelop the floral apex, which has become clearly five-angled (Figs. 5, 6, 8). Sepal growth exceeds the inner flower primordium (Figs. 17, 22). At the time the petals take over the protective function the erect sepals enclose the bud loosely (Figs. 17, 20, 22). Each sepal becomes covered on its adaxial surface with numerous multicellular and capitate trichomes (Figs. 17, 22). These trichomes are similar to those on the vegetative parts of the stem and inflorescence. Sepals may be curved abruptly in the middle with an angle of ≈90° (Fig. 22). Sepals, as well as leaves on the stem, bracts, and bracteoles bear stipules at their base (Fig. 22).

Initiation of the petals—As the sepals start to cover the floral bud, the corners of the flattened, nearly pentagonal floral apex start to bulge out into five broad protuberances (Figs. 5, 6). These protuberances, the petal primordia, become progressively flattened and grow into a weak cowl (Figs. 7, 8). Petal primordia arise almost simultaneously, though one side of the flower bud may precede the other (Figs. 5, 8). This unequal size may persist in older stages (Figs. 12, 14). Later the apical parts of the petals arch inwardly (Figs. 10, 12, 14). Petal primordia are slightly asymmetrical by unequal growth (Figs. 12, 16). The primordia only start to hide the apex at the inception of the carpels (Figs. 12, 17). They remain free at the base and have an imbricate-contorted aestivation (Figs. 16, 19). At maturity petals develop a weak dorsal crest (Figs. 14, 16).

Initiation of the androecium—Immediately after or simultaneously with the inception of the petal primordia, five stamen primordia emerge in antesepalous positions about halfway up the apical meristem (Fig. 6, arrows). The initiation of stamen primordia is usually simultaneous but can be sequential; in one case a stamen primordium was larger on the adaxial side of the apex (Fig. 8). Also in older buds stamens may have different sizes, suggesting a sequential initiation (Fig. 10). As soon as the inception of the antesepalous stamens is completed, two smaller primordia arise opposite each of the petals and are pressed in the limited space between antesepalous stamens and petals (Figs. 7–9). The time of inception of each primordial stamen pair relative to the initiation of another pair may be variable (Figs. 7–9). Stamen primordia in each pair are closely linked and are oriented obliquely toward each other (Figs. 10, 11, 13). This oblique insertion and growth is accentuated in later stages (Figs. 13, 14). This may lead to the impression that each antepetalous stamen of one pair belongs to a triplet formed by a large, central, antesepalous stamen and two smaller, lateral, antepetalous stamens (Figs. 13, 14). The stamen primordia become progressively covered by the petals and are pressed toward the center of the flower, covering the gynoecium by their apices (Figs. 13, 14, 18). Each stamen develops a broad triangular anther primordium. The inner stamen primordia, that is, the antesepalous ones that arise before the antepetalous pairs, are larger and touch each other centrally over the young gynoecium (Figs. 13, 14, 18); the outer antepetalous stamen primordia remain smaller at first (about two-thirds the size of the inner stamens; Figs. 14, 15, 17, 18). Before anthesis the outer antepetalous stamen primordia increase dramatically in size and overtop the inner stamens, which are squeezed between the outer stamens and the developing style (Fig. 20). Anthers are linear-oblong, crescen-

tic, dithecal structures, and a stout filament is formed at the time of inception of the style (Figs. 18–20). Filament bases are inflated at anthesis.

Initiation of the gynoecium and the nectary—When all stamens have been initiated, the central area of the floral apex develops as a pentangular platform (Figs. 10, 12). Soon the five angles become distorted by the appearance of three flat protuberances that are unevenly distributed on the pentagon (Figs. 11, 13, 15). The protuberances rapidly grow into three horseshoe-shaped carpel primordia. The shape of the pentagon is still visible as the three carpels become clearly demarcated. Two carpel primordia are closer together than the third, leaving a naked area on the platform (Fig. 15). By growth of the peripheral tissue of the primordia three small depressions are formed and become progressively enclosed by the surrounding carpellary tissue (Figs. 15, 18). The three carpel primordia are lifted by common peripheral growth; they extend upward as elongated closely pressed fingers, and the original division between primordia is only visible as a long slit. The three septa, which arise from the fused lateral walls of the carpels, become axially joined. A single clublike style is thus differentiated and grows upward through the overarching inner stamens (Figs. 20, 21). At fruiting the style splits open into twisted segments corresponding to the carpels. The ovary is globose and clearly separated from the style; it encloses numerous ovules inserted in paired rows (Fig. 19). Placentation is axile where the septa have met in the center of the gynoecium (Figs. 19–21). An apical concentration of the ovules results from the elongation of a column in the lower part of the locule (Figs. 21, 23). The anatropous ovules arise in four equal rows on each placenta (Figs. 19, 21, 23). Later, the lower ones hang down to fill up the locular cavity in its lower section.

A weak intrastaminal disc-like nectary develops around the base of the gynoecium (Figs. 21, 23). A number of stomata occur on the surface of the nectary. The mature ovary is situated in a depression formed by the raised nectary, stamens and perianth parts (Fig. 20, 23).

Floral anatomy—The pedicel contains a eustele with ten collateral bundles separated by considerable interfascicular parenchyma (Fig. 24); four bundles may be situated closer to each other and be superficially continuous in transverse sectional view (Fig. 24, arrows). Higher up in the pedicel the bundles become arranged in a sinuous circle as the outline of the three outer sepal bases becomes visible (Figs. 25, 26). A few micrometres higher, one of the bundles diverges to the periphery; a second and a third one follow soon, and at a higher level a fourth and fifth (Figs. 25, 26); they ultimately yield the median traces of the sepals. A higher section shows the five di-

verging bundles in the base of the receptacle, alternating with five larger inner areas of vascular tissue (Fig. 27).

Two small lateral traces become visible next to the firstly diverging median sepal trace (Figs. 26, 27). They depart within the parenchymatous tissue without connection with the central stele. These laterals may occasionally divide into a number of small traces but reunite at a higher level (Figs. 27 [arrow], 28).

The five remaining bundles alternating with the sepal median traces extend tangentially and become reorganized into an inner star-shaped ring (Fig. 28). The five angles of this inner ring run into two ventral loops or clear invaginations of tissue (Fig. 29, arrow). These are detached from the ring and contribute to a second inner, triangular ring (Figs. 30, 31). In this way the ring is divided in ten units; five large horseshoe-shaped bundles are left in the angles, while five smaller traces are detached opposite the median sepal traces (Figs. 30 [arrow], 31). These traces constitute the supply for the antesepalous stamens. At the same level the second triangular ring is sectioned in three outer arcs of tissue in the angles of the triangle (the dorsals) and three alternating inner arcs of vascular tissue (the ventrals; Figs. 31, 32). At a higher level the horseshoe-shaped bundles divide into three units; two lateral traces are separated as the antepetalous stamen traces. The resultant central trace is made up of the supply to petals and commissural sepal lateral traces (Figs. 31, 33).

Centrally, the outer arcs of tissue around the ventrals break up into numerous traces. A slightly darker area of small cells can be seen at this level, inside the stamen traces (Fig. 32, broken line). This constitutes the nectariferous tissue surrounding the base of the gynoecium. Petal–sepal lateral bundles branch into their respective units (Fig. 33). The antesepalous filaments are detached by a gap in the nectarial tissue; on each side of the antesepalous stamen an antepetalous stamen joins in (Figs. 33, 34). The sepals are also separated from the central core of tissue, but remain linked with the petals for some distance (Fig. 33). At this level the carpellary tissue is completely detached from the receptacle. The external traces are arranged in a continuous ring, which we termed dorsals (Fig. 36). The alternating, centrally placed bundles represent the ventrals; higher up the ventrals are detached as groups of two units that converge centrally and proceed toward the placentae, dividing repeatedly (Figs. 35, 36). In each of the three locules four rows of small ovules are attached pairwise on each placental ridge (Figs. 33–36). All bundles run throughout the ovarian wall and into the massive cylindrical style. The paired ventrals converge centrally and end blindly in the style (Fig. 36).

