

MACROEVOLUTIONARY EVENTS AND THE ORIGIN OF HIGHER TAXA

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Abstract: The role of macromutation as a source of evolutionary novelty is discussed in relation to the repeatedly appearing reticulate pollen grain morphology; the origin of stomata by pedomorphic transformation of gametangial conceptacles in the alga-like precursors of vascular plants; the fixation of environmentally induced anomalous stomatography as a genus-specific character; the origin of specialized seedling morphology in mangroves through changes of developmental rates; the cyclic evolution (retroconvergence) of reproductive and foliar characters; the possibility of pathogenic cecidogenous origin of plant organs; and the diversification burst (anastrophes) on the basis of macropolymorphic post-crisis populations. Macromutation can be involved in both micro- and macroevolutionary processes, yet the origin of higher taxa is not reducible to a single macromutation event. Rather, it is an accumulation of macromutational novelties arising in different lineages, as well as a retrieval of ancestral characters lost in the immediate ancestors, but retained in the genomic memory and their integration in the new adaptive context.

1. INTRODUCTION

The term macroevolution is commonly applied to evolutionary events at or above the species level, while the modern evolutionary studies are focused, mostly or exclusively, on the processes that are not, or at least not in the time-scale of the experiment, consummated in speciation and are, therefore, considered as microevolutionary. A well-trod way from micro-

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evolutionary observation to macroevolutionary deduction lies in the assumption that macroevolution is a gradual accumulation of microevolutionary events through geological time.

A different line of thought ascribes macroevolution to saltational changes, or macromutations, that are rare and abnormal for the gradual microevolutionary developments. The latter theory was forcefully advanced by Goldschmidt (1958 and earlier work), who defined macromutation (systemic mutation) as "a shift of developmental processes by a single mutation event to such an extent that a structural departure appears which is of the order of magnitude of macroevolutionary differences". Arguing with Dobzhansky and Stebbins, who dubbed his theory "cataclismic", Goldschmidt (1958, p. 491) bitterly remarked: "If cataclisms enter this theorizing at all, it is the cataclism of the orthodox and extreme Neo-Darwinism".

It was later discovered that at least some macromutations are the developmental effects of genome – plasmon interactions, potentially of a great evolutionary significance (Jinks, 1964; Løvtrup, 1974). Developmental studies lend support to macromutational effects of rate changes, or heterochronies (Arthur, 1975; Gould, 1977), in particular those occurring early in the ontogeny (archallaxes of Severtsov, 1939).

Long before the advent of macromutation theory, the synthesis of developmental and paleontological evidence gave rise to the theory of orthogenesis, which held that morphological evolution results from either acceleration or retardation of developmental rates, accompanied by addition or deletion of developmental stages (e.g., in the evolutionary series of ammonites: Neumayr, 1879). The orthogenetic views shared by such eminent 19th century paleontologists as Cope, Hyatt, Neumayr, Grabau, and others (reviewed in Krassilov, 1977) were expelled from the modern synthesis and all the voluminous supportive evidence came to be viewed with suspicion. Yet there are more recent paleontological examples of speciation through halted development (Gould, 1970; Soulé, 1973; Niklas et al., 1976), and even the modern studies of interpopulation polymorphism occasionally reveal morphological and/or genetic distinctions that correspond to consecutive developmental stages or retention of successional isozymes (Nair et al., 1977).

Paleontological models of episodic high rate macroevolution go back to the XIX century catastrophism (mass extinctions) and anastrophism (bursts of diversification at higher taxonomic levels), later furnished with the macromutation mechanism (Schindewolf, 1958). Their milder versions are represented by the quantum evolution concept (Simpson, 1944) and its derived model of punctuated equilibrium (Eldredge and Gould, 1972).

The Goldschmidtian macromutations were rediscovered as "genetic revolutions" in founder populations (Mayr, 1954) or saltational reorgani-

zations of supergenes (Carson, 1975). Yet, it is commonly held (e.g., Stanley, 1979) that although quantum evolution is a possibility, the extreme views of Goldschmidt, Schindewolf, and their followers only discredited the idea.

Thus, the old dilemma of gradualism vs. saltationism is still with us, but the problem of macroevolution is far more comprehensive than that.

2. MATERIALS AND METHODS

This study is based on paleobotanical materials from the Devonian, Permian, Mesozoic and Paleogene deposits of the Far East, Central Asia, Eastern Europe, and the Middle East preserved as impressions and compressions of macroscopic plant remains, pollen grains, gut compressions of fossil insects, fossil galls, and other traces of plant – animal interactions. Stratigraphic, taphonomic, and paleoecological studies were conducted in the major localities. The material was subjected to macro- and micromorphological studies, the latter assisted with the scanning electron microscopy. Fossils selected for the analysis of macroevolutionary events came from the following localities:

Cutinized thalloid plant *Shuguria ornata* Tschirkova-Zalesskaya: The Pavlosk Quarry, Voronezh Region, central European Russia, Middle Devonian (Givetian).

Cutinized thalloid plant *Orestovia devonica* Ergolskaya: The Barzas River, Kuznetsk Basin, Western Siberia, Middle Devonian.

Conifer *Ullmannia* cf. *bronnii* Goeppert: The Kitchmenga River near Nedubrovo Village, Vologda Region, northern European Russia, the latest Permian to lowermost Triassic.

Dispersed pollen grains *Reticulatina* sp. (courtesy of Natalia Zavialova): The Tschekarda locality, Cis-Urals, Lower Permian (Kungurian).

Pollen grains *Lunatisporites* sp., from the gut compression of Permian insect *Idelopsocus diradiatus* Rasnitsyn: The Tschekarda locality, Cis-Urals, Lower Permian (Kungurian).

Peltasperm *Scytophyllum vulgare* (Prynada) Dobruskina (courtesy of Vera Vladimirovitch): The Bogoslovskoye Coal Mine, the Eastern Urals, Middle Triassic.

Cycadophyte *Baruligyna disticha* Krassilov et Doludenko: The Barula River, Georgia, Middle Jurassic (Callovian).

Pollen grains from the angiosperm flower *Freyantha sibirica* Krassilov et Golovneva: The Kem' River, Tchulymo-Yeniseysk Basin, West Siberia, mid-Cretaceous (Cenomanian).

Aquatic fern megasporae: The Kem' River, Tchulymo-Yeniseysk Basin, West Siberia, mid-Cretaceous (Cenomanian).

Fossil seedlings: The Gerofit locality, southern Negev, Israel, mid-Cretaceous (Turonian).

Fossil galls: The Gerofit locality, southern Negev, Israel, mid-Cretaceous (Turonian).

The collections are deposited in the Institute of Biology and Pedology, Vladivostok (Russia), Institute of Paleontology, Moscow (Russia), and the Institute of Evolution, University of Haifa (Israel).

