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Solitary and/or colonial growth in the Palaeozoic superorder Heterocorallia SCHINDEWOLF, 1941 (Eifelian–Serpukhovian)

by Dieter Weyer (Berlin) with 9 figures and 11 plates

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Abstract

The slowly growing evidence for colonial habit in the Palaeozoic Heterocorallia is supported by the first record of nearly complete colonies, found in the Upper Famennian of Morocco (Anti-Atlas, Tafilalt). Rich collections of *Oligophylloides* RóżKOWSKA, 1969 allow the proposal of *Oligophylloides maroccanus* sp. nov., found in cephalopod limestones, where a thicket of about six colonies was observed (length 2.30 m, height 0.3–0.4 m, planar dendroid growth). The sessile benthonic genus lived rarely solitary, mostly colonial within one species population. These corals constructed a special type of colonies, starting with several (observed up to 16) protocorallites, which united their tissue without any genetic barrier. The new term paracolony is introduced for such coral colonies, which are also known among Rugosa, as demonstrated by the Lower Silurian *Schlotheimophyllum patellatum* (SCHLOTHEIM, 1820) from Gotland Island, Sweden. Obviously also the typical Viséan–Serpukhovian heterocorallian genera *Hexaphyllia* STUCKENBERG, 1904 and *Heterophyllia* MCCOY, 1849 were both colonial and solitary, as indicated by their locally sediment-filling rich assemblages, already recorded in the literature. The worldwide usual, always strongly fragmented preservation could be caused by fish-like predators, feeding (perhaps similar to some recent parrot fishes) the unprotected soft parts, which covered greater parts of the distal Heterocorallia skeleton.

Zusammenfassung

Allmählich zunehmende Beweise für die Existenz kolonialer Heterocorallia werden durch die ersten Funde nahezu vollständiger Kolonien im Oberen Famenne von Marokko (Anti-Atlas, Tafilalt) gestützt. Anhand reicher Kollektionen von *Oligophylloides* RóżKOWSKA, 1969 wird *Oligophylloides maroccanus* sp. nov. für Funde aus Cephalopoden-Kalken aufgestellt. Ein Heterocorallia-Dickicht aus etwa sechs planaren dendroiden Kolonien wurde beobachtet (Länge 2,30 m, Höhe 0,3–0,4 m). Arten des sessil benthonischen Genus lebten selten solitär, meist kolonial. Sie bauten einen speziellen Kolonie-Typ, der mit mehreren (bis zu 16 beobachteten) Protocoralliten startete, die ihre Weichteile ohne irgendeine genetische Barriere vereinen konnten. Dafür wird der neue Terminus Parakolonie vorgeschlagen; er kommt auch unter Rugosa vor, was durch *Schlotheimophyllum patellatum* (SCHLOTHEIM, 1820) aus dem Unteren Silur der Insel Gotland (Schweden) belegt wird. Höchstwahrscheinlich waren auch die typischen Heterocorallia des Visé–Serpukhov, *Hexaphyllia* STUCKENBERG, 1904 und *Heterophyllia* MCCOY, 1849, sowohl solitär als auch kolonial, wie ihre aus der Literatur bekannten, lokal öfter stark angereicherten, nahezu gesteinsbildenden Populationen belegen. Ihre weltweit übliche, immer stark fragmentierte Erhaltung dürfte auf Fressfeinden beruhen, die (vielleicht ähnlich wie einige rezente Papagei-Fische) die ungeschützten Weichteile abweideten, von denen erhebliche Teile des distalen Heterocorallia-Skeletts äußerlich bedeckt waren.

1 Introduction

Since their first description (genus *Heterophyllia* M'COY, 1849), heterocorals have been diagnosed mostly as solitary (ROEMER, 1880: p. 412; THOMSON, 1883: p. 411; SCHINDEWOLF, 1941: p. 224; HILL, 1940: p. 196; FONTAINE, 1961: p. 203; SUTHERLAND & MITCHELL, 1980: p.2; KABAKOVICH, 1962: p. 344; OLIVER, 1968: p. 19; SCRUTTON, 1985/1990: p. 34; LAFUSTE, 1987: p. 811). On the other hand, already DUNCAN (1868: p. 646, pl. 31/6a) had noticed budding in the Late Viséan species *Heterophyllia sedgwicki* DUNCAN, 1868 (later partly redescribed by THOMSON, 1883: p. 414, pl. 10/17,17A, without mentioning buds). This was critically analyzed by SCHINDEWOLF (1941: p. 225, 284), who never had seen any budding in his own material of Heterocorallia: he doubted that this species belongs to his newly proposed suborder.

His opinion was based on the regular alternating of ten longer and ten shorter septa (like major and minor ones of Rugosa, with axially free ending catasepta *sensu* EZAKI, 1989) in one calicular view of DUNCAN (1868: pl. 31/6e, probably the same specimen as pl. 31/6c) and might be correct, though such a morphology with well developed costae (everted calice) is at present unknown among Scottish Late Viséan Rugosa. The illustrated transverse section of DUNCAN (1868: pl. 31/6b) is a real *Heterophyllia*, and perhaps not conspecific with his calicular view, pending a future revision (with choice of a lectotype) of the species *Heterophyllia sedgwicki* DUNCAN, 1868, which was not possible for HILL (1940: p. 197), having no access to the DUNCAN (1868) materials collected by THOMSON (see 1883: p. 415).

Obviously, the case of *Heterophyllia sedgwicki* DUNCAN, 1868, was the reason, why HILL (1956: p. F324) mentioned "but rare indications of branching" in Heterocorallia, getting access to the publication of SCHINDEWOLF (1941) since 1945 after the end of the Second World War, which had interrupted all scientific exchange. Later she accepted probably SCHINDEWOLF's exclusion of this species from the Heterocorallia and omitted such an indication for coloniality in the revised second edition of her Palaeozoic Coral Treatise (1981), as written to WRZOŁEK (1981: p. 514).

The doubtless existence of colonial Heterocoralla was demonstrated at first by WRZOŁEK (1978 in a preliminary abstract, 1981) for the genus *Oligophylloides* RóżKOWSKA, 1969, based on lower Famennian materials from the Polish Holy Cross Mountains in the common fragmentary preservation. He illustrated asexual budding (1981: fig. 1, KARWOWSKI & WRZOŁEK, 1987: fig. 1A), analyzed by narrow serial sections. Similar fragments with buds were already illustrated in RóżKOWSKA (1969: p.169, fig. 71A₁₋₂, though interpreted as separate individuals settled as sexually produced larvae. CHWIEDUK (2001) supplemented these studies by a fundamental morphological-biological revision. Budding was also mentioned for Upper Famennian *Oligophylloides* from Germany (WEYER, 1995: p. 121, figs. 10/1–14; PIECHA, 2004a: 127, pl. 1–2).

Lower Carboniferous colonies of Heterocorallia were first recorded by SUGIYAMA (1984: fig. 17, pl. 7/6a–b) in his new dendroid genus *Radiciphyllia* from the Upper Viséan (Asbian) of Japan. Later he showed a reconstruction of the benthic life habit (SUGIYAMA, 1991: fig. 4b). A second new genus was announced by TOURNEUR et al. (1995). It comes from Serpukhovian beds in the French Pyrenees and had been misidentified previously as *"Lithostrotion?* cf. *tareense* PICKETT", 1966 (PERRET & SEMENOFF-TIAN-CHANSKY, 1971: p. 570, pl.1/1a–c). COSSEY (1997: p. 1032. 1059 cited it as *Anomalophyllia* nomen nudum. Markus ARETZ (Toulouse) received the material after the death of Pierre SEMENOFF-TIAN-CHANSKY (1926–2003) and plans the publication.

The profound revision of the Viséan *Hexaphyllia* STUCKENBERG, 1904, by COSSEY (1997: p. 1031) – based in *Hexaphyllia marginata* (FLEMING, 1828) from England – declares the genus to be typically solitary, bur rarely weakly colonial and benthic. SCRUTTON (1977: p. 12) had already announced this current study reporting

branching *Hexaphyllia*. But COSSEY (1997: p. 1038) speaks about the difficulty to distinguish between branching by asexual budding from attachment by larval encrustation, and he thinks that encrustation is prevailing. This idea is supported by CHWIEDUK (2001: p. 1191) declaring for *Oligophylloides*: "the offsets are never connected with the tabularium of the parental corallite" (confirmed by PIECHA, 2004a: pl. 2/7a–b, and here by Fig. 1, but opposed by Fig. 2 and Pl. 3/1b). A further colonial Lower Carboniferous heterocoral seems to be *Hexaphyllia? ayzenvergi* WEYER & POLYAKOVA, 1995, from the Upper Serpukhovian of the Donez Basin, Ukraine (WEYER & POLYAKOVA, 1995: pl. 1/2a–c). Several fragmented and extremely enriched occurrences of other records of Viséan *Hexaphyllia* and *Heterophyllia* allow the suggestion that they are not solitary individuals as suggested by authors, but represent most probably former colonies (PAREYN, 1959: pl. 24/B; POTY, 1981: pl. 24/12, RODRÍGUEZ & COMAS-RENGIFO, 1989 – pl.1/1, Chinese localities studied by LIN Ying-dang and his students). Chinese authors accepted the increasing discovery of coloniality (LIN et al., 1992), and cases of budding were studied, sometimes also using serial sections (LIN, WU & QIU, 1992).



Fig. 1: Oligophylloides pachythecus RóżKOWSKA, 1969, Upper Famennian, upper Clymenia Genozone, borehole Refrath 1/1992 10 km E of Cologne, Rhenish Mountains, collection M. PIECHA 1992; branch fragments with either asexual budding (?) or new larval settlements. 1 – borehole core of marly mudstone with straight and curved cylindrical branches, sometimes showing small "buds" (no. MB.K.7999.8.), x 1. 2 &3 – external configuration (nos. MB.K.7999.1–2.), x 6. 4, 5, 6 – median longitudinal thin sections (nos. MB.K.7999.7, 5, 4), always with a complete heterotheca separating the two corallites, this favouring an interpretation as postmortal attachment of a next larval generation. x 20.

Heterocorallia, living during lower Eifelian – upper Serpukhovian times, had developed both solitary and colonial (dendroid) growth forms, which for the moment seem to be unimportant for the taxonomic definition of genera (especially in view of missing records in the Givetian and Frasnian, and nearly missing records in the Tournaisian). Probably, their species even had the ability of "free" choice between the two growth habits, conditional upon solely ecological circumstances.

The rare oldest representatives are known only from small fragments, which could be either solitary or colonial: *Stellaphyllia* FERNÁNDEZ-MARTÍNEZ, TOURNEUR & LÓPEZ-ALCÁNTARA, 2003, lower Eifelian, Cantabrian

Mountains, Spain (FERNÁNDEZ-MARTÍNEZ et al., 2003), "*Mariaephyllia eifeliensis* GLINSKI, 1998", middle Eifelian, Rhenish Mountains, Germany. The latter name is invalid, because of the unhappy holotype selection of GLINSKI (1998: pl. 1/1), which is not a heterocoral as all illustrated paratypes, but a Rugosa with some short catasepta, namely a juvenile *Metriophyllum gracile* SCHLÜTER, 1884.

Lower Devonian Heterocorallia did not exist or are still unknown. The Upper Emsian *Pseudopetraia* SOSHKINA, 1951 (Ural Mountains, Russia), questionably included into the Heterophylliidae DYBOWSKI, 1873 by HILL (1981: p. F425) and accepted as a monotypic family Pseudopetraiidae FEDOROWSKI, 1991 (order Calyxcorallia FEDOROWSKI, 1991), is a normal Rugosa coral, as demonstrated by the ontogeny of the second species *Pseudopetraia issa* WEYER, 1991 (Pragian, Thuringia, Germany).



Fig. 2: *Oligophylloides* sp., Upper Famennian, upper *Clymenia* Genozone, Ouidane Chebbi section 43 km ESE of Erfoud (bed 114), collection D. WEYER 1995 (MB.K.2425.13.), median longitudinal thin section of a budding branch fragment (photo see Pl. 10/13) with connected tabularia. x 5.

Tetraphyllia YOH, JIN, ZHEN & XIE, 1984, (Upper Emsian, Yunnan, China) has no heterocorallian wall of heterotheca type (growing centrifugally), but clearly an archaeotheca of normal Rugosa type (growing centripetally), as visible in YOH et al. (1984: p. 5, pl. 1/1–6) or even better in JIN (2005: p. 138, pl. 24/6–16, in higher printing quality) and criticized in WEYER (1991: p. 20, 1995: p. 112). This is evident in transverse sections from the well-rounded transition of the last tangential internal wall layer into the radial outer septal flank layer, both formed finally as one stereoplasmatic thickening process. In heterocorals this contact is angular (WEYER, 1995: p. 109, figs. 1–2), and schematic drawings as those of FEDOROWSKI (1993: p. 85, figs. 5a–c) are incorrect in that detail. Tentatively *Tetraphyllia* was reclassified as Tetraphylliinae YOH, JIN, ZHEN & XIE, 1984, within the Polycoeliidae FROMENTEL, 1861 (WEYER, 2014: p. 130). Thus, the suborder Tetraphylliina FEDOROWSKI, 1991, (of order Heterocorallia SCHINDEWOLF, 1941) is cancelled, a priori owing to nomenclatural reasons; the later taxonomic discussion will show that no replacement name is necessary, also because of morphological reasons, as an order subdivision (*sensu* FEDOROWSKI, 1991: p. 52, 63, fig. 7) based on symmetrical or asymmetrical septal arrangement does not work.

The youngest heterocorals in the Serpukhovian include colonial ones; the presence of solitary forms remains undecided due to the only very fragmentary preservation. Their survival in Upper Carboniferous times is unproven. *Hexaphyllia concavia* METCALFE, IDRIS & TAN, 1980, was dated as *Homoceras* Genozone by parallel conodont studies (METCALFE, 1980), but the precise layer in the interval topmost Serpukhovian to basal Bashkirian is not fixed. Presumed findings of Heterocorallia from the late Upper Carboniferous (Mapingian, Gzhelian) in China by LIN & PENG (1990) are crass misidentifications (WEYER & POLYAKOVA, 1995: p. 144): their monotypic new genus *Dichophyllia* (and thus the subfamily name Dichophyllina LIN, HUANG, WU, PENG & QIU, 1992) is a Bryozoan; their *Heterophyllia* sp. (p. 372, pl. 1/1) and *Heterophyllia henanensis* (p. 372, pl. 1/2-3) are Rugosa.

2 Material, localities & age

The best samples of Famennian Heterocorallia (including nearly complete, well preserved colonies of *Oligophylloides* RÓŻKOWSKA, 1969) were observed, collected, or bought in the Anti-Atlas of Morocco (Tafilalt). First records had been announced by TOURNEUR (1994) and described by WEYER (1995). In addition to the materials studied here, there are further, often rich faunas from several other places (map in HARTENFELS &

BECKER, 2016: fig. 3): Bordj Est near Erfoud = Djebel Erfoud (*Cheiloceras* Genozone), El Atrous (*Clymenia* Genozone), Oum el Jerane (*Clymenia* Genozone), Rich Harun (*Cheiloceras* Genozone). All figured and supplementary specimens are stored in the Museum of Natural History (LEIBNIZ Institution) at the HUMBOLDT-University in Berlin (no. MB.K. xxx), excepting one colony (Pl. 8/1) donated to the Institute of Geology at the Technical University (Mining Academy) in Freiberg (no. FG.663).