Petals are detached as flat appendages with a dorsal crest (Fig. 34), that are disposed in an imbricate-contorted

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Figs. 1–8. SEM micrographs of the inflorescence and floral buds of *Peganum harmala* during sepal, petal, and stamen initiation. **1.** Lateral view of main inflorescence axis showing initiation of a lateral branch between a bract and two bracteoles; arrow points to a lateral stipule primordium. **2.** Lateral view of a secondary inflorescence. Note the successive appearance of bracts (numbers) with the initiation of flower primordia in their axil. **3.** Apical view of young flower at the initiation of the sepals (numbers); bracts removed. Note the successive initiation of lateral flowers subtended by bracteoles. **4.** Apical view of older bud showing the progressive covering of the apex by the sepals. **5.** Early initiation of the petal primordia. Note that the adaxial side precedes the development of the other side; all sepals (numbers) except sepals four and five removed. **6.**
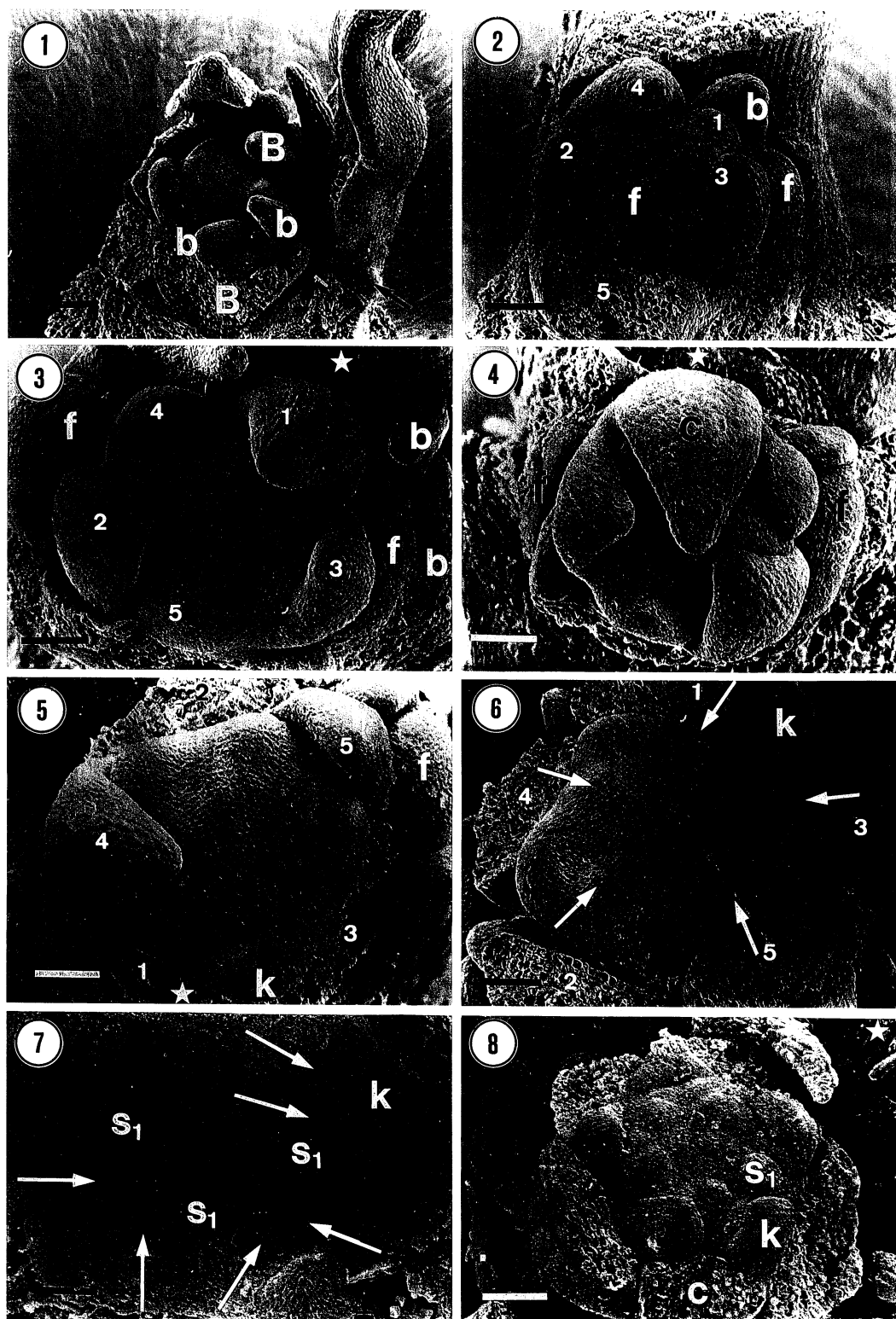
Lateral view at the initiation of five antesepalous stamen primordia (arrows) alternating with five petal primordia; all sepals (numbers) removed. **7.** Partial apical view at the initiation of the antepetalous stamen primordia (arrows). **8.** Slightly older bud showing unequal size of the antesepalous stamens and petals. All bars = 58 μm, except Fig. 1: bar = 114 μm and Fig. 7: bar = 29 μm.

Figure abbreviations: B, bract; b, bracteole; C, sepal; CB, common bundle to petals, sepal laterals and antepetalous stamens; C_M, sepal median trace; C_L, sepal lateral trace; C_W, carpel wall; D, dorsal traces; f, flower bud or lateral flower primordium; G, carpel primordium; K, petal primordium or petal trace; L, smaller sepal lateral trace; N, nectary; O, ovule; OS, ovule supply; P, placenta; S_1, inner (antesepalous) stamen; S_2, outer (antepetalous) stamen; V, ventral traces. The adaxial side of the flower is shown with an asterisk.
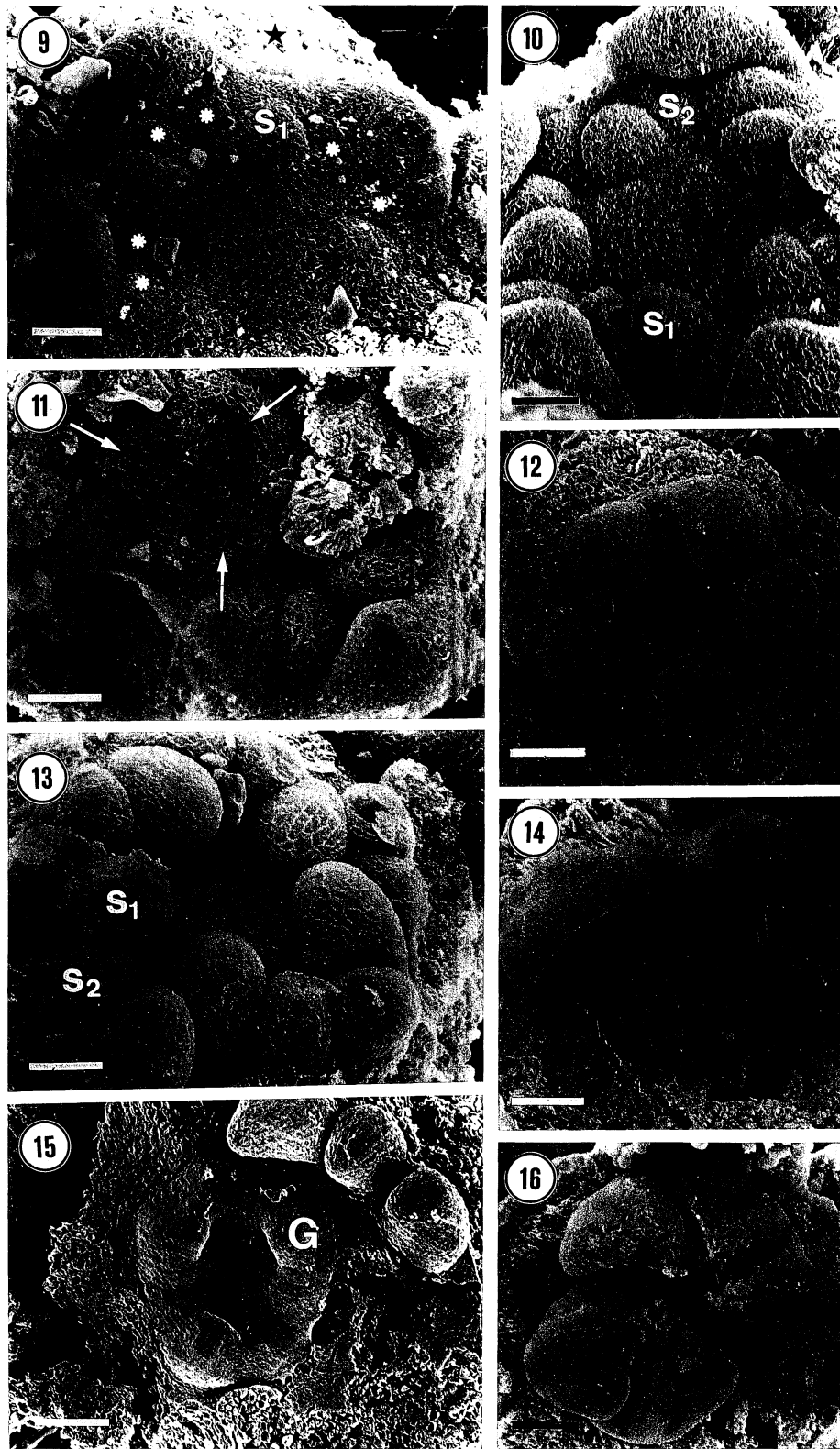
Figs. 9–16.   Floral development of *Peganum harmala* at stamen and carpel initiation (sepals removed in all figures). **9.** Partial view of a flower bud; sepals removed. Three pairs of antepetalous stamen primordia are visible (white asterisks). **10.** View of older bud. Note the central pentagonal apex and oblique growth of the antepetalous stamens. **11.** Formation of three unequal carpel protuberances (arrows). **12.** Similar but older view as Fig. 10 with pentagonal gynoecial apex. Note the growth of the petals. **13.** Unequal inception of three carpel primordia visible between the overarching stamen primordia. **14.** Lateral view with the overtopping of the gynoecium by the stamens. **15.** Apical view of developing gynoecium. Note the three unevenly distributed carpel primordia. **16.** Apical view of flower bud showing the contorted aestivation of the crested petals. All bars = 29 μm, except Figs. 12 and 14: bar = 59 μm and Fig. 16: bar = 115 μm.
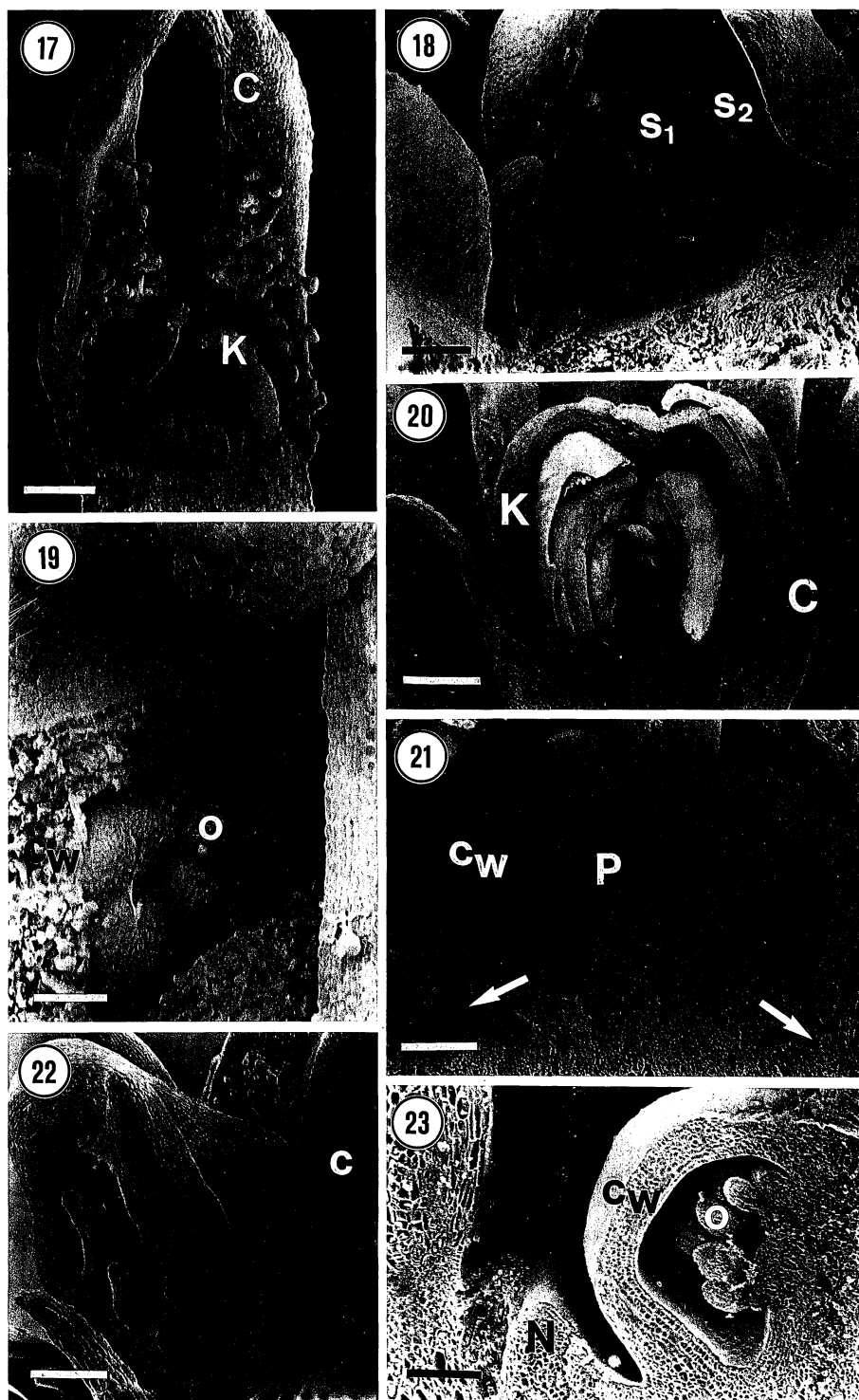
Figs. 17–23. Floral buds of *Peganum harmala* prior to anthesis. **17.** Lateral view of nearly mature bud; some petals and sepals removed. Note the large erect sepals with stalked trichomes on their inner surface. Bar = 114 μm. **18.** Development of stylar tissue by the growth of the dorsal part of the carpel primordia; some stamens removed. Note the overtopping of the antesepalous stamen primordia by the antepetalous stamen primordia. Bar = 114 μm. **19.** View of two rows of ovules within a locular chamber. Bar = 29 μm. **20.** Longitudinal section through a nearly mature flower. Bar = 450 μm. **21.** Longisection through the ovary. Note the axile placentation. Arrows point to the nectary. Bar = 228 μm. **22.** Lateral view of nearly mature bud. Note the characteristic curving of the sepals and presence of stipules. Bar = 228 μm. **23.** Longisection through part of the flower. Note the invagination of the gynoecium surrounded by the nectary. Bar = 114 μm.
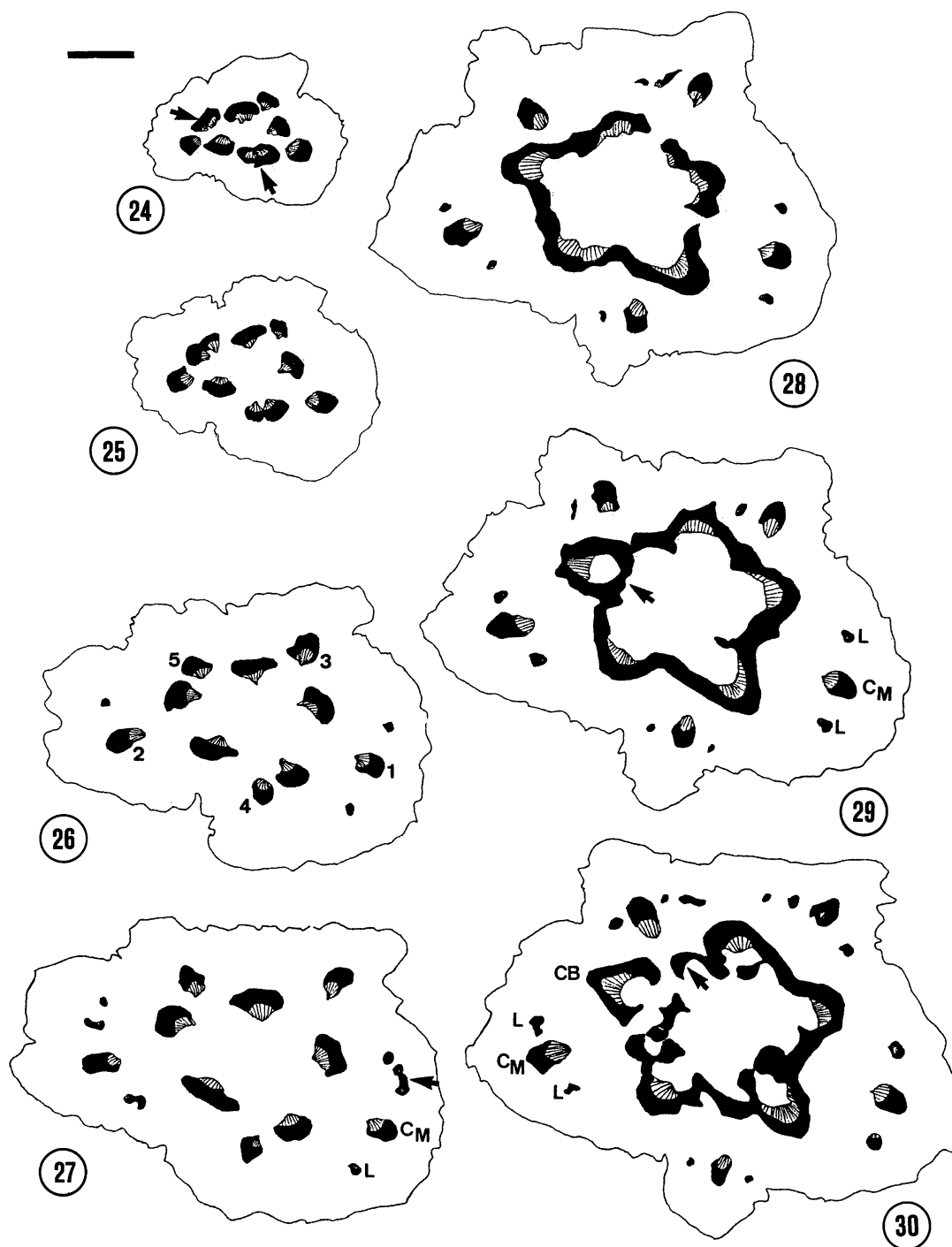
Figs. 24–30. Successive camera lucida drawings of transverse sections of the flower of *Peganum harmala.* Xylem shown by a radial striation (xylem not shown in Figs. 33, 35, 36); the distance between successive sections is indicated in micrometres, starting at Fig. 24. Bar = 120 μm. **24.** Section at the base of the flower (upper part of the pedicel) with dissected eustele consisting of ten bundles. Note two laterally fused pairs (arrows). **25.** Section 100 μm higher. Divergence of bundles corresponding to sepals and separation of fused bundles. **26.** Section 200 μm higher. Separation of five sepal median traces. The numbers indicate the order of separation; note the appearance of small lateral traces next to the sepal medians. **27.** Section 110 μm higher. Lateral extension of remaining central bundles. The laterals of the sepals may occasionally branch (arrow). **28.** Section 90 μm higher. The central bundles extend laterally to form a continuous girdle. **29.** Section 40 μm higher. Formation of central invaginations lateral of each xylem element, which become connected into loops (arrow). **30.** Section 30 μm higher. The girdle breaks up in separate sections; the inner section moves to the center. Note the separation of an antesepalous stamen trace (arrow).
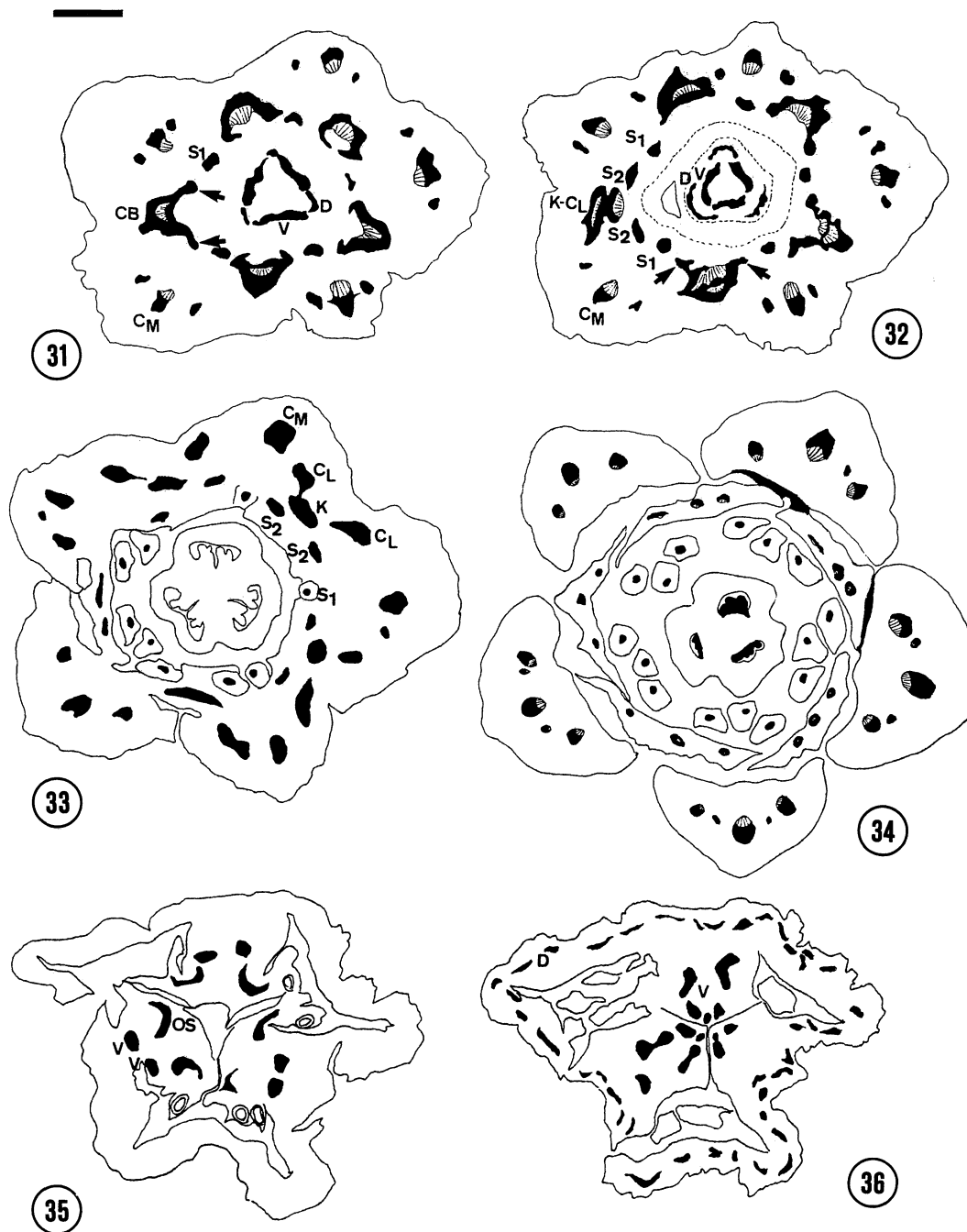
Figs. 31–36. Camera lucida drawings of successive transverse sections of the flower of *Peganum harmala*. (Same remarks as for Figs. 24–30). Bar = 160 μm, except for Figs. 35, 36 where bars = 150 μm. **31.** Section 50 μm higher than Fig. 30. Separation of five antesepalous traces (S₁), formation of central triangle, breaking up in ventrals and dorsals. Note the lateral extensions on the large common bundle. **32.** Section 50 μm higher. Breaking-up of common bundles in a petal trace, sepal lateral traces, and two lateral stamen traces (S₂). The arrow points to the separation of S₂; the broken line represents the darkly staining nectary. **33.** Section 60 μm higher. Separation of gynoecium and stamens from the receptacle. The sepal laterals diverge toward their respective sepals and may occasionally fuse with the smaller laterals. Note the pairs of ovules. **34.** Section 120 μm higher. Separation of sepals and petals. Note the arrangement of stamens in triplets. **35.** Detail of the gynoecium; dorsal traces have been omitted. Note paired ventral bundles and divergence of traces to the placentae and ovules. **36.** Section through the upper part of the gynoecium. The ventral bundles converge toward the center.

manner. In each petal the trace trifurcates into a median and two lateral traces (Figs. 33, 34). Sepals are distinctly triangular units with three to five traces and cover the flower in a valvate arrangement (Fig. 34). At this level stamens appear grouped in antesepalous triplets.

Cladistic analysis—In the unweighted analysis a single most parsimonious tree of 97 steps (Fig. 39) with an ensemble consistency index of 0.53 and an ensemble retention index of 0.42 was obtained. Using implied weighting, this is also the cladogram with highest total fit for a
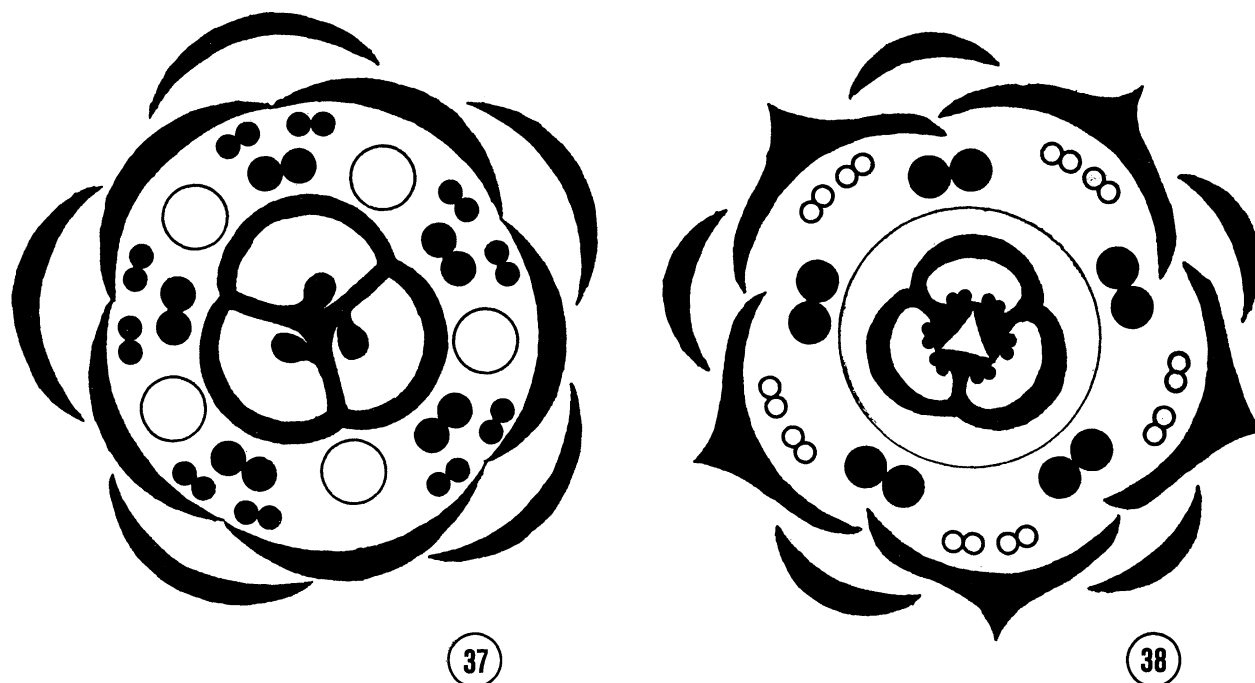
Figs. 37–38. **37.** Floral diagram of *Nitraria retusa* L. (arcs, sepals and petals; paired black dots, stamens; hollow circles, nectary). **38.** Floral diagram of *Peganum harmala* L. (arcs, sepals and petals; paired white dots, antepetalous stamens; paired black dots, antesepalous stamens; hollow circle surrounding gynoecium, nectary).

concavity constant K between 2 and 6. For $K = 3$, the total fit equals 281.5 and the implied weights vary between 6 and 10. With $K = 1$ (i.e., relatively stronger downweighting of homoplasy) a different fittest cladogram was obtained (Fig. 40; the total fit is 201.3, the implied weights vary between 2.5 and 10).

DISCUSSION

Floral development—Flowers of *Peganum* have been studied ontogenetically by Payer (1857), Beille (1901), and Eckert (1966), as well as anatomically in several other studies (Beille, 1901; Saunders, 1931, 1934; Nair and Nathawat, 1958; Eckert, 1966; Kumar, 1976). Payer (1857) noted that in *Peganum harmala* the five antesepalous stamen primordia emerge before the antepetalous primordia. We confirmed his observation that the ten antepetalous stamens arise as independent entities centrifugally to the antesepalous stamens. Beille (1901) mentioned that a stamen–petal complex is initiated in *Peganum harmala*; the primordium was said to split radially into two halves and the inner section to split laterally again into two antepetalous stamens. We could not confirm his observations in our study.

The floral inception and vasculature demonstrate that each stamen pair is an integral part of the antepetalous flower sector and has not arisen by the division of the antesepalous stamens, for the following reasons. Firstly, the stamen pairs emerge clearly opposite the petals (Figs. 7, 9) and are independent from the antesepalous stamens. Antepetalous stamen primordia of one pair usually grow at equal rate, possibly differing from a neighboring pair in size, which indicates that one cannot mix up stamens from different pairs. Within each pair stamens grow to-

ward each other and appear as a unit (Figs. 10, 11, 13). Secondly, the vasculature of the antepetalous stamens is usually connected to that of the petals and is independent of that of the antesepalous sector. Antesepalous stamen traces are detached at a lower level in the flower by the fragmentation of the vascular girdle (Fig. 30); antepetalous stamen traces are derived from the common sepal lateral-petal supply (Figs. 31, 32, 33).

Most members of the Zygophyllaceae have an obdiplostemonous androecium. Indeed, diplostemony or obdiplostemony are ubiquitous in the Geraniales-Rutales-Linales complex (Ronse Decraene and Smets, 1987, 1995). There is no other alternative for interpreting the stamen pairs of *Peganum* than as the result of a secondary increase, as they would otherwise not fit within the widespread pattern of two-whorled androecia. *Peganum* is derived from an obdiplostemonous androecium via a secondary increase of the antepetalous stamens. Eckert (1966, pp. 549–550) reaches the same conclusions: "Zwei Kronstamina von *Peganum* entsprechen ungefähr einem Kronstaubblatt von *Tribulus* oder *Zygophyllum*."

Recently, several authors have demonstrated that obdiplostemony is often a derived phenomenon brought about by different growth rates between the antepetalous and antesepalous stamens and by a displacement of primordia (e.g., Leins, 1964; Eckert, 1966; Gelius, 1967; Eckardt, 1963; Mayr, 1969; Klopfer, 1968, 1972, 1973). In all these cases the antepetalous stamens are initiated more centrally or at the same level as the antesepalous stamens as is current for diplostemonous flowers. At later stages of development differential growth rates between the antepetalous and antesepalous sectors re-orient the antepetalous stamens to the periphery. We observed a sim-

ilar development in members of the Zygophyllaceae, such as *Zygophyllum album* L., *Tribulus terrestris* L. (L. P. Ronse Decraene, unpublished data) and *Fagonia cretica* L. (Ronse Decraene and Smets, 1995). These species show the initiation of antepetalous and antesepalous stamen primordia at the same level. Later displacements of the stamen primordia make the androecium appear obdiplostemonous. According to Eckert (1966) the antepetalous stamen pairs of *Peganum* similarly arise at the same level as the antesepalous stamen primordia. In later stages the antepetalous stamens are said to be pressed to the outside. However, our observations on *Peganum harmala* contradict those of Eckert (1966) and demonstrate that the antepetalous stamen primordia are initiated outside of the antesepalous stamens and are not pushed to the periphery by a process of displacement (Figs. 7–10). Thus, the obdiplostemonous androecium of *Peganum* clearly arises in a manner different from the other Zygophyllaceae. The antepetalous stamens are initiated centrifugally to the antesepalous stamens on a meristematic area between antesepalous stamens and petals. Such development was described by Corner (1946) as "centrifugal obdiplostemony" (see below). Dickson (1865) derived obdiplostemonous flowers by a congenital fusion in pairs of the outer stamens of *Monsonia* (Geraniaceae). He interpreted the outer stamens as secondarily derived lateral lobes of the inner stamens, comparable to interpetiolar stipules. Another, more plausible explanation is that the centrifugal appearance of the antepetalous stamens in *Peganum* is linked with a retardation in development of the antepetalous sector. Therefore, antepetalous stamen primordia are initiated later and more externally to the antesepalous stamen primordia on a limited area of the floral apex. A secondary increase makes the androecium of *Peganum* polyandrous; one cannot escape the fact that the presence of stamen pairs is a derived condition in diplostemonous groups (see also Ronse Decraene and Smets, 1992; Endress, 1994).

The example of *Peganum* shows that everything has not been elucidated yet about obdiplostemony (see also Ronse Decraene and Smets, 1987, 1995). Floral development in other unusual Geraniales with 15 stamens, especially in relation to their floral vascular arrangement, should be studied.

Besides the fact that the androecium is obdiplostemonous, the origin of the stamen pairs has been interpreted variously in the past. Payer (1857), Baillon (1874), and Eichler (1878) on the one hand considered the antepetalous stamen pairs to have arisen by "congenital dédoublement." This means that the stamens do not arise as the result of splitting of a complex primordium during floral ontogeny but arise as paired but independent structures (see Ronse Decraene and Smets, 1993). It was believed that a visible process of splitting had occurred in an ancestral stage but that it has vanished in the extant species. Corner (1946) on the other hand derived the androecium of *Peganum* (and all other cases with 15 stamens) from an original centrifugal androecium. In this case *Peganum* is considered as a transitional form in a reduction series, leading from a multistaminate androecium to a two-whorled androecium. However, it remains difficult to interpret the androecium of *Peganum* as an-

cestral to that of other Zygophyllaceae with obdiplostemonous flowers.

The idea that the dédoublement occurred "congenitally" is vague and confusing; it cannot be checked because it links a phylogenetic step with an ontogenetic process (Ronse Decraene and Smets, 1993). Moreover, it is unnecessary to invent a process such as "congenital dédoublement" to explain the paired position of the antepetalous stamens, when the inception of the two primordia occurs independently. The occurrence of paired stamens in *Peganum* most probably arose de novo from originally single stamens in its ancestor. It is possible that a sudden switch happened in the evolution of the androecium leading to the initiation of two smaller stamens instead of one. No process of splitting has to be involved in this case. However, this does not exclude the idea that a flower with 15 stamens is derived from an obdiplostemonous ancestor. As we have discussed for *Nitraria* (Ronse Decraene and Smets, 1991) the distinction between the inception of complex (primary) primordia splitting in two or more (secondary) primordia, and the independent inception of two or more (secondary) primordia, can be explained as extremes of a gradation or as an example of the concept of variable proportions (sensu Troll, 1956). The outer stamens of *Peganum* and other similar species can be explained in the same way; no phylogenetic speculations such as "congenital dédoublement" are needed.

In other Geraniales certain families have genera with the same floral construction as in *Peganum* (e.g., *Monsonia* and *Sarcocaulon* in Geraniaceae: Payer, 1857; Saunders, 1937; *Hypseocharis* in Oxalidaceae: Saunders, 1937; Rama Devi, 1991; *Ixonanthes* in Ixonanthaceae: Narayana and Rao, 1966). In these taxa the "doubled" stamens occupy the space that is available in a given flower sector (usually the antepetalous). More should be known about their floral development.

Petals of *Peganum* are not retarded in their ontogeny (cf. Eckert, 1966). This corresponds to a similar development of *Nitraria* (Ronse Decraene and Smets, 1991) and differs from the common situation in the Zygophyllaceae (Eckert, 1966; L. P. Ronse Decraene, personal observations). Whether this has much significance can only be inferred by the ontogenetic study of a wider group of genera of the Zygophyllaceae (see below). The same developmental difference has been used for discussing the relationship of the Hydrangeaceae to the Saxifragaceae (see Eckert, 1966; Klopfer, 1973). The gynoecium of *Peganum* is trimerous. However, the pentagonal primordial shape and uneven distribution of the three carpel primordia seem to indicate that the trimerous gynoecium of *Peganum* has been derived by the loss of two carpels. The general morphology of the gynoecium of *Peganum* closely resembles that of most other Zygophyllaceae in its globose ovary with long style and confined stigmatic area, and axile placentation with two rows of ovules within each locule.

Floral vasculature—The vascular anatomy of the paired stamens of *Peganum* has been the subject of many studies and provides a more consistent scheme of discussion than the ontogeny. Kumar (1976) on the one hand found that the antesepalous stamen traces run always independently of the antepetalous traces. He also believed

that the antepetalous traces are either linked with the petal traces (*Monsonia*: Geraniaceae; see also Narayana and Arora, 1963), or run independently (*Peganum*). On the other hand, Beille (1901), Saunders (1934, 1937), and Eckert (1966), as well as this study (Figs. 31, 32), confirmed that there are common traces for the antepetalous stamens and petals in *Peganum*. Saunders (1931, 1937) described a similar situation for other members of Geraniales with paired stamens (e.g., *Monsonia, Sarcocaulon, Hypseocharis*). Rama Devi (1991) also pointed to differences in the vascular arrangement of different genera of Geraniales. *Hypseocharis* shares a similar complex of fused traces to petals, sepal laterals, and antepetalous stamen pairs with *Peganum*. Nair and Nathawat (1958) stated that the antepetalous stamen supply in *Peganum* is delimited before the antesepalous traces, but that the traces are independently derived from the angles of gaps formed by the petal traces. We found that the antesepalous traces were derived below the antepetalous traces by the fragmentation of the outer vascular ring (Figs. 30, 31).

It is clear that opinions diverge considerably about the origin of traces, as their departure from the stele can be variable or difficult to detect. However, all agree that the antepetalous stamen traces are more or less independent of the antesepalous traces. It must also be kept in mind that the variable fusions of petal traces with antepetalous stamen traces are often correlated with a displacement of stamen primordia, the tendency to build a hypanthium by invagination of the gynoecium, compressions within the flower, and lack of space. The nearer two primordia are initiated, the more likely is the fusion of their traces.

Cladistic analysis and conclusion—Zygophyllaceae are monophyletic on both reported cladograms (Figs. 39, 40). Presence of stipules, a cymose inflorescence and capsular fruits with loculicidal dehiscence are unambiguous synapomorphies for the family on both trees (i.e., these states are synapomorphies under every possible optimization of those characters). On the cladogram with strong weighting against homoplasious characters (Fig. 40), simple leaves are an additional unambiguous familial synapomorphy. Among the symplesiomorphic states are the woody habit, alternate leaves, an obdiplostemonous stamen configuration with filaments that are not basally fused, a gynoecium with numerous dorsal traces and paired ventral bundles.

In both reported cladograms the basal division within the Zygophyllaceae separates *Peganum* from the other genera. On the basis of the high number of character state changes on the branch leading to *Peganum,* the recognition of a separate family Peganaceae might be defended. However, such long branches can also be an indication that taxon sampling was inappropriate, i.e., *Peganum* may actually belong outside the sampled Zygophyllaceae, or its placement inside the family can only be understood by more extensive sampling. In both trees, the fusion of the sepal lateral traces and the petal traces in *Peganum, Nitraria,* and *Zygophyllum* is a convergent similarity; it is ambiguous whether the rapid petal growth in *Peganum* on the one hand and *Nitraria* and *Balanites* on the other is homologous or convergent.

The position of *Fagonia, Zygophyllum,* and *Tribulus*

on the most parsimonious tree supports their inclusion in the same subfamily. On the tree with strong weighting against homoplasious characters, *Augea* and *Morkillea* are also included in this clade. This is in line with the results of Sheahan and Cutler (1993), who found little evidence in vegetative anatomy to separate Morkillioideae and Augeoideae from Zygophylloideae. The close relationship between *Fagonia* and *Zygophyllum* is also supported by wood anatomical evidence (Fahn, Werker, and Baas, 1986).

Balanites and *Nitraria* are sister groups on both trees. The presence of thorns that are homologous to stems, the single ovule per carpel (two degenerate at maturity, leaving only one in each flower), and the drupaceous fruit are unambiguous synapomorphies. On the most parsimonious cladogram, the apical insertion of the ovule on the placenta is an additional unambiguous synapomorphy. It is known that *Balanites* differs from the Zygophyllaceae by its embryology (Nair and Jain, 1956; Boesewinkel, 1994), the presence of S-sieve tube plastids (Behnke, 1988) and details of vegetative anatomy (Sheahan and Cutler, 1993). It resembles the family in its floral anatomy (Nair and Jain, 1956), epidermal characteristics (Vijayalakshmi Sarma and Raja Shanmukha Rao, 1991), and flavonoid composition (Maksoud and El-Hadidi, 1988). Its retention in Zygophyllaceae is supported by our analysis. The high number of character state changes on the branch leading to *Nitraria* exemplifies the deviant anatomy (Ronse Decraene and Smets, 1991; Sheahan and Cutler, 1993) and embryology (Li and Tu, 1991) of the genus. Among the derived character states that set *Nitraria* apart are the valvate cucullate petals, the haplostemonous stamen configuration with a secondary increase (haplostemony, however, is also found in *Tetradiclis*; Engler, 1931), and the external morphology of the nectary. *Nitraria* has a fragmented intrastaminal receptacular nectary, which is covered with long nonsecreting laciniate trichomes (Ronse Decraene and Smets, 1991, figs. 18, 31). The other Zygophyllaceae have usually well developed axial disc-like nectaries similar to the nectary of *Peganum* (they may be dissected or lobed). The circular disc-shaped nectary of *Peganum* possesses stomata and occurs around the base of the gynoecium (Figs. 21, 23, 32). Both types of nectaries belong to the axial nectary type (sensu Smets, 1986, 1988; Smets and Cresens, 1988) but with a different external texture.

At first glance, the floral development seems to be very much alike in *Peganum* and *Nitraria* (see also Ronse Decraene and Smets, 1991). Paired stamens are present in both species in almost the same position. However, the floral construction of *Peganum* differs from that of *Nitraria* in certain essential details. Differences are expressed by Table 2 and two floral diagrams (Figs. 37, 38), which are a reflection of our interpretation of the nature of the flower in the two genera.

In *Nitraria* (Fig. 37), the outer stamens are seemingly arranged in antepetalous pairs in mature flowers, as is the case in *Peganum*. However, during early ontogeny, the two stamens of such an antepetalous pair are not associated; on the contrary: the outer stamens arise in pairs in relation to the inner antesepalous stamens. In this way triplets consisting of one inner and two outer stamens are formed. The outer stamen primordia of a single triplet

Quassia   Ptelea   Peganum Morkillia   Nitraria   Balanites   Augea   Tribulus   Fagonia Zygophyllum

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 19:0    17:0     0:1      7:2(1)    8:1      2:2(0)    4:0       2:2(0)    20:0(1)  10:1
 28:1(0) 24:1     6:0               9:1      22:1      6:0       25:1
 33:1    27:0     10:1              10:1     34:1      12:0      36:1
 34:0    29:0     22:1              12:0     40:2(1)   26:0      37:2(1)    7:2(1)
 42:1    41:1     29:2(1)           13:1               34:1                 14:1
                  36:1              17:0               38:0                 24:0
                  38:0              20:2(1)                                 33:1
                  39:0              25:1
                  40:0(1)           26:0                                   18:1
                                    38:0                                   23:1
                                    42:0                                   29 0

                                  1:1                 0:1
                                  28:0(1or2)          3:0
                                  29:2(1)             35:1
                                  31:0

                                           24:1
                                           33:0

                                  5:0
                                  9:0
                                  23:0

                        4:1
                        7:1(0)
                        31:1(2)
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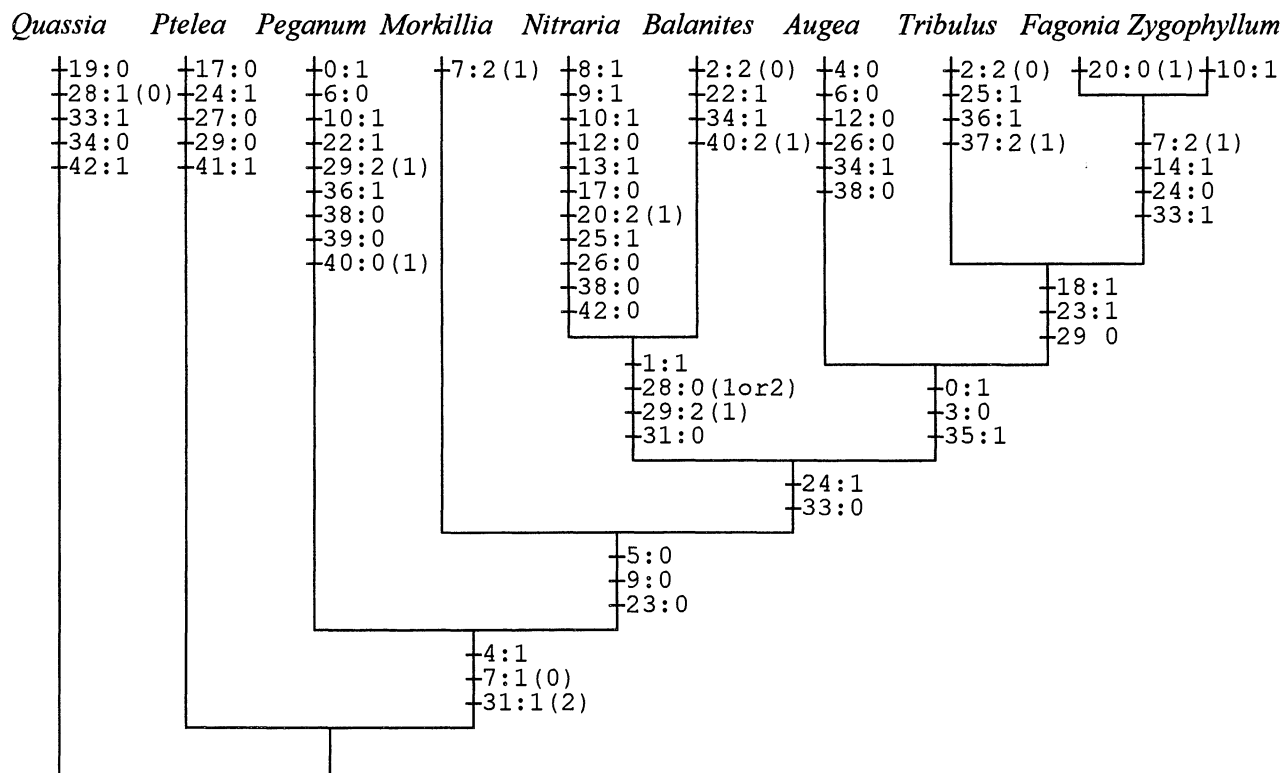
Fig. 39. Most parsimonious cladogram (length = 97; CI = 0.53; RI = 0.42). This is also the cladogram with the highest total fit for a concavity constant between 2 and 6. The numbers of the characters and character states refer to Table 1; the analysis is based on the data matrix given in Table 2. Only the unambiguous synapomorphies are shown (a:b stands for state b of character a; for the multistate characters, the number between brackets indicates the character state that transforms into the synapomorphic state).

always have the same size, but the differentiation of the outer stamens of different triplets is not synchronous (cf. Ronse Decraene and Smets, 1991, figs. 7, 15). So, in mature flowers, the size of the stamens of an antepetalous pair may be different. The vascular supply of the outer stamens of a triplet is connected with the inner stamens in the antesepalous sector (cf. Ronse Decraene and Smets, 1991, figs. 23–27). Based on these observations, the androecium can be described as complex haplostemonous (see Ronse Decraene and Smets, 1992); it has probably been derived by the division of single antesepalous stamen primordia, and therefore it is a case of secondary polyandry.

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┌──────────────────── Quassia
└┬─────────────────── Ptelea
 └┬────────────────── Peganum
  └┬───────────────── Nitraria
   └┬──────────────── Balanites
    └┬─────────────── Tribulus
     └┬────────────── Augea
      └┬───────────── Morkillia
       └┬──────────── Fagonia
        └──────────── Zygophyllum
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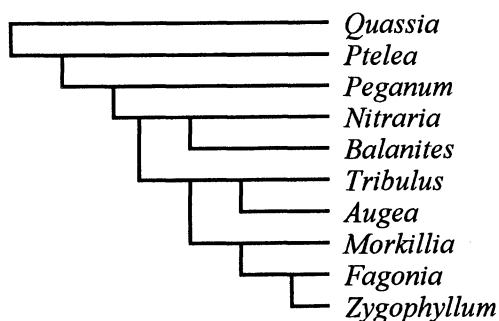
Fig. 40. Cladogram with the highest total fit for the data matrix given in Table 2 with the concavity constant equal to one (i.e., with strong downweighting of homoplasy).

In *Peganum* (Fig. 38) the outer stamens arise as antepetalous pairs without close link to the antesepalous inner stamens. Stamens of a pair were not seen to differ in size during development although different pairs may differ in size (Figs. 7–10). The traces of the antepetalous stamens are completely separate from the antesepalous sector and are fused with the traces to the petals and sepal laterals. The antepetalous stamens are clearly linked to the petals by their position and vasculature. Hence, the androecium can be described as complex obdiplostemonous, which means that secondary polyandry is coupled to an obdiplostemonous androecium. For a clarification of this terminology we refer to Ronse Decraene and Smets (1987, 1992). The superposition of polyandry on an obdiplostemonous condition makes a comparison with the other obdiplostemonous Zygophyllaceae relevant. That the androecium of *Nitraria* can be derived from that of *Peganum* by the intercalation of portions of the nectarial disc is unlikely because of the very late appearance of the nectarial tissue in the ontogeny of both genera.

Other differences between *Peganum* and *Nitraria* exist in the morphology of the gynoecium; *Nitraria* has a short style and a one-seeded ovary with an apically inserted pendulous ovule without endosperm (Ronse Decraene and Smets, 1991, fig. 21). *Peganum* has a long erect style and an ovary with numerous axillary inserted anatropous ovules with endosperm (Engler, 1931; Figs. 19–21, 23). Nevertheless both genera have a tricarpellate gynoecium, contrary to most other Zygophyllaceae. The vascular sup-

ply to the gynoecium tends to be more uniform: *Peganum* and *Nitraria* have the same arrangement of outer (dorsal and marginal) traces, but the ventral traces of *Peganum* are paired.

The position of *Nitraria* within the Zygophyllaceae or close to the Zygophyllaceae is contradicted in a recent cladistic analysis of the *rbc*L gene in the Zygophyllaceae and related families (Sheahan and Chase, 1994). In that analysis, *Nitraria, Peganum,* and *Malacocarpus* form a clade linked to Sapindales/Rutales, while the other genera of the Zygophyllaceae (including *Balanites*) appear together with Krameriaceae near a large clade containing, among others, a number of Rosaceae and Fabaceae. It is clear that an increased understanding of the internal relationships within and among Rutales, Linales, and Geraniales will be as important as an intensified study of Zygophyllaceae to settle the discussion of whether or not it should be split up into a number of smaller families.

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ERRATUM

An error in the Charles L. Argue paper (*American Journal of Botany* 80: 723–733, 1993) is hereby corrected. The length of the polar axis for *Walafrida* in Table 1, p. 728, should read: "15–26" instead of "15–16."