3. **PROPHETIC CHARACTERS: RETICULATE POLLEN GRAINS**

Characters may appear earlier, sometimes much earlier, than the taxon for which they are diagnostic. For instance, practically all the diagnostic characters of angiosperms, including double fertilization, occur in phylogenetically older seed plant lineages (Krassilov, 1997). The mystery of angiosperm origins, although not resolved yet, is becoming less abominable with accumulation of paleobotanical evidence. Transitional forms combining angiospermous and gymnospermous characters are presently known from the Late Jurassic to Early Cretaceous deposits (Krassilov, 1997; Krassilov and Bugdaeva, 1999, 2000).

It is commonly believed that the easily dispersed pollen grains, rather than macrofossils, provide the most reliable records of angiosperm entries into the Mesozoic plant communities. In particular, the records of semi-tectate reticulate pollen grains are widely used for dating the angiosperm origins (Hughes, 1976). A steady increase in both frequencies and diversity of such pollen morphotypes over the Early Cretaceous is commonly held as evidence of high rate macroevolution in early angiosperms. Actually, such pollen grains have been extracted from staminate organs of more than one group of mid-Cretaceous angiosperms (Friis et al., 1986; Krassilov and Shilin, 1986; Krassilov and Golovneva, 2001), thus, suggesting a widespread parallelism of pollen morphology at this level.

Yet the angiosperm-like pollen grains are occasionally found in much older deposits. Fig. 1A depicts a reticulate pollen grain at least 230 million years older than the earliest Cretaceous reticuliform records. Such pollen morphotypes (*Reticulatina* Koloda) are known from the Early and Middle Permian (Kungurian to Kazanian) of northern Russia and the stratotypic Cis-Uralian Region (Koloda, 1996). They are presently studied with SEM and TEM from the Kungurian of Tschekarda, the Cis-Urals (Zavialova, in preparation) where *Reticulatina* spp. constitute up to 4% of palynological assemblage dominated by the widespread Permian pollen types *Lunatisporites*, *Protohaploxypinus*, *Cladaitina*, *Platisaccus*, *Vittatina*, and *Cor-*

daitina. These latter have either smooth or taeniate (with the surface layer divided into parallel stripes, or taeniae) exine. In *Reticulatina*, the surface reticulum has thick walls (muri) enclosing the irregularly polygonal, triangular, elliptical or slit-like lumina (Fig. 1B). Joints of the muri are sometimes perforated with a minute circular pore. Occasional lumina are traversed by a thin wall. The reticulum is coarser in the polar region fining out to the periphery. All these characters occur in the reticulate angiosperm pollen found *in situ* in the anthers of *Freyantha sibirica* Krassilov et Golovneva, the mid-Cretaceous angiosperm (Fig. 1C, D).

One can suspect that *Reticulatina* was produced by some primordial angiosperms hiding in the uplands of the proto-Uralian ranges. Yet this is scarcely the case. Not only is the time gap (150 million years) between the Permian and Cretaceous reticulate forms too large for their phylogenetic continuity, but also the Permian reticulatinas were both morphologically and ultrastructurally similar to the common types of non-reticulate Permian pollen grains found both dispersed and *in situ* in the pollen organs of Permian pteridosperms. Almost all types of taeniate pollen grains occur in the pollen load of Permian insects (Krassilov and Rasnitsyn, 1997, 1998) providing evidence of widespread pollen-feeding. In the pollen clumps extracted from the gut compressions, some grains are fully intact (Fig. 1C), whereas in the others the surface layer is partly digested exposing the infrastructure, which is reticulate and practically identical to the surface reticulum in *Reticulatina* (Fig. 1F). Reticulate infrastructure was observed also in smooth pollen grains of Cretaceous proangiosperms such as *Baisia* (Krassilov and Bugdaeva, 1982).

These findings indicate that sexinal reticulum first developed as infrastructure covered with a non perforate tectum. Dispensing of the latter as a late developmental stage resulted in surfacing of the reticulum in few Permian species, and the same repeated on a larger scale in the Cretaceous.

The surface reticulum in early angiosperms is interpreted (Zavada, 1984) as a component of self-incompatibility syndrome related to the pollen – stigma interaction. In the Permian seed plants, its functional meaning might have been entirely different. Our data show that most Permian pollinivores were visually attracted by taeniate surfaces promoting their parallel development in a number of insect-pollinated gymnosperm lineages (Krassilov and Rasnitsyn, 1997, 1998). With the build-up of ecological and morphological diversity through the Early Permian, the reticulate surface structures might have appeared as an alternative of taeniate structures breaking the monotony of contemporaneous pollen grain morphology.

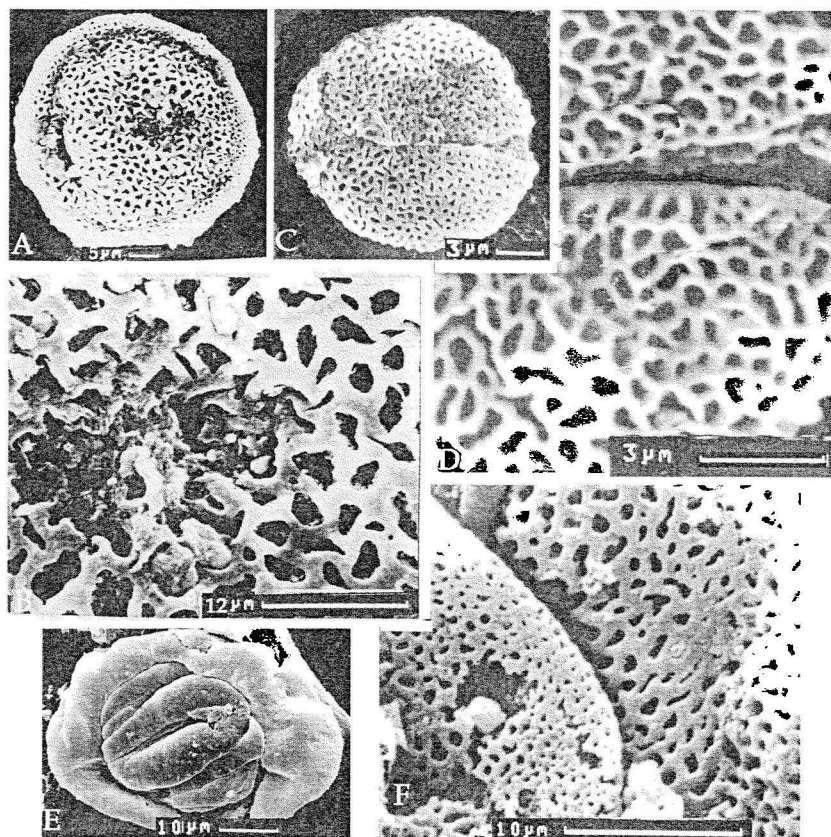


Figure 1. Reticulate pollen grains as an example of prophetic character repeatedly appearing due to the surfacing of infratectal structures: A. *Reticulatina* sp., dispersed pollen grain from the Lower Permian (Kungurian) of the Cis-Urals (courtesy of Natalia Zavialova); B. Reticulate surface structure of the same grain, enlarged; C. *In situ* pollen grain of *Freyantha sibirica* Krassilov et Golovneva, angiosperm flower from the mid-Cretaceous (Cenomanian) of West Siberia (Krassilov and Golovneva, 2001); D. Surface structure of the same grain, enlarged; E. *Lunatisporites* sp., taeniate pollen grain from gut compression of fossil insect *Idelopsocus diradiatus* Rasn. from the Lower Permian (Kungurian) of the Cis-Urals (Krassilov and Rasnitsyn, 1997); F. Reticulate infratectal structure of another *Lunatisporites*-type pollen grain from the same pollen load, with the tectum partly eroded by intestinal exudates.

Irrespective of functional interpretation, the loss of continuous tectum - surfacing of infratectal structure is a striking example of macromutation through abbreviated development resulting in a distinctive new morphology. This example also shows that a single character, however typical, does not unequivocally testify to the origin of the respective higher taxon. The

character may develop prophetically in a different adaptive context to acquire a new function much later in evolutionary history.

4. GENOCOPY: FIXATION OF ANOMALOUS STOMATOGRAPHY

Epidermal structures are a promising object of developmental studies. In particular, the types and arrangements of stomata are thought to reflect a morphogene concentration that (1) induces differentiation of epidermis into stomatal and stomata-free areas, (2) inhibits stomatal initials (meristemoids) in the vicinity of the developing stoma, and (3) modifies the adjacent epidermal cells (Bloch, 1965; Ursprung, 1966; Lewis et al., 1977). These features are of a certain taxonomic significance. At the same time, the ratio of stomata to ordinary epidermal cells is under strong environmental (atmospheric CO₂ concentration) control (Kürschner, 1996) and the other stomatographic characters are also liable to environmental induction.

Uneven distribution of stomata over leaf surface is sometimes ascribed to standing waves of morphogene concentration (Ursprung, 1966). Yet stomata typically tend to develop between veins, in parallel bands or polygonal areas depending on the type of venation. Such distribution has a functional meaning in respect to concentration of vapor and CO₂ in the boundary layer separating leaf surface from the ambient air. A decoupling efficiency of the boundary layer depends on the leaf surface micromorphology (Meinzer, 1993). It is typically higher between the vein ridges, hence, the intercostal concentration of stomata. My study of bennettitalean stomata (Krassilov, 1978a) has shown that in the microshadow of prominent lateral veins, not only is the distribution of stomata less regular, but also the frequency of contiguous stomata (only one cell apart) is considerably higher than in the stomatal mid-zones.

The configuration of stomatal bands in respect to vascular bundles is diagnostic for species or even genera in many angiosperm families and in the vast majority of gymnosperms. It can persist even after the loss of the veins. Thus, in conifers, several longitudinal stomatal bands are sometimes retained in single-veined needle-leaves derived from broad leaves with several veins (e.g., in the single-veined podocarp leaves with three stomatal bands: Florin, 1931; Krassilov, 1967). Yet the differentiation of stomatal initials in respect to veins is often obliterated or nearly so in enrolled leaves or those with deeply embedded vascular bundles. Epidermal topography thus falls under an intricately combined control of genetically determined morphogenic gradients and environmental induction.

The taxonomically significant configurations of subsidiary cells are related to the meristemoid developmental rates. Ontogenetically, subsidiary cells are either perigenous, derived from adjacent epidermal cells, or mesogenous, produced by the rapid successive divisions of meristemoid itself. The latter can be seen as an atavistic mutation betraying the evolutionary origin of stomata from multicellular structures (part 5). Yet the mesogenous subsidiaries are distinctive for a number of angiosperm families and for bennettites among gymnosperms (Florin, 1933; Krassilov, 1978a). At the same time, in the bennettitalean cataphylls, the configuration of subsidiaries is different from that in the foliage leaf and is more typically perigenous. Thus, in this group at least, the stomatotype depends on the developmental program of organogenesis.

An exceptionally high frequency of epidermal anomalies such as irregular epidermal zones, interrupted stomatal rows, underdeveloped and/or contiguous stomata, disorganized arrangements of subsidiary cells, etc., are recorded in the transboundary Permian - Triassic fossil plant assemblage of Nedubrovo, central European Russia (Krassilov et al., 1999). As this stratigraphic level is marked by huge volcanic eruptions, the anomalous epidermal developments might have been related either to the massive ash falls or to the mutagenic effect of UV radiation (increased with the discharge of ozone-destroying volcanic aerosols) or both.

A conspicuous anomaly is an occasional increase of subsidiary cells from 4 – 6, typical for peltasperms and conifers, to 8 – 12, exceptional for these plant groups. Remarkably, in the monotypic conifer genus *Ullmannia* Goeppert, appearing during the large-scale environmental disturbance in the latest Permian, a ring of 10 – 12 subsidiary cells is a diagnostic character (Fig. 2A). The subsidiary cells are considerably smaller than the ordinary epidermal cells and they are radially disposed encircling the guard cells. Occasional aborted stomata appear as a group of minute cells resulting from proliferation of meristemoid, in which the guard cells failed to differentiate. These are evidence of mesogenous origin for all or most subsidiaries (the intruding larger cells, as in Fig. 2B, are probably perigenous).

Since the typical stomatal structure in *Ullmannia* corresponds to the anomalous environmentally induced condition in other contemporaneous conifers, a fixation through genocopy is the most probable mechanism of macromutational origin for this genus-specific epidermal character.

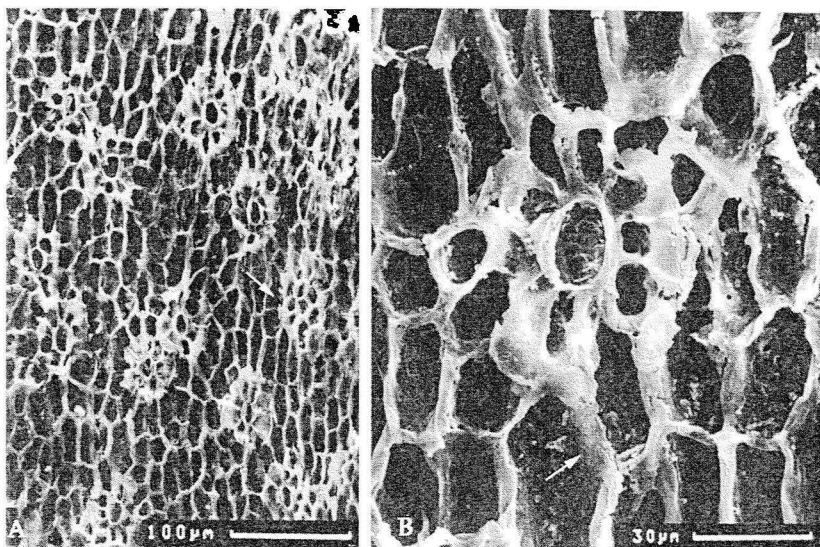


Figure 2. Teratological origin of stomatal structure in *Ullmannia* cf. *bronnii* Goeppert., a conifer from the transitional Permian – Triassic deposits of Nedubrovo, European Russia: A. Stomata with numerous (10 – 12) small subsidiary cells and a similar configuration of small cells produced by prolific divisions of a meristomoid that failed to develop into stoma (arrow); B. Stoma with a ring of small mesogenous cells intruded by a larger perigenous cell (arrow).

5. PEDOMORPHIC ORGANOGENESIS: ORIGIN OF STOMATA

Stomata are obligatory for photosynthetic tissues of terrestrial plants, therefore, conceivably appearing at a very early stage of their evolution. Genuine transitional stages between early land plants and their algal ancestors are not known, yet the conservative morphology of thickly cutinized (hence terrestrial) alga-like Devonian plants give some idea of how the basic structures might look. The most primitive among the cutinized thalloids is *Shuguria* Tchirkova-Zalesskaya emend Krassilov from the mid-Devonian of European Russia having tubular shoots with two-layered cortex. The cortical layers probably correspond to the mesoderm and subcortex of brown algae. The medullar tissues comprise the subcortical parenchymatous layer and the central bundle of pitted conducting cells resembling the conducting tubes of extant laminarialean algae and *Ascoseira* (Moe and Henry, 1982).

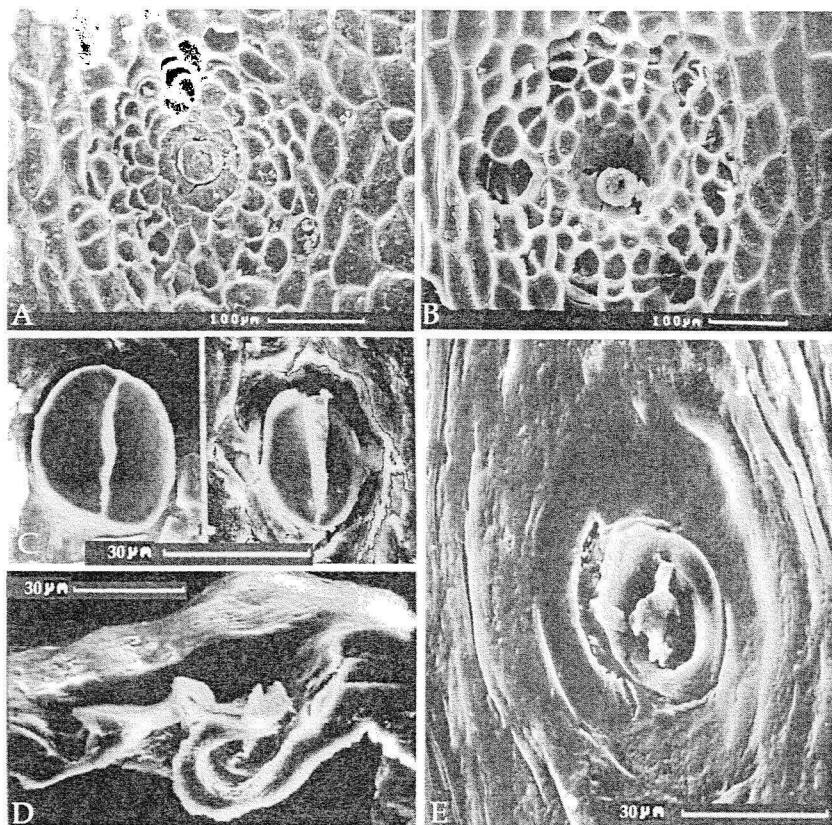


Figure 3. The supposed homology of sex organs and stomata in the Devonian alga-like plants: A. Gametangial conceptacle of *Shuguria ornata* Tchirkova-Zaleskaya B. Conceptacle of the same plant with the neck cell detached; C – E. Stomata of *Orestovia devonica* Ergolskaya, interior view and transverse section showing cuticle of guard cells extending to substomatal chamber (Krassilov, 1981a).

The most conspicuous structures of *Shuguria*-type thalloids are spherical bodies developing subcortically and opening by a pore that is covered with a detachable neck cell (Fig. 3A). These structures are closely comparable with gametangial conceptacles of brown algae, in particular the Fucales and Ascoseirales, in which they develop from the initial cells, or prospores, that differentiate in the meristoderm and are developmentally shifted to the subcortex. Consecutive developmental stages preserved in *Shuguria* are closely comparable with those in extant *Ascoseira* (Moe and Henry, 1982). In both, the conceptacle initial appears as an enlarged thick-walled cell of the inner cortical layer producing by successive anticlinal divisions the basal chamber with gametangial or sporangial sori and with a neck reaching to the

shoot surface. The surrounding cortical cells undergo mitotic divisions forming concentric rings.

In *Shuguria*, the terminal neck cell is puck-shaped, about 50 μm in the larger diameter, divided by thin median septa, with the parts gaping in the middle forming the central canal. The neck cell appears as a terminal periclinal derivative of the stem cell. After maturation, the neck cell is detached as a lid and drops out or sticks near the circular orifice (Fig. 3B). With continuing stretching of the cortex, the conceptacles are destroyed, their orifices developing into irregular pores scattered over the shoot surface.

New conceptacles are often initiated in close proximity to, occasionally even contiguous with, the older ones. The conceptacles of the same developmental stage, however, are nearly equidistant from each other. Such arrangements suggest an inhibitory interaction between simultaneously developing structures and the lack of such between successive generations.

Shuguria has been compared and even synonymized (Istchenko and Istchenko, 1981) with *Orestovia* Ergolskaya from the Devonian of Siberia, to which it is similar in the general habit and the cell pattern of cutinized cortical tissues. In *Orestovia*, however, the conducting cylinder is much thicker, consisting of tracheid-like cells with helical or reticulate thickenings (Krassilov, 1981a). Moreover, *Orestovia* shows the regularly disposed stomata or stomata-like structures lacking in *Shuguria*, the tubular shoots of which might have been ventilated through the pores left of the shed conceptacles. *Orestovia* clearly represents a more advanced stage of terrestrial plant life requiring a more specialized organ of gas exchange. Here, the stomata-like structures consist of two cells with a cutinized canal between them extending to the cavity beneath (Fig. 3C - E). They are similar to the detachable neck cells of gametangial conceptacles in *Shuguria*, thus confirming the hypothetical derivation of stomata from sex organs (Pant, 1960). In their distinctive shape and morphogenic control over development of surrounding cells, the conceptacle initials are exactly like stomatal initials.

The morphologically feasible steps in derivation of *Orestovia*-type stomata from *Shuguria*-type conceptacles would have been an abbreviation of proliferative activity in the stem cells after a few divisions, a reduction of the gametangial chamber leaving the residual substomatal chamber, and a direct transformation of stem cell into the neck complex bypassing the intermediate stages. Instead of being detached at maturation, the neck complex would remain intact providing a more sophisticated mechanism of gas exchange than the residual pores of the *Shuguria*-type conceptacles.

