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SERGIO RODRIGUEZ

The taxonomic status of the geyerophyllid corals

ABSTRACT: The geyerophyllid rugose corals comprise several genera broadly distributed during the Middle and Upper Carboniferous. Their specific and generic variability is so great that some authors have recently considered most of the geyerophyllids as synonyms of the genera *Geyerophyllum* or *Kionophyllum*. The present paper analyses the relationships between the solitary geyerphyllid genera in order to prove whether they constitute a simple genus or a true family. In the author's opinion, fully justified is their family status, *viz.* the Geyerophyllidae MINATO, 1955.

INTRODUCTION

The Upper Carboniferous rugose coral family Geyerophyllidae was proposed by MINATO (1955) to include the genera *Geyerophyllum* HERITSCH, 1936, *Carinthiaphyllum* HERITSCH, 1936, *Carniaphyllum* HERITSCH, 1936, *Lonsdaleoides* HERITSCH, 1936, *Cionodendron* BENSON & SMITH, 1923, and *Akiyosiphyllum* YABE & SUGIYAMA, 1942. This family was based on the presence of a clisiophylloid axial structure composed of septal lamellae and axial tabellae in the adult stage and a lophophyllidiid axial structure, simple and solid in the young stage. This concept of the Geyerophyllidae was changed by DOBROLYUBOVA (1962) and deGROOT (1963). The first author placed the genus *Kionophyllum* CHI, 1931, in the Geyerophyllidae and pointed out that the tabulae are horizontal and concave, whereas deGROOT (1963) described one species of *Lonsdaleoides* and pointed out that this species has clinotabulae. According to deGROOT (1963), the presence of clinotabulae is an important character to distinguish the Geyerophyllidae from similar forms; he also proved that the axial structure in *Lonsdaleoides* is joined to the cardinal septum, not the counter septum, as thought by MINATO (1955).

HAYASAKA & MINATO (1966) stated that the axial structure is continuous with the cardinal septum in *Carinthiaphyllum*, *Carniaphyllum*, *Geyerophyllum*, and *Lonsdaleoides*, and concluded that this may be the case in all the geyerophyllids.

MINATO & KATO (1967) described *Carinthiaphyllum carnicum* HERITSCH, 1936, from the Carnic Alps and recognized the presence of clinotabulae, ROWETT & KATO (1968) described *Darwasophyllum irregulare* PYZHANOV from Japan and found that this species has clinotabulae and clinotabellae; therefore, they placed *Darwasophyllum* in the Geyerophyllidae and considered *Geyerophyllum* as a synonym of *Kionophyllum*.

COCKE (1970) described some geyerophyllids from Kansas and interpreted *Geyerophyllum* as a "broad spectrum of morphological types"; he considered *Lonsdaleoides*, *Carinthiaphyllum*, *Carniaphyllum*, *Axolithophyllum*, *Koninckocarinia*, and *Amygdalophylloides*, as synonymous of *Geyerophyllum*.

MINATO & KATO (1971) and ROWETT & KATO (1968) regarded the family Koninckocariniidae DOBROLYUBOVA as possibly synonymous with Geyerophyllidae. WU & ZHAO (1974) also described some species of the genera *Axolithophyllum*, *Carinthiaphyllum*, and *Kionophyllum*.

As a result of these papers, MINATO & KATO (1975) revised the family diagnosis and pointed out that diagnostic characters of the geyerophyllids are the presence of clinotabulae and a solid columella connected to the cardinal septum. Thus, the new diagnosis of the Geyerophyllidae (MINATO & KATO 1975) was given as follows.

"This family includes solitary and fasciculate corals having diffusotrabecular septa (KATO 1963), clinotabulae (MINATO & KATO 1965a, b) as well as transverse tabulae. The axial structure is a swollen solid columella in the early stage, but may become denticulated as far as it reaches carcinophylloid axial column in the later stage. Lonsdaleoid dissepiments may develop with variable degrees in the mature stage. Septa are arranged in bilateral symmetry in the early stage and radial pattern in the later stage. Septa occur in two orders. Cardinal septum unites with swollen and solid columella in the early stage. Peripheral thickening of septa may sometimes be laterally coalesced with each other to form a distinct stereozone. Normal dissepimentarium is often masked by the well developed stereozone. Fossula indistinct. Rejuvenescence common".

MINATO & KATO (1975) included in the family the following genera: *Kionophyllum* CHI, 1931, *Carinthiaphyllum* HERITSCH, 1936, *Lonsdaleoides* HERITSCH, 1936, *Geyerophyllum* HERITSCH, 1936, *Amygdalophylloides* DOBROLYUBOVA & KABAKOVICH, 1948, *Axolithophyllum* FOMICHEV, 1953, *Darwasophyllum* PYZHANOV, 1964, and with slight doubt, *Carniaphyllum* HERITSCH, 1936, and *Paracarruthersella* YOH, 1961. The genus *Koninckocarinia* DOBROLYUBOVA, 1937, was placed in the Koninckocariniidae DOBROLYUBOVA, 1962.

The author (RODRIGUEZ 1983) described a new geyerophyllid genus, *Geyeronaotia*, and several species of *Amygdalophylloides*, *Kionophyllum*, *Axolithophyllum*, and *Koninckocarinia*. Finally, BOLL (1985) described several species of *Kionophyllum* and returned to COCKE's (1970) idea that the geyerophyllids belong to a single genus. BOLL considered *Axolithophyllum*, *Geyerophyllum*, *Lonsdaleoides*, *Koninckocarinia* and some species of *Amygdalophylloides* as synonymous with *Kionophyllum*. Thus, we are again faced with the question of whether the geyerophyllids are really a family or only a very variable genus.

DISCUSSION ON THE TAXONOMIC STATUS

The geyerophyllids are a very common group in the Upper Carboniferous, when they appeared in many zoogeographic provinces. They constitute a complicated group with very great variability which is why COCKE (1970) would not distinguish clear boundaries between the genera, and concluded that most of the family belonged to one genus. COCKE (1970) considered that the range of variation between *Lonsdaleoides* HERITSCH, 1936, *Carinthiaphyllum* HERITSCH, 1936, *Carniaphyllum* HERITSCH, 1936, *Axolithophyllum* FOMICHEV, 1953, and *Ko-*

ninckocarinia DOBROLYUBOVA & KABAKOVICH, 1948, does not greatly exceed intraspecific variation in *Geyerophyllum* sp. (cf. *G. broilli*) from the Wyandotte Formation.

COCKE (1970) signad that the most common criteria used to erect the geyerophyllid genera are: (*1*) Habit, (*2*) Character of the axial structure, (*3*) Character of the septa, (*4*) Presence or absence of lonsdaleoid dissepiments, and (*5*) Width and character of the dissepimentarium. In addition, he indicated that specimens of *Geyerophyllum* sp. (cf. *G. broilli*) collected from algal-rich calcilutite are solitary, gently flaring, and have a denticulate columella and well developed lonsdaleoid dissepiments, but the specimens of the same species collected in calcarenite are conicocylindrical, may be weakly fasciculate, have a less consistently denticulate columella, and do not have lonsdaleoid dissepiments in all individuals. Accordingly, he placed the whole family in one genus, *Geyerophyllum*. To accept COCKE's thesis, coloniality must be proved and variations in the columella and the dissepimentarium must be shown to be entirely ecologic. In the author's opinion, neither COCKE's descriptions nor his illustrations prove the coloniality of his specimens. Secondly, the axial structure of some geyerophyllids is so variable that lesser or greater denticulation of the columella is not significant. The presence of cavernous septa is more important, but is not a decisive argument, because COCKE referred to "slightly cavernous to regular septa", but not generallized cavernous or divided septa, and he did not explain the nature of the septa of specimens collected in the calcarenite.

The variability in *Geyerophyllum* sp. (cf. *G. broilli*) seems to be no greater than that in *Kionophyllum variabile* RODRIGUEZ, 1983. Because of such great variability, BOLL (1985) described specimens of *Kionophyllum* from the same level as 6 different subspecies of 5 species. BOLL, like COCKE, considered almost the whole family as a simple genus, but accepted the differentiation of *Amygdalophylloides* as a separate genus; he placed most of the geyerophyllids in *Kionophyllum* because this genus, not *Geyerophyllum*, has priority. In the author's opinion, some of the geyerophyllid genera are synonymous with *Kionophyllum*, but placing almost the whole family in only a genus is an oversimplification.

An analysis of descriptions and figures of type species of all these genera allows to place *Carniaphyllum* and *Geyerophyllum* into the synonymy of *Kionophyllum*, which is a genus with a broad spectrum of variability. The genera *Darwasophyllum*, *Lonsdaleoides*, and *Carinthiaphyllum*, because they are colonial, are separate from *Kionophyllum*, although differences between *Lonsdaleoides* and *Darwasophyllum* must be rechecked, because the type species of these genera seem to be very similar.

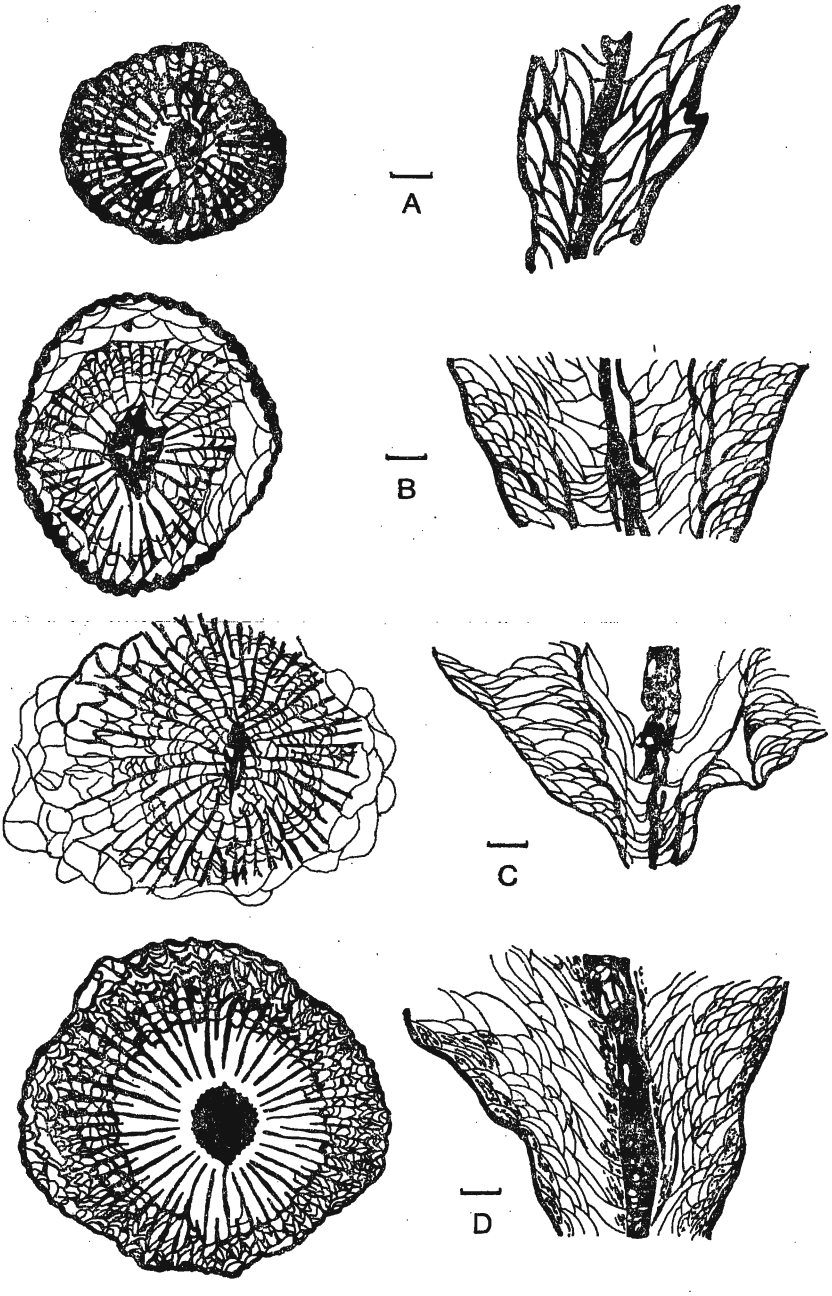
The genus *Koninckocarinia* is clearly different from *Kionophyllum*, because of its very simple axial structure, but in the author's opinion, *Koninckocarinia* belongs in the Geyerophyllidae and not in the Koninckocarinidae as MINATO & KATO (1975) proposed, because its remaining features agree totally with those of the Geyerophyllidae.

The type species of *Paracarruthersella* YOH, 1961, needs revision and it seems to be distinguishable from *Kionophyllum* by the notable presence of carinae on the septa.

The genera *Amygdalophylloides*, *Axolithophyllum* and *Geyeronaotia* are closely related to *Kionophyllum*, but they can be distinguished by an analysis of the criteria used to erect these genera as given in the forthcoming subchapters.

DISSEPIMENTARIUM

According to COCKE (1970) the main taxonomic character in the geyerophyllids is the presence or absence of lonsdaleoid dissepiments. The dissepimentarium (Text-



-fig. 1) is a very important criterion to distinguishing genera in the Geyerophyllidae, but not only the presence of lonsdaleoid dissepiments must be used. Differences between the dissepimentariums of *Amygdalophylloides*, *Axolithophyllum*, *Kionophyllum*, and *Geyeronaotia* are important.

The genus *Amygdalophylloides* has a narrow, regular dissepimentarium, which can be replaced in the young stage by a stereozone and may have some rare lonsdaleoid dissepiments in adult stage but never a true, well developed lonsdaleoid dissepimentarium.

The genus *Kionophyllum* has a normally developed lonsdaleoid dissepimentarium in the late young stage. In the adult stage the dissepimentarium may be either mainly lonsdaleoid with some regular dissepiments in the inner zone or entirely lonsdaleoid. The inner wall of the dissepimentarium, which MINATO & KATO (1975) regarded as a diagnostic feature of *Geyerophyllum*, is also present in the type species of *Kionophyllum*. This wall is formed normally by thickened regular dissepiments. Moreover, this character is so variable, that it may or may not appear in different sections of the same specimen.

The genus *Axolithophyllum*, which is very close to *Kionophyllum* in some aspects, can be distinguished easily because it has a broad lonsdaleoid dissepimentarium with peripheral flat dissepiments. Nevertheless, this genus has regular dissepiments that first appear in the young stage and continue into the adult stages. The lonsdaleoid dissepimentarium is developed when the diameter increases. An inner wall can appear also, but in *Axolithophyllum* it is normally composed of several rows of regular dissepiments very close one to another.

The dissepimentarium of *Geyeronaotia* resembles in some aspects that of *Kionophyllum*, having lonsdaleoid and regular dissepiments, but having frequently naotic dissepiments (called also the naotic septa). Moreover, it has regular lateral dissepiments, which are very rare in other geyerophyllids.

MICROSTRUCTURE OF SEPTA

The microstructure of the septa (Text-fig. 2) in *Amygdalophylloides* and *Kionophyllum* is not very different. It is trabecular, pseudotrabecular or diffusotrabecular. The septa normally reach the wall in *Amygdalophylloides*, but not in *Kionophyllum* because of the lonsdaleoid dissepimentarium. Both genera have regular septa, but *Kionophyllum* sometimes shows slightly cavenous septa. According to MINATO & KATO (1975), *Kionophyllum* differs from *Amygdalophylloides* in having longer minor septa. Comparison of this character in most of the species assignable to both genera indicates that this is not a distinctiv feature. The type species of *Amygdalophylloides* has rather long minor septa, and this character is very variable in some of the species assignable to *Kionophyllum*.

Fig. 1. Dissepimentarium and tabularium structure in some solitary geyerophyllid corals

A — cross and longitudinal sections of *Amygdalophylloides liebanensis*, RODRIGUEZ, 1983; Upper Bashkirian of the Cantabrian Mts, NW Spain; B — cross and longitudinal sections of *Kionophyllum variabile* RODRIGUEZ, 1983; Upper Bashkirian of the Cantabrian Mts, NW Spain; C — cross and longitudinal sections of *Axolithophyllum hontoriense* RODRIGUEZ, 1983; Moscovian of the Cantabrian Mts, NW Spain; D — cross and longitudinal sections of *Geyeronaotia hispanica* RODRIGUEZ, 1983; Kasimovian of the Cantabrian Mts, NW Spain

Scale bars are 2 mm

In *Axolithophyllum*, the septa are extremely variable; they may be regular, cavernous, or "divided" (RODRIGUEZ 1983). The microstructure is trabecular or multitrabecular, and normally shows a complex system of two or three rows of trabeculae. When they are isolated, the septa show cavernous structure, but when the rows are separated, the septa show a "divided" structure. This

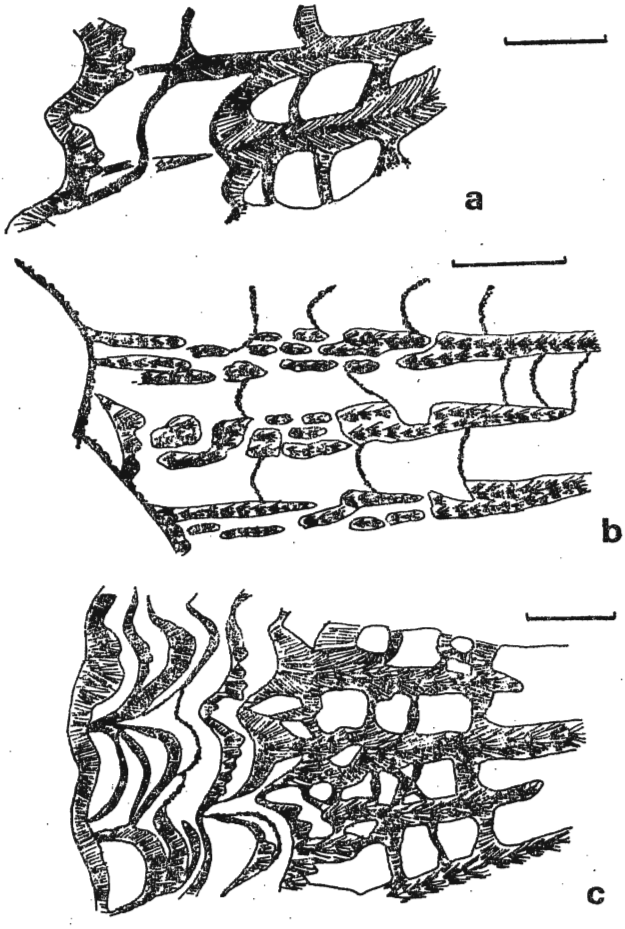


Fig. 2. Microstructure of the septa in: a — *Kionophyllum variabile* RODRIGUEZ, 1983; b — *Axolithophyllum hontoriense* RODRIGUEZ, 1983; c — *Geyeronaotia hispanica* RODRIGUEZ, 1983; all from the Cantabrian Mts, NW Spain; scale bars are 1 mm

septal architecture is only evident in peripheral areas and not in all septa, but it is always present. In addition, the septa of *Axolithophyllum* do not normally reach the wall, but may be present as septal crests on the lonsdaleoid dissepiments. The minor septa are often sparsely developed. Then are generally short and, in some species, appear only as septal crests on the dissepiments between major septa ("transeptal dissepiments of second order" of SEMENOFF-TIANCHANSKY 1974).

The septa of *Geyeronaotia* have a structure close to *Axolithophyllum*. They are trabecular and sometimes, not very often, may be "divided", but the most characteristic feature is the presence of naotic structures in the peripheral area near the wall. The typical structure of *Geyeronaotia* shows some curved fibrous lamellae perpendicular to the septa. The number of lamellae does not exceed five or six, and the lamellae are not present in each septum. Sometimes they are loosely packed and sometimes they are closely packed. Some of these lamellae can be related to lonsdaleoid distepi-

ments. Minor septa are well developed, but they are restricted to a median zone; they do not penetrate the lonsdaleoid dissepimentarium and barely reach the tabularium. Their structure is trabecular or multitrabecular, like that of major septa.

TABULARIUM

No distinctive feature distinguishes the tabularium of different geyerophyllid genera (*see* Text-fig. 1): all of them have clinotabulae and transverse tabulae, which is the most representative character of the family. Minor differences in tabularium structure are only useful for differenciating species.

AXIAL STRUCTURE

The presence of an axial structure (Text-fig. 3) is a general character in all the geyerophyllids. In young stages it is always a swollen solid columella joined to the cardinal septum, but in adult stages it shows extreme variability.

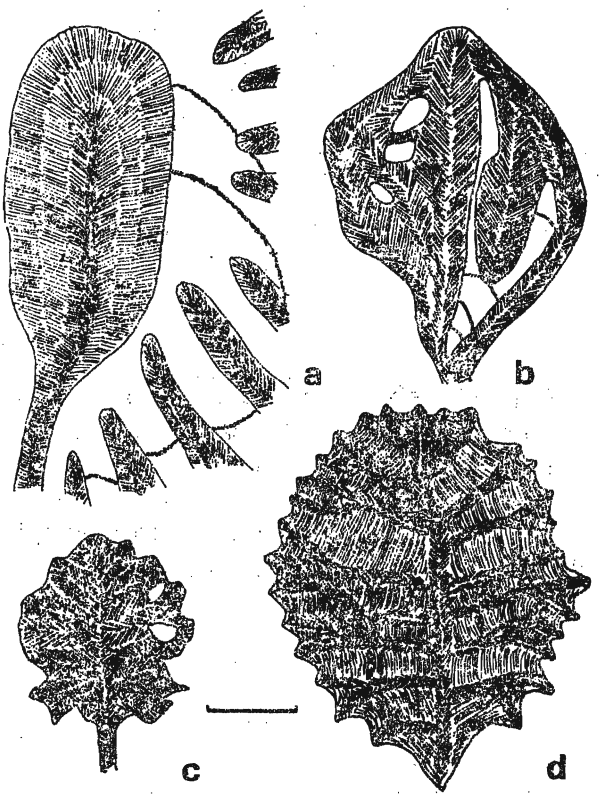


Fig. 3. Microstructure of the axial structure in: **a** — *Amygdalophylloides ivanovi* DOBROLYUBOVA, 1937, from the Moscovian of the Cantabrian Mts, NW Spain; **b** — *Axolithophyllum quiringui* WEISSERMEL, 1935, from the Upper Bashkirian of the Cantabrian Mts, NW Spain; **c** — *Kionophyllum cosgayense* RODRIGUEZ, 1983, from the Lower Bashkirian of the Cantabrian Mts, NW Spain; **d** — *Geyeronaotia hispanica* RODRIGUEZ, 1983, from the Kasimovian of the Cantabrian Mts, NW Spain; scale bar is 1 mm

The genus *Koninckocarinia* which closely resembles *Kionophyllum*, can be distinguished by having a simple columella formed by thin prolongation of the cardinal septum. Differences between and relationships with columellae of other genera are much more complex.

The genus *Amygdalophylloides* has a simple axial structure composed of a solid columella with or without rare irregularly arranged and poorly developed axial tabellae.

The genus *Kionophyllum* shows a complex axial structure that is extremely variable ontogenetically. Variability in the axial structure of *Kionophyllum* is exemplified in the description of the columella in the original diagnosis of CHI (1931):

"The structural divisions are... and a very large median solid stereocolumella. Septa alternating in size, ... having projections from their extremities which unite with the central pseudocolumella. They are straight or very slightly twisted. Between septa at the center of the corallum there is a deposit of stereoplasma a pseudocolumella of very peculiar appearance somewhat resembling the stereocolumella of *Stereolasma* SIMPSON. This consist of a median plate which is continuous with both cardinal and counter septa. The section of the columella is oval shaped with a distinct boundary".

Thus, the main features are solid columella with septal lamellae and stereoplasmic deposits. Septal lamellae are always present in *Kionophyllum*, but their development is very variable; sometimes they are sparse and sometimes they constitute a very complex axial structure (e.g., *Axophyllum wagneri* deGROOT, 1963 = *Kionophyllum wagneri*, deGROOT 1963; *see* RODRIGUEZ 1983).

The axial structure of *Axolithophyllum* does not differ greatly from that of *Kionophyllum*. Normally, it is a little more irregular and complex because of the presence of lamellae which are parallel to the median plate. Some tabellae may also appear between the lamellae. Septal lamellae are normally not so extensive as in *Kionophyllum*. The axial structure can not be a determining factor to distinguish *Kionophyllum* from *Axolithophyllum* because of its great variability in both genera, but it can be an important subordinate factor. On the contrary, the axial structure of *Geyeronaotia* is its most characteristic feature; it is a solid, oval, large columella with denticulated margins. Its diameter can reach 1/5 of the lumen of the coral. The inner structure of the columella is very characteristic, having a trabecular medial plate and many fibrous, radial, branching lamellae. Between the lamellae are some holes which are normally filled with stereoplasm, but rarely the holes are open.

HABIT

The habit of *Amygdalophylloides* is generally ceratoid to conicocylindrical; *Kionophyllum*, *Koninckocarinia* and *Geyeronaotia* are ceratoid or trocoid, whereas *Axolithophyllum* is patelate or turbinate. The range of variation within a species is frequently very great with the exception perhaps of *Axolithophyllum*, the genus which can tentatively be distinguished on the basis of its habit, but this character must be used only as an accesory criterion.

STRATIGRAPHIC RANGE AND PHYLOGENY

The stratigraphic range and geographic distribution of solitary geyerophyllids (Text-fig. 4) are based on the data compiled by several authors (*e. g.*, MINATO & KATO 1975, p. 19; COTTON 1983, pp. 18, 25, 38, 94—95; RODRIGUEZ 1983, p. 525) and on the unpublished data from Spain (BOLL 1985).