2.1 Bou Ifarherioun

This region in the southern Tafilalt platform, 15 km south of Rissani (WENDT et al., 1984: p. 620, map fig. 16) offers some trenches in the Upper Famennian *Gonioclymenia*-Limestone, exploited for its ammonoid fossils and marble stones. In 1995, a rich collection of Heterocorallia (*Oligophylloides, Mariaephyllia*) was sampled from areas with masses of loose pebbles from this horizon. Accompanying fragments of the index fossil *Gonioclymenia* HYATT, 1884, were found several times. Some limestone pebbles yielding heterocorals allowed an age control by their conodont faunas of the Subzone of *Bispathodus costatus (Bispathodus aculeatus aculeatus Zone)*, according to the zonation of HARTENFELS (2011: p. 35, fig. 3) and HARTENFELS & BECKER (2016: fig. 7), which is an equivalent of the Middle *Palmatolepis gracilis expansa* Zone *sensu* ZIEGLER & SANDBERG 1984: *Bispathodus aculeatus aculeatus* (BRANSON & MEHL, 1934), *Bispathodus aculeatus anteposicornis* (SCOTT, 1961), *Bispathodus costatus* (BRANSON, 1934), *Bispathodus bischoffi* (RHODES, AUSTIN & DRUCE, 1969). Some few loose pebbles with *Bispathodus ultimus ultimus* (BISCHOFF, 1957) are younger: *Bispahodus ultimus ultimus* Zone [Lower *Wocklumeria* Genozone, Zone of *Kalloclymenia subarmata* (MÜNSTER, 1832) *sensu* SCHINDEWOLF, 1937], as explained in HARTENFELS & BECKER (2016). But the majority of the big Heterocorallia comes definitely from the *Clymenia* Genozone.

Oligophylloides specimens of the enormous size typical at the Bou Ifarherioun locality, though from an older lower Famennian horizon, had been misinterpreted as crinoid holdfasts in life position (WENDT et al., 1984: p. 612, fig. 11A). Perhaps the same misidentification happened in HARTENFELS & BECKER (2016: fig. 2c-insert) – Upper Famennian *Costaclymenia* Limestone at the Djebel Ihrt locality.

2.2 Djebel Amre

The now big quarry Djebel Amre (31°13.47' N, 04°23.00' W), WSW of Rissani, is situated near to the trench outcrops (*Gonioclymenia* Limestone) of the Djebel Ihrs-West and Djebel Amelane localities in HARTENFELS & BECKER (2016: fig. 3). A first visit in 2006 allowed surprising observations of about 6–8 *Oligophylloides* colonies in life position, standing in a row to form a thicket of 2.30 m length and 0.3–0.4 m height. The predominantly planar colonies had started to grow attached to some few crinoid roots. Sampling of that *in situ* material was impossible, but another turned over colony (Pl. 9/1) was found embedded parallel to stratification. Sediment from this specimen yielded conodonts of the *Bispathodus costatus* Subzone (*Clymenia* Genozone), and Ostracoda of Thuringian ecotype (in chlorite preservation: *Tricornina, Acratia, Villozona*, Rectonariidae).

In 2006, it was already possible to buy another small colony (Pl. 10/16) in a big fossil shop in Erfoud. During our visit, Arab workers of the quarry had observed our interests in these corals; now they started to look intensively not only for ammonoids (*Gonioclymenia*). Thus I could buy two further colonies in 2007 (Pl. 7/1) and in 2009 (Pl. 8/1).

2.3 Ouidane Chebbi

The section ca. 43 km ESE of Erfoud was studied by KORN (1999: p. 149, figs. 1, 4). In 1995, I collected under his guidance a rich assemblage of *Oligophylloides* from bed 114, which was dated by ammonoids as upper *Clymenia* Genozone.

64 fragments (length 9–73 mm, diameter 2–6 mm, Pl. 10/1-15) were found in an area of ca. 1 m²; surely there had been even more, but smaller debris. Together, my specimens amount to a length of 1.66 m; asexual budding is visible four times. It seems very probable that all pieces could be broken parts of one (or more?) colonies, comparable to the locally enriched occurrence in the German borehole Refrath 1/1992 (PIECHA, 2004a: pl. 1).

2.4 Seheb el Rhassal

One Mid-Famennian *Oligophylloides* fragment (Fig. 4, collection R.T. BECKER 1999) is published here because of its budding and epibiont. The locality Scheb El Rhassal in the central Tafilalt (31°21'19.2'' N, 04°11'14.2'' W)

is an unpublished section of R. T. BECKER, where I could collect some Rugosa and Heterocorallia in 2000. The *Oligophylloides* sp. comes from a bed "9e-top", ammonoid Zone of *Planitornoceras euryomphalum* (WEDEKIND, 1918), zone DU III-B *sensu* BECKER et al. (2002), Moroccan equivalent of the mid-European Zone of *Pseudoclymenia pseudogoniatites* (SANDBERGER, 1853) = conodont Zone of *Scaphignathus velifer* HELMS, 1959 (lower part).

2.5 Borehole Refrath 1/1992 (near Cologne, Germany)

The borehole was situated in the golf course of Bergisch Gladbach–Refrath (R 85 79275, N 56 49075), ca. 10 km east of Cologne (map 1 : 25.000, sheet Köln-Mülheim, no. 5008) (see map in PIECHA, 2004a: p. 124, fig. 1). Masses of Heterocorallia (*Oligophylloides*) were found in Late Famennian grey mudstones (depth 3–38 m) and studied by PIECHA (2004a). The horizon was dated as Middle Conodont Zone of *Palmatolepis gracilis expansa* SANDBERG & ZIEGLER, 1979 (PIECHA, 2004b), as lower *Clymenia*-Genozone, mainly Ammonoid Zone of *Clymenia laevigata* (MÜNSTER, 1832) (KORN, 2004), and as Lower Entomozoid Ostracod Zone of *Maternella hemisphaerica* (RICHTER, 1848) and *Maternella dichotoma* (PAECKELMANN, 1913) (GROOS-UFFENORDE, 2004). In 2002, a part of his samples was given to me and is now – by permission of the Geologischer Dienst Nordrhein-Westfalen – stored in the Museum of Natural History in Berlin: no. MB.K.7999.1-11. (partly illustrated in Fig. 1), MB.K.8000.1-21. (collection M. PIECHA, 1992).

3 Morphology

The classical and outstanding study of SCHINDEWOLF (1941) with the up to that date most intensive morphological analysis, resulting in the proposal of the suborder Heterocorallia equal in rank to Rugosa and Tabulata, nowadays has also some tragic aspects. His corallum orientation juvenile \rightarrow adult was opposite to the truth; therefore his data on septal ontogenesis could not always be trusted. Even he did not find Famennian heterocorals, though in his times he was the one person who had collected most intensively (especially ammonoids, but always looking for all faunal groups) in Famennian cephalopod limestones of Germany. After their surprising discovery by RÓŻKOWSKA (1969) in Poland, I could find them in four of SCHINDEWOLF's localities: Ebersdorf (Lower Silesia, now Poland: Dzikowiec), Schübelhammer near Köstenhof (Upper Franconia), Wocklum, and his favourite Hönnetal railway cut Oberrödinghausen (Rhenish Mountains).

The incorrect growth direction (with concave or saucered tabulae) was the original opinion up to SCHINDEWOLF (1941): MCCOY (1849, 1851/1855), DUNCAN (1868), KUNTH (1869), STUCKENBERG (1904). A remarkable exception was THOMSON (1883: p. 412, pl. 10 – tabulae domed, excepting pl. 10/18A = *Heterophyllia angulata* DUNCAN, 1868, in opposite orientation). Of special interest is his longitudinal section pl. 10/19B of *Heterophyllia granulata* DUNCAN, 1868, showing in the left upper third an incomplete tabella, the adhesion of which is a doubtless proof of the chosen growth direction (probably the source of HILL's argumentation about tabellae in 1956: p. F326). An ambiguous view offered CARRUTHERS (1909: p. 155 - domed, pl. 1/9 – concave). HILL (1940: p.196–197) proclaimed domed tabulae, with steeply inclined edges, which run together to form a wall between the peripheral ends of the septa (unknown in Rugosa). Unfortunately, her illustrations are too small to show the necessary details, but her argumentation could have been the same as in HILL (1956).

The solution of the ostensible problem is rather simple looking only at those central parts of the longitudinal sections illustrated in KUNTH (1869) and SCHINDEWOLF (1941), where tabulae touch the cut septa. Using their wrong orientation (concave tabulae), the contact always is angular above, well rounded below a tabula, thus indicating the true opposite growth direction, when the last stereoplasmatic thickening of the tabulae changes by gradual transition into the last stereoplasmatic thickening of the septal flanks (KUNTH, 1869: pl. 2/1f; SCHINDEWOLF, 1941: pl. 10/2a, 6, 7, 8).

HILL (1956: p. F325–326, fig. 221, using copied figures from SCHINDEWOLF, 1941), argued with the curvature of tabulae between two septa in transverse sections being concave on the growing surface (as in Rugosa), and with scattered incomplete tabulae [= tabellae], which indicate by their manner of adhesion that the tabulae are domes, not saucers. These interpretations are irrefutable: for sure in pl. 12/1a–b of SCHINDEWOLF (1941) tabulae are sloping down towards the periphery according to the sequence of growth lamellae. The answer of SCHINDEWOLF (1967: p. 143) insisting in his way of orientation, can be replied with his own words, when he (SCHINDEWOLF 1952: p. 172) criticised (correctly) HERITSCH (1941) "zeugt – leider muß es gesagt werden – von mangelnder Vertrautheit mit dem Aufbau der Pterokorallen" ["testifies - sorry to say so - insufficient familiarity with the structure of Rugosa"].

In 1967, I could manage to revise the complete Hetercorallia collection of SCHINDEWOLF (1941) in order to find the correct growth direction in those cases, where two or more transverse sections had been illustrated (WEYER, 1995: p. 108–111). This was possible when parts of the cylindrical corals had remained unsectioned and allowed

to be arranged in proper order with the transverse sections – rather easy using all geometrical details of the interseptal lumina. Then tangential polished surfaces of these remaining parts showed the orientation of tabulae. The result for the 16 specimens figured by SCHINDEWOLF (1941) with two or more transverse sections (see tab. 1, WEYER, 1995): a) 4 specimens unrevised because of absence of remaining parts of the coral; b) 4 specimens need the expected opposite orientation; c) 8 specimens are already correctly arranged (tabulae domed); this "mistake" (*sensu* SCHINDEWOLF, 1941) could be explained perhaps by the fact that his thin sections had been prepared already around 1930, without precise documentation of the preparation ways.

All discussions about domed or concave tabulae were finished, when RóŻKOWSKA (1969: figs. 67–71) discovered the basal attachment in her new Famennian genus *Oligophylloides*. These talons belong to smaller solitary specimens and proof the benthic adult life. The larval corals preferred any hardground object on the sea bottom and even could settle on a living crinoid stem (WEYER, 1995: p. 115, fig. 7/6–9). Perhaps, attachment on soft bottom areas was also possible (Pl. 2/3a). Curious lateral talon outgrowths (perhaps fixing to algae) in a certain height above the basal talon were observed in a Famennian *Mariaephyllia*; they could have given additional support to continue some vertical growth (WEYER, 1997: fig. 1/6, pl. 2/2–4).

The now discovered, nearly complete colonies from Morocco (Pl. 1–4, 6–9, 10/16–17; WEYER 1997: pl. 1) have strong roots formed by excessive growth of their heterotheca, often using additional holdfast around crinoid roots. These are not normal colonies or clons, but always somewhat alike composite colonies (FEDOROWSKI, 1978: p. 180), built by several sexually produced larvae, though different by fusing after settlement and uniting their tissue. The largest available, though incomplete root specimen (Pl. 10/17a–b) contains at least about 16 larvae, but only few of them reached greater height, overgrown by massive protoheterotheca layers or ending as lateral everted calices ("distal cones") on the root surface, and finally only one or two produced the not preserved main part of the colony. Obviously, coloniality in *Oligophylloides* depended from the offer of plenty larvae settled near to each other; perhaps these larvae also should descend from the same parent or hermaphrodite, at least from genetically very close ancestors.

Nowadays the term "colony" often is used for corals in a more specified way (quasicolony, protocolony, pseudocolony, gregarium – after OLIVER (1968) and COATES & OLIVER (1973) mainly FEDOROWSKI (1978, 1979, 1981). The case of the here described *Oligophylloides* colonies affords a new term: **paracolony**, defined by the presence of two or more protocorallites, uniting their soft tissue during growth without any genetic barrier. The term is typified in Heterocorallia by *Oligophylloides maroccanus* sp. nov. (Pl. 10/17a–b). It occurs also, though rarely, in the superorder Rugosa; there it is here typified by the Silurian (Lower Wenlock, Sheinwoodian, top of Upper Visby Marls, Gotland Island, Sweden) *Schlotheimophyllum patellatum* (SCHLOTHEIM, 1820), which is both solitary and paracolonial (Pl. 11/1–2; NEUMAN & KERSHAW 1991: p. 91, fig. 43; MCLEAN & COPPER 1013: pl. 39/1–6). Once, a paracolony among Rugosa was already figured as temporary fusion in solitary corals: two Lower Permian specimens of "*Duplophyllum*" (FEDOROWSKI 1981: p. 434, pl. 27/1a–b, 29/1a–d), now *Paraduplophyllum* FEDOROWSKI, 1987). The few hitherto known paracolonial Palaeozoic corals lived also as solitary forms.

It is well known from Rugosa that the growth form – solitary or colonial – is by no means "automatically" a generic or even specific criterion. There are several intensive studies, which could ascribe only an intraspecific value to this feature (especially in the Lower–Middle Devonian genus *Heliophyllum* HALL in DANA, 1846 – OLIVER, 1997). Such an intraspecific variation is also accepted for Heterocorallia (here proofed in *Oligophylloides* RÓŻKOWSKA, 1969).

All branches of the large colonies are arranged in nearly one plane. This planar structure starts already in the root (Pl. 1/1, 10/17b). Branchlets diminish their diameters discontinuously in smaller or greater steps – therefore older estimations of heterocorallian length up to 0.75-1 m (SCHINDEWOLF 1941: p. 223, 228), connected with a pseudoplanctonic life habit, are now unrealistic. In the specimen of Pl. 10/16, 13 cm height are enough to diminish the corallite diameter from 10 mm to 1.5 mm. Once separated, neighbouring budded branches can touch again and grow together (Pl. 6/1–2); in such rare cases even a *Syringopora*-like, only much thicker connecting bridge may arise (Pl. 9/1).

The wall of Heterocorallia was named heterotheca by SCHINDEWOLF (1941: p. 265). He knew the centrifugal growth direction in spite of his incorrect orientation of tabulae. FEDOROWSKI (1991: p. 22) proposed some useful revisions for special cases in the Lower Carboniferous (radicitheca for *Radiciphyllia* SUGIYAMA, 1984, reticulotheca for *Vassiljukaephyllia* FEDOROWSKI, 1991) and in the Famennian (protoheterotheca for *Oligophylloides* RóżKOWSKA, 1969). The latter differs from a normal heterotheca in the septa, which enter the wall only in its interior parts and are absent in its outer lamellar zone. This was seen as the ancestral phylogenetic step (FEDOROWSKI 1991: p. 49, fig. 16), but the later discovered Eifelian heterocorals (GLINSKI 1998, *Stellaphyllia* FERNÁNDEZ-MARTÍNEZ & TOURNEUR, 2003) possess already the apomorph heterotheca. Sometimes the protoheterotheca of *Oligophylloides* is not massive, but contains few or many open lumina – in the root/talon region (Pl. 1/1; WEYER, 1995: fig. 12/10–15) and in budding branches (Pl. 4/1–7). The right third of Pl. 4/4–5 shows a row of such heterothecal tabulae occurring between two buds, which after separation and increase of diameter become united again by enveloping outer wall layers; this reminds of the principally tabular nature of a heterotheca (therefore WRZOŁEK, 1981 preferred the term tabulotheca).

Among the models of septal insertion and ontogenesis in Heterocorallia, those of SUTHERLAND & FORBES (1981) and FEDOROWSKI (1991) are followed; they revised older ideas of YABE & SUGIYAMA (1940), SCHINDEWOLF (1941), and POTY (1978a, b).

4 Life habits

Surely, Heterocorallia started their life with a planctonic larval phase, probably of rather long duration in view of their nearly cosmopolitic distribution. A pseudoplanctonic post-larval continuation, as suggested by SCHINDEWOLF (1941), is now not longer discussed – the proofs for a maturity as sessile benthos are irrefutable. It was necessary to find any hardground on the sea bottom to become fixed by a talon (solitary growth) or a root (colonial growth), which both occurred. Big complex talons were described by RÓŻKOWSKA (1969: figs. 68, 69); also small simple attachment discs are found in the Famennian of Morocco (comparable to the Rugosa example in RÓŻKOWSKA, 1869: fig. 10F). One case of settling above the sea ground on a living crinoid column is known (WEYER, 1995: fig. 7). Roots of the mainly Famennian *Oligophylloides* are presented here, mostly connected with nearly complete colonies (reaching heights of 20–40 cm); usually they used crinoid roots to support their vertical growth. Similar well preserved colonies have not yet been found in the Lower Carboniferous, but there some signs allow the suspicion that many or most *Hexaphyllia* and *Heterophyllia* also had the ability to grow up either as solitary or as colonial.

Heterocorallia lived in the shallow water photic zone (majority of Viséan–Serpukhovian localities, often together with reefal Rugosa corals, and in mudmounds) and in the cephalopod facies of deeper shelf areas (most Famennian records). Such a differentiation must be estimated very cautiously, as up to now there exist no Givetian–Frasnian and nearly no Tournaisian representatives; the two Eifelian taxa come from shallow marine beds. The hitherto only Uppermost Famennian (Strunian) specimen outside the cephalopod limestones was communicated by VACHARD (1981) and VACHARD & MONTENAT (1996: p. 479, pl. 1/3) from Afghanistan.

The dendroid colonies – here named paracolonies – of *Oligophylloides* possess several protocorallites – they are not clons derived from only one sexually produced larva. Numerous larvae united their tissue without any genetic or immunological barrier, and their power of calcitic skeleton construction to achieve stable higher vertical growth. Perhaps all protocorallite larvae should come from the same parent or from very closely related ancestors. The primary condition was the nearest settlement of many larvae in a narrow area. If larvae attached isolated only in greater distances, their destiny would be the solitary growth, remaining very small. The biggest, but even still incomplete available root (Pl. 10/17a–b) contains ca. 16 protocorallites. The greater part of them was overgrown by enormous thick protoheterothecal layers; only few could continue to grow as highly everted calices on the flanks of the root, and only one, two or three strongest produced the higher branches of the paracolony.

One reason, why heterocorals are normally found only as smaller fragments, could be their soft parts, covering extended parts of the skeleton and not retractile into a protecting calice, and thus being easily taken food for predators, grazing through the coral colonies. Their presence is indicated by the case of a specimen of an Upper Viséan *Hexaphyllia marginata* (FLEMING, 1828) with completely damaged dark median line in the central six septa (attacked by a probably "fish"-like enemy, when these septa still formed the top of the highly everted calice or distal cone). After being beaten but not eaten (perhaps because of any poison), the coral survived and could repair the damage by the usual stereoplasmatic thickening of the septal apparatus (illustrated in WEYER, 1995: p. 109, fig. 2). Other predators might have acquired immunity against coral poisons and fed systematically in Heterocorallia thickets, similar to some parrot-fishes in recent Scleractinia reefs.

5 Epibionts

Heterocorallia lived in the shallow water photic zone and deep shelf areas of the Tafilalt platform (limestones, marls, pelites); they are absent in the deeper facies of the Maider basin. Similar circumstances characterize the Famennian of Germany, where heterocorals could not be found in the deeper "cypridinic (entomozoid) shale" facies of e.g. the Bohlen section near Saalfeld (Thuringia).

There the most common epibiont on Crinoida was the auloporid Tabulata coral *Cladochonus* MCCOY, 1847, which did not enter the photic zone of shallow shelfs. Five rare cases of *Cladochonus* encrusting also *Oligophylloides* were observed, two of them sectioned (Fig. 3a–c, Pl. 4/1–2); this had happened during life time, as indicated by the typical holdfast ring fixed around the coral in vertical position. The generic determination is affirmed by calicular fragments of tobacco-pipe configuration, often found in sediment and thin sections around the heterocorals. Such an attached calice is seen in Pl. 4/1, bearing in its base the typical reticulate tissue (well figured by HILL & SMYTH, 1938).

Also during life time, another (favositid) Tabulata coral determined as *Sutherlandia*? sp. had settled on *Oligophylloides* (Fig. 4b). The genus *Sutherlandia* COCKE & BOWSHER, 1968 is a widespread Lower–Upper Carboniferous crinoidal epibiont, which includes the classical species *Emmonsia parasitica* (PHILLIPS, 1836) and

Pleurodictyum dechenianum KAYSER, 1882 (WEYER, 1972). Rare Uppermost Famennian specimens were collected from the *Wocklumeria* Genozone in the Bohlen section of Saalfeld (Thuringia, Germany).



Fig. 4: *Oligophylloides* sp., Middle Famennian, conodont zone of *Scaphignathus velifer* HELMS, 1959 (lower part), locality Seheb El Rhassal (central Tafilalt), collection R.T. BECKER 1999 (unpublished section, bed 9e-top), no. MB.K.2426.

a) small branch fragment with two budding corallites, x 4;

b) transverse thin section at proximal end, x 15, with a spherical epibiont *Sutherlandia*? sp. (squamulate favositid).

Older species as the mid-Famennian one of Fig. 4b still offer problems to separate them precisely from mainly Lower–Middle Devonian taxa, also spherical and squamulate epibionts on Crinoida, as *Emmonsia* MILNE-EDWARDS & HAIME, 1851, or *Hamarilopora* LEMAîTRE, 1956.

Fig. 5 presents borings in the big basal root part of an *Oligophylloides* paracolony. They were produced by an unknown animal, surely during life times, because the small borings of uniform shape are arranged in different density on all sides of the vertically positioned root.

COSSEY (1997: p. 1055) had mentioned circum-corallite encrustations by rhodophyte algae.



Fig. 5: Oligophylloides maroccanus sp. nov., Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, no. MB.K.400.5.; characteristic borings of an unknown animal on the flanks of a big paracolonial root (see Pl. 10/17a), x 2.5.

Such epibionts support the views of WRZOŁEK (1981, 1993a) and COSSEY (1997) that the heterocorallian skeleton was only partially covered by soft tissue, which during upward growth left the older proximal protoheterotheca. There encrusting animals or plants were not disturbed and enveloped by outer heterothecal layers, as seen by WRZOŁEK (1981: p. 516, pl. 49/2) for the distal part. CHWIEDUK (2001: p. 1206) assumed a complete cover by soft parts for *Oligophylloides*. I would agree with the estimated amount of external polyp tissue lobes in the reconstructions of COSSEY (1997: figs. 3, 5, 12, 13).

6 Taxonomy

The following abbreviations are used: CS transverse (cross) section, LS longitudinal section, TS thin section, P peel, R remaining coral part. Serial transverse sections of all illustrations are correctly oriented to each other.

Class Anthozoa EHRENBERG, 1834 Subclass Zoantharia BLAINVILLE, 1830 Superorder Heterocorallia SCHINDEWOLF, 1941

This taxon is classified of equal rank as all other Palaeozoic superorders – Tabulata MILNE-EDWARDS & HAIME, 1850, Heliolitida FRECH, 1897, Kilbuchophyllida SCRUTTON & CLARKSON, 1991, Rugosa MILNE-EDWARDS & HAIME, 1850. The Calyxcorallia FEDOROWSKI, 1991, are not accepted, being normal Rugosa (WRZOŁEK, 1993b; POTY & XU, 1997; BERKOWSKI, 1997, 2001, 2002); then Dividocorallia FEDOROWSKI, 1991, are not longer necessary,

For a long period, Heterocorallia comprised only one family Heterophylliidae DYBOWSKI, 1873 (up to HILL, 1981). Six new family/subfamily taxa were proposed mostly in Chinese literature, without intensive morphological and ontogenetic studies: two do not belong to the superorder (Tetraphylliidae YOH, JIN, ZHEN & XIE, 1984 = Rugosa;

Dichophylliinae LIN, HUANG, WU, PENG & QIU, 1992 = Bryozoa), three are synonyms of Heterophylliidae (Crepidophylliidae YU, LIN, SHI, HUANG & YU, 1983; Hexaphylliidae HUANG & MA, 1986; Fossaphylliidae LIN, HUANG, WU, PENG & QIU, 1992), and only one (Longlinophylliidae LIN & WU, 1985) was accepted by FEDOROWSKI (1991). Finally the Radiciphylliidae FEDOROWSKI, 1991, followed.

FEDOROWSKI (1991: p. 52, 63, fig. 7) subdivided the Heterocorallia (as order) into two suborders, the Devonian Tetraphylliina FEDOROWSKI, 1991, and the Lower Carboniferous Heterocorallia SCHINDEWOLF, 1941, on the basis of symmetrical or asymmetrical arranged septa (and of course not happy to be forced by the International Code of Zoological Nomenclature to use according to his taxonomic evaluation just the unsure Tetraphylliidae name as base for his new suborder). Symmetrical arranged septa are not always visible in the here studied *Oligophylloides* (e.g. Pl. 5/2a–c). Besides, a sequence of serial sections to present the ontogenetic septal development should be correctly orientated in order to be reliable and trusted. This is not the case for *Mariaephyllia famenniana* RÓŻKOWSKA, 1969 in FEDOROWSKI (1991: e.g. figs. 18/1e–1f are horizontal mirror images; or fig. 19/2c–2d, where the latter must be rotated 45° against the clock and horizontally mirrored; further cases can be judged on only during the preparation process, especially in view of "septal shifting" and "rearrangement of the septal apparatus", well illustrated in CHWIEDUK, 2001: p. 1215). Thus, for the moment it seems better to avoid a separation of *Oligophylloides* from *Heterophyllia* at the family level, reminding the nearly complete vacuum of Heterocorallia during the Tournaisian after the global Hangenberg Event, where the genus had survived – *Heterophyllia* sp. of VACHARD (1988: pl. 2/1), re-illustrated as *Oligophylloides* sp. in WEYER (1995: fig. 5).

Family Heterophylliidaa DYBOWSKI, 1873

Genus Oligophylloides Ròżkowska, 1969

<u>Type species</u>: *Oligophylloides pachythecus* RÒŻKOWSKA, 1969, Upper Famennian, *Bispathodus costatus* Zone *sensu* ZIEGLER (1962), bed 1 of Gałęzice, Holy Cross Mountains, Poland (according to WOŁSKA, 1967: tab. 4 with *Palmatolepis gonioclymeniae* MÜLLER, 1956 = *Wocklumeria* Genozone).

<u>Species</u>: Discrimination of species and their precise diagnoses within the genus are problematic after the study of CHWIEDUK (2001), who synonymized *Oligophylloides pachythecus pentagonus* RóżKOWSKA, 1969, and *Oligophylloides tenuicinctus* RóżKOWSKA, 1969, with the type species. Also the here published colonies support this: corallite diameter and thickness of the heterotheca alone are not longer suitable specific criterions. The diameter of the tabularium seems to be more stable. *Oligophylloides parvulus* WEYER, 1995, could probably be only extreme distal fragments of *Oligophylloides pachythecus*, when conpared with the measurements of CHWIEDUK (2001: fig. 17). *Oligophylloides weyeri* BERKOWSKI, 2002, differs by its more heterothecal wall (completely crossed by septa) and perhaps should be excluded from the genus.

<u>Stratigraphic range</u>: At present, *Oligophylloides* is known in Middle Famennian – Lower Tournaisian times, from the Lower *Palmatolepis marginifera* Zone (upper *Cheiloceras* Genozone) to the *Siphonodella sulcata* Zone (Lower *Gattendorfia* Genozone) in Poland, Germany, France, and Morocco. A more extended geographical distribution can be expected especially in Europa, Asia, and North Africa.

Oligophylloides maroccanus sp. nov. Fig. 3, 5–6, 7/2–3, 9, Pl. 1–2, 3/1, 4–9, 10/16–17

1997 Oligophylloides sp. – WEYER: p. 146, pl. 1/1.

<u>Holotype</u>: specimen no. MB.K.400.1. (Fig. 9, Pl. 1/1–3, 2/2) = 5CS (4TS, 1P), 5 R, collection D. WEYER, 1995.

Type locality: Bou Ifarherioun south of Rissani, Tafilalt, Anti-Atlas, Morocco.

Type horizon: Gonioclymenia Limestone (Clymenia Genozone).

<u>Materials</u>: A – locality Bou Ifarherioun – 136 specimens (mostly fragmented branches of paracolonies), from loose pebbles of *Gonioclymenia* Limestone, Coll. D. WEYER, 1995: no. MB.K.400.1-13. (illustrated paratypes), MB.K.8002.1-21. (paratypes, cut, not thin-sectioned), MB.K.8003.1-102. (fragmented isolated, often distal



branches, cut, not thin-sectioned). B – locality Djebel Amre – 7 paracolonies from *Gonioclymenia* Limestone, no. MB.K.8001.1-3. (1 Collection D. WEYER, 2006, 2–3 bought in fossil shop 2006, 2007), MB.K.8001.4-6. (3 fragmentary specimens not sectioned and not illustrated, coll. D. WEYER, 2006, 2 of them with root region), and no. FG.633. (bought in fossil shop 2009).

<u>Diagnosis</u>: Solitary and mainly colonial growth, small attachment talon or big root (built by extremely thickened heterotheca layers, often using crinoid support, with more than one to many protocorallites), branching by intratentacular bifurcate budding; planar paracolonies up to 20-40 cm height, proximal corallites starting with 10-20 mm diameter, which diminishes distally and discontinuously to 1 mm; tabularium with 0.4-0.7 mm diameter, small in relation to the thick protoheterotheca; 8-12 septa (3 generations).

<u>Description</u>: The majority of collected specimens are branch fragments, sometimes with a bud, thus indicating that they represent colonies. Only one definitely solitary coral is available (Pl. 2/3a–b), characterized by its special protoheterothecal talon without visible hardground. Unable to construct a paracolony because no further larvae had settled nearby, this specimen reached only 2.5 mm diameter and perhaps about 1 cm height. Its small tabularium diameter (Pl. 2/3a – 0.68 mm) is conformable to larger colonial paratypes.

Fig. 6: Oligophylloides maroccanus sp. nov., Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, no. MB.K.400.13.

1a, b, c – series of transverse thin sections, x 12, primary corallite (in SE, and distal 1c) with 8 septa, bud with 9 septa.

2 – isolated distal transverse section with 8 septa (diameter 1,5 mm), x 12.

Nearly complete paracolonies (Pl. 7–10) found for the first time are dendroid and planar (similar to some sea pens), as sessile benthos fixed by a rather massive root of excessive protoheterothecal layers (mostly massive, rarely as thinner or thicker tabulae – Pl. 1/1, 10/17b). Sometimes the root includes crinoid columns (Pl. 10/16); *in situ* observations have demonstrated a repeated settlement on crinoidal roots providing additional support for vertical growth of the dichotomous branches, which amounts to 20–40 cm. The largest, still incomplete root specimen (Pl. 10/17b) includes 16 protocorallites. Branches become slowly or discontinuously thinner; often a bud starts much smaller than the parent branch. Budding proceeds usually towards divergence of the branches, though sometimes also narrowing leads to secondary touches and connections (Pl. 6/1–2). Preserved most distal branches reached minimum corallite diameters of 1.5 mm /Pl. 7/1), 2.0 mm (Pl. 8/1), 2.5 mm (Pl. 9/1), and 1.3 mm (Pl. 10/16). Rare isolated, even smaller branch fragments (Pl. 5/3–4) of 0.7 mm diameter could already come near the distal cone (or highly everted calice) and differ here in the wall, being not a protoheterotheca, but a typical heterotheca fully traversed by the septa.

During budding, the parent corallite and the new one have connected tabularia (Pl. 3/1b, 5/1b–c), against the opinion of CHWIEDUK (2001: p. 1191). This means that longitudinal sections in such a "budding area", with a strong dividing wall (as in PIECHA, 2004a: pl. 2/7a–b, CHWIEDUK 2001: pl. 2/2a, or here Fig. 1/1–6) indicate rather the settling of another larva than an asexual budding process. Many transverse sections offer 8 septa = 2 generations (*sensu* FEDOROWSKI, 1991). A complete 3^{rd} generation was never observed. Axial septal connections are identical in the series of Pl. 4/1–7; in the sequence of Pl. 5/2a–c they change remarkably.

The thick protoheterotheca – comparable to continuous uninterrupted stereoplasma layers in Rugosa – mostly is massive. Exceptions occur in talons and roots (similar to fig. 68F in RóżKowsKA, 1969) and between still connected buds after longer growth periods (Pl. 4/1–6). Such tabulae within the protoheterotheca reflect a quite economic calcite secretion to achieve a stable skeleton. The wall in the colonial branches was protected against borings by the external soft parts, which during growth certainly had left the proximal parts of the skeleton, thus allowing settlements of epibionts and boring organisms.

Discussion: At present, there are now (after the synonymy proposed by CHWIEDUK, 2001) three *Oligophylloides* species, which should be compared and diffentiated. The long-lasting corallite diameter of about 10 mm in main branches (Pl. 6/1) is about double size (*pachythecus*) or more (*parvulus*, *weyeri*) than in the hitherto known *Oligophylloides*. Contrary, the tabularium diameter of the new species is distinctly less than in *Oligophylloides pachythecus* RóżKOWSKA, 1969 (CHWIEDUK, 2001: p. 1204, fig. 17). *Oligophylloides parvulus* WEYER, 1995, can no longer be seen as a valid species; it was based on extreme distal fragments of (surely) a colony and their corallite diameters, which are now obsolete criteria. *Oligophylloides weyeri* BERKOWSKI, 2002, has a much smaller tabularium (0.2 mm), and its wall is a perfect heterotheca , not a protoheterotheca. The mostly colonial nature of the genus is now evident; thus a lot of hitherto found fragments might allow in future only generic, but no longer specific determinations.

Occurrence: Only known from two localities in the Upper Famennian *Gonioclymenia* Limestone (Bou Ifarherioun and Jebel Amre, Tafilalt, Anti-Atlas, Morocco).

Oligophylloides sp. Fig. 2, 7/1a–d, 8/1–3, Pl. 3/2a–c, 10/1–15

<u>Material</u>: A – 64 smaller and larger branch fragments of perhaps(?) one destroyed colony, found in ca. 1 m² of clay bed no. 114, upper *Clymenia* Genozone, Ouidane Chebbi section, 43 km ESE Erfoud, MB.K.2425.1-18. (illustrated specimens), MB.K.2425.19. (46 branch fragments, not thin-sectioned), collection D. WEYER, 1995. B – 2 specimens from the *Gonioclymenia* Limestone of Bou Ifarherioun locality (loose pebbles), MB.K.8004.1. (6CS, 1LS), MB.K.8004.2. (5CS, 1LS), collection D. WEYER, 1995.

<u>Discussion</u>: The population from the Ouidane Chebbi section (Fig. 2, 8/1–3, Pl. 10/1–15) could represent either distal parts of *Oligophylloides maroccanus* sp. nov., or might be identified as *Oligophylloides pachythecus* RÓŻKOWSKA, 1969 (in the broader sense of CHWIEDUK, 2001). The typical thicker proximal corallite branches (diameter 10–15 mm) of the new species are absent. The tabularium diameters (1.0–1.1 mm) are larger than in the new species (there: 0.4–0.7, mostly 0.5–0.6 mm).

Modern ammonoid studies (KORN et al., 2014; KLEIN & KORN, 2014) demonstrated that Moroccan goniatite and clymeniid species mostly differ from the mid-European taxa, which earlier were thought to be identical; now a clear faunal provincialism becomes evident. This might occur also in corals, but can not be verified, as Rugosa, Tabulata, and Heterocorallia offer much less suitable skeleton features – they are described as pure

palaeontological morphospecies, which could comprise quite different biological species, defined in addition by soft part, behaviour, and genetic criteria.



Fig. 7: 1 - Oligophylloides sp., Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, no. MB.K.8004.2., x 12. a, b, c, d distal branch fragment (diameter 2.7-2.5 mm, 10–11 septa) in transverse and median longitudinal thin sections. 2 & 3 -Oligophylloides maroccanus sp. nov., Upper Famennian, Gonioclymenia Limestone (loose pebbles), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, 2 transverse thin section of a short branch fragment (diameter 4.2 mm, 10 septa), no. MB.K.400.12., x 12; 3 - isolated transverse thin section (diameter 2.7 mm, 11 septa), no. MB.K.400.10. (in section 4), the originally circular tabularium appears longdue to some stereoplasmatic oval thickening of tabulae, x 20.