6. RESTRUCTURING THROUGH DEVELOPMENTAL RATES: MANGROVE SEEDLINGS

All morphological changes involve developmental rates. Yet examples of a rapid and conspicuous restructuring solely resulting from a definable shift of developmental rates are not so common. Perhaps the best of these are provided by the viviparous seedlings of mangroves, the woody plants of intertidal mangal communities. In the typically viviparous *Rhizophora* L., the proximal seedling axis, or hypocotyl, emerges from the fruit while it is still attached to the parent tree. As a matter of fact, neither fruit nor seed take any part in propagation that is totally assigned to the hypocotyl, which detaches itself from the cotyledons (left with the fruit), falls to the muddy ground, and develops into a new plant. This peculiar form of propagule results from the early shift of high rate growth from cotyledons to the intercallary meristematic zone below the cotyledonary node (Juncosa, 1984). As a result, the cotyledons never develop as distinct foliar structures, but instead are completely fused into the gaustorial cotyledonary body. Prior to detachment, growth is once more shifted to the base of cotyledons forming the cotyledonary collar that protrudes from the fruit enclosing the epicotyl. Even the radicle meristem is suppressed in favor of lateral roots arising from the hypocotyl. A high rate growth of hypocotyl is shared by the other rhizophoracean genera, although the base of cotyledons may not be so excessively developed, and the abscission line may remain inside the fruit.

Due to their relative robustness, mangrove seedlings are often preserved as fossils. Various types of seedling development are recorded in the mid-Cretaceous mangrove assemblage (recognized as such on the basis of root morphology primarily) of Gerofit, southern Israel. One of them was cryptoviviparous, germinating from the seed, but enclosed in the fruit that developed from epigynous flower (Fig. 4A). The hypocotyl apex emerged from the fruit after shedding (Fig. 4B). Another type of propagule is represented by a detached seedling consisting of a relatively short and warty hypocotyl with a well-developed pair of lateral roots near the apex and with shorter lateral roots above (Fig. 4C). It shows no evidence of radicle, the development of which might have been totally suppressed. Here the developmental pattern should have been much as in *Rhizophora*, yet with the hypocotyl less excessively elongated before shedding.

Fig. 5A – C shows an uprooted seedling with fruit remains attached near the base and with a well-developed cotyledonary collar emerging from it. The epicotyledonary axis and leaves are well developed. This seedling morphology appears less specialized than in the *Rhizophoraceae*, with epicotyl overgrowing the cotyledons and the fruit abscised with the seedling.

However, the cotyledonary collar indicates an excessive basal growth of cotyledonary body as an early appearing specialized feature (playing a role in regulation of salt content) of mangrove seedlings. In this respect, the seedling morphology in the Cretaceous mangrove plant is more advanced than in the extant *Bruguiera* Lamark, in which the intercalary meristematic zone between the cotyledons and hypocotyl remains inside the fruit (Jancosa, 1982, 1984). Fossil seedlings thus add new variants of heterochronous development unknown in the extant mangroves.

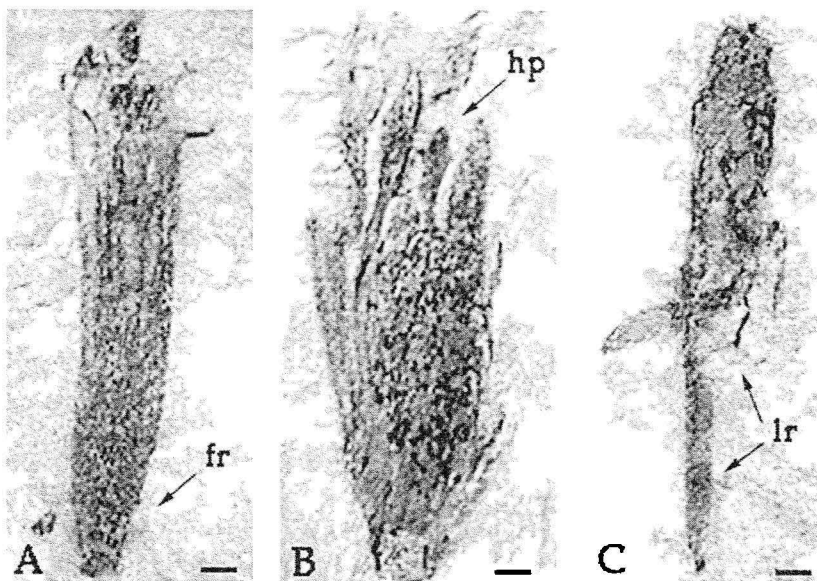


Figure 4. Seedling morphologies in the early mangroves (mid-Cretaceous of Gerofit, Israel) arising through developmental shifts: A. Early stage of fruit (fr) development from the epigynous flower; B. Flower in fruit with the hypocotyl (hp) emerging from the fruit; C. Detached hypocotyl with lateral roots (lr). Scale bar 0.5 mm.

The diversity of specialized seedling morphologies in the mid-Cretaceous assemblage is remarkable considering that this is the earliest record of just appearing angiosperm mangroves, which attests to a high rate macromorphological evolution through the shifting growth rates in the early development.

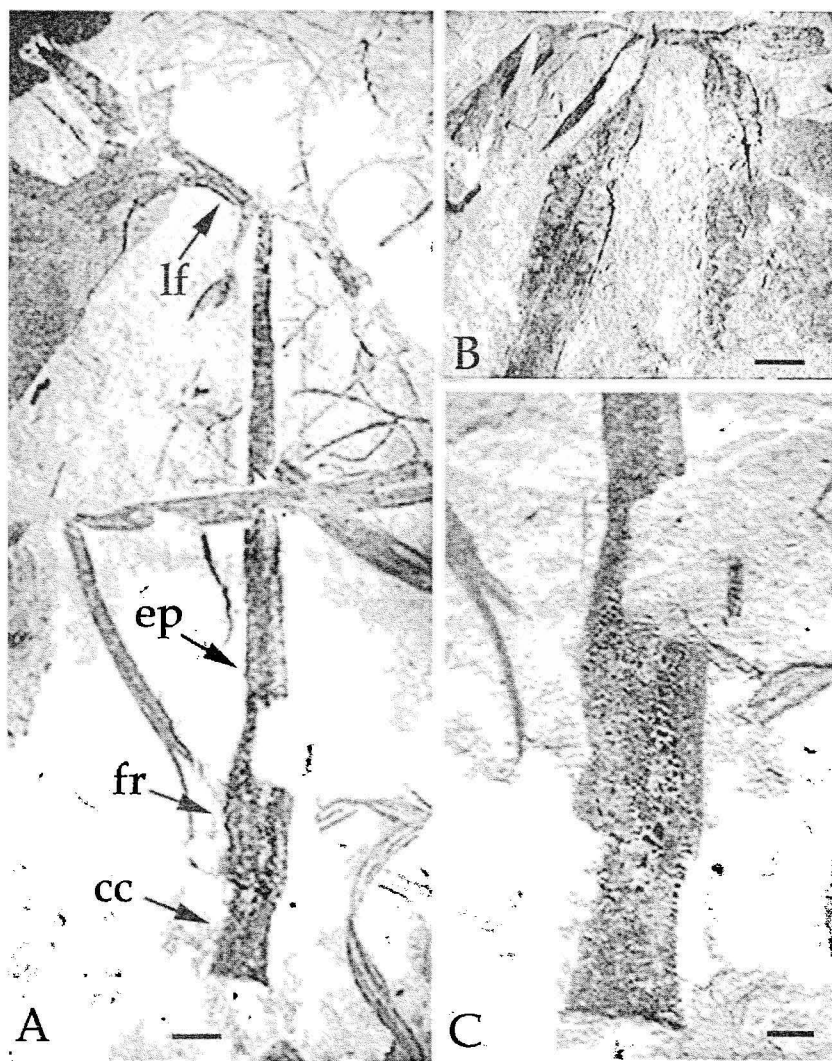


Figure 5. Seedling morphology in the early mangroves (mid-Cretaceous of Gerofit, Negev, Israel) arising through developmental shifts: A. Seedling uprooted below the cotyledonary collar (cc – cotyledonary collar emerging from the fruit, ep – epicotyl, fr – fruit coat, lf – leaf); B. Proximal part enlarged to show cotyledonary collar; C. Seedling leaf from counterpart of the same specimen. Scale bar 0.3 mm.

7. RETROCONVERGENT MORPHOLOGY

This category comprises macroevolutionary events, which bring back character states that had once appeared and were lost in the course of historic development. The well-known examples from plant morphology are the leafy "megasporephylls" of *Cycas* L., as well as the anomalous ovules on leaves in *Ginkgo biloba* L. As both these structures resemble leafy ovulate organs of Paleozoic pteridosperms, the putative forerunners of all modern gymnosperms, they were interpreted as a retention of ancestral character state, a peculiar case of evolutionary conservatism. Plant morphologists even considered *Ginkgo* (and, by implication, *Cycas*) as "living pteridosperms" (Meyen, 1987).

Leafy ovuliphores, however, never occurred in the Mesozoic ginkgophytes and cycadophytes that intervened between the Paleozoic and extant forms. Typical of the Mesozoic ginkgophytes were ovulate strobili (Krassilov, 1970) that showed no evidence of either leafy prototype or secondary planation.



Figure 6. Retroconvergence of *Cycas* like "megasporephyll" in Jurassic cycad *Baruligyna* Krassilov and Doludenko, with scars of subtending bracts (arrows) betraying its origin from a planated strobilate structure.

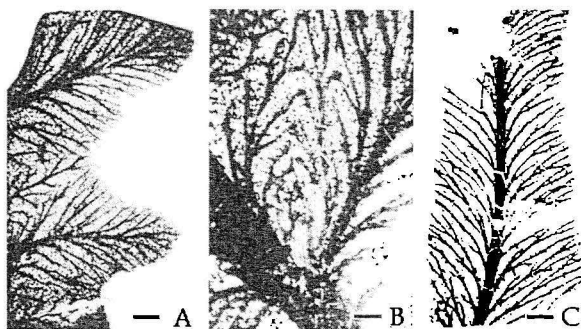


Figure 7. Retroconvergence of pinnule shape and venation in Triassic pteridosperm *Scytophyllum vulgare* (Prynada) Dobruskina: A. Proximal fusion of pinnules with open dichotomous venation. Scale bar 1.5 mm; B. Fused portion of the pinna with areolate venation around interstitial pinnule incorporated in the web. Scale bar 0.75 mm; C. Later stage appearing as a simple pinnule with dichotomous lateral veins, except the occasional anastomoses and irregular branching of basal veins. Scale bar 1.5 mm (Krassilov, 1995).

The reproductive structures of Mesozoic cycadophytes were likewise strobilate, yet showing a planation tendency in at least two forms of ovulate organs, *Semionogyna* from the Early Cretaceous of Transbaikalia (Krassilov and Bugdaeva, 1988) and *Baruligyna* from the Jurassic of Georgia. Both were flat axes bearing ovules in two lateral rows. In *Semionogyna*, the

ovules developed in the axils of subtending bracts that were shed at maturity. *Baruligyna*, although chronologically an earlier form, was further advanced in the direction of *Cycas*-type "megasporephyll" morphology. Here the subtending bracts were lost early in development leaving inconspicuous scars at the base of the ovules that were decurrent at the base, webbing the axis (Fig. 6). These forms preceded the first appearance of *Cycas* in the Late Cretaceous (Krassilov, 1978b) definitely suggesting a derivation of leaf-like ovulate organs from a strobilate precursor. The pteridospermous aspect of "megasporephylls" in *Cycas* and the anomalous ovuliferous leaves in *Ginkgo* are, thus, of secondary nature, falling in the category of retroconvergence (Krassilov, 1995).

The phenomenon of retroconvergence is most spectacular in the case of complex structures homomorphous to their constituent units, as in the compound strobili (of conifers) converging upon their progenitorial simple cones, inflorescences imitating solitary flowers, fruits shaped as seeds, permanent pollen tetrads resembling solitary pollen grains, etc. In the Mesozoic peltasperm *Scytophyllum vulgare* (Prynada) Dobruskina, segments of bi- to tripinnate leaves fuse marginally webbing the axes and, at a more advanced stage, forming the entire leaf blade. Although the pinnules are lost in fusion, their venation remains distinct over the coalescent blade. Areolate venation develops by arching and anastomosing of veins around an interstitial pinnule imbedded in the web (Fig. 7A, B). Yet at the later stages, all traces of fusion are obliterated, the venation is reduced to the conventional dichotomous pattern, and the coalescent blade appears as a segment of the initial pinnate leaf (Fig. 7C). An adaptive meaning of such cyclic transformations is scarcely conceivable. Rather, the meaning is related to the nature of genomic memory retaining images of lost basic structures, which can be conferred upon their derivative organs.

8. PATHOGENIC ORGANOGENESIS: ORGANOID GALLS

Symbionts render not only physiological but also morphological effects (reviewed in Buchner, 1965), most conspicuous in the case of organoid galls, which are induced by various organisms, from bacteria to arthropods. Gall formation, or cecidogenesis, often simulates normal organogenesis, even to the extent of pathogenic "organocopies". Familiar examples are the "green petal" disease induced by mycoplasmas, the polyclady (witches' brooms) caused by rust fungi that inflict also hypertrophy of leaf tissues and fusion of leaf lobes, the inhibition of apical growth bringing about a sympodial branching or aggregation of lateral shoots or pinnae (e.g., in the familiar fern

species *Athyrium filix-femina* (L.) Roth galled by dipteran larvae), the swelling of petioles and pathogenic leaf dehiscence, the production of epiphyllous buds and dwarf shoots, the transformation of paniculate inflorescences into heads by inhibition of internodes (by cecidogenous larvae of a homopteran species *Philaenus spumarius* L.), the enlargement and closure of corolla in flower galls or, conversely, the inhibition of corolla (e.g., by a heteropteran galler *Copium cornatum* Thumb.), the development of pouch galls resembling ascidiform carpels, inflicted by various insect gallers such as aphids, gall midges, etc. (reviewed in Meyer, 1987).

In the above examples, the cecidogenesis involves both hypertrophy and inhibition of growth. The parallelism of evolutionary derived morphogenetic processes and pathogenic organogenesis indicates that developmental pathways may be the same in both. If the galls are organocopies of evolutionary developments, can the reverse be true for non pathogenic characters that look like galls? In other words, can certain plant morphologies, such as the fusion of needles, cecidogenic in *Pinus silvestris* L., but a generic character in *Sciadopitys verticillata* Sieb et Zucc. or the ascidiform gynoeceia of archaic angiosperms that look like pouch galls, be acquired as genocopies of respective pathogenic transformations?

Since galling is mediated by the gene transducing plasmids (Manulis, 1992), it seems fairly possible that the same transposons are involved in normal morphogenetic processes and their cecidogenous organocopies. A genomic study addressing this problem would have been rewarding. From the morphological point of view, the possibility is confirmed by the existence of pseudogalls, or plant structures of nonpathogenic origin that appear like galls and are colonized by cecidicolous insects (Monod and Schmitt, 1968). Pseudogalls obviously result from a genetic fixation of pathogenic induction. If so, then certain plant organ morphologies might, in principle, originate in the same way.

A paleobotanical observation perhaps relevant to the problem of cecidogenous organocopies is that the diversity of both organogenesis and gall formation had immensely and simultaneously increased with the advent of flowering plants, the coincidence that was scarcely accidental. Although galls are recorded since the Carboniferous at least (Van Amerom, 1973), their fossil record is meager until the mid-Cretaceous and the causative agents remained unknown. In contrast, in the Turonian fossil plant assemblage of Gerofit, southern Israel, almost every leaf is parasitized by gallers, sometimes of two or more kinds. The most common are the pouch galls (Fig. 8A) induced by cecidomiids (their larvae are occasionally preserved). As their extant progeny, the Cretaceous cecidomiids were able to break loose their galls, which are found detached, abandoned by imago, with the pupal horns emerging from the exit (Fig. 8B). Such remains can easily be confused with detached fruits from the same locality, and it is still to be learned

whether this morphology first appeared in fruits or in galls. Anyway, the abundance and diversity of galls on early angiosperms testifies to an explosive cecidogenesis for which the appropriate mechanism has to be sought.

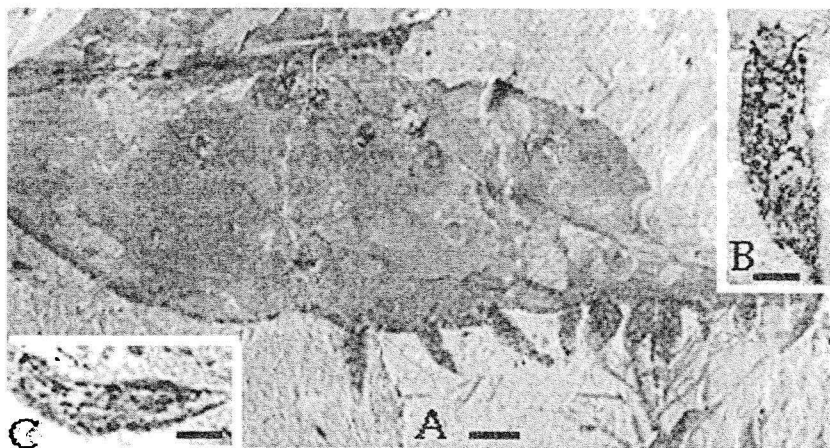


Figure 8. Gall and fruit remains from the mid-Cretaceous of Gerofit, southern Negev, Israel: A. Poach galls on leaf margin, scale bar 2 mm; B. Poach gall detached, with cephalic horns of the pupa protruding from the exit, scale bar 0.3 mm. C. Detached fruit of *Gerofitia* Krassilov et Dobruskina for comparison with the gall, scale bar 0.3 mm.

9. ANASTROPHES

No matter how loyal to the *natura non facit saltum* slogan and how suspicious of the fossil record one may be, one has to accept the non-uniform evolution rates as an undeniable fact of nature.

New orders of plants and animals appear in dozens within rather short intervals of geological time followed by the much longer periods of evolutionary quiescence (examples in Simpson, 1944, 1949; House, 1963; Newell, 1967; Boucot, 1975; Krassilov, 1977; Vermeij, 1987 and elsewhere). Seed plant phylogeny (Fig. 9) clearly shows the clustered appearance of orders in gymnosperms and proangiosperms, whereas angiosperms accomplished their basic radiation in the mid-Cretaceous (Krassilov, 1997).

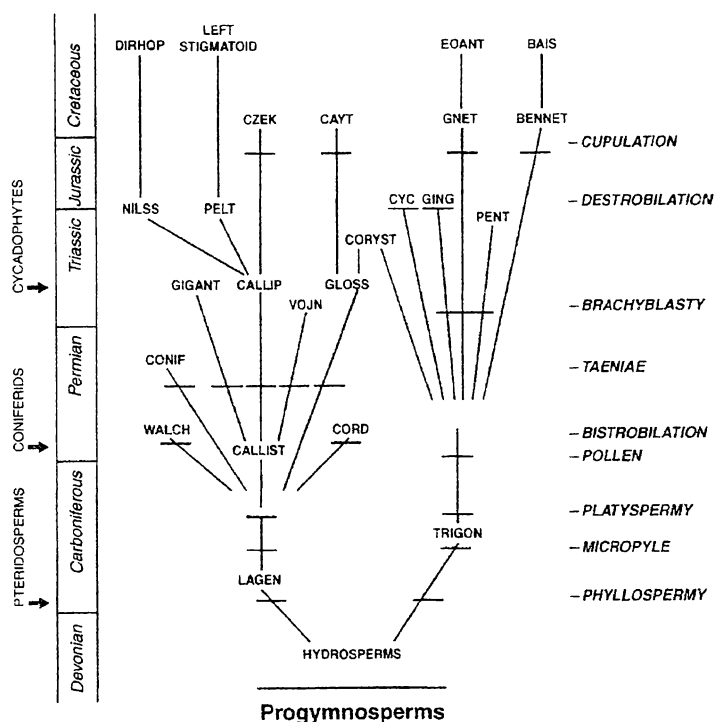


Figure 9. Phylogeny of gymnosperms and proangiosperms (Krassilov, 1997) showing radiation bursts (anastrophes) and parallel developments of morphological traits (horizontal dashes). Abbreviations: Bais, *Baisia*; Bennet, bennettites; Callist, callistophytes; Callipt, callipterids; Conif, conifers; Cord, cordaiteae; Cayt, catonias; Cyc, cycads; Czek, czekanowskians; Dirhop, *Dirhopalostachys*; Eoant, *Eoantha*; Gigant, gigantopterids; Ging, ginkgoaleans; Gnet, gnetophytes; Gloss, glossopterids; Lagen, lagenopstoms; Lept, *Leptostrobus*; Nilss, nilssonias; Pelt, peltasperms; Trigon, trigonocarps; Walch, walchians.

The anastrophes are commonly thought to be consequential to colonization of new biotopes, which explains why diversification bursts closely followed the first appearances, e.g., of land plants in the Devonian. A striking example is the rapid diversification of aquatic ferns and angiosperms at the initial stage of their entry into lacustrine ecosystems in the mid-Cretaceous including the bizarre forms producing amphispores, the megaspores bearing microspores (Fig. 10) retroconvergent upon the Devonian *Kryshfovichia* Nikitin (Krassilov and Golovneva, 1999). Likewise, the diversity of specialized seedling morphologies in the mid-Cretaceous mangrove assemblage of southern Israel (part 6) is evidence of explosive macroevolution at the first appearance of a new adaptive type.

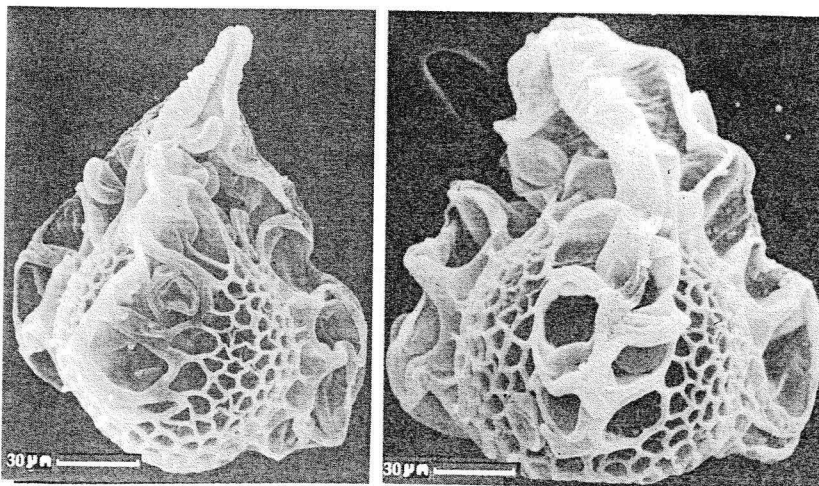


Figure 10. Innovation at anastrophe in aquatic ferns: the water-borne megaspores bearing microspores in their laesural pockets as a single dispersal unit (Krassilov and Golovneva 1999).

Yet anastrophes are sometimes delayed for several periods, as in the case of mammals (the first appearance in the mid-Triassic, anastrophe in the Paleogene), or they happen more than once, as in ammonoids (in the Devonian and Jurassic) or dinosaurs (in the Jurassic and mid-Cretaceous). In such cases, the bursts of diversification were preceded by near-extinctions which corroborate a causal link between catastrophes and anastrophes.

The coincidence of anastrophes in dinosaurs and angiosperms can be explained by their links through trophic cascades (Krassilov, 1981b). However, such trophically unrelated groups as planktonic foraminifers, marine bivalves (aucellinas, rudistids), craniid brachiopods, terrestrial insects, etc., also experienced anastrophes at the same time, which requires a more general explanation. According to the model of coherent vs. non-coherent evolution (Krassilov, 1969, 1977, 2003, and elsewhere), anastrophes are consequential to disruption of co-evolved biotic communities (simultaneous in marine and terrestrial realms under global environmental change). With stabilizing selection relaxed, high premium is placed on accelerated development and early reproduction promoting heterochronic shifts of growth rates. All kinds of macromutation described above may appear jointly because they are interrelated. In effect, the morphological disparity is greatly enhanced bringing about macropolymorphic populations typical of post-crisis situations.

Examples of post-crisis macropolymorphism could have been concealed by the routine paleontological treatment of any deviating morphology as a separate taxon. This, in fact, has been revealed in my studies (Krassilov

1976, 1989) of morphological variation in the Early Paleocene species *Trochdendroides arctica* (Heer) Berry and *Platanus raynoldsii* Newberry, previously described under a dozen generic names each (Kryshtovovich and Baikovskaya, 1966). At this pre-anastrophic stage, macromutation does not result in the origin of new taxon and must be considered as a micro-evolutionary event. Yet the macropolymorphic population might serve as a basis for diversification at the species and higher levels with evolution recessing to the coherent coevolution mode.

10. CONCLUSIONS

There is ample evidence of taxonomically important characters arising from developmental changes that can hardly be anything but saltational. Yet the appearance of such characters does not mean that the higher taxa, for which they are typical, came into being in the same saltational way. Characters appear, disappear, and reappear each time in a different adaptive context. They become typical for a higher taxon as a part of its adaptive syndrome through interaction with other typical characters having a separate history of macroevolutionary developments.

Higher taxa are commonly conceived of as constant combinations of characters indicating a monophyletic origin. However, although the latter remains an unverifiable assumption, a more realistic cause for morphological distinctness is its functional adaptive significance. Conifers or angiosperms are essentially the distinct adaptive types in the same way that amphibians or mammals are. As such they make use of structures that appeared in a different adaptive context and for different functions. Such prophetic structures (e.g., the reticulate pollen grains, part 3) might have evolved in a remote rather than immediate ancestor of the group to be retrieved as retroconvergent characters (e.g., the "pteridospermous" megasporophyll morphology in cycads, part 6) from a silent part of genomic memory. In particular, the angiosperms show typical characters of cycads, ferns, horsetails, charophytes even. Each of these groups has been claimed to be ancestral at one time or another and, in a sense, they all contributed to the origin of angiosperms (Krassilov, 2002). An essential feature of the latter is the accelerate development opening the way to a retrieval of the seemingly long-forgotten traits. The phenomenon of retroconvergence suggests that, once appearing, a morphological trait would seldom or maybe never escape from the genomic memory.

Ample opportunities for macromutational developmental shifts arise with accelerated growth and precocious sexual maturation. Moreover, pedomorphic forms are especially vulnerable to environmental induction including the pathogenic organogenesis. Therefore, one can expect a high rate

macroevolution under circumstances that encourage precocious development. Just such circumstances arise with global environmental crises and the collapse of stable biotic communities. The post-crisis populations tend to be macropolymorphic incorporating morphological effects of macromutations. In such populations, macromutations are microevolutionary, rather than macroevolutionary, events enhancing morphological disparity that is not accompanied by an adequate increase in taxonomic diversity. The diversification bursts start with adaptive segregation of macropolymorphic phenotypes.

The traditional speciation theory holds that separation by a physical barrier is necessary for interruption of gene flow. It has been shown, however, that ecological differences may be even more important than geographic separation (Ehrlich and Raven, 1969). Rapid accumulation of evidence for sympatric genetic divergence in respect to differentiation of habitats, greatly enhanced by Eviatar Nevo and his collaborators (Nevo et al., 1997a,b, and elsewhere), makes clear that the traditional theory of isolation first – adaptive divergence next, just started at the wrong end. Effective interruption of gene flow is achievable, without geographic barrier, through a phenotypic modification (such as dwarfing or a shift of flowering time) that interferes with crossing.

Vast evidence collected under the orthogenetic paradigm (part 1) and a few more recent examples attest to developmental shifts as an immediate response to environmental induction. The effects typically fall in the category of phenocopies (Goldschmidt, 1958), which means that the environmentally induced phenotype is reproducible by mutation and, therefore, can be fixed as genocopy.

Thus, recognition of the evolutionary role of macromutation does not necessarily imply that mechanisms of micro- and macroevolution are different. It implies only that our understanding of both is impeded by the tenacious, yet hopefully surmountable, dogmas of traditional evolutionism.

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