Transverse division in a Miocene scleractinian coral

JAROSŁAW STOLARSKI

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Specimens of *'Discotrochus' duncani*, at various stages of transverse division occur abundantly in the Miocene Korytnica clays in the Holy Cross Mountains, Poland. This mode of asexual reproduction probably predominated in the studied population, and is here put forward as an adaptation for rapid colonization of soft bottoms. *Truncatocyathus* gen. n. is proposed to include *'D.' duncani*.

Key words: asexual reproduction, transverse division, Scleractinia, Tertiary.

Jarosław Stolarski, Instytut Paleobiologii PAN, Aleja Żwirki i Wigury 93, 02-089 Warszawa, Poland.

Introduction

Transverse division is a common mode of asexual reproduction among skeletonless coelenterates. Several sea-anemones [*Goniactinia prolifera* (Blockman & Hilger 1888), *Aiptasia couchii* (Stephenson 1935) and *Anthopleura stallula* (Schmidt 1970)] reproduce in this way (see Chia 1976). Strobilation, a form of transverse division, is also the usual mode of reproduction in many scyphozoans (e.g. *Aurelia*) and hydrozoans. This form of clonopary (*sensu* Rosen 1986) occurs also among skeletal anthozoans (division of the soft body must be associated with division of the skeleton).

In Scleractinia transverse division has been observed at the monostomatous stage only, even if the adult stages of the descendant individuals are polystomatous (for example in *Polyphyllia*, *Zoopilus*, *Herpolitha*; see Fig. 7; Wells 1966, Hoeksema 1989). Transversely dividing forms are known almost exclusively in the suborder Caryophylliina (9 genera in 3 families, i.e. about 8 percent of the whole number of the genera and subgenera in the suborder) and Fungiina (8 out of 11 genera of the family Fungiidae (*sensu* Hoeksema 1989 *non* Wells 1956), i.e. about 7 percent.

In the suborder Dendrophylliina (with 26 genera/subgenera), only members of *Endopachys* divide transversely. Within the suborder Faviina, which includes the highest number of scleractinian genera and subgenera (i.e. 191), solitary forms are rare and these do not reproduce asexually by transverse division. The proximal parts of coralla are separated from the living polyp by well developed endothecal dissepiments, so the soft tissue cannot penetrate the skeleton and dissolve it. *Pleuropodia* from the Eocene of Australia, which possibly divides transversely, resembles faviid Rhizangiidae in its calice structure (see Dennant 1903; Vaughan & Wells 1943; Wells 1956) but other morphological features suggest rather its caryophylliid origin. The genus *Dunocyathus* was previously also assigned to Rhizangiidae (=Astrangiidae; see Vaughan & Wells 1943) but later it was placed in the Caryophylliinae (see Wells 1956).

There is remarkably little evidence for transverse division in Rugosa, the majority of which are represented by solitary taxa. Members of four genera are supposed to divide transversely: the cyathaxoniids *Gymnaxon*, *Duncanella* and *Petronella* and the hapsiphyllid *Adradosia* (see Birenheide & Soto 1977, Weyer 1982). These are forms that lack a wall in the apical parts of the skeleton (like in the just detached individuals of transversely dividing scleractinians). In the lumen of their calices, transverse partitions are relatively rare. Transverse division in other Rugosa was thus probably impossible because the proximal parts of the skeleton were closed off by dissepiments and tabulae (as in the solitary faviids).

More than 5000 excellently preserved specimens of '*Discotrochus*' *duncani* Reuss 1871 (the type species of *Truncatocyathus* gen. n.) have been collected from the Miocene (Badenian) Korytnica clays in the Holy Cross Mountains (localities: Korytnica-Las, Korytnica-Plebania and Góra Łysa; see Stolarski 1992). In the present paper the phenomenon of transverse division in this species will be described and discussed.

The collection is housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL).

The Korytnica turbinoliid

Unseparated specimens.– About 3 percent of the examined specimens of *Truncatocyathus duncani* are represented by parent and descendant forms joined together (Figs 1A, B, E, 2B, C). Usually they are parent-descendant pairs but some specimens are joined in triads (Fig. 6D, 7; Stolarski 1991: Pl. 8: 10). The number of radial elements in descendant individuals is always inherited from their parents. The diameter of a descendant is almost invariably the same as that of parent individuals (occasionally, diameter of a descendant can be slightly smaller than that of a parent specimen e.g. Fig. 1B, E).

The majority of non-detached forms possess intercostal perforations (about 0.1-0.2 mm in diameter) regularly distributed in a horizontal plane

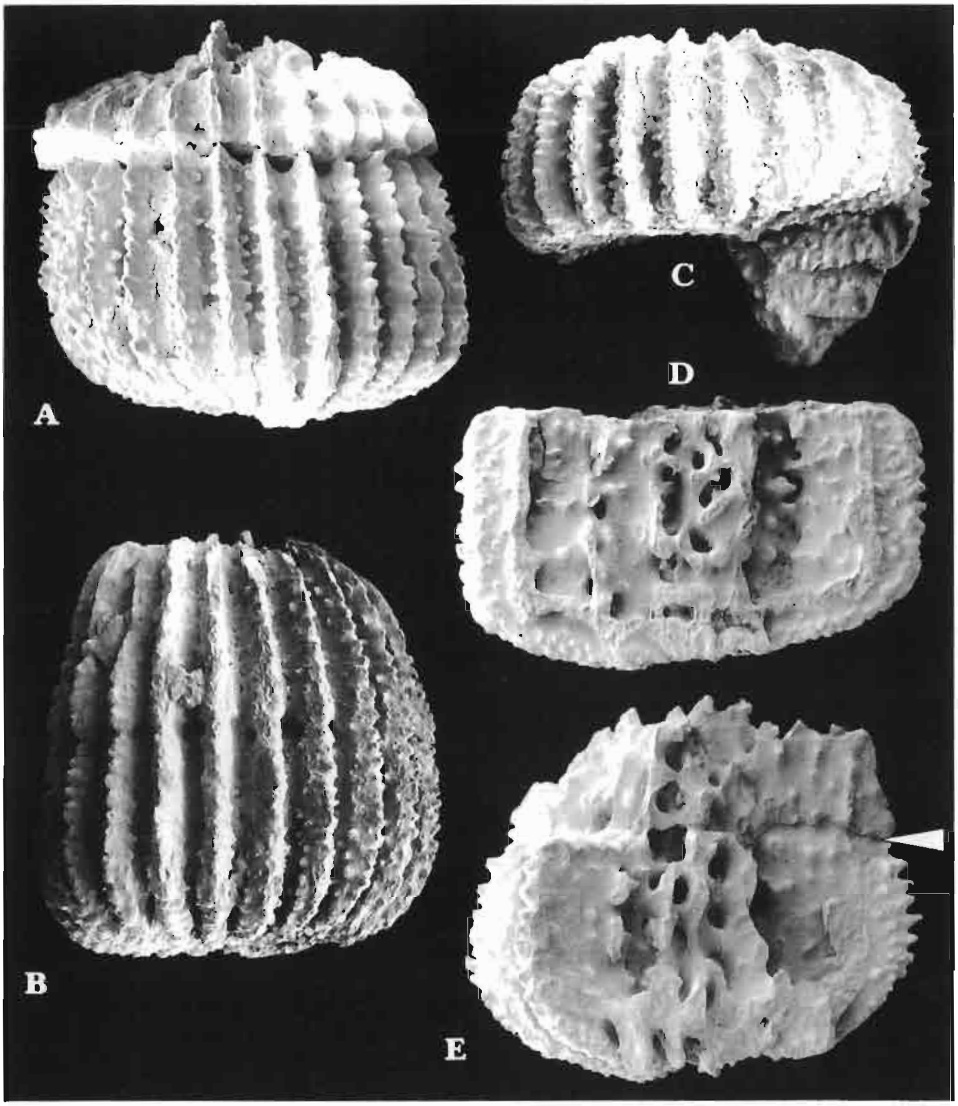


Fig. 1. Specimens of *Truncatocyathus duncani* (Reuss 1871) from the Miocene (Badenian) clays of Korytnica, Holy Cross Mts, Poland. ☐A, B. Unseparated parent/descendant pairs. Note intercostal perforations in the plane of separation and different heights of descendant forms (ZPAL H.IX/512 and ZPAL H.IX/513 respectively). ☐C. Imperfectly separated descendant form (ZPAL H.IX/514). ☐D. Parent form with flat distal side (ZPAL H.IX/515). ☐E. Unseparated parent/descendant pair with a furrow (arrowed) in a plane of separation crossing the skeleton (ZPAL H.IX/516). All × 23.

of separation (Fig. 1A, B). In broken sections of joined parent-descendant pairs there can be found both forms with continuous and forms with discontinuous septal blades in the separation zone. On the lateral surfaces of radial elements continuing from parent to descendant individuals, there is a linear (sometimes fan-like) pattern in the distribution of granular (or menianae-like) ornamentation (Fig. 1E). Some furrows on the faces of the radial elements can be seen in the plane of separation (Fig. 1E arrow). In other specimens the septa are interrupted, particularly in the axial zone (Fig. 2B, C), and the junction between the parent and descendant skeletons is kept only in the costal region.

Descendant individuals.– About 2 percent of specimens almost completely lack any wall in the proximal part of the skeleton. Generally, they have fully developed distal structures of the corallum (arched septa, pali etc.). An incomplete development of the proximal part of detached anthocyathi is known in Recent Scleractinia (e.g. in *Truncatoflabellum, Truncatoguynia, Placotrochides* - see Cairns 1989b) and possibly also in Rugosa (Birenheide & Soto 1977, Weyer 1982). In corals having no external soft tissue cover of the skeleton, like the flabellids, the detachment scar remains unchanged throughout the rest of the coral's life (Fig. 7) or becomes corroded. The empty intercostal spaces are filled (from the inside of the corallum) with stereome. In forms with the corallum fully invested by the polyp (e.g. *Fungia*) a detachment scar can be completely masked by new skeletal elements (see Wells 1966; Hoeksema 1989). The Korytnica species, like other Turbinoliinae, belong to the latter category of corals (compare Vaughan & Wells 1943).

In completion of the proximal part of the skeleton (Fig. 3), two main phases can be distinguished:

(1) Formation of the basal wall. The specimens just after division usually have no basal skeleton (Fig. 3A). Successively, from the sides of the septa and the column wall a very thin, film-like basal wall is developed (Fig. 3B-D). A granulation (Fig. 4D), as well as polygonal ridges (about 10-20 μm in diameter), characteristic of newly formed surfaces of the coral skeleton, then appear over its external surface (Fig. 4A, B; see also Sorauf & Podoff 1977: Pl. 2: 5, 6).

After filling the intercostal gaps (sometimes somewhat earlier) new skeletal material, costae (Fig. 3C, D), is deposited on the proximal radial elements.

(2) Formation of proximal costae. The proximal, cut edges of the septa are continuous with newly forming costae. At first, along the edges, narrow lists appear (Fig. 3C, D). Their structure is often modular (Fig. 4C). The costal modules represent trabeculae growing in the opposite direction to those of the septa and their diameter is equal to that of the septal ones (about 20 μm). The height and width of costae progressively increases. Having reached a height of about 0.2 mm, the costae grow almost exclusively in width. Ornamentation of the proximal costae is granular. At the incipient stage of ornamentation development, granulae are relatively rare and thick (Fig. 3E, F), while at the mature stage they are numerous and minute (Fig. 3G, H).

Coralla with atypically developed proximal sides, in which a very thin, often incomplete, basal wall with empty intercostal spaces coexists with

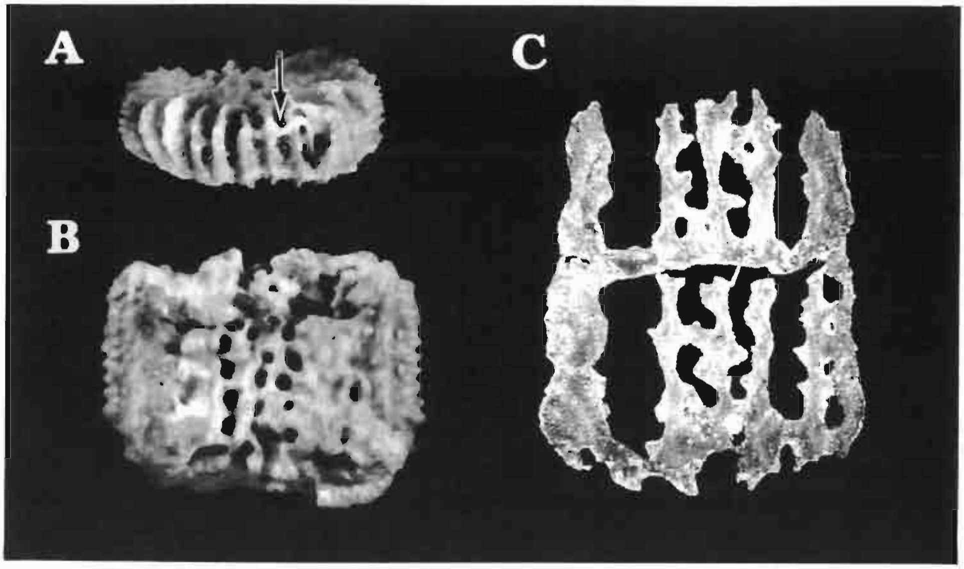


Fig. 2. *Truncatocyathus duncani* (Reuss 1871) from the Badenian of Korytnica. ❑A. Specimen (ZPAL H.IX/139) with incompletely developed synapticular column wall. Arrowed synapticular connections between septa. ❑B. Undetached parent/descendant pair ZPAL H.IX/159. ❑C. Longitudinal section of parent/descendant pair (ZPAL H.IX/38). In this case the parent individual probably died following the formation of the basal wall of the descendant individual. All × 15.

large, fully developed costae on the lateral side of corallum (Fig. 3I), are relatively rare. Such a difference in the development of wall and septa could be caused by a relatively long retention of descendant individuals on the parental stock. They would have had much more time to develop large, fully ornamented lateral costae than the basal wall. Another possible explanation is that the skeleton of a descendant was not entirely covered with the soft tissue and therefore the exposed proximal parts of the skeleton could not be completed after division. In this case, only the ectoderm inside the corallum could have been responsible for filling up the intercostal gaps.

The proximal parts in the transversely dividing coral *Bourneotrochus veroni* Wells 1984 (=*Deltocyathus stellulatus* Cairns 1984), illustrated by Wells (1984: Fig. 3: 18) and Cairns (1984: Pl. 3D), are similar in appearance to those in the Miocene species.

Parent individuals.– About 20 percent of the examined specimens have a completely flat distal side of the corallum (Fig. 1D), the distal edges of septa, pali (P2) and the parietal columella being cut horizontally. Specimens of this type usually have well preserved, ornamented lateral costae and fully developed proximal sides with complete basal wall and a mature, fine-granular pattern of costal ornamentation. These forms are interpreted here as parent individuals which possibly died after releasing descendant forms before having been able to restore distal ends of the coralla.

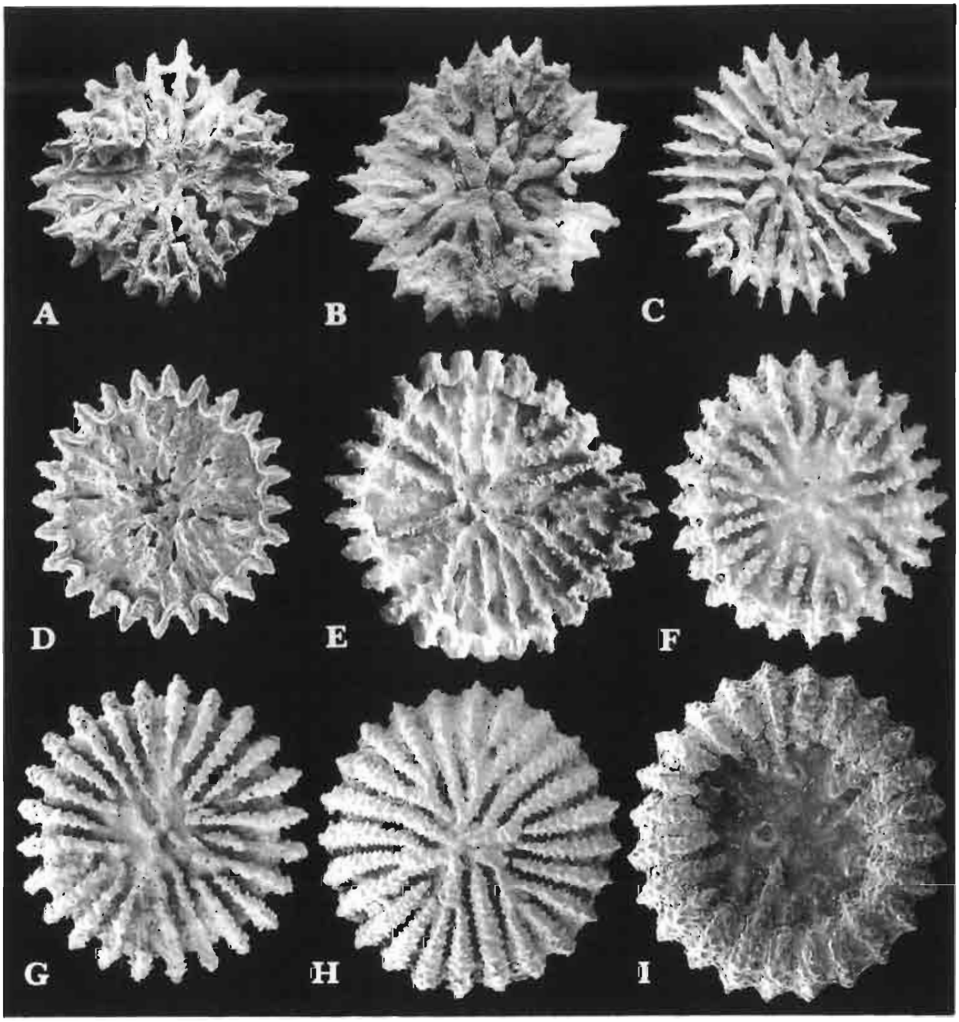


Fig. 3. Proximal side of specimens of *Truncatocyathus duncani* (Reuss 1871) from thevBadenian of Korytnica. ❑A-I. Stages in the wall and costae completion; ZPAL H.IX/503-511. All × 15.

Recent fungiid analogues

The process which leads to the separation of individuals after transverse division has been described in detail by Yamashiro & Yamazato (1987a, b) in two Recent fungiids, *Fungia fungites* (Linnaeus 1758) and *Sandalolitha robusta* (Quelch 1886). In both, the separation of a descendant individual (anthocyathus) from the parent stock (anthocaulus) is possible due to local chemical dissolution of the skeleton. These processes affect the separation

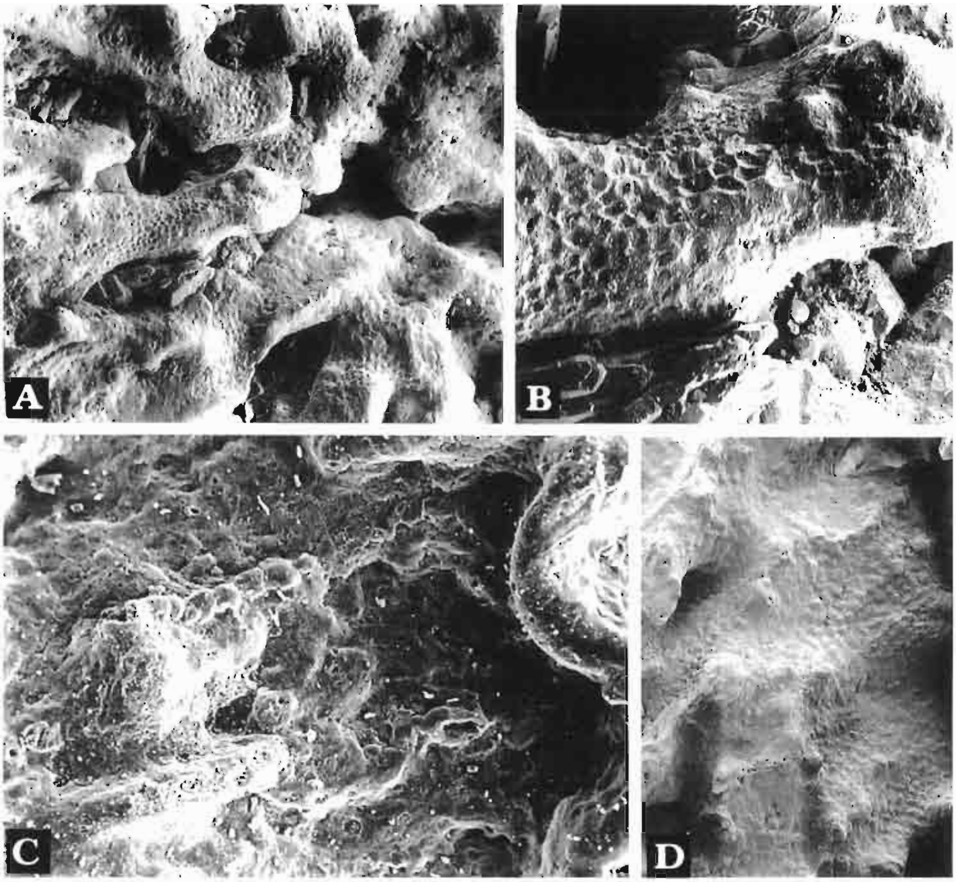


Fig. 4. Descendant specimens *of Truncatocyathus duncani* (Reuss 1871) from proximal side, Badenian of Korytnica. ❑A. Polygonal ridges developed on newly formed wall (ZPAL H.IX/163); × 65. ❑B. Enlargement of the proximal side with polygonal structures (ZPAL H.IX/163); × 200. ❑C. Newly formed list- shaped costae with trabecular modules (ZPAL H.IX/506); × 170. ❑D. Granulae on the newly formed proximal wall (ZPAL H.IX/512); × 65.

plane of the specimens and start with pulverized spots on the internal surfaces of the wall and septa. Later the zone of disintegration expands to the entire internal surface of septa and columella (Yamashiro & Yamazato 1987a: Fig. 3). At the last stage of detachment, the anthocyathus is joined to the anthocaulus only by non-dissolved costae. Yamashiro & Yamazato (1987a) proposed an extracellular secretion of acidic metabolic products as the demineralizing factor.

Intercostal perforation, furrows in the separation plane and other evidence of skeletal demineralization in *Truncatocyathus duncani* suggest that the process of transverse division was comparable with that in fungiids.

Palaeoebiology

The morphology of the skeleton of *T. duncani* provides the following information on the ontogeny of the species:

(1) There is a lack of thecal rings (compare Durham 1949).

(2) The final septal number of an individual equals the number of septa on its proximal side and does not increase through the later stage of ontogeny, i.e. during growth in height. This indicates that all septa appeared simultaneously at the earliest stages of ontogeny (compare Mori & Minoura 1983). There are extremely rare specimens in which septal number changes during ontogeny, but at most 1 or 2 septa can appear or disappear.

(3) Specimens reaching the final septal number develop a column wall (synapticulotheca-like), and they grow almost exclusively in height.

(4) The cylindrical shape is kept throughout ontogeny (proximal diameter is essentially the same as distal diameter of the corallum).

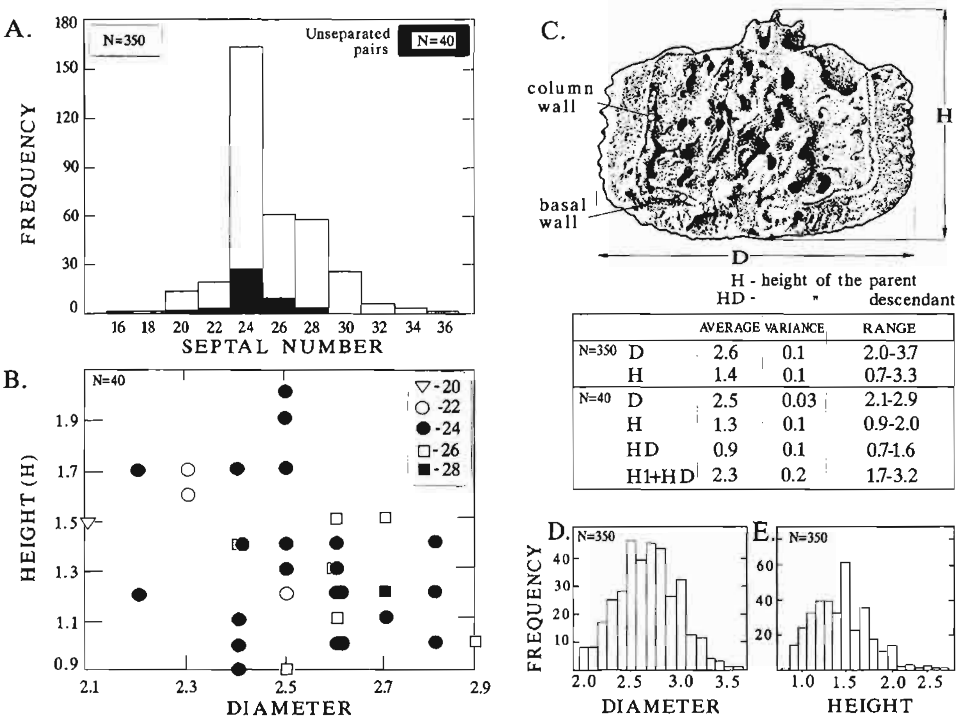
Larger numbers of septa generally correlate with shorter calices (N=350; r=0.66). The frequency histogram of septal number in specimens with final septal number is, however, right skewed (Fig. 5A). Specimens with 24 septa (with 3 complete septal cycles) and strict hexameral symmetry are the most frequent. Specimens with smaller septal number (16-22) may have different corallum symmetry e.g. tetrameral, pentameral, but often also hexameral symmetry with an incomplete third cycle of septa. In specimens having a larger number of septa (26-36), additional septa appear, mainly, as an incomplete fourth cycle in typical hexameral plan; some individuals were also found with septameral symmetry.

It seems that in the Korytnica population both the histogram skewing and domination of 24-septal specimens reflect a specific, genetic determination of septal number and hexameral symmetry (compare Mori & Minoura 1983, Mori 1987). Distributions of other morphological features, e.g diameter, or height of coralla, are more normal (see Fig. 5E, F).

The lack of any attachment to the substrate is a distinctive feature of many turbinoliids (compare Zibrowius 1984: p. 83), including *T. duncani*. Longitudinal sections of coralla do not reveal any mineral grains which could be used as an initial support (as there is in a Jurassic *Chomatoseris*; see Gill & Coates 1977).

There are no characters of *T. duncani* that allow asexually produced descendant individuals with completely regenerated detachment scar to be distinguished from sexually produced oozoids. Parent individuals of the unseparated pairs could be, in fact, either oozoids or may already belong to asexual generations. Morphologic features that might be expected to characterize oozoids cannot be used as indirect evidence of the sexual origin of any forms, e.g.:

(1) Small height (0.7 mm), because some descendant individuals of unseparated pairs can likewise be short (Fig. 5D).



		AVERAGE	VARIANCE	RANGE
N=350	D	2.6	0.1	2.0-3.7
	H	1.4	0.1	0.7-3.3
N=40	D	2.5	0.03	2.1-2.9
	H	1.3	0.1	0.9-2.0
	HD	0.9	0.1	0.7-1.6
	H1+HD	2.3	0.2	1.7-3.2

Fig. 5. Morphologic variability of the Korytnica population of *Truncatocyathus duncani* (Reuss 1871). □A. Frequency distribution for septal numbers. □B. Scattergram of diameter *versus* height of parent individuals in unseparated pairs (symbols indicate septal numbers of individuals). □C. Statistics for basic dimensions. □D, E. Size (diameter and height, respectively) distributions of 350 specimens.

(2) Small number of septa, because transverse division can be recognized in specimens having less than 24 septa (Fig. 5A, B).

(3) Fully developed proximal side, because transverse division is followed by a complete regeneration of the basal part of the corallum.

Another interesting phenomenon is the lack of any specimens less than 2 mm in diameter, of height less than 0.7 mm, and of septal number less than 16. This cannot be an artefact produced by selective winnowing of the material because in the same site much smaller juveniles of *Stephanophyllia elegans* (Bronn 1837) and *Ceratotrochus granulatus* Dembińska-Różkowska 1932 occur (see Stolarski 1992).

It is therefore proposed here that transverse division was the predominant reproductive strategy of *T. duncani* (Fig. 6).

The question of whether all the parent individuals survived division still remains open for there is no way to prove that regeneration of the distal septal edges took place. The frequency of specimens of parental generation without any regeneration, thus died after transverse division, is about 20 percent. This means that the actual mortality at this stage was much

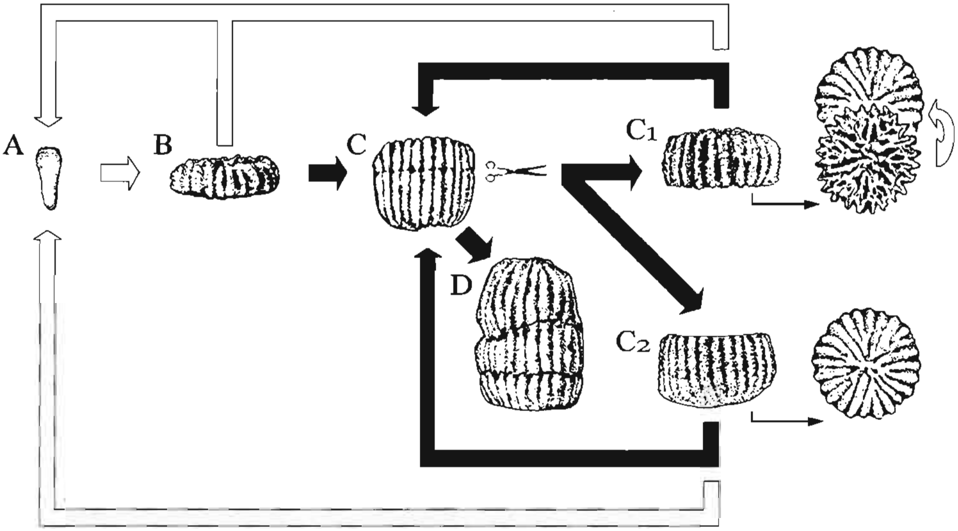


Fig. 6. Proposed life cycle of *Truncatocyathus duncani* (Reuss 1871).

much smaller, still allowing good reproduction effects. The phenomenon of transverse truncation thus had a tremendous influence on the population dynamics of *T. duncani*. The clonemates had similar diameters and septal number to their parents. Hence, it resulted in a great increase of identical individuals (see Cairns 1989a). Differences in septal number between asexually reproducing forms, although rare, increase the intrapopulational variability of *T. duncani*.

In corals, transverse division appears to be an adaptation to soft bottom conditions (see Cairns 1989a). Presumably, difficulties for planula settlement (or subsequent survival) on a soft substrate is disadvantageous compared with having cloned offspring that are equal (e.g. *Truncatocyathus*) or larger (e.g. *Fungia*, *Truncatoflabellum*) in size than those of the parents.

Discoidal coralla completely invested by the edge zone are considered as potentially auto-mobile forms (Gill & Coates 1977). Auto-mobile corals are also adapted to soft, loose sandy, or sandy mud substrates. In small-sized *T. duncani*, self-induced movement might be used for righting action, recovery from sediment burial, or for migration across substrate. Potential auto-mobility capacities together with releasing of relatively 'large' clonal offspring suggest that representatives of the genus *Truncatocyathus* are forms particularly well adapted to soft bottom conditions.

Taxonomy

Family Caryophylliidae Dana 1864
Subfamily Turbinoliinae Milne Edwards & Haime 1848

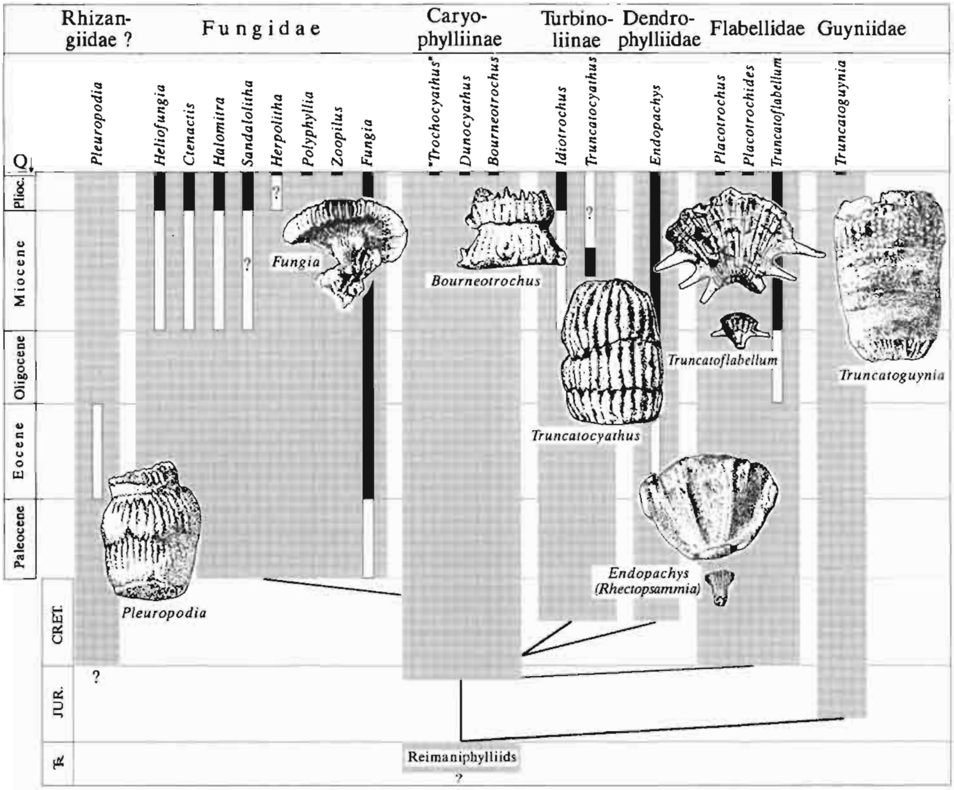


Fig. 7. Genera with transverse division and presumed relationships among families they are representing. Dark bars - precise stratigraphic occurrence, white bars - conjectured occurrence, question mark - uncertain occurrence. Illustrations after photos from: Cairns 1989b, Dennant 1903, Stolarski 1992, Vaughan 1900, Wells 1984, Yamashiro & Yamazato 1987. Presumed phylogeny after Wells 1956 and Roniewicz & Morycowa (in press).

Genus *Truncatocyathus* nov.

Type species: *Discotrochus duncani* Reuss 1871

Derivation of the name: The genus name is from the Latin *trunco* =truncate and refers to transverse division.

Diagnosis.– Like *Peponocyathus*, but reproducing asexually by transverse division. Non-attached parent and descendant forms are generally similar in their cylindrical shape. The detachment scar on the proximal side of descendant corallite is gradually hidden by the development of the wall and costae.

Species assigned.– *Discotrochus duncani* Reuss 1871.

Discussion.– Adaptive character of this mode of asexual reproduction and facility in distinguishing transversely divided forms suggests that this mode of reproduction is an important character above the species level (Cairns 1989a, b; compare also Zibrowius & Gili 1990). Thus, I propose a new genus, *Truncatocyathus*, for those species previously assigned to the genus *Peponocyathus* which divide transversely.

There are differences in opinion regarding asexual reproduction of Recent representatives of *Peponocyathus* species. There seems to be a consensus amongst authors regarding a lack of transverse division in *P. australiensis* (Duncan 1870). In Zibrowius' (1984) opinion coralla of the type species *P. folliculus* (Pourtalés 1868) divide transversely, but Cairns (1989b) considers that this species never does this. My personal observations of Recent skeletons of *P. folliculus* suggest that two developmental phenomena cause that interpretational divergences:
(1) Many of the representatives of *P. folliculus* revealed features of rejuvenescence (i.e. parricidal budding; see Zibrowius 1980; Pl. 58L, Pl. 59A, G, H, K). The descendant buds can have a number of septa identical to their parents. Often however, the number is smaller than in the parent individual. Some buds look like forms which clonally detach from the parental stock. If such 'total rejuvenescence' (after Birenheide & Soto 1977) takes place, the genesis of the descendant individuals growing as buds on the parents which die away, would be fundamentally different from those which originate by transverse division.
(2) Very rare juvenile forms attached a broad base to a hard substrate was described as *P. folliculus* by Zibrowius (1980: Pl. 58D, E). Although many of transversely dividing corals posses attached anthocauli stages, Zibrowius' forms show no traces of transverse division. There is also a lack of convincing evidences that morphologically similar forms described by Squires (1964: Pl. 2, Fig. 10, 11, 14) as trophozooids (anthocauli) of *Kionotrochus (K.) suteri* could actually divide transversely.

It is worthy of note that all parental individuals in unseparated pairs of *T. duncani* were free-living and any attached forms have not yet been found (the Korytnica Basin was thoroughly sampled in various environments; compare Bałuk & Radwański 1977).

The specimens described by Vašíček (1946: Tab. 1: 6) as *Discotrochus minutus* with underdeveloped proximal wall and characteristic rare and thick granulae on the basal costae are interpreted here as just detached individuals of *T. duncani* (comparable with stage Fig. 3A-C).

The corals illustrated and assigned by Weyer (1982) to *Kionotrochus (Cylindrophyllia) duncani* (Reuss 1871) and *to K. (C.) lecomptei* Wells 1937 (synonymized later as *P. duncani;* see Stolarski 1992) are represented by unseparated individuals (Pl. 7: 1, 8, 9) and individuals with weakly developed proximal side (Pl. 2: 3-5).

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Streszczenie

W ilastych osadach miocenu Gór Świętokrzyskich (Korytnica) zostały znalezione liczne okazy korali osobniczych, z gatunku opisywanego poprzednio jako *Peponocyathus duncani* (patrz Stolarski 1992). Korale te rozmnażały się bezpłciowo na drodze podziału poprzecznego. Podział poprzeczny uważany jest za cechę o znaczeniu ponadgatunkowym. Dlatego zaproponowano zaliczenie tego gatunku do nowego rodzaju - *Truncatocyathus*.

Formy potomne *T. duncani*, świeżo odseparowane od form macierzystych, nie mają na stronie proksymalnej koralita ściany ani żeber. W związku z pokrywaniem od zewnątrz bazalnej strony szkieletu przez tkanki miękkie korala, następuje stopniowy proces uzupełniania brakujących części szkieletu. Zregenerowane formy potomne są praktycznie nieodróżnialne od form macierzystych. Biorąc pod uwagę m.in. brak form młodocianych *T. duncani* (przy współwystępujących w badanych stanowiskach formach młodocianych innych gatunków korali) wysunięto przypuszczenie, że podział poprzeczny mógł dominować jako forma rozmnażania w populacji korytnickich *T. duncani*. Tę potencjalnie automobilną, rozmnażającą się przez podział poprzeczny formę uznano za wyjątkowo dobrze przystosowaną do życia na miękkim dnie (środowisko niekorzystne dla większości korali Scleractinia, wymagających twardego podłoża).

W artykule omówiono też taksonomiczną różnorodność korali Scleractinia rozmnażających się przez podział poprzeczny. U korali Rugosa ten typ rozmnażania należy do rzadkości. Za główną przyczynę tego stanu uