On the morphological nature of the cupules of some Upper Devonian/Lower Carboniferous seed plants

Alexander B. Doweld

National Institute of Carpology (Gaertnerian Institution),
P.O. Box 72, RUS-119517, Moscow, Russian Federation

The morphology of ovule - and microsynangia-bearing systems of most primitive Upper Devonian (*Elkinsia polymorpha*, *Moresnetia zalesskyi*) and Lower Carboniferous gymnosperms (*Kerryia mattenii*, *Pullaritheca longii*) has been reinterpreted and redescribed in the terms of a shoot morphology. The cupules alone and the cupuliferous complex constructions are a single morphofunctional unit being a system of modified reproductive shoots bearing synangia- insynangescence. These gymnosperms are characterized by aggregate insynangescences, or synsynangescences of pleiochasidial type representing in itself a whole hierarchy of insynangescences. The cupules of *Elkinsia* and *Moresnetia*, and also those of *Kerryia* are interpreted as partial insynangescences (synangescences) aggregated into compound insynangescences (cincinni) and constituted in its turn an aggregate synsynangescence of pleiochasidial type. The cupules of *Moresnetia* and *Elkinsia* are interpreted as dichasidia, those of *Kerryia* as trichasidia, whereas cupules of *Pullaritheca* are interpreted to represent another type of the compound insynangescent system - a condensed calathiform aggregation of two dichasidial insynangescences, termed a pocule. The bisexuality of the synsynangescence of *Pullaritheca longii* obviously indicates that it belongs to some seed plants having a bisexual assemblage of ovules and microsynangia. It does emphasize that known unisexual and possible dioecious Upper Devonian/Lower Carboniferous gymnosperms were far too specialized to be the only initial group for all spermatophytes. It is more likely to hold them as a blind branch of gymnospermous evolution taking into consideration its retaining imperfect telomic organisation of the reproductive shoot. In such a case in the starting naked insynangescence there are not any potentialities for a formation of the additional protective epi-integumentary systems enveloping an ovule as seen within more advanced spermatophytes. The insynangescence concept finally debunks views on the origin of integument from the vegetative segments like tegoclades of dichasidium, trichasidium or pocule. On the basis of comparative morphology of insynangescences, *Pullaritheca* has been segregated into a distinct family Pullarithecaceae and order Pullarithecales. Thus it has been formally ascertained an existence of two distinct highly specialized phyla within the Upper Devonian and Lower Carboniferous seed plants.

Key-words - Ovule, origin, integument, inflorescences, shoot.

INTRODUCTION

THE last few years have greatly expanded our interest on the structure of reproductive organs of the earliest seed plants (Meyen 1987; Stewart & Rothwell 1993; Taylor & Taylor 1993) mainly dealing with the problems of their biology (Rothwell & Scheckler 1988; Rothwell & Serbet 1992). These studies have contributed numerous additions and corrections both to morphological descriptions and to the understanding of the biology of the complex constructions of lobed integument, "cupule" and "cupuliferous branching system". Paradoxically, the fact is that the expanded and modified reconstructions of reproductive organs of these seed plants have not pushed forward our knowledge to the necessary reappraisal and redescription of their stucture in terms of the analogies and homologies of the same structures in more advanced spermatophytes. Evidently, it might be explained by the lack, for many years, of the terminology in organography of fossil seed plants, permitting cogent comparison of the described structures. It was possible, in part, due to the lack of a clear understanding of the phylogenetic relationships between described taxa. But at the same time some students of fossil forms, following settled views of previous authors, often reject or do not see the necessity to re-evaluate the morphological nature of the studied organs. They frequently use the same name for comparatively different structures. So, Rothwell and Scheckler (1988 : 104) defined the pre-Carboniferous cupule

as "... the unit that encircles or encloses a single space into which one or more ovules protrude...". Following such an approach, the carpel of angiosperms, cupule of seed ferns, 'capsule' of *Umkomasia* and seed-scale complex of Pinophyta would have the same morphological nature, with which, plainly, it is impossible to agree. Meyen's attempt (1982, 1984) to introduce a "new terminology" for description of gymnospermous fructifications, dividing them into two artificial groups - monosperms and polysperms, - did not solve the problems of their homologies and morphogenetic relationships. This "new terminology" resembles an inventarisation only of available objects rather than a terminology being able to emphasize the individuality of a structure and its morphological nature, making it comparable with other structures of seed plants.

According to the modern widely accepted theory (Meyen 1984, 1987; Stewart & Rothwell 1993; Taylor & Taylor 1993) the first ovules were enclosed into the peculiar cupule. It has been also claimed (Meyen 1984) that these cupule lobes became adnate, enveloped an ovule, and simultaneously transformed into the outer integument of Trigonocarpales (Oliver & Scott 1904; Stopes 1905; Oliver 1909; Smith 1964; Walton 1953; Meyen 1984; Stewart & Rothwell 1993; Taylor & Taylor 1993). In this respect, the occurrence of microsynangia within such cupules appears somewhat strange and hardly explicable, since there are no rudiments of any other vestiges of such structures in the cupules of higher spermatophytes. Moreover, the recorded unequal number of ovules within the cupules does not agree with numbers of dichotomous distal elements. It looks somewhat strange, since the pedicel of the ovule, as it has been determined, is a derivate of the dichotomy of an axis of a lower order, and we should expect a certain correspondence between the number of ovules and distal elements of a cupule. But there is no correspondence. On the contrary, the Upper Devonian cupules are characterized by their inconstancy, variability and sometimes lack of both ovules and microsynangia. In other words, its structure is rather independent (i.e. developing by themselves) from the subtending sporangiate processes. Such a variability is more comparable with the polymorphism of distinct shoot systems

(Arber 1950). Nevertheless, in modern palaeobotany the view point (Walton 1953) on the origin of ovular integument by the coalescence of telomes (belonging to such a cupular system) around megasporangium (= *collar syntelome*) is retained. In our opinion, the unexpected occurrence of *microsynangia* (sic!, = microsporangia of Long 1977; Matten *et al.* 1980; Rothwell & Wight 1989) in these cupules casts doubt on the correctness of the interpretation of such synangia-bearing telomic systems as a cupule (or forerunner of it) comparable to that of other advanced gymnosperms, interpreting in modern evolutionary plant morphology as having yet a leafy origin (Takhtajan 1956, 1991). Evidently, from the view point of current evolutionary morphology such a misconception should be rejected and replaced by a new one. The latter should improve the language of the Upper Devonian/Lower Carboniferous botany by putting into order of modern used terminology.

MATERIALS

In the present paper the structures of some of the most ancient seed plants are discussed. At the moment seven complex reproductive structures of the Upper Devonian and Lower Carboniferous age were described, such as: *Archaeosperma arnoldii* Beck & Pettitt (1968; Arnold 1935), *Moresnetia zalesskyi* Stockmans (1948), *Kerryia mattenii* Rothwell & Wight (1989), *Pullaritheca longii* (Matten, Lacey & Lucas) Rothwell & Wight (1989), *Elkinsia polymorpha* Rothwell, Scheckler & Gillespie (1989), *Xenotheca devonica* Arber & Goode (1915; Rogers, 1926) and *Spermolithus devonicus* Johnson (1917; Chaloner *et al.*, 1977). Fragmentary preservation of *Archaeosperma arnoldii*, *Xenotheca devonica*, *Spermolithus devonicus* and Russian species of *Moresnetia* (Lepekhina *et al.*, 1962) does not allow a dicussion of their structure in the present paper. To emphasize our attention on some overlooked aspects of the morphology of reproductive systems we have specially limited ourselves to the consideration of the exclusively most primitive ovulate fructifications, as defined by Rothwell (1986), leaving out other cupulate systems from the closely-boundered sediments and thus reducing to a minimum, the variation in ovule morphology.

Shoot and cupule as an insynangescence

The theory of the shoot as the main morphological unit in the higher plants (Arber 1937, 1941, 1950; Zimmermann 1959), being the foundation-stone in modern evolutionary plant morphology (Esau 1977; Takhtajan 1991), unfortunately, did not exert a continued revolutionizing influence on the minds of palaeobotanists as it had done earlier in the thinking of the classic morphologists during 1930-60 (Pervukhina 1970). However, it is impossible to make any analysis of the diversity of forms within vascular plants without the shoot concept. Nevertheless, its use in palaeobotanical analysis is very limited owing to incomplete preservation of whole organs.

Fairon-Demaret and Scheckler (1987) who re-examined the structure of seed-bearing structures of *Moresnetia*, have pointed out that the so-called cupules of this plant were assembled in *raceme*-like aggregations forming complex so-called "cupuliferous branching system". Later it has been noticed by Rothwell and Scheckler (1988: 107) that cupule symmetry and therefore its morphology depend upon its (cupules) arrangement in the whole system. Serbet and Rothwell (1992) who reconstructed similar *Elkinsia* synangia-bearing structures, had not found any difference in the anatomy of cupuliferous branching system and cupules. In addition, they noticed its likeness with the structure of sterile fronds. Thus, all this has emphasized the structural and functional unity of cupule and cupuliferous branching systems as a single whole (Rothwell & Scheckler 1988). But the analysis of the structure of these branching systems and cupules is carried out separately up to our days.

As far back as Walton (1949: 726) and then Barnard (1960) noted that the cupule of *Calathospermum* (Upper Tournaisian, Lower Carboniferous) being undoubtedly a derivative of the Upper Devonian gymnosperms represents itself "a frond or part of a frond" (!) "morphologically comparable to the vegetative part of a Neuropterid frond" (Barnard 1960: 275). In our opinion, there is no necessity to remind a homology of the aforementioned frond with a partial vegetative shoot (Arber 1950; Zimmermann 1959). Their conclusions were fully justified by the resemblance of the morphology and vascular anatomy of the cupule stalk of *Calathospermum* with a rachis of the *Lyginorachis*-type. This homology indicates that the cupule of Upper Devonian/Lower Carboniferous age represents itself a modified reproductive shoot. In such a case the whole system bearing numerous cupules is interpreted as a system ("whole-shoot", after Arber 1950) of modified shoots with synangia, or *insynangescence (insynangescentia, lat.)*. This system resembles (to some extent) inflorescences of angiosperms, but in this case we deal with synangia (both micro- and macro-) instead of flowers. Introducing this term and following Benson (1904, 1914) we emphasize thereby the unity of the synangial nature of ovule (as a gynosynangium) and of microsporangia corresponding to it. Thus we assign cupules of Upper Devonian/Lower Carboniferous age to a distinct morphological category.

The likeness of the insynangescence with inflorescences is also added by the occurrence of peculiar bracts (tegoclades) subtending macro-synangia (ovules) within insynangescences. The *tegoclade* represents itself a compound modified vegetative shoot (bract) consisting of three main parts (Fig. 1). The basal part, or *basiclade*, originates as a result of dichotomy of the common stalk with a synangium. It dichotomizes and forms two
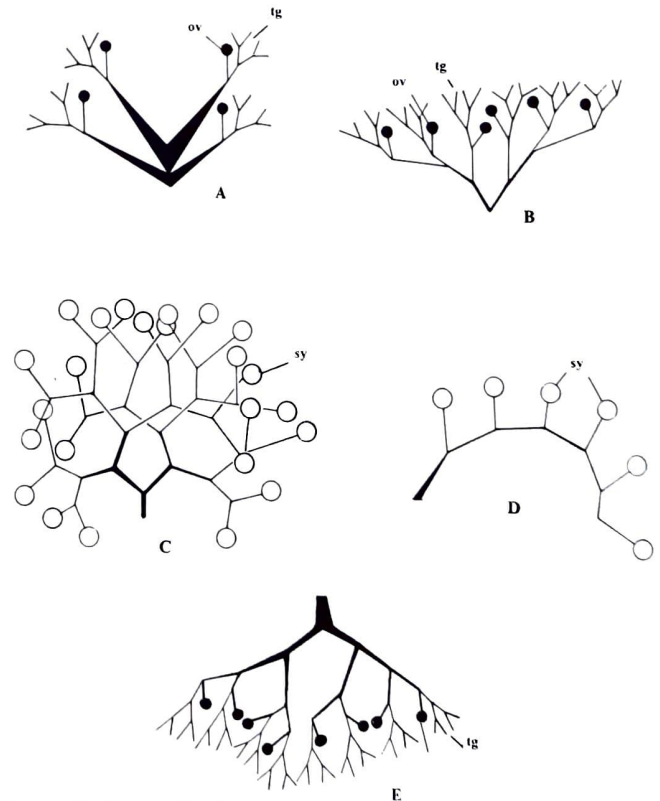

Figure 1. General schemes of the structural types of insynangescences. - A. Dichasidium. - B. Trichasidium. - C. Pleiochasidium. -D. Cincinnus. -E. Pocule. - Abbreviations: ov, ovules; sy, synangescences; tg, tegoclades.

mesoclades (middle branches) in its turn bifurcating and forming two pairs of ultimate units, or *acroclades*. It is noteworthy that such a complex construction of the tegoclade is constant within all Upper Devonian/Lower Carboniferous ovulate cupules.

Morphology and typology of insynangescence as a system of modified reproductive shoots bearing synangia mainly would rest upon the progress and achievements in the morphology of analogous inflorescences (Roeper 1826; Guillard 1857; Celakovsky 1892; Parkin 1914; Pilger 1922, 1933; Goebel 1931; Zimmermann 1935, 1935, 1965; Bolle 1940; Croizat 1943; Rickett 1944; Eames 1961; Troll 1964, 1969; Weberling 1965, 1989; Theodorov & Artjuschenko 1979; Weberling *et al.*, 1994). But in constrast to inflorescences, the Upper Devonian insynangescences bore synangia, had a basically dichotomous branching and completely lacked any leaf-like formations. Therefore, their morphology and typology would have a certain resemblance only with that of inflorescences.

We refuse to describe insynangescences in the terms of similar cymose inflorescences (dichasium, pleiochasium, etc: Wydler 1843, 1851, 1878) as in present case the question is that the true dichotomous or dichopodial types of branching are characteristic only to plants of telomic morphology, but not to highly advanced angiosperms. And, therefore, we have substituted them by similar terms, *dichasidium* (Fig. 1 A) and *pleiochasidium* (Fig. 1 C). We also consider it necessary to refuse straight and tough analogies with a (part of) frond and all the ensuing descriptive terminology (petioles, pinnae, pinnules, etc.), as the object of present comparative morphological survey would not be a single cupule alone, but a single morphofunctional shoot unit - insynangescence. It should be also pointed out that emphasis on quantitative characters in the general descriptions of synsynangescences or their constituent parts do not amount to overstatement. In the following account we have completely omitted these characters.

Besides this, we also deprecate the use of monopodial branching, sometimes ascribed to these plants, and replace it by a more natural *dichopodial* one. Thus it would emphasize the essential, sometimes overlooked, difference between monopodial branching with a single prevailing axis and dichopodial one with an unequal real dichotomy reminiscent in part of a tendency to monopodial branching pattern. This delimitation of the branching pattern types permits to reveal an essential difference in the branching pattern between basal (dichotomy) and distal parts (dichopody) within the insynangescences of *Elkinsia* and *Moresnetia*, and thus to establish an aggregate nature of these compound shoot systems (analogous to some extent to the aggregate inflorescences *sensu* Theodorov & Artjuschenko 1979).

Thus, it appears to be necessary to form an original own terminology for insynangescences, permitting to describe their structure in detail, and we provide a special glossary of new terms.

Glossary of new descriptive terms

Acroclade (acrocladum, lat.) - an ultimate branch of a tegoclade.

Basiclade (basicladum, lat.) - a basal branch of a tegoclade.

Cincinnus (cincinnus, lat.) (Fig. 1 D) - an insynangescence, the lateral branches of higher order of which are successively diverged from one side.

Dichasidium (dichasidium, lat.) (Fig. 1 A) - an insynangescence consisting of two pairs of synangia-bearing shoots originated as a result of dichopodial branching of the main axis.

Dichopodial (branching) - a distinct type of branching with an unequal real dichotomy reminiscent only of a tendency to monopodial branching pattern.

Dicincinnus (dicincinnus, lat.) (Fig. B) - an insynangescence consisting of two successively, several times dichopodially branched synagia-bearing shoots diverging from one side.

Insynangescence (insynangescentia, lat.) - a system of modified reproductive shoots bearing synangia.

Insynangescence aggregate (insynangescentia aggregata, seu complexa, lat.), or *synsynangescence* - an insynangescence, the type of branching pattern of the main axis of which does not coincide with that of partial insynangescences or their aggregations.

Insynangescence bisexual (insynangescentia bisexualis, lat.) - an insynangescence bearing both macrosynangia (ovules) and microsynangia.

Insynangescence compound (insynangescentia composita, lat.) - an insynangescence the lateral

branches of which are represented by a branching system of axes bearing synangia (partial insynangescences).

Insynangescence definite (insynangescentia definita, lat.) - an insynangescence each axis of which in turn is terminated with a synangium.

Insynangescence female (insynangescentia feminea, lat.) - an insynangescence bearing macrosynangia (ovules).

Insynangescence indefinite (insynangescentia indefinita, lat.) - an insynangescence the main axis of which has an unlimited growth, i.e. does not terminate with a synangium.

Insynangescence male (insynangescentia mascula, lat.) - an insynangescence bearing microsynangia.

Insynangescence monotelic (insynangescentia monotelica, lat.) - an insynangescence the main and lateral axes of which terminate in a synangium.

Insynangescence partial (insynangescentia partialis, lat.), or synangescence - a lateral branching system of axes bearing synangia of any compound insynangescence.

Insynangescence unisexual (insynangescentia unisexualis, lat.) - an insynangescence bearing only macrosynangia (ovules) or microsynangia.

Mesoclade (mesocladum, lat.)- a middle branch of a tegoclade.

Pleiochasidium (pleiochasidium, lat.) (Fig. 1 C) - an insynangescence consisting of several (more than three) pairs of synangia-bearing shoots originated as a result of several dichotomies of the main axis.

Pocule (poculum, lat.) - a condensed calathiform compound insynangescence consisting of two dichasidial insynangescences.

Synangescence (synangescentia, lat.) - see *Insynangescence partial*.

Synsynangescence (synsynangescentia, lat.) - see *Insynangescence aggregate*.

Tegoclade (tegocladum, lat.) - a compound modified vegetative shoot (bract) subtending a synangium.

Trichasidium (trichasidium, lat.) (Fig. 1 B) - an insynangescence consisting of three pairs of synangia-bearing shoots originated as a result of successive dichopodial branchings of the main axis (= three-parted dicincinnus).

Typification of insynangescences

Female pleiochasidial cincinnus of dichasidia

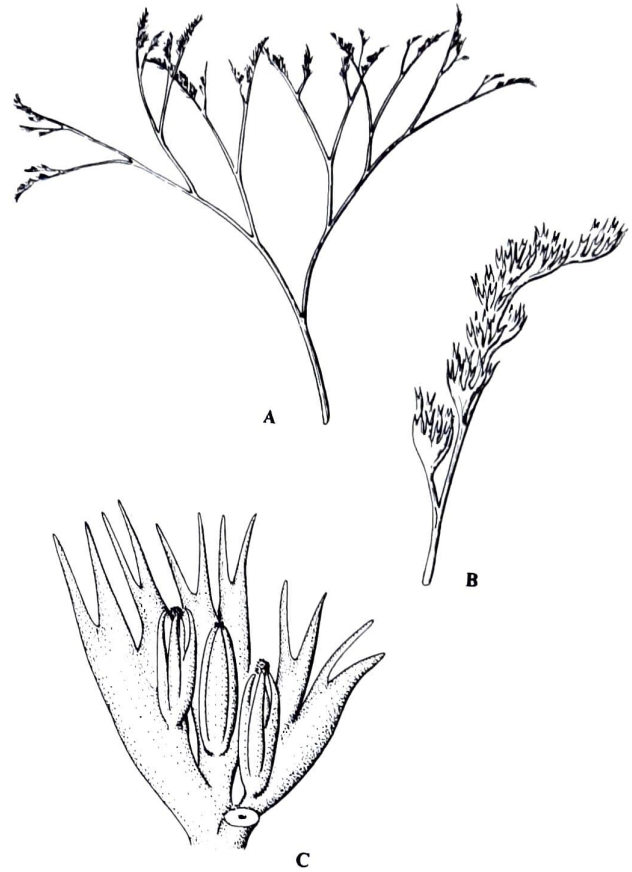#### *Elkinsia polymorpha* Rothwell, Scheckler & Gillespie (Fig. 2)

Figure 2. Synsynangescence of *Elkinsia polymorpha*. - A. General view of pleiochasidial synsynangescence (modified after Serbet & Rothwell, 1992). - B. Cincinnus of dichasidia. - C. Dichasidium, one branch removed (B, C- modified after Rothwell & Scheckler, 1988).

Rothwell, Scheckler & Gillespie 1989; Rothwell & Scheckler 1988; Serbet & Rothwell 1992.

Moresnetia zalesskyi Stockmans (Fig. 3)

Stockmans 1948; Fairon-Demaret & Scheckler 1987; Rothwell & Scheckler 1988.

This synsynangescence we define to be aggregate so far as the often dichotomous branching in its basal part is distinct from the dichopodial branching of insynangescences and its partial constituents. Such a type of the synsynangescence should be defined as a *pleiochasidium*, since the synsynangescence is basically highly branched. And therefore the aggregations of cupules, i.e. the compound insynangescence, are arranged on the branches of 4-5 and higher orders. These aggrega-
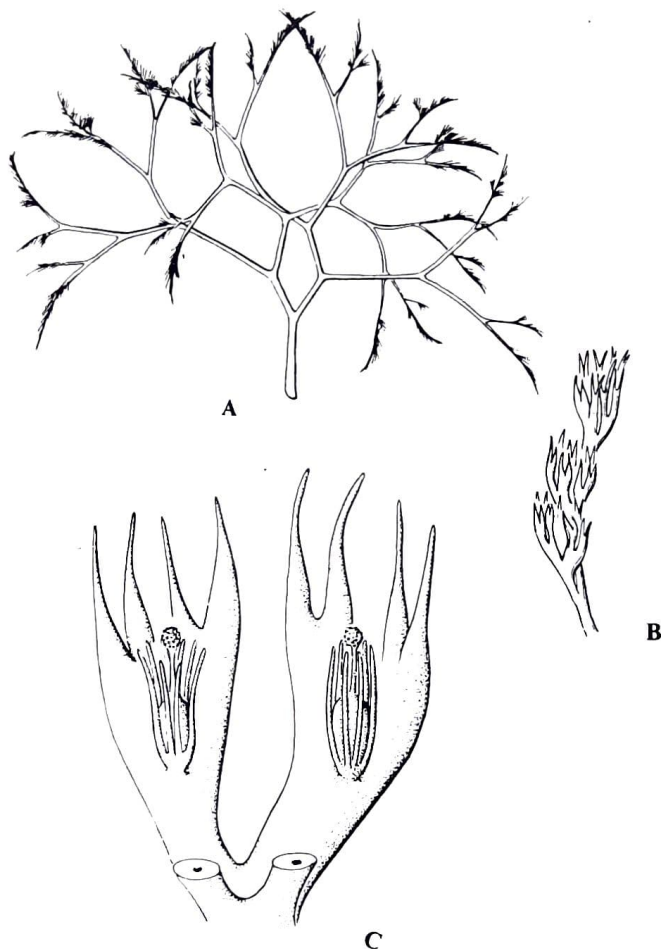
Figure 3. Synsynangescence of *Moresnetia zalesskyi*. - A. General view of pleiochasidial synsynangescence (modified after Fairon-Demaret & Scheckler, 1987). - B. Cincinnus of dichasidia. - C. Dichasidium, a half removed (B, C- modified after Rothwell & Scheckler, 1988).

tions of cupules ('racemes' of Rothwell & Scheckler 1988: 108) are reminiscent in architecture, the cincinnus (not racemes!), of analogous inflorescences (Wydler 1851, 1878; Weberling 1989) owing to the prevailing dichopodial type of successive one-sided branching pattern. The cupules of *Moresnetia* and *Elkinsia* represent only partial shoots (synangescences) in this compound insynangescences, and coming in the field of descriptive morphoogy, we term them as *dichasidia* (to some extent only being analogous to a dichasium of inflorescences). Dichasidia as partial insynangescences (synangescences) should be characterized in addition as being monotelic and definite, as the synangescence terminates in an ovule.

Female pleiochasidial (?) cincinnus (?) of trichasidia

Kerryia mattenii Rothwell & Wight (Fig. 4 A)

Long 1961; Matten, Lacey & Lucas 1980; Rothwell & Scheckler 1988; Rothwell & Wight 1989.

As far as possible to judge from the data of Long (1961), Matten *et al.* (1980) and Rothwell and Wight (1989), the partial insynangescence of *Kerryia mattenii* is a reproductive shoot consisting of 6 axes (24 distal tegoclades) and producing up to 6 ovules. In point of fact, this synangescence is reminiscent of a *trimerous dicincinnus*, but in order to emphasize its peculiar 6-axity we introduce a special term *trichasidium* for such a type of synangescence. In spite of the claimed symmetry of the structure of trichasidium (Rothwell & Wight 1989), we accept its asymmetry illustrated by Matten *et al.* (1980) meaning that one of the branches of basic dichasidium dichotomizes additionally (not trichotomy) forming a total of three branches, two of which are of higher order.

It is unknown whether trichasidia of *Kerryia*, like dichasidia of *Elkinsia* and *Moresnetia*, were borne on the pleiochasidial system or were organized in a more altered cincinnate compound insynangescences. But we provisionally suppose such a structure of synsynangescence, thus emphasizing a possible morphogenetic relationship with a partial insynangescence of dichasidial type. Our suggestion sufficiently agrees with the asymmetry of trichasidium which is similar to the asymmetry of dichasidia, caused by their arrangement in the compound cincinnate insynangescent system. In our opinion, the trichasidial type of synangescence, appeared in the later stages of gymnosperm evolution (Tournaisian, Lower Carboniferous), is a direct derivative of such a dichasidial type. But the enrichment of the partial insynangescences should correlate normally with a further progressive reduction of the branching of the main axis of the whole aggregate insynangescence (synsynangescence). This circumstance should be clarified by fossil record.

In spite of Matten *et al.* (1980) we are inclined to recognize all six main branches as to be ovuliferous writing off the variation in ovule numbers (2, 4-6) to the irregularity of the development of trichasidia as partial insynangescences (in certain extent analogous to the watering down of cymoids in the thyrsoidal systems of inflorescences). In addition it should be mentioned that trichasidia are also monotelic and definite as dichasidia.

Bisexual pleiochasidium of pocules

Pullaritheca longii (Matten, Lacey & Lucas) Rothwell & Wight (Fig. 4B, C)
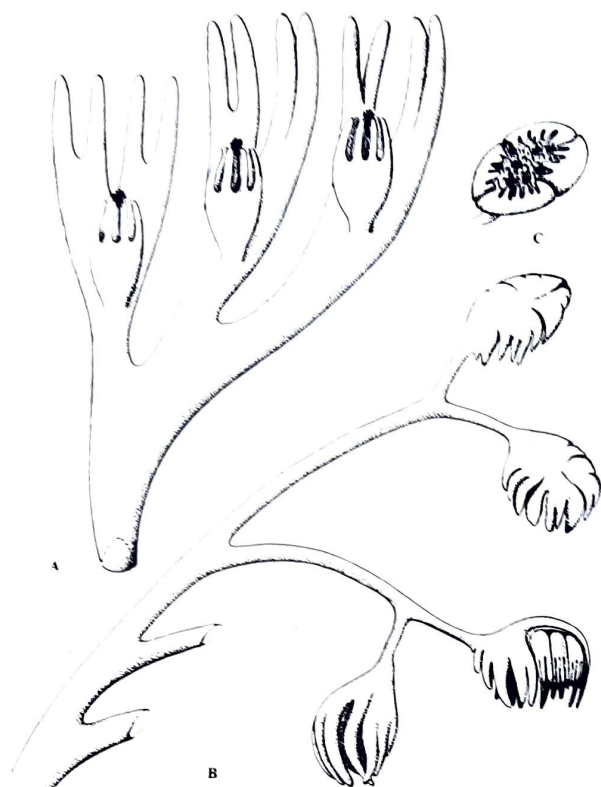
Figure 4. Synsynangescences of *Kerryia* and *Pullaritheca*. - A. Trichasidium of *Kerryia mattenii*, a half removed. - B. General view of synsynangescence of *Pullaritheca longii* (several branches removed). - C. A view of the distal part of the pocule of *Pullaritheca longii* showing numerous ovules and microsynangia.

Long, 1961; Long, 1977a, b; Long, 1979; Matten, Lacey & Lucas, 1980; Rothwell & Scheckler, 1988; Rothwell & Wight, 1989.

The reconstruction of the synsynangescence of *Pullaritheca longii* is based upon the published material of Long (1977b; 1979, Pl. 1, figs. 10-11; cupules: figs. 8-9). We omitted new data of Rothwell and Wight (1989) because they did not present clear descriptions of the sterile cupule parts.

According to the comprehensive descriptions of Long (1977b: specimens 4 & 6), each cupule (hemi-cupule) has two halves with 6-8 lobes (in sum nearly 16 distal segments) and bears four (!) ovules (Long 1977b : 17). Such a construction unquestionably resembles a dichasidium of *Moresnetia*-type (Figs. 1A, 3): four axes with four ovules subtending by four compound tegoclades having 16 acroclades (= distal segments of Long, *ibid.*). The

reported variability of acroclades (16-18) does not allow to determine with a certainty the character of this insynangescence: in case of 16 acroclades - it should be characterized as being monotelic and definite, but in case of 18 - as being polytelic and indefinite. We are inclined to think that these insynangescences retain a common feature of the insynangescence growth with definite and monotelic insynangescences of *Elkinsia*, *Kerryia* and *Moresnetia*.

The two such cupules ('hemi-cupules') having a compound stalk constitute a single 'megacupule', or a *double dichasidium (dichasidium duplex, lat.)* The reduction and shortening of the axes between these two dichasidia leads to the formation of a new specialized calathiform type of the compound insynangescence, and we segregated it into a distinct type termed a *pocule (poculum, lat. - a goblet)*. It is necessary to emphasize that the pocule of *Pullaritheca* is a natural insynangescent entity of higher order (compound insynangescence) in contrast to the 'cupules' (partial insynangescences) of other Upper Devonian spermatophytes *Elkinsia* and *Moresnetia*.

These pocules were arranged on the dichotomical highly branching system resembling in part a pleiochasidial base of the aggregate insynangescence (synsynangescence) of pleiochasidial type, or bisexual pleiochasidium of pocules (as in some pocules several microsporangia have been recorded).

However, our interpretation of the cupule structure of *Pullaritheca longii* clearly indicates for a highest possible number of ovules in a pocule:eight ovules only. The another reported number (16) by Long (1977a), Matten *et al.* (1980) and even 25 by Rothwell and Wight (1989) could be better explained by a further possible aggregation of dichasidia due to the reduction and shortening of axes within such an insynangescence, caused probably by stress of ecological factors provoking attenuation of intercalary activity. Such multiovulate structures are a whole ensemble of pocules distinct from pocules alone by the presence of several tegoclades in a 'common cavity'. To all appearance, besides the possible ecological explanation of such a phenomenon, an alternative explanation should recognize such an agregation as a temporary ontogenetical stage (± coinciding

with a period of ovule formation and the following growth of a pocule alone) up to the beginning of intercalary activity in the basal forking parts, spreading pocules before the period of ovule abscission. This scenario could explain a large number of ovules if we could take into consideration the revealed correlation between number of ovules (16) and number of cupule distal segments (16) in these systems. In our opinion, knowing the complex construction of the 4-lobed tegoclade subtending Upper Devonian/Lower Carboniferous macrosynangia (ovules), we may state that these sructures represent a temporary immature stage with still undifferentiated tegoclades (it appears that only basiclades (16) were formed).

The significance of the insynangescence theory

The insynangescence theory with improved terminology brings new perspectives in the analysis of complicatedly arranged synangia-bearing branching systems of some early seed plants. Typified and redescribed, the above three principal types of insynangescences show sharp qualitative differences with hitherto mentioned quantitative ones (Rothwell & Scheckler 1988; Rothwell & Wight 1989) between structures traditionally described as the Upper Devonian and Lower Carboniferous cupules. The dichasidia (partial insynangescences) of Famennian *Elkinsia* and *Moresnetia* being aggregated in a cincinnate complex system turn out to be more simply organized than the partial insynangescences of younger Tournaisian *Kerryia* representing by trichasidia, and than modified condensed forms of the compound dichasidial insynangescences of also Tournaisian *Pullaritheca* (pocules). As a minimum, such a new approach permits us to recognize already in the Upper Devonian/Lower Carboniferous two principal distinct phyla of the evolution of seed plants. It seems that in that space of geological time they were not closely related to each other, and therefore seem to have, as a minimum, the ranks of orders *Elkinsiales* (*Moresnetia*, *Elkinsia* and *Kerryia*) and *Pullarithecales* (*Pullaritheca*) [1]. A new terminology avails also to describe in detail a structure of the insynangescences of other Lower Carboniferous spermatophytes,

and thereby to analyze their probable phylogenetic relationships in the terms of a shoot morphology. In general it permits to introduce new additional important characters into the systematics and phylogeny of early seed plants. A full account of the insynangescence morphology of all Lower Carboniferous spermatophytes would be published elsewhere.

The complex nature of the aggregate insynangescences of the Upper Devonian and some Lower Carboniferous spermatophytes together with their prevailing unisexuality (possible dioecy in Elkinsiales) indicate for a rather higher specialisation of the latter. It does not speak well of a doctrine to suggest its close nearness to the ancestral complex of all spermatophytes and also their basality for all other groups of gymnosperms. Moreover, the occurrence of bisexual pocules (although recorded from later strata of Tournaisian 1a) directly evidences for the possible existence of a more primitive ancestor for all spermatophytes in more lower sediments having a bisexual ordered ensemble (? a strobile, *devanthus*) of synangia (both micro- and ovules). We may note that only general construction of the less specialized reproductive organs of Aneurophytales shows a certain resemblance with that of the Upper Devonian spermatophytes (Matten *et al*. 1980; Rothwell & Scheckler 1988), but for a grounding rooting of gymnosperms in Aneurophytales (Rothwell & Erwin 1987) it is necessary to carry out additional studies on the structure of its sporangiate systems. In future it may turn out that Aneurophytales are not a sole candidate to be an ancestral link to gymnosperms, and it would be necessary to look for another progymnosperm with a bisexual ensemble (*devanthus*) of synangia.

The interpretation of the Upper Devonian cupules as partial shoots (insynangescences) finally debunks illusory views on the origin of integument from the sterile vegetative segments like tegoclades of dichasidia, trichasidia or pocules (Oliver & Scott 1904; Stopes 1905; Oliver 1909; Andrews 1940; Walton 1953; Smith 1964; Long 1966; Meyen 1984; DiMichele *et al*. 1989). It is very unlikely that such variable shoots-branchlets of insynangescences

---

[1]   *Pullarithecales* A. Doweld, ord. nov., *Pullarithecaceae* A. Doweld, fam. nov. Bisexual pleiochasidial synsynangescences consisting of two condensed calathiform compound insynangescences of the dichasidial type (pocules). 8 microsporangia and 8 ovules per pocule with a 8-10-lobed outer integument. TYPE: *Pullaritheca* Rothwell & Wight (1989).

could form so strongly determined and regular lobed 'integument' system (Andrews 1963). It is also hardly probable that further these lobes could form a syntelome or its accrescent likeness as an outer integument (Camp & Hubbard 1963), since in such a case it would be necessary to accept a polyphyletic origin of seed habit. The variability of integument lobes is very great: from 2 lobes (*Lyrasperma scotica*) to 8-12 (*Moresnetia zalesskyi*). It has been also recorded 3-lobed constructions (*Eurystoma trigona*), a 4-5-lobed (*Elkinsia polymorpha, Dolichosperma pentagounum*) and even a 6-7-lobed system (*Dolichosperma sexangulatum*) (Long 1975). These processes around an indehiscent megasporangium (Stewart 1983; Chaloner & Pettitt 1987) or, in our opinion, correctly *a nucellus enveloped by the inner integument* (Camp & Hubbard 1963; Doweld, in prep.), resemble most likely some sort of perianth of angiosperms and its variables in particular. Both *Moresnetia* having 8-12 lobes of such an integument and *Elkinsia* with only 4-5 lobes have a similar type of insynangescence - a female pleiochasidial cincinnus of dichasidia. It seems very strange and improbable that the similar insynangescences or cupular systems of nearly similar time of record could give rise to the different number of such lobes. Moreover, this variability of integument lobes within the spermatophytes of the Upper Devonian age suggests that these processes are not analogues to the outer integument at all. It seems that they were rather specialized processes in a distinctive seed reproduction of the Upper Devonian seed plants (Andrews 1963). Otherwise, it would be necessary to accept an absurd polyphletic view on the formation of seed habit by the independent coalescence of 2, 3, 4, 8, etc. telomes. The rejection of the telomic (i.e. sterile leafy) origin of the integument also coincides with the occurrence of integumentary embryony (Naumova 1993) which is quite impossible in the initially sterile (telomic) structures. This circumstance emphasizes a validity of the synangial sterilized theory of the ovule origin advanced by Benson (1904, 1914). In this respect, we prefer to consider these lobes as rather sterilised processes of the single sporangiate system than representing any part of telomic or insynangescent system.

The rejection of the "branchlets" theory of integument origin shows another morphogenetic

field for the evolution of the cupulate or telomic reproductive branching systems of the Upper Devonian and Lower Carboniferous spermatophytes. It seems more probable that at this geological epoch the evolution of ovule and its bearing shoot systems has been directed to the formation of the protective additional adaptations to make the ovule more autonomous to abiotic stress factors. This is illustrated in part by the formation of specialized type of compound insynangescences - pocules - by shortening, aggregation and further reduction of branches within the compound insynangescences. At the same time the appearance of the compact aggregations of ovules in the unisexual specialized insynangescences like pocules sufficiently raised their chances for pollination and therefore successful seed reproduction. The similar pocules of *Calathiops* (Benson 1935), *Calathospermum* (Walton 1949; Barnard, 1960), *Geminitheca* (Smith 1959) and *Gnetopsis* (Renault & Zeiller 1884; Renault 1885; Gensel & Skog 1977) recorded in the higher Carboniferous strata have confirmed the existence of such a mode in the evolution of insynangescent shoot structures.

However, the extinction of such a blind phylum of seed plants was bound up with the exhausting of the potentialities of its structure for further evolution. It was due to the probable specialisation of the system of partial consitituents of the reproductive whole-shoot to produce frondose, frondulose or bracteose reproductive shoot and to use its partial shoots, modifying them, for a construction of protective epi-integumentary systems. In other words, only the seed plants, which managed to change telomic organisation of a reproductive shoot to frondose or frond-like organisation, had given rise to various irradiating phyla of higher spermatophytes (*sensu* Crane 1988). It was possible, in our opinion, by having a lesser degree of specialisation of the whole-shoot system or, more probable, by an escape from the specialisation proceeding parallel with the evolution of basic branching from dichotomous (pleiochasidial insynangescences) through dichopodial to monopodial and sympodial ones. It seems to us, at present time, that the Upper Devonian and some Lower Carboniferous spermatophytes bearing pocules, trichasidia or dichasidia have been too highly specialized to change their imperfect, prac-

tically still telomic organisation of the insynangescence. And therefore they find themselves in the blind branches of gymnospermous evolution.

Thus owing to the insynangescence theory we may obtain a key to analysis of the extent of specialisation of seed plants judging by the structure of their reproductive shoot with an associated vegetative partial shoot to show its real place in the phylogeny of gymnosperms (blind branch vs. progressive line).

The introduction of a shoot morphology into the analysis of female (ovulate) reproductive structures should be applied equally to the same analysis of male fructifications. It could be illustrated by the known fact that microsynangia of *Elkinsia* were organized in exactly the same shoot aggregations (male synsynangescence) as the ovules did (Serbet & Rothwell 1992: 617, figs. 45, 48). In a comprehensive review of morphology and phylogeny of early spermatophytes Galtier (1988: 169) pointed out the diversity of a frond architecture of pollen-bearing organs. This opinion has been also shared by Millay and Taylor (1979) and Taylor (1988). To all appearance, only using the insynangescence concept we could obtain a neat morphological interpretation of the early spore-bearing organs, such as *Telangium* (Benson 1904; Kidston 1924; Jennings 1976; Long, 1979), *Melissiotheca* (Meyer-Beerthaud 1986), *Phacelotheca* (Meyer-Berthaud & Galtier 1986), and so forth. It avails finally to get out artificial terminology employing to male fructifications and its complex aggregations, thus more naturally connecting them with the corresponding female organs. However, at the present time it is not possible for us to analyse "frond" morphology of pollen-bearing organs with clearly associated female ones due to numerous outstanding problems and misunderstanding in morphology and evolution of the very sporangia and synangia (Millay & Taylor 1979; Meyen 1984; Taylor 1988).

In conclusion, it would be appropriate to point out that the above introduced term *insynangescence* should be applied only to shoots bearing naked synangia, i.e. without any epi-integumentary coats in the case of female ones. The insynangescence concept cannot be applied to the explanation of any other aggregations of the reproductive organs within the seed plants. They ought to receive another terminological sounding reflecting a nature of bearing reproductive organs.

REFERENCES

Andrews H. N. 1940. A new cupule from the Lower Carboniferous of Scotland. *Bull. Torrey bot. Club* **67**: 595-601.

Andrews, H. N. 1963. Early seed plants. *Science* **142**: 925-931.

Arber A. 1937. The interpretation of the flower: a study of some aspects of morphological thought. *Biol. Rev. Cambridge Philos. Soc.* **12**: 157-184.

Arber A. 1941. The interpretation of leaf and root in the angiosperms. *Biol. Rev. Cambridge Philos. Soc.* **16**: 81-105.

Arber A. 1950. *The Natural Philosophy of Plant Form*. Cambridge: Cambridge University Press.

Arber E. A. N. & Goode R. H. 1915. On some fossil plants from the Devonian rocks of North Devon. *Proc. Cambridge Philos. Soc.* **18**: 89-104.

Arnold C. A. 1935. On seed like structures associated with *Archaeopteris*, from the Upper Devonian of Northern Pennsylvania. *Contr. Mus. Paleont., Univ. Michigan (Ann Arbor)* **4**: 283-286.

Barnard P. D. W. 1960. *Calathospermum fimbriatum* sp. nov., a Lower Carboniferous pteridosperm cupule from Scotland. *Palaeontology* **3**: 265-275.

Benson M. J. 1904. *Telangium scotti*, a new species of *Telangium* (*Calymmatotheca*) showing structure. *Ann. Bot. (Lond.)* **18**: 161-177.

Benson M. J. 1914. *Sphaerostoma ovale* (*Conostoma ovale et intermedium*, Williamson). A Lower Carboniferous ovule from Pettycur, Fifeshire, Scotland. *Trans. R Soc. Edinb.* **50**: 1-15.

Benson M. J. 1935. The fructification, *Calathiops bernhardti* n. sp. *Ann. Bot. (Lond.)* **49**: 155-160.

Bolle F. 1940. Theorie der Blütenstände. *Verh. Bot. Ver. Prov. Brandenburg* **80**: 53-81.

Camp W. H. & Hubbard, M. M. 1963. On the origins of the ovule and cupule in lyginopterid pteridosperms. *A.J. Bot.* **50**: 235-243.

Celakovsky L. F. 1892. Gedanken über eine zeitgemässe Reform der Theorie der Blütenstände. *Bot. Jahrb. Syst.* **16**: 33-51.

Chaloner W. G., Hill A. J. & Lacey W.S 1977. First Devonian platysper-mic seed and its implications in gymnosperm evolution. *Nature (Lond.)* 265: 233-235.

Chaloner W. G. & Pettitt J. M. 1987. The inevitable seed. *Bull. Soc. Bot. Fr., Actual. Bot.* 134(2): 39-49.

Crane P. R. 1988. Major clades and relationships in the "higher" Gymnosperms. *In:* C. B. Beck (Ed.) - *Origin and evolution of gym-nosperms:* 218-272. New York: Columbia University Press.

Croizat L. 1943. The concept of inflorescence. *Bull. Torrey bot. Club* 70: 489-495.

Dimichele W. A., Davis J. I. & Olmstead R. G. 1989. Origins of heterospory and the seed habit: the role of heterochrony. *Taxon* 38: 1-11.

Eames A. 1961. *Morphology of the Angiosperms.* New York: McGraw-Hill Book Co.

Esau K. 1977. *Anatomy of Seed Plants.* 2nd ed. New York: Wiley.

Fairon-demaret M. & Scheckler S. E. 1987. Typification and redescrip-tion of *Moresnetia zalesskyi* Stockmans, 1948, an early seed plant from the Upper Famennian of Belgium. *Bull. Inst. R Sci. Nat. Belg., Sci. Terr.* 57: 183-199.

Galtier J. 1988. Morphology and phylogenetic relationships of early pteridosperms. In: C.B. Beck (Ed.) - *Origin and evolution of gym-nosperm:* 135-176. New York: Columbia University Press.

Gensel P. G. & Skog J.E. 1977. Two early Mississippian seeds from the Price Formation of southwestern Virginia. *Brittonia* 29: 332-351.

Gillespie W. H., Rothwell G. W. & Scheckler, S. E. 1981. The earliest seeds. *Nature (Lond.)* 293: 462-464.

Goebel K. I. E. 1931. *Blütenbildung and Sprossgestaltung. (Anthokladien and Infloreszenzen). Zweiter Ergänzungsband zur Organograpie der Pflanzen.* Jena: Fischer.

Guillard J. C. 1857. Idée générale de linflorescence. *Bull. Soc. bot. Fr.* 4:29-41, 116-124.

Jennings J. R. 1976. The morphology and relationships of *Rhodea, Telangium, Telangiopsis* and *Heterangium. A.J. Bot.* 63: 1119-1133.

Johnson T. 1917. *Spermolithus devonicus* gen. *et* sp. nov., and other pteridosperms from the Upper Devonian beds of Kiltorcan, Co. Kilkenny. *Roy. Soc. Dublin, Sci. Proc.* 15: 245-254.

Kidston R. 1924. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. geol. Surv. Gr. Brit., Palaeontol.* 2(5): 1-670.

Lepekhina V. G., Petrosyan N. M. & Radchenko G. P. 1962. Vazhneishie devonskie rasteniya Altaye-Sayanskoy gornoy oblasti [The most important Devonian plants of the Altai-Sayan mountain region]. *In:* G. P. Radchenko (Ed.) - *Materialy k fitostratigrafii devonskikh otlozheniy Altaye- Sayanskoy gornoy oblasti [Materials on the phytostratigraphy of the Devonian sediments of Altai-Sayan mountain region]:* 61-189 (*Trudy VSEGEI, N. S.,* fase. 70). Leningrad: Nauka. [InRuss.].

Long A. G. 1961. Some pteridosperm seeds from the Calciferous Sandstone Series of Berwickshire. *Trans. R Soc. Edinb.* 64: 401-419.

Long A. G. 1966. Some Lower Carboniferous Fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules, and carpels. *Trans. R Soc. Edinb.* 64: 345-375.

Long A. G. 1975. Further observations on some Lower Carboniferous seeds and cupules. *Trans. R Soc. Edinb.* 69: 267-293.

Long A. G. 1977a. Some Lower Carboniferous pteridosperm cupules bearing ovules and microsporangia. *Trans. R Soc. Edinb.* 70: 1-11.

Long A. G. 1977b. Lower Carboniferous pteridosperm cupules and the origin of angiosperms. *Trans. R Soc. Edinb.* 70. 13-35.

Long A. G. 1979. The resemblance between the Lower Carboniferous cupules of *Hydrasperma* cf. *tenuis* Long and *Sphenopteris bifida* Lindley & Hutton. *Trans. R Soc. Edinb.* 70. 129-137.

Matten L.C. & Lacey W. S. 1981. Cupule organization in early seed plants. *In:* R.C. Romans (Ed.) - *Geobotany II:* 221-234. New York: Plenum Press.

Matten L.C., Lacey W.S. & Lucas R.C. 1980. Studies on the cupulate seed genus *Hydrasperma* Long from Berwickshire and East Lothian in Scotland and County Kerry in Ireland. *Bot. J. Linn. Soc.* 81: 249-273.

Meyen S.V. 1982. Organy razmnozheniya golosemennykh i ikh evolut-siya po dannym paleobotaniki [Reproductive organs of gym-nosperms and its evolution as evidenced by palaeobotany]. *Zhurn. Obshch. Biol. (Moscow)* 43: 303-323. (In Russ.].

Meyen S. V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot. Rev. (Lancaster)* 50: 1-111.

Meyen S. V. 1987. *Fundamentals of Palaeobotany.* London, New York: Chapman & Hall.

Meyer-berthaud B. 1986. *Melissiotheca* : a new pteridosperm pollen organ from the Lower Carboniferous of Scotland. *Bot. J. Linn. Soc.* 93: 277-290.

Meyer-berthaud B. & Galtier, J. 1986. Studies on a Lower Car-boniferous flora from Kingswood near Pettycur, Scotland. 2. *Phacelotheca,* a new synangiate fructification of pteridospermous affinity. *Rev. Palaeobot. Palynol.* 48. 181-198.

Millay M. A. & Taylor T. N. 1979. Paleozoic seed fern pollen organs. *Bot. Rev. (Lancaster)* 45: 301-375.

Naumova T. N. 1993. *Apomixis in angiosperms: nucellar and integumen-tary embryony.* Boca Raton, Fla: CRC Press.

Oliver F. W. 1909. On *Physostoma elegans* Will. *Ann. Bot. (Lond.)* 23: 73: 73-116.

Oliver F. W. & Scot D. H. 1904. On the structure of the Palaeozoic seed *Lagenostoma lomaxi,* with a statement of the evidence upon which it is referred to *Lyginodendron. Phil. Trans. R Soc. London* 197B: 193-247.

Parkin J. 1914. The evolution of the inflorescence. *J. Linn. Soc. London* 42: 511-553.

Pervukhina N. V. 1970. *Problemy morfologii i biologii tsvetka [Problems of the morphology and biology of the flower].* Leningrad: Nauka. [In Russ.].

Pettitt J. 1970 Heterospory and the origin of the seed habit. *Biol. Rev. Cambridge Philos. Soc.* 45: 404-415.

Pettitt J. & Beck C. B. 1968. *Archaeosperma arnoldii* - a cupulate seed from the Upper Devonian of North America. *Contr. Mus. Paleont. Univ. Michigan (Ann Arbor)* 22: 139-154.

Pilger R. K. F. 1922. Über Verzweigung und Blütenstandsbildung bei den Holzgewächsen. *Biblioth. Bot.* 23(90): 1-38.

Pilger R. K. F. 1933. Bemerkungen über Anthokladien und Infloreszen-zen. *Bot. Jahrb. Syst.* 65: 75-96.

Renault B. 1885. *Cours de botanique fossile fait au Muséum d'histoire naturelle. Conifères, Gnétacées. Annee 4.* Paris: Masson.

Renault B. & Zeiller R. 1884. Sur un nouveau genre de graines du Terrain Houiller Supérieur. *C. R. Acad. Sci. Paris* 99: 56-58.

Rickett H. W. 1944. The classification of inflorescences. *Bot. Rev. (Lan-caster)* 10: 187-231.

Roeper J. A. C. 1826. Observationes aliquot in florum inflorescen-tiarumque naturam. *Linnaea* : 433-466.

Rogers I. 1926. On the discovery of fossil fishes and plants in the Devonian rocks of North Devon. *Trans. Devonshire Assoc. Adv. Sci. Lit. Art* 58: 223-234.

Rothwell G. W. 1986. Classifying the earliest gymnosperms. *In:* R. A. Spicer & B. A. Thomas (Eds) - *Systematic and taxonomic approaches in palaeobotany* : 137-161. The Systematics Association Special Volume No. 31. Oxford: Clarendon Press.

Rothwell G. W. & Erwin D. M. 1987. Origin of seed plants : an aneurophyte/seed fern link elaborated. A.J. Bot. 74: 970-973.

Rothwell G. W. & Scheckler S. E. 1988. Biology of ancestral gynosperms. In: C. B. Beck (Ed.) - Origin and evolution of gymnosperms: 85-134. New York: Columbia University Press.

Rothwell G. W., Scheckler S. E. & Gillespie, W. H. 1989. Elkinsia gen. nov., a late Devonian gymnosperm with cupulate ovules. Bot. Gaz. 150: 170-189.

Rothwell G. W. & Serbet R. 1992. Pollination biology of Elkinsia polymorpha, implications for the origins of gymnosperms. Cour. Forsch.- Inst. Senckenberg 147: 225-231.

Rothwell G. W. & Wight D. C. 1989. Pullaritheca longii gen. nov. and Kerryia mattenii gen. et sp. nov., Lower Carboniferous cupules with ovules of the Hydrasperma tenuis-type. Rev. Palaeobot. Palynol. 60: 289-309.

Serbet R. & Rothwell G. W. 1992. Characterizing the most primitive seed fern. I. Reconstruction of Elkinsia polymorpha. Int. J. Plant Sci. 153: 602-621.

Stewart W. N. 1983 Paleobotany and the Evolution of Plants. Cambridge: Cambridge University Press.

Stewart W. N. & Rothwell G. W. 1993. Paleobotany and the Evolution of Plants. 2nd ed. Cambridge: Cambridge University Press.

Smith D. L. 1959. Geminitheca scotica gen. et sp. nov.: a pteridosperm from the Lower Carboniferous of Dunbartonshire. Ann. Bot. (Lond.) N. S., 23: 477-491.

Smith D. L. 1964. The evolution of the ovule. Biol. Rev. Cambridge Philos. Soc. 39: 137-159.

Stockmans F. 1948. Végétaux du Dévonien Supériur de la Belgique. Mém. Mus. R d'His. Nat. Belgique 110: 1-85.

Stopes M. 1905. On the double nature of the cycadean integument. Ann. Bot. (Lond.) 19: 561-566.

Takhtajan A. L. 1956. Vysshie rasteniya. Ot psilofitovykh do khvoynykh [The higher plants. Psilophytales-Coniferales]. Vol 1. Moscow & Leningrad: Nauka. [In Russ.].

Takhtajan A. L. 1991 Evolutionary Trends in Flowering Plants. New York: Columbia University Press.

Tylor T. N. 1988. Pollen and pollen organs of fossil gymnosperms: phylogeny and reproductive biology. In: C. B. Beck (Ed.) - Origin and evolution of gymnosperms: 177-217. New York: Columbia University Press.

Taylor T. N. & Taylor E. L. 1993. The Biology and Evolution of Fossil Plants. Englewood Cliffs, New Jersey: Prentice-Hall.

Theodorov [Fedorov]. AL. A. & Artjuscenko Z. T. 1979. Organographia Illustrata Plantarum Vascularium. Inflorescentia. Leningrad: Nauka. [In Russ.].

Troll W. 1964. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. Bd. 1. Jena: Fischer.

Troll W. 1969. Die Inloreszenzen. Typologie und Stellungim Aufbau des Vegetationskörpers. Bd. 2 (1). Jena: Fischer.

Walton J. 1949. Calathospermum scoticum - an ovuliferous fructification of Lower Carboniferous age from Dunbartonshire. Trans. R Soc. Edinb. 61: 719-728.

Walton J. 1953. The evolution of the ovule in the pteridosperms. Adv. Sci. 10:223-230.

Weberling F. 1965. Typology of inflorescences. Bot. J. Linn. Soc. 59: 215-220.

Weberling F. 1989. Morphology of Flowers and Inflorescences. Cambridge: Cambridge University Press.

Weberling F., Müller-doblies U. & Müller-doblies D. 1994. Zur deskriptiven and vergleichend-morphologischen Terminologie komplexer Infloreszenzen. Beitr. Biol. Pflanz. 67: 453-473.

Wydler H. 1843. Über dichotome Verzweigung der Blütenaxen (cymöse Infloreszenz) dicotyledonischer Gewächse. Linnaea 17: 153-192, 408-409.

Wydler H. 1851. Über die symmetrische Verzeigungsweise dichotmer Infloreszenzen. Flora 34: 289-312, 321-330, 337-348, 353-365, 369-378, 385-398, 400-412, 417-426, 433-448.

Wydler H. 1878. Zur Morphologie, hauptsächlich der dichotomen Blütenstände. Jahrb. wiss. Bot. 11: 313-379.

Zimmermann W. M. 1935. Die Phylogenie der Angiospermen-Blütenstände. Beih. Bot. Centralbl. 53A: 95-121.

Zimmermann W. M. 1959. Die Phylogenie der Pflanzen. 2 Aufl. Stuttgart: Fischer.

Zimmermann W. M. 1965. Die Blütenstände, ihr System und ihre Phylogenie. Ber. Dtsch. bot. Ges. 78: 3-12.