(see opposite page)

Fig. 8: Oligophylloides sp., Upper Famennian, upper Clymenia Genozone, Ouidane Chebbi section 43 km ESE of Erfoud (bed 114), collection D. WEYER 1995, three cylindrical fragments of different diameters. 1a, b, c, d, e, f- thicker branch (length 37 mm, diameter 6.0-5.7 mm, 12 septa), no. MB.K.2425.17; a - basal transverse thin section, x 10; b - median longitudinal thin section, x 10; c - top transverse thin section, x10; d - drawing of 1b, x 5; e - septa of 1a, x 20; f - septa of 1c, x 20. 2a, b, c - mid-sized branch (length 22 mm, diameter 4.5 mm, 10 septa), no. MB.K.2425.16.; a - top transverse thin section, x 10; b – median longitudinal thin section, x10; c - septa of 2a, x 20. 3a, b, c,thinner branch (length 25 mm. d – diameter 3.2 mm, 12 septa), no MB.K.2425.18.; a - basal transverse thin section, x 10; b – median longitudinal thin section, x 10; c - top transverse thin section, x 10; d – septa of 3a, x 20.

The two specimens from Bou Ifarherioun locality (Fig. 7/1a–d, Pl. 3/2a–c, the latter of solitary growth) are found together with many *Oligophylloides maroccanus* sp. nov., but differ by their wider tabularium (diameter 0.9–1.1 mm) and somewhat more densely spaced tabulae. For the moment, an open nomenclature is preferred in view of the still unsure way how to define species within the genus.



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Fig. 9: Sketch of the paracolony, holotype of *Oligophylloides maroccanus* sp. nov. (no. MB.K.400.1.), indicating the position of the prepared transverse sections, x 1. These demonstrate the presence of further branches inside the sediment.



Plate 1

Oligophylloides maroccanus sp. nov., holotype, no. MB.K.400.1., x 0.75; Upper Famennian, *Gonioclymenia* Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995 (already figured in WEYER, 1997: pl. 1/1).

Fig. 1–3: Transverse thin sections in the root part of a paracolony (no. 2, 4, 5 in Fig. 9), x 3 (enlarged transverse section of left corallite in Fig. 2 see Pl. 2/2).



Oligophylloides maroccanus sp. nov., Upper Famennian, *Gonioclymenia* Limestone (loose pebbles), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995;

- Fig. 1: a, b, c, d Budding branch of a paratype, no. MB.K.400.4. Serial transverse thin sections (no. 1, 3, 4, 6), all with 8 septa, x 5.
- Fig. 2: Holotype, no. MB.K.400.1. Left corallite from Pl. 1/2 (diameter 10.4 mm, 8 septa), x 8 (further photos see Pl. 1/1–3).
- Fig. 3: a, b small solitary specimen, no. MB.K.400.6. a median longitudinal section of basal part (broader talon without basal plate), x 10; b transverse thin section of the uppermost preserved part, with 15 septa, x 15.



- Fig. 1: Oligophylloides maroccanus sp. nov., paratype no. MB.K.400.7., x 0.75; Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, budding branch fragment.
 a transverse thin section (no. 1, 8 septa), x 8; b longitudinal thin section (no. 2a), x 10; c transverse thin section (no. 3, 8 septa), x 8.
- Fig. 2: Oligophylloides sp., Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995, no. MB.K.8004.1. Small solitary specimen.

a - basal transverse thin section (11 septa) with talon, x 12; b - top transverse thin section (20 septa), x 15; c - middle longitudinal thin section, x 12.



Figs. 1–7: Oligophylloides maroccanus sp. nov., paratype, no. MB.K.400.8.; Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995; serial sections (always with only 8 septa) of a budding branch fragment (length ca. 80 mm), x 8. 1 & 2 – older transverse thin sections, with a Cladochonus sp. attachment ring and calice as epibiont, bearing in 1 an undeterminable coral as second epibiont; 3 & 4 – median longitudinal thin sections showing at first the tabulae within the heterotheca between the two buds re-united again by later wall layers (the tiny tabularia are only occasionally cutted); 5, 6, 7 – younger transverse sections with the finally separated bud.



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Oligophylloides maroccanus sp. nov., paratypes, x 0.75; Upper Famennian, *Gonioclymenia* Limestone (loose pebbles), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995.

- Fig. 1a-e: Paratype, no. MB.K.400.9. Serial transverse thin sections of a branch fragment budding twice, x 6; the primary corallite has 9 septa, its first but has 10 septa; the tabularia cutted in 1b-c indicate a direct connection of the two corallites without dividing wall.
- Fig. 2–6: Small distal, mostly isolated transverse sections, found in five serial thin sections, no. MB.K.400.10. 2a, b, c – corallite with 9 septa, x 50 (in section 3, 4, 5), diameter diminishes towards the top of the distal cone (a – 1.01 mm, b – 0.97 mm, c – 0.94 mm).
 - 3-8-septal stage at 0.7 mm diameter , x 50 (in section 5).
 - 4 11-septal stage at 0.7 mm diameter, x 50 (in section 3).
 - 5-10-septal stage at diameter 1.5 mm (in thin section 2).
 - 6-10-septal stage at 2.04 mm diameter (in thin section 1).



Oligophylloides maroccanus sp. nov., paratypes, x 0.75; Upper Famennian, *Gonioclymenia* Limestone (loose pebbles), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995; arrows mark secondary contacts of neighbouring branches, which have been freed from the hard limestone sediment by careful preparation.

- Fig. 1: No. MB.K.400.2. (fragment of a paracolony).
- Fig. 2: No. MB.K.400.3. (fragment of a paracolony).



Fig. 1: Oligophylloides maroccanus sp. nov., paratype, paracolony, no. MB.K.8001.3., x 0.75; Upper Famennian, Gonioclymenia Limestone, quarry Djebel Amre WSW of Rissani, Tafilalt, Morocco; bought 2007 in a fossil shop of Erfoud.



Fig. 1: Oligophylloides maroccanus sp. nov., paratype, paracolony, no. FG663. (Geological Institute, Freiberg University, Freiberg/Saxony), x 0.75; Upper Famennian, Gonioclymenia Limestone, quarry Djebel Amre WSW of Rissani, Tafilalt, Morocco; bought 2009 in a fossil shop of Erfoud.



Fig. 1: Oligophylloides maroccanus sp. nov., paratype, paracolony, no. MB.K.8001.1., x 0.75; Upper Famennian, Gonioclymenia Limestone, quarry Djebel Amre WSW of Rissani, Tafilalt, Morocco; collection D. WEYER 2006.



- Figs. 1–15: Oligophylloides sp., paracolonial fragments from largest to smallest diameter (13–15 with budding), no. MB.K.2425.1-15., x 1; Upper Famennian, upper Clymenia Genozone, Ouidane Chebbi section 43 km ESE of Erfoud, bed 114; collection D. WEYER 1995 (thin section of Fig. 13 see text-Fig. 2).
- Fig. 16: *Oligophylloides maroccanus* sp. nov., paratype, small paracolony, no. MB.K.8001.2., x 0.75; Upper Famennian, *Gonioclymenia* Limestone, quarry Djebel Amre WSW of Rissani, Tafilalt, Morocco; bought 2006 in a fossil shop of Erfoud.
- Fig. 17: Oligophylloides maroccanus sp. nov., paratype, no. MB.K.400.5., Upper Famennian, Gonioclymenia Limestone (loose pebble), Bou Ifarherioun 15 km S of Rissani, Tafilalt, Morocco; collection D. WEYER 1995. a root portion of a big paracolony, x 0.75; b basal transverse section (peel), x 1.5.



Schlotheimophyllum patellatum (SCHLOTHEIM, 1820), Lower Wenlock (Sheinwoodian, top of Upper Visby Marls), cliff Ireviken, Gotland Island, Sweden, collection F. TROSTHEIDE 1997 (still in his private collection). Protocorallites marked by an X.

- Fig. 1: Paracolony of two corallites, no. 4089, x 1; a upper view; b lower view.
- Fig. 2: Paracolony of three corallites, no. 2180, x 1; a upper view; b lower view.



psf-Paläontologie, Stratigraphie, Fazies

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