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Characters and homologies of ancient angiosperms as related to their origin

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Morphogenetics and interpretative morphology of ancient angiosperms, as evidenced by pollen and leaves from the Middle and Lower Cretaceous, are discussed. The similarity of pollen in Chloranthaceae and *Austrobaileya* shows close relationship which confirms Meeuse's Anthocorm Theory. General morphology of Monimiaceae and Piperaceae is investigated to find some morphological peculiarities of their organs concerning their phylogenetic ambiguity. The flowers of Monimiaceae resemble those of *Whittleseya* and the inflorescences of Piperales (Saururales) resemble some so-called teratologies in modern hybrids of certain Rosaceae. The lack of petals in *Neviusia* as well as certain inflorescences of Bennettitales need consideration.

Key-words—Angiosperms, Origin, Morphogenetics, Monimiaceae, Piperaceae.

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सारॉंश

प्राचीन आवृतबीजीयों के उद्‌भव से सम्बद्ध इनके संलक्षण एवं समजाततायें

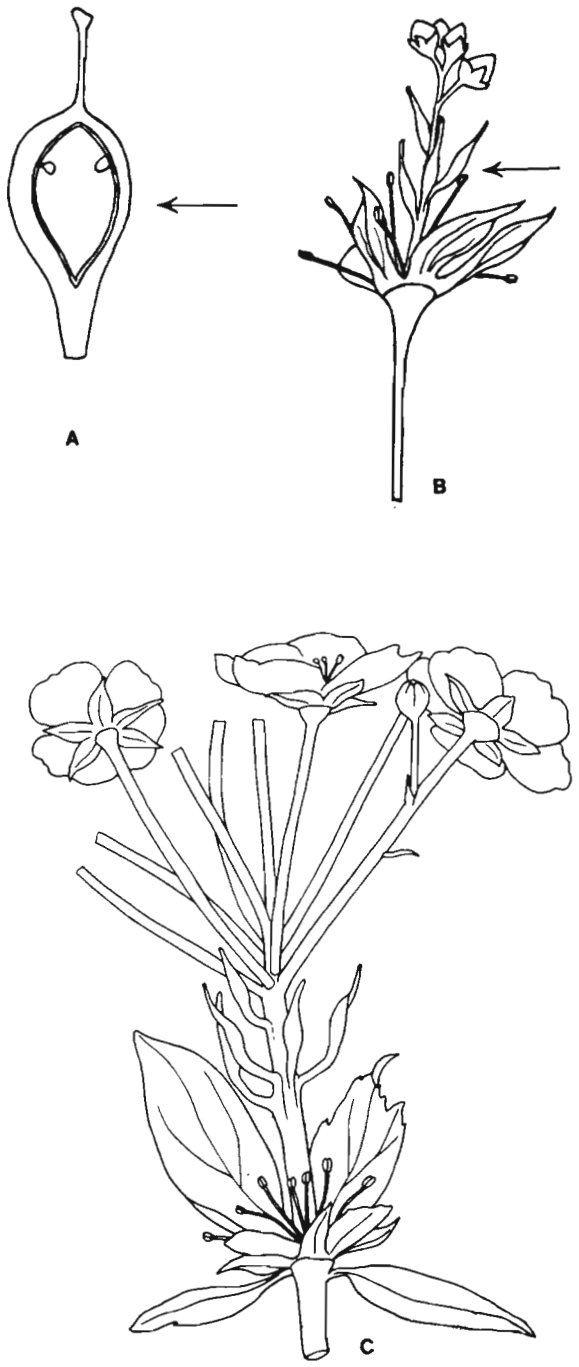
लुडविग रफ़ले

मध्य एवं अधरि क्रीटेशी काल से उपलब्ध अश्मित परागकणों एवं पत्तीयों के प्रमाणों के आधार पर प्राचीन आवृतबीजीयों का संरचनाविकास तथा इनकी व्याख्यात्मक आकारिकी विवेचित किये गये हैं। क्लोरेन्थेसी एवं ऑस्ट्रोबैलया के परागकणों की परस्पर समानता से इनका घनिष्ठ सम्बन्ध व्यक्त होता है जिससे मीयूस के ऍन्थोकॉर्म सिद्धान्त की पुष्टी होती है। मोनीमिएसी एवं पाइपरेसी नामक कुलों के सम्बद्ध अंगों की जातिवृत्तीय संदिग्धता अन्वेषित करने हेतु इनकी सामान्य आकारिकी का अध्ययन किया गया है। मोनीमिएसी कुल के पुष्प ड्हिटलेसिआ से समानता प्रदर्शित करते हैं तथा पाइपरेल्स (सोरुरेल्स) के पुष्पक्रम रोज़ेसी कुल के कुछ वर्तमान संकरों से सजातीयता व्यक्त करते हैं। नेवियूसिआ एवं कुछ बेन्त्रिटाइटेल्स के पुष्पक्रमों में दलपुंज की अनुपस्थिति विचारणीय है।

AFTER Zimmermann's (1966) view of "Hologeny" qualitative new organs (characters) in plant phylogeny can be developed by a certain heterobathmic composition ("mosaic") of partial multiplications and partial stability of older ones. While some organs and characters remain in ancient stature and shape, an other part becomes comparably smaller and increases in quantity. The combination of all these parts by fusion forms a new organ (character). Referring to this there seem to be no differences between genetics and phylogenetics. Some examples of hybrids and so-called teratologies show the same (Guédès). If reduction in the above mentioned manner becomes evident in a high degree, this mode of phylogenetic evolution would be called neoteny by Takhtajan. As far as an organism may be reduced or not, paleobotanical record can demonstrate.

It seems that the more principles of neoteny became acknowledged by botanists, the more was it possible to judge ontogenetical (and some teratological?) events in connection with phylogenesis and last but not least with paleobotany. Enlargement of organisms by new organs does not take place in continuity as well in phylogeny as in ontogeny.

It seems to be of importance that most of the higher plants [particularly angiosperms



Text-figure 1—A-C, *Spiracea* van Houttei ZBI. (hybrid of species) : Prolification of flower, ca × 10, ca × 20, ca × 30 respectively.

(Magnoliophyta) in a high degree] are similar in cotyledonar and reproductive (floral) regions: shape of foliar appendages, gonophylls, semaphylls ("bracts, petals"), venation, marginal meristems, trichotomy, dichotomy (particularly in default of buds), central steles, dedifferentiation of adaxial and abaxial surfaces (particularly in some monocots) Rüffle (1969, 1980). The higher coordinations and differentiations as angiosperm phylogeny has produced them, seem to be a heterobathmic mixture of intermediate programs of several morphogenetic events resembling loops of computers. If any loop lacks, regeneration of morphogeny becomes neoteny. New characters of organisms cannot simply be added terminally in ontogenesis or phylogenesis at least. This may be the main reason that for derivation of angiosperms (Magnoliophyta) from ancient groups, comparisons (and definitions) with flowers only are insufficient; paleobotany needs more or less parts in connection or the whole plant for reconstruction of ontogeny. Knowledge of modern plants can make it easy. It seems that in angiosperms many buds (perhaps certain flowers), intercalary growth of leaves and shoots (Doyle & Hickey) and secondary thickening or the whole stem of trees from cotyledons to the reproductive region are such inter-mediated programs, characterized rather by many postgenital adnations.

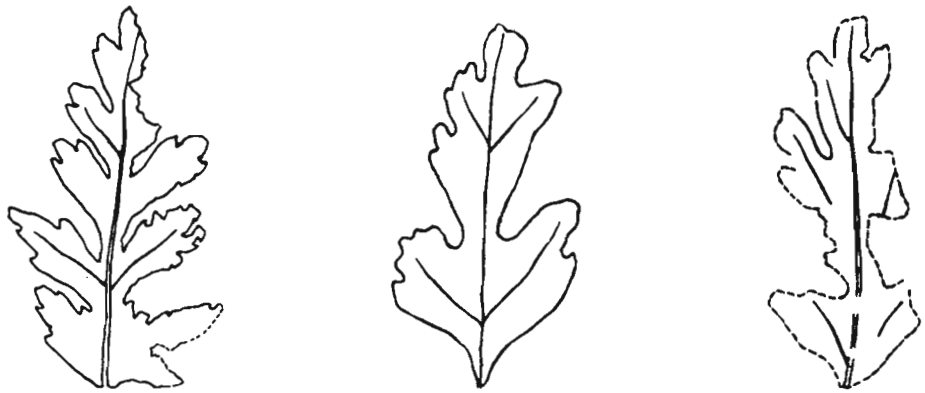
Hagemann has shown that in *Helleborus* (and obviously in *Platanus, Dewalquea* (Fagaceae) and Araceae too) the pedate shape of foliar leaves originates from a secondary meristem which is arranged across the petiole. The leaves though compound are homologous to any other simple leaf of Ranunculaceae (Platanaceae, Fagaceae, Araceae). But the more leaves are compound in the pedate manner, the so-called leaflets are at the same time homologous with simple leaves concerning the groups mentioned above. In view of phylogeny (and neoteny) each homology seems to be ambiguous.

Obviously plant organs can produce more plant organs close to the former by neotenic regeneration. The present author postulates that the median prolifications in the flowers of some hybrids in *Spiracea* or *Geum* producing small clusters of new flowers instead of carpels, etc. are not only teratological, they are atavisms resembling the inflorescences of Piperales (Saururales), which are regarded by Kuprianova and Meeuse to be one of the oldest angiosperm families close to Araceae. For *Peperomia* Leinfellner has found out that the hypopeltate bracts within the spica resemble the mode of growth of the so-called "Querzone" of angiospermous carpels and some cotyledons. To the present author it seems possible to interpret the inflorescences of Piperales nearly as an inflorescence as well as only one cone-like flower. The basal bracts seem to be petals. This recalls the anthocorm theory with a small correction: The inflorescences of Piperales (Saururales) seem to be homologous pro parte to the flowers of *Magnolia* (holanthocormoid) but the single flowers of Piperales (anthoid) likewise pro parte.

This could explain many premises of the anthocorm theory (theory of polyaxis in floral region). Meeuse (1976) draws the attention also to

Figure 1—**A**, *Spiracea* van Houttei ZBL (hybrid of species): Prolification of flower; **B**, *Geum rivale* L. (hybrid ?) after Krechetowich, 1952; prolification of flower; **C**, *Cercidiphyllum arachiodes* (Lesq.) Brown: "*Trochodendrocarpus*" by Meeuse, 1974 supposed to be related with *Amborella* (Monimiaceae sensu lato), vessel-less wood, Anthoid or Holanthocormoid?; **D**, "*Myrica*" *pseudoquercifolia* Kräusel, 1922: Monimiaceae from the Senonian of Quedlinburg (×2). *Protohedycarya pseudoquercifolia* (Kräusel) Rüffle comb. nov.

Monimiaceae, particularly the similarity between *Trochodendrocarpus* and *Amborella* fructifications. The present author wants to emphasize that the flowers of *Amborella* and some Monimioideae harmonize very well with Meeuse's anthocorm theory. In Europe some Upper Cretaceous leaves of Monimioideae with cuticles ("*Myrica*" *pseudoquercifolia*) Kräusel (1922), Rüffle (1965), Knappe & Rüffle (1975, figure 5) are close to some Cissites ("*Cissus tavaredensis*" Teixeira) from Aptian and Albian (Potomac flora) in shape and morphology, particularly in the broad undulated margin. The nearly anemochore diclinic flowers of *Amborella* and some Monimioideae (Monimiaceae) and their fossil and extant distribution could demonstrate that in fact this family would be one of the oldest angiosperms on the whole as well as Piperales. This corresponds to the anthocorm theory (in both being homoxylous woods). Perhaps Magnoliaceae arose much later (see inflorescences of Bennettitales).



Text-figure 2—**A**, Protohedycarya pseudoquercifolia (Kräusel) Ruffle comb. nov.; **B**, *Cissites tavaredensis* Teixeira, 1948 from Aptial/Albian, Portugal; **C**, *Cissites* sp. after Lebedev, 1974 from Aptian/Albian, Siberia (**B** and **C** are supposed to be related with *Protohedycarya pseudoquercifolia* (Krausel) Rüffle comb. nov. based on cuticles.

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