Understanding of the young stages of geyerophyllid corals is essential for the recognition of the ancestor of that family. The presence of an amygdalophylloid stage has been recorded in most of species of *Kionophyllum*, *Axolithophyllum* and

also in *Geyeronaotia*. Sometimes, young stages of the *Kionophyllum* species have been described as *Amygdalophylloides*, but the later genus is conicocylindrical and when the adult stage is attained the coral mantains the same diameter and the some features.

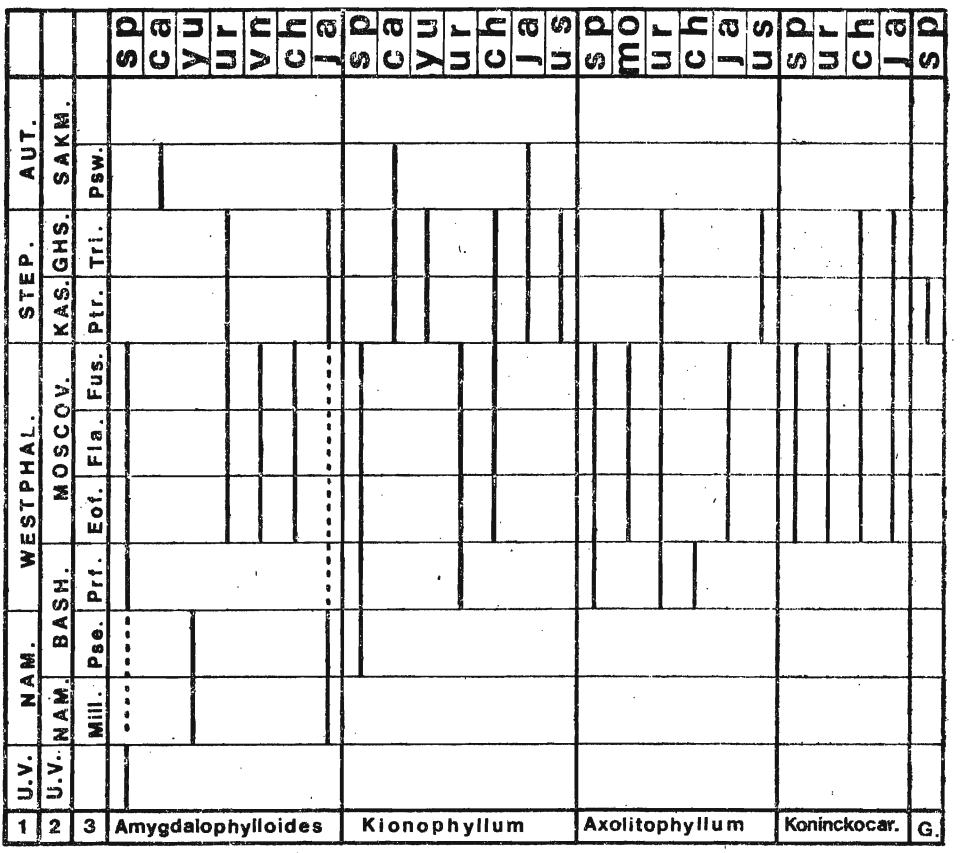


Fig. 4. Stratigraphic range of the solitary geyerophyllid genera (*1* West European scale, *2* Soviet Union scale, *3* foraminiferal zones)

Geographic names: **sp** — Spanien, **ca** — Carnic Alps, **yu** — Yugoslavia, **ur** — U.S.S.R., **vn** — Vietnam, **ch** — China, **ja** — Japan, **us** — U.S.A., **mo** — Morocco

Stratigraphic names: **U.V.** — Upper Viséan, **Nam.** — Namurian, **Westphal.** — Westphalian, **Step.** — Stephanian, **Aut.** — Autunian, **Bash.** — Bashkirian, **Moscov.** — Moscovian, **Kas.** — Kasimovian, **Ghs.** — Ghselian, **Sakm.** — Sakmarian

Foraminiferal zones: **Mill.** — Millerella Zone, **Pse.** — Pseudostafella Zone, **Prf.** — Profusulinella Zone, **Eof.** — Eofusulina Zone, **Fla.** — Fusulinella Zone, **Ptr.** — Protriticites Zone, **Tri.** — Triticites Zone, **Psw.** — Pseudoschwagerina Zone

In addition, the oldest geyerophyllid species may be assigned to *Amygdalophylloides*, as has been recorded from the Upper Viséan of southern Spain. This species is small and has a large solid columella with a smooth surface. Nevertheless, the presence of some lonsdaleoid dissepiments in the adult stage indicates close relationships to *Kionophyllum* and suggests that is an ancestor of both genera.

Another species of *Amygdalophylloides* are recorded in the Lower Namurian of Yugoslavia and Japan, but the first true *Kionophyllum* is not recorded until the Namurian/Bashkirian boundary is reached. Species recorded at that position are small, but show all the characters of *Kionophyllum* (e. g., complex axial structure, and well developed lonsdaleoid dissepiments) and are appreciably simpler than the species of that genus from the Upper Bashkirian, Moscovian and Kasimovian. This seems to indicate that the geyerophyllids became more complex during the Bashkirian and Moscovian.

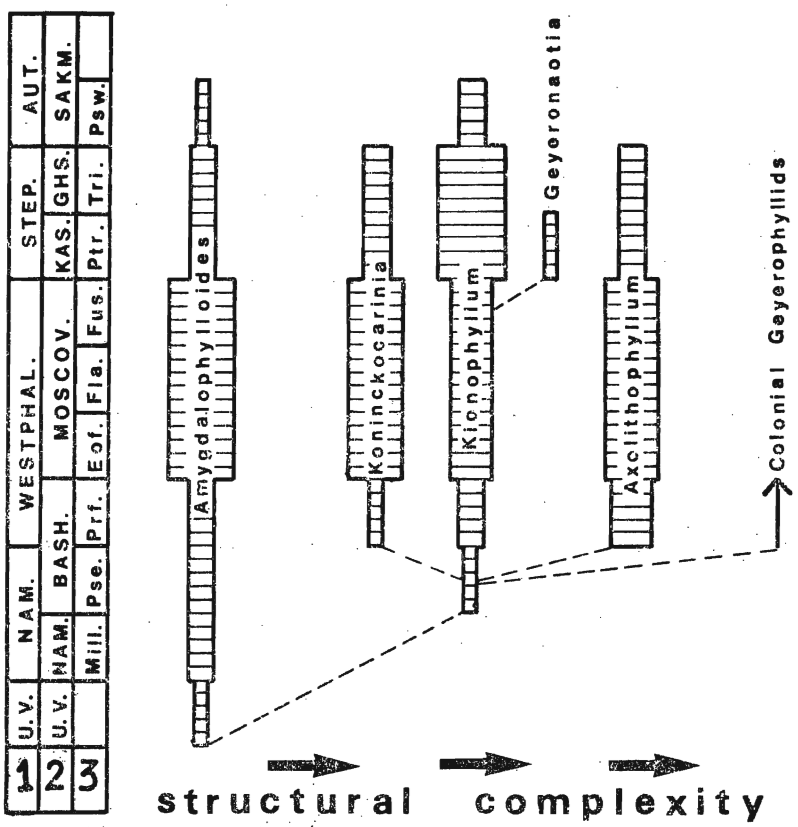


Fig. 5. Tentative phylogenetic relationships between the geyerophyllid solitary genera (stratigraphic scales as in Text-fig. 4); the thickness of the columns depends on the number of areas where the genera have been recorded

The first records of *Axolithophyllum* and *Koninckocarinia* are in the Upper Bashkirian. The both genera are close to *Kionophyllum* but show important variations: *Koninckocarinia* develops a simple axial structure, and *Axolithophyllum* does special septal structures as well as a pateloid habit. These genera seem to be variations from the main trunk of the Geyerophyllidae, probably represented by *Kionophyllum*. Such variations succeed and develop broadly during the whole Upper Carboniferous (Text-fig. 5), although *Axolithophyllum* has broader geographic distribution than *Koninckocarinia*. Nevertheless they are extinguished at the end

of the Carboniferous, but *Amygdalophylloides* and *Kionophyllum* reach into the Lower Permian.

The genus *Geyeronaotia* seems to be another, very characteristic variation, but with lesser stratigraphic and geographic development in the Kasimovian of the Cantabrian Mts of Spain.

Colonial geyerophyllids were derived probably also from *Kionophyllum*. The presence of some calicular budding in specimens of *K. variabile* and *Axolithophyllum hontoriense* from the Cantabrian Mts seems to evidence a tendency toward colonial development during the Upper Bashkirian and Moscovian stages.

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Departamento de Paleontologia,
Facultad de Ciencias Geologicas,
Universidad Complutense de Madrid,
28040 Madrid, Espana

Institut und Museum
für Geologie und Paläontologie
der Universität Tübingen,
Sigwartstrasse 10
7400 Tübingen, Bundesrepublik Deutschland

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