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DEVELOPMENT AND EVOLUTION OF BASAL CAULINE PLACENTATION: BASELLA RUBRA[1]

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ABSTRACT

In Angiosperms placentae or ovules are formed on carpels or the floral apex. Hence, in a developmental sense, there are carpellate and acarpellate gynoecia. The latter occur in about 11% of all Angiosperm families. *Basella rubra* is an example of the noncarpellate condition. Its single basal ovule is formed directly from the floral apex. In young developmental stages it even retains the tunica-corpus organization of the floral apex. In later developmental stages, three septa arise only at the base of the ovule. The single vascular strand of the ovule is symmetrically derived from the bases of all six strands that supply the ovary wall, i.e., it is not associated with the vascular strand of only one of the three gynoecial appendages. Hence, neither development nor vascularization support a carpellate interpretation of the *Basella* gynoecium. With regard to the evolution of basal placentation in *Basella* and other taxa of Angiosperms three possibilities exist: 1) It is derived from the carpellate condition, 2) It is primitive and the carpellate condition is derived, 3) Both carpellate and noncarpellate organizations have coexisted during the evolution of Angiosperms which may have been monophyletic or polyphyletic.

ARE PLACENTAE integral parts of carpels, as they are commonly thought to be, or are they better considered additional structures, as Croizat (1962), Sattler (1974) and others have suggested? Are the gynoecia of all taxa of Angiosperms carpellate or do acarpellate (noncarpellary) gynoecia with cauline placentae and ovules occur? How do gynoecia with basal placentation develop and how have they evolved? Answers to these and related questions may depend on detailed observations of floral development, ways of drawing lines between parts of the flower, the methodology of comparison, phylogenetic hypotheses, and general views of evolutionary and phylogenetic biology.

It has generally been acknowledged that the single ovule of *Basella* is basal (Eichler, 1878; Melchior, 1964; Maheshwari Devi and Pullaiah, 1975; Cronquist, 1981). Nonetheless, there has been much disagreement on whether it is cauline or carpellary. Payer (1857) who studied the floral development of *Basella rubra* documented its cauline origin from the floral apex. Moeliono (1970) came to the same conclusion. However, Eckardt (1955) and Sharma (1961) claimed that the ovule is inserted at the base of one of the three carpels that compose the gynoecium of *Basella* and related genera of the Basellaceae such as *Anredera* (*Boussingaultia*). The majority of morphologists and taxonomists seem to accept this interpretation when referring to basal placentation. However, since neither Eckardt (1955) nor Sharma (1961) provided sufficient developmental data for their carpellary interpretation, a developmental study of the *Basella* gynoecium was undertaken. In addition we will present the results of a survey on the occurrence of basal placentation in Angiosperms. The discussion will deal with the implications of basal placentation for developmental and evolutionary morphology. It will also touch on the origin of Angiosperms and placentation.

MATERIALS AND METHODS—Developing inflorescences of *Basella rubra* L. were periodically collected from October 1984 to December 1985 from the McGill University greenhouse. Three hundred fifty flower buds of different developmental stages and approximately 100 mature flowers were examined. The plants were grown under normal greenhouse conditions. Material was identified according to the key in the Flora of Java by Backer and Bakhuizen van den Brink (1963) and Flora Malesiana by van Steenis (1958) at the genus level and in the Manual of Cultivated Plants by Bailey (1949) and in an article by Fathima, Boraiah, and Shivashankar (1971) at the species level. A

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voucher specimen has been deposited at the McGill University herbarium at the Macdonald College campus in Ste. Anne de Bellevue, Quebec.

Some FAA fixed flower buds and inflorescences were cleared according to the technique of Fuchs (1963) to reveal vasculature. For the other techniques used, the reader is referred to Lacroix and Sattler (1988).

RESULTS—The mature flower of *Basella rubra* consists of two involucral bracts (that have also been interpreted as sepals), five tepals (or petals), five stamens and a tristigmate gynoecium with one basal ovule that is bitegmic and orthoamphitropous (see Lacroix and Sattler, 1988).

When all of the tepals and stamens have been initiated and have grown to a certain size (Fig. 1), the slightly convex floral apex gradually assumes a triangular shape as a result of the inception of three gynoecial primordia (Fig. 1, 2). These primordia arise from anticlinal and periclinal divisions in the second cell layer and underlying cells with concomitant anticlinal divisions in the outermost layer (Fig. 12). As the three appendages grow, the remaining floral apex becomes more rounded and dome-shaped, thus gradually transforming into a single ovule (Fig. 3–6). The transformation from floral apex into ovule is so gradual that it is impossible to pinpoint exactly when the floral apex becomes the ovule. As the ovule primordium develops, the meristematic appearance of cells such as dense cytoplasm, numerous small vacuoles and actively dividing nuclei shows no change, at least at the light microscope level (Fig. 12–15). A two-layered tunica, apparent in the earlier stages of floral development is maintained until the primordium has become distinctly dome-shaped (Fig. 14). In subsequent stages, periclinal divisions occur in the second layer (Fig. 15, 16). The inner integument is initiated before the outer one through anticlinal and periclinal divisions in the outer cell layer and the underlying layer (Fig. 8, 16). The gynoecial primordia form the three stylar branches and stigmas. Interprimordial growth at the base of the gynoecial primordia forms the common base of the stylar branches and the ovary that encloses the ovule (Fig. 7, 10).

When the two integuments have completely developed and the ovule has become orthoamphitropous (Fig. 11), the gynoecium appears trilocular at the base. The locules are approximately 0.17–0.2 mm deep (approx. 15% of total ovary height) as was determined by serial cross sections. The ovule is not enclosed in any of the three locules, but rather lies on top of them (Fig. 9). However, the micropylar end of the ovule is in one of the locules (Fig. 17, 18).

The procambial supply to the gynoecium develops from branches of the tepal-stamen strands (see Lacroix and Sattler, 1988). These branches converge in the center of the axis, thus forming a nearly circular ring of provascular tissue (Fig. 19). From this, three gynoecial strands originate, each supplying one of the three developing gynoecial appendages. In more mature stages, six strands are seen in the gynoecial wall: three major strands and three additional ones (Fig. 17). At their base in the receptacle, branch strands from these six merge centrally to form one strand to the single central ovule (Fig. 20–22).

DISCUSSION—The results of this study show that the basal ovule of *Basella rubra* arises from the floral apex. The latter is transformed into the ovule in such a gradual manner that it is impossible to decide at which stage the floral apex becomes the ovule primordium. Hence, all available evidence from the early stages of ovular and gynoecial development support the axial or cauline interpretation of the ovule. This implies that the three gynoecial primordia are not carpels in a developmental sense because they do not give rise to the ovule. The latter is simply enclosed by the ovary wall that develops through interprimordial growth at the base of the three gynoecial primordia which form three stylar branches and three stigmata. If the ovary wall is considered to be part of the gynoecial appendages (Philipson, 1978) and if a carpel, as suggested by Sattler and Perlin (1982), is redefined as a gynoecial appendage that encloses the ovule(s) but does not necessarily bear them, the gynoecium of *Basella* can be interpreted as tricarpellate. This interpretation is, however, in sharp contrast to the classical carpel interpretation according to which carpels are viewed as folded megasporophylls, i.e., appendages that *bear* and enclose ovules.

In the past, attempts have been made to interpret the *Basella* gynoecium in terms of carpels in the classical sense. Thus, the occurrence of the three septa at the base of the ovary has been emphasized (Eckardt, 1955; Sharma, 1961, 1968). Furthermore, it has been pointed out that the ovule is not positioned exactly in the center of the ovary but rather toward the adaxial gynoecial appendage (Eckardt, 1955). These observations have been regarded as evidence that "clearly shows the ovule to be a lateral organ" (Sharma, 1961). Our investigations have demonstrated, however, that the

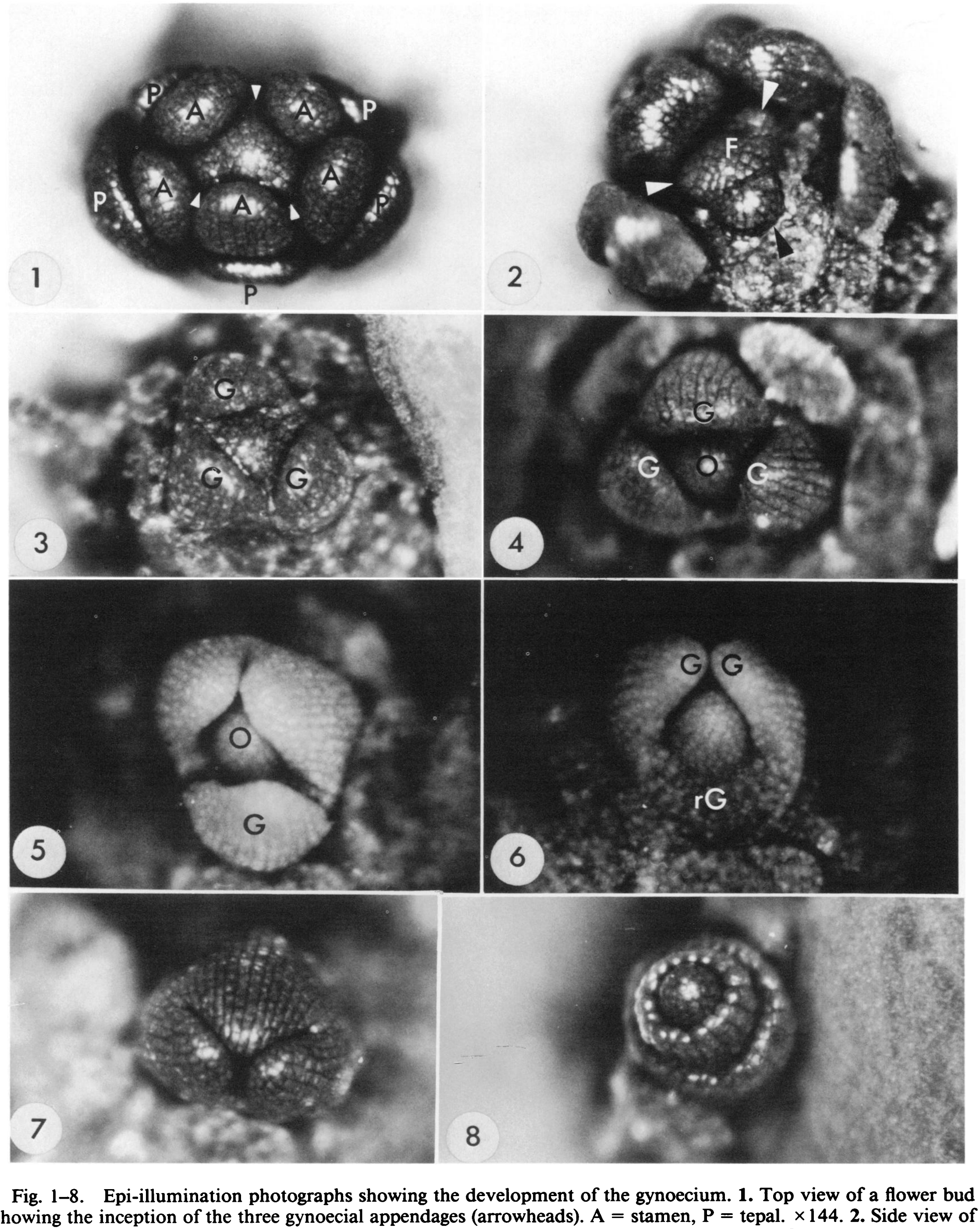

Fig. 1–8. Epi-illumination photographs showing the development of the gynoecium. **1.** Top view of a flower bud showing the inception of the three gynoecial appendages (arrowheads). A = stamen, P = tepal. ×144. **2.** Side view of floral apex (F) on which three gynoecial appendages have been initiated (arrowheads). Some of the stamen and tepal primordia have been removed. ×144. **3.** Top view of the three gynoecial appendages (G) and site of ovule formation. ×162. **4.** Top view of an older stage showing young ovule primordium (O) surrounded by the three gynoecial appendages (G). ×162. **5.** Top view of a young gynoecium where the lower gynoecial appendage (G) has been moved to show the central ovule primordium (O). ×162. **6.** Same gynoecium as that of Fig. 5 with lower appendage removed completely (rG) to show that the ovule primordium is not borne on any of the three gynoecial appendages. ×162. **7.** Top view of an older gynoecium showing upgrowth below the appendages as evidenced by regular cell files. ×162. **8.** Top view of young ovule with developing inner and outer integuments. ×162.

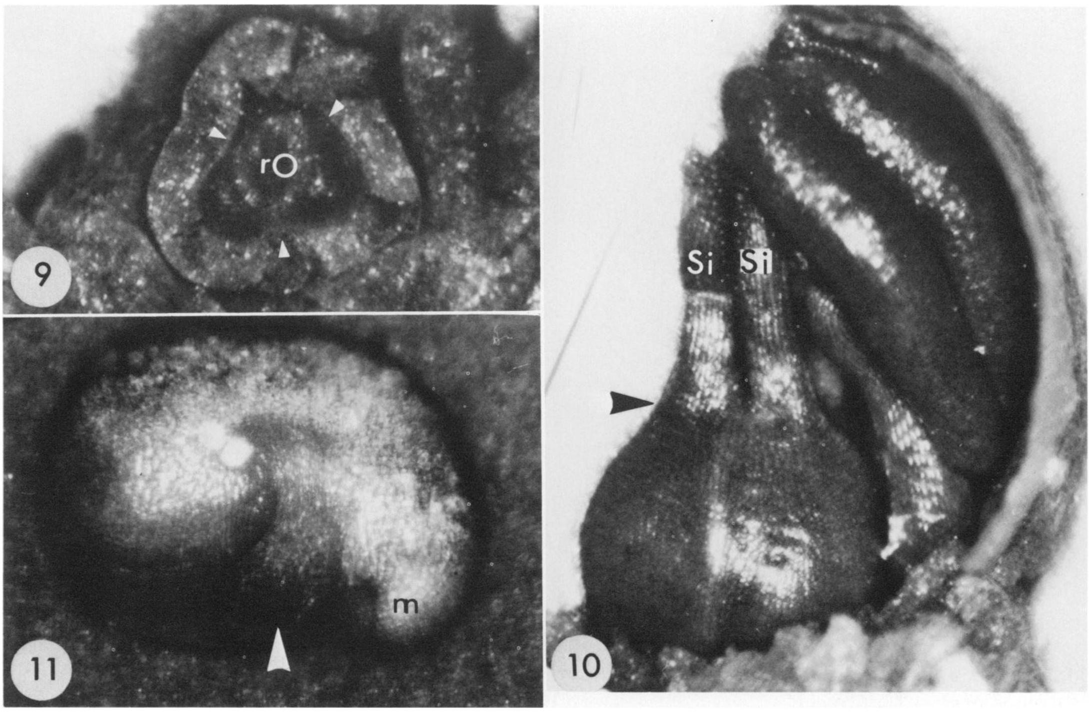

Fig. 9–11. Epi-illumination photographs of the young gynoecium and ovule. **9.** Top view of the inside of the gynoecium at the base. The ovule (rO), at a slightly older stage of development than that of Fig. 8, has been removed to show the early formation of septa (arrowheads) and locules. ×84. **10.** Side view of a gynoecium showing two of the three stigmas (Si). The short common style will form below (arrowhead). ×74. **11.** Side view of the ovule of a gynoecium at a stage similar to that of Fig. 10. Note location of the micropyle (m) and the insertion of the ovule (arrowhead). ×63.

ovule originates directly from the floral apex in the center of the ovary. A very slight displacement toward the adaxial side occurs only in later developmental stages when the ovule becomes campylotropous. The septa also develop relatively late at the base of the ovule primordium. This is not in conformity with the pattern of axile placentation. Hence, the carpellate interpretation (in the classical sense) of the *Basella* gynoecium is ill-founded when early developmental stages are taken into consideration. It should also be noted that the single vascular strand of the ovule comes from all six strands supplying the ovary wall, i.e., the ovular strand is not associated with only one gynoecial appendage.

Calvin Sperling (personal communication) observed flowers in which, instead of forming an ovule, the floral apex had given rise to another flower inside the gynoecium and that flower in turn produced another flower inside its gynoecium. This underlines the organogenetic potential of the floral apex that may not only form an ovule (under normal circumstances) but may even produce additional flower(s).

Our assertion that the gynoecium of *Basella* is acarpellate (or perhaps carpellate according to the redefinition by Sattler and Perlin [1982]) is a conclusion of developmental morphology. It is not an evolutionary or phylogenetic hypothesis. With regard to evolution and phylogeny, the following two possibilities can be envisaged:

1) *Basella* with its basal ovule evolved from plants with a typically carpellate gynoecium as, for example, a gynoecium with axile placentation. This hypothesis requires a reduction of both the septa and the number of ovules along with a phylogenetic shifting of one ovule from an axile position onto the floral apex. The septa at the base of the ovary could be considered support for this hypothesis. Since they are formed in later developmental stages, this hypothesis implies, however, that the changes leading to the evolution of the *Basella* gynoecium occurred in early developmental stages when the ovular shift is expressed. This is contrary to the commonly accepted view that evolutionary changes more likely affect later developmental stages because changes in early stages would disrupt morphogenesis (see, e.g.,

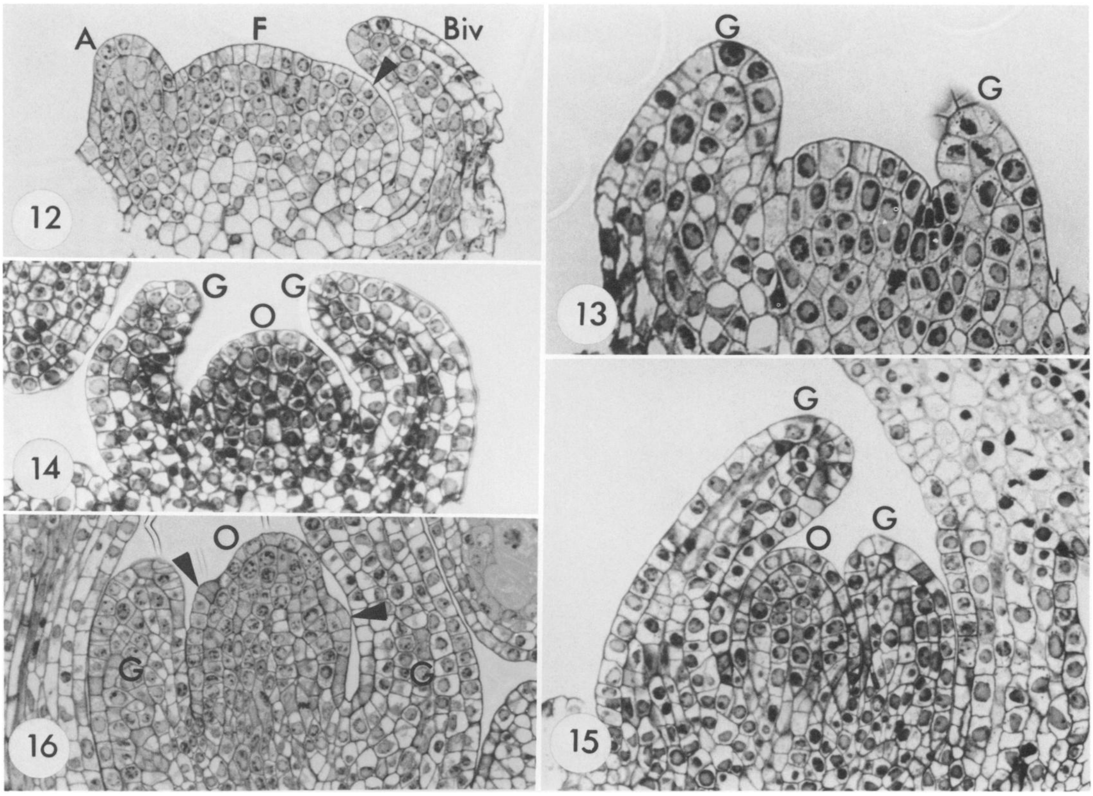

Fig. 12–16. Longitudinal sections of different developmental stages of gynoecia in the adaxial-abaxial plane. **12.** Nearly median section through the floral apex (F) showing the initiation of the adaxial gynoecial appendage through periclinal divisions below the outermost cell layer (arrowhead). Biv = involucral bract, A = stamen. ×256. **13.** Nearly median section showing the gradual transformation of the floral apex into the ovule. G = gynoecial appendage. ×400. **14.** Tunica-corpus organization still apparent in the ovule primordium (O). ×256. **15.** Older stage of gynoecial development. Periclinal divisions have occurred in the second cell layer of the ovule (O). ×256. **16.** Inner integument initiation through periclinal and anticlinal divisions (arrowheads) in the outermost cell layer and below. ×224.

Sachs, 1982). If, nonetheless, the *Basella* gynoecium evolved from a carpellate condition (in the classical sense), it is an exception to the rule of evolutionary conservation of early development (see Sachs, 1982). If, in addition, other cases of basal placentation (see below) and other features evolved in a similar manner, exceptions to this rule are so frequent that its validity may become questionable. Changes affecting early developmental stages may then be seen as a mechanism of macroevolution leading to a transgression of a common type of organization. (See Cooney-Sovetts and Sattler [1987] for other examples.)

In cladistic terms, this hypothesis implies different conclusions at different levels of the cladogram (Stevens, 1984: 402). At the level of the Basellaceae (all of whose members appear to exhibit the same organization as *Basella rubra*), *Basella rubra* does not have carpels in the classical sense. However, at the level of Angiosperms, *Basella rubra* has carpels (in the classical sense) if Angiosperms are monophyletically derived from a carpellate ancestor. This conclusion appears strange and misleading to us. It is like saying that multicellular organisms are unicellular at an inclusive hierarchical level. To us they are simply multicellular, although we think that they have evolved from unicellular ancestors. Likewise, *Basella* is simply acarpellate (in the classical sense), although it may have evolved from carpellate ancestors.

2) The second possibility for the evolution of the basal ovule of *Basella* is contrary to the first: the basal, cauline ovule is considered a primitive feature. This implies that the ancestors of *Basella* never possessed carpels (in the classical sense). Since we do not have sufficient fossil evidence, the question is which extant taxa of Angiosperms might be closely related to ancestral taxa of the Basellaceae. Many authors such as, for example, Takhtajan (1980) consider the Phytolaccaceae the most primitive family within the Centrospermae (Cary-

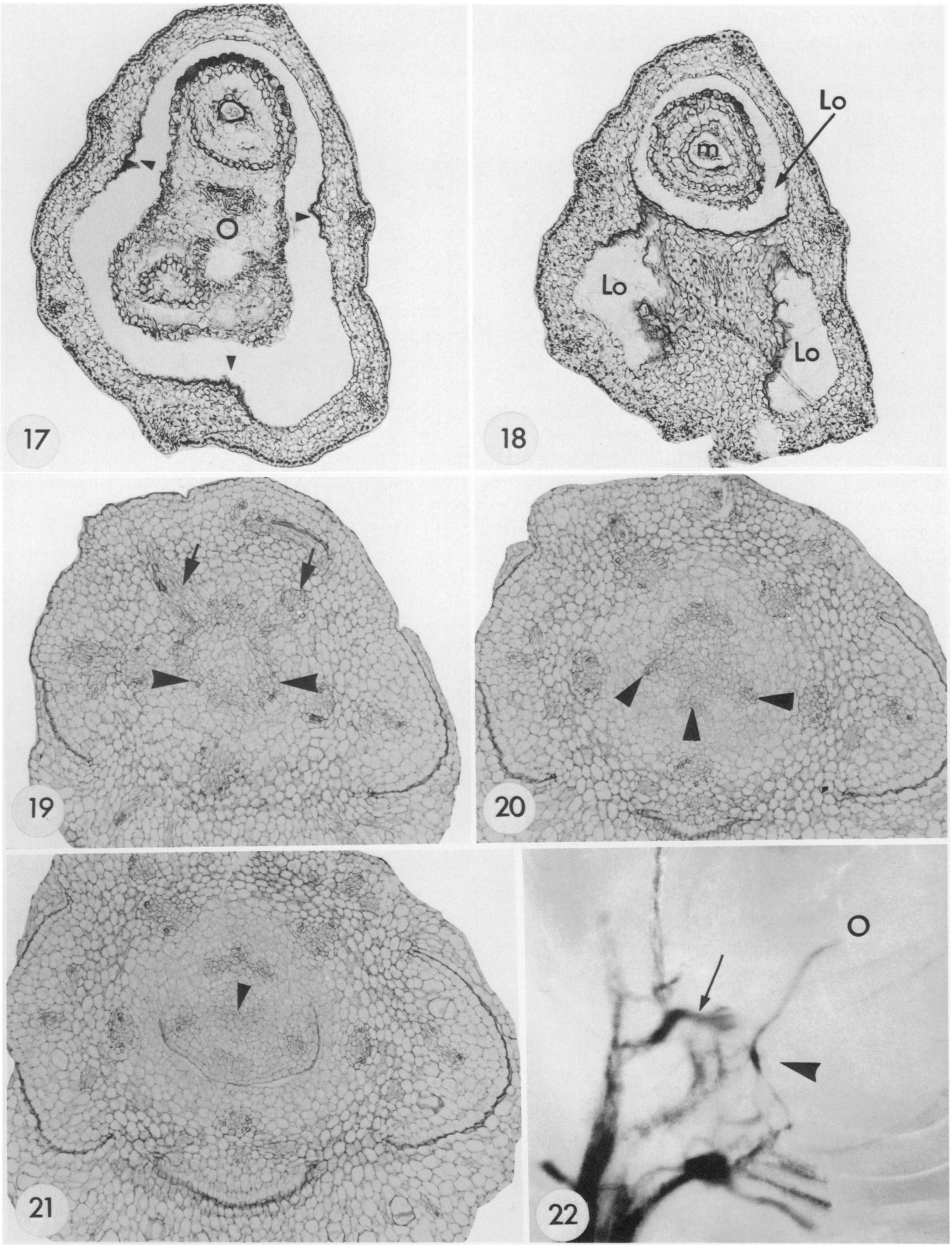

Fig. 17–22. **17.** Cross section through the gynoecium of a mature flower near its base showing the ovule (O) and beginning of partitions (arrowheads). ×76. **18.** Cross section of the base of the same gynoecium revealing the three locules (Lo), one of them slightly deeper than the other two. The micropylar end of the ovule (m) is in this particular locule. ×76. Fig. 19–22. Cross sections of a nearly mature flower bud showing the vascular supply to the gynoecium. **19.** Strands from major traces supplying the tepals and stamens (small arrows) merge to the center forming a ring (arrowheads). ×76. **20.** The vascular supply to the gynoecial wall is derived from this ring (arrowheads). ×76. **21.** The vascular supply to the ovule is also derived from this ring (arrowhead). ×76. **22.** Clearing of the base of a gynoecium showing anastomosing of strands (arrowhead) to form the single strand to the ovule (O). The arrow points to a strand unrelated to the gynoecium. ×63.

ophyllales). Rodman et al. (1984) emphasize the primitive status of both Phytolaccaceae and Nyctaginaceae. Takhtajan (1980: 268) assumes furthermore that "the Phytolaccaceae in particular is linked with both the Ranunculales . . . and with the Illiciales," the latter being considered to be among the most primitive Angiosperms. In the context of the *Basella* placentation it may then be phylogenetically significant that developmentally acarpellate gynoecia seem to exist in the Nyctaginaceae, the Phytolaccaceae and in *Illicium.* In the Nyctaginaceae the floral apex is transformed into the basal ovule as observed in *Basella* (Sattler and Perlin, 1982). Although Eckardt (1955) stated that the ovule in the Phytolaccaceae is borne on a cross zone and therefore the gynoecium is carpellate (in the classical sense), Rohweder (1965) questioned the occurrence of cross zones in *Phytolacca*; thus, the ovules may be borne at the periphery of the floral apex in the axil of gynoecial appendages. Robertson and Tucker (1979) also reported an axillary position of ovule inception in *Illicium floridanum.* They noted that the single ovule of a "carpel" is "between, but not attached to the appressed margins of the carpel." Nonetheless they hesitated to consider this condition as acarpellate. Erbar (1983) confirmed the axillary position of the ovule in *Illicium anisatum.* An evolutionary derivation of *Basella* from plants exhibiting an axillary ovule such as *Illicium* would involve a reduction of the number of gynoecial appendages and ovules and a phylogenetic shifting of one ovule from an axillary to a basal central position. There are, of course, other cauline ways of deriving the basal ovule of the Basellaceae (e.g., Hagerup, 1936). All of these derivations are speculative as is the classical derivation from carpellate ancestors.

Occurrence of cauline placentation in Angiosperms—Apart from the Basellaceae, morphologically cauline placentae or ovules are not rare (see, e.g., Maze, Dengler, and Bohm, 1971; Philipson, 1975, 1978). According to a survey conducted by the second author, they occur in about 11% of all Angiosperm families of the system by Dahlgren (1983) for the dicotyledons and Dahlgren, Clifford, and Yeo (1985) for the monocotyledons (a list of these families is available from the authors). Developmental documentation of the cauline origin of placentae or ovules exists for *Illicium* in the Illiciaceae (Erbar, 1983; but see also Robertson and Tucker, 1979), Piperaceae (Tucker, 1980, 1982), Nyctaginaceae (Sattler and Perlin, 1982), Chenopodiaceae (see Sattler, 1973), Polygonaceae (Galle, 1977), Malvaceae (van Heel, 1978), Urticaceae (Macdonald, 1974), Scyphostegiaceae (van Heel, 1967), *Ochna* in the Ochnaceae (Pauzé and Sattler, 1979), Primulales (Aymard, 1967; Sattler, 1973), Juglandaceae (see Sattler, 1973), Myricaceae (Macdonald and Sattler, 1973; Macdonald, 1979), Santalaceae (see Sattler, 1973), Asteraceae (see Sattler, 1973), Najadaceae (Posluszny and Sattler, 1976), *Luzula* in the Juncaceae (Barnard, 1958), Cyperaceae (see Sattler, 1973), Poaceae (Maze et al., 1971; Sattler, 1973; Kam, 1974; Cheng, Greyson, and Walden, 1983) and others. There even may be cases where cauline and carpellary ovules occur in the same flower (see Dupuy and Guédès, 1975; Puri, 1978).

Evolution of cauline placentation—With regard to the evolution of developmentally cauline placentation in Angiosperms, we see three possibilities:

1) The ancestors of Angiosperms possessed only carpellate gynoecia (in the classical sense). Hence, all cases of developmentally cauline placentae and ovules are phylogenetically derived. Whatever the likelihood of this commonly held view may be, it appears strange and misleading to us to conclude that because the ancestors were carpellate, the descendants have essentially the same organization. Such statements seem to deny the reality of evolutionary change. Why can't it more generally be admitted, except by very few authors such as Croizat (1962), Philipson (1975), Maze (in Scagel et al., 1984) and Stevens (1984), that during the evolution of Angiosperms basic types of organization such as the megasporophyllous condition might have been transgressed? This admission would, of course, entail that, developmentally, carpels (in the classical sense) are not a diagnostic feature of Angiosperms. If, however, the "carpel" is redefined as a gynoecial appendage that encloses ovule(s) and may or may not bear them, more, though not all, taxa of Angiosperms might be morphologically characterized by carpels. This redefinition by Sattler and Perlin (1982) focuses on the functional aspect of carpels: that they protect the ovules. As long as the ovules are protected, it does not seem important whether they develop from the gynoecial appendages or the floral apex. Their protection seems to allow a considerable freedom with regard to shifts in their position ranging from basal to apical.

2) The ancestors of Angiosperms possessed only cauline placentae and ovules (e. g., Meeuse, 1980, 1986).

3) The ancestors of Angiosperms possessed both cauline and phyllomic placentae and

ovules (Sattler and Perlin, 1982). This view need not imply two fundamentally distinct lineages of Angiosperm evolution, the Stachyosporae and the Phyllosporae, as postulated by Lam (e.g., 1962). And it need not imply that the whole plexus of Angiosperm features has evolved more than once independently, but instead gradually (see Nicklas, Tiffney, and Knoll, 1980; Tiffney, 1981). This might mean that typical features of this plexus such as the reduction of the gametophytes and double fertilization evolved first and perhaps monophyletically, but that the gynoecium may have evolved in different ways ranging from typically carpellate to acarpellate. This view may also allow for transgressions between the extreme types of gynoecial construction during the evolution of Angiosperms due to the fluidity of organizational patterns (see Philipson, 1975: 76; Tiffney, 1981). The fact that axillary and basal ovules occur in some taxa that are relatively primitive such as *Illicium* (Erbar, 1983), *Ochna* (Pauzé and Sattler, 1979), *Piper* (Tucker, 1982) and *Myrica* (Macdonald and Sattler, 1973) is compatible with this as well as the two other views. It would be interesting to know whether in Cretaceous fossils of flowers with only one ovule per carpel (see, e.g., Dilcher and Crane, 1984), this ovule was initiated in an axillary position as in *Illicium* or on a cross zone as in many members of the Ranunculales and Laurales (see, e.g., Endress, 1972a, b; van Heel, 1981, 1983). In the absence of such detailed fossil evidence, it is difficult to decide which of the three possibilities is the most probable one. We can, however, extrapolate some basic evolutionary processes that may have shaped the evolution of Angiosperms with their various types of gynoecia and placentation (Sattler, 1974). Phylogenetic shifting leading to heterochrony and heterotopy is one of these processes that has played a role regardless of which phylogenetic hypothesis on the origin and evolution of Angiosperms is favored.

Conclusions—As in many families of Angiosperms, the basal ovule of *Basella rubra* and probably of all other members of the Basellaceae arises directly from the floral apex. Hence, in a developmental sense, the gynoecium is acarpellate. Although one may continue to debate whether this condition is primitive or derived in the Centrospermae (Caryophyllales) or even in Angiosperms, this discussion is not necessarily appropriate because carpellate and acarpellate gynoecia may have co-existed during the evolution of the Centrospermae and perhaps even the Angiosperms (Sattler and Perlin, 1982). The occurrence of both carpellate and acarpellate gynoecia within the Centrospermae and relatively primitive Angiosperms is compatible with this view that also allows for a fluidity of organization leading to transgressions from cauline to phyllomic placentation and vice versa (see also Maze et al., 1971; Philipson, 1975).

Regardless of which phylogenetic speculation on the origin and evolution of Angiosperms one prefers, phylogenetic shifting in the timing and positioning of placental or ovular inception (heterochrony and heterotopy) appears to have played an important role in the evolution of gynoecial diversity (see Sattler, 1974). Thus, the position of the placenta or ovule(s) may range from typically carpellary to typically cauline. From a functional point of view (see Maze et al., 1971; Maze in Scagel et al., 1984: 626), this positional variation need not necessarily be very significant. What appears to be most important is the enclosure and hence the protection of the ovule(s). Obviously, different taxa of Angiosperms have succeeded in enclosing and protecting ovules in different ways ranging from cauline to carpellary. Both of these extremes including the intermediates seem equally functional and efficient. This may be the simple reason why they coexist in different angiospermous taxa and why they may have coexisted perhaps since the origin of Angiosperms.

It should also be kept in mind that a plant is a whole. This whole can be conceptually dismembered in different ways (see Meyen, 1978; Rutishauser and Sattler, 1985). Besides the classical dismemberment that delimits roots, stems and leaves (and their homologues), there are at least four others. According to one, the fertile leaf model, the axillary bud is part of the leaf. According to another, the metameric model, the shoot is composed of growth units each of which comprises a leaf with the stem segment below, i.e., stems and leaves no longer exist as separate units (see Rutishauser and Sattler, 1985). Since one or another model of dismemberment is always presupposed, any morphological discussion is relative to the conceptual framework of the model adopted. Thus, the discussion and conclusion of this study reflects the caulome-phyllome framework of the classical model or its pyramid extension by Sattler (1986: 105). From the point of view of the metamer model, the question of whether ovules are cauline or phyllomic does not exist because the categories caulome and phyllome are not used. Ovules are always borne on metamers. Hence this model underlines the unity of the various types of placentation. According to the fertile leaf model, axillary placentation as reported in *Illicium* (Erbar, 1983) or *Ochna* (Pauzé and Sattler, 1979) would be compatible with the classical carpel concept if the latter were extended to include axillary structures.

What constitutes a problem in the framework of one model need not at all be problematic in terms of another model. For example, the stachyospory-phyllospory problem does not exist within the framework of the metameric model. Problems, questions, and answers are relative to the conceptual framework adopted. Since the frameworks of the five models discussed by Rutishauser and Sattler (1985) are complementary to each other, the consideration of all of them provides a more encompassing view than the restricted perspective of only one of them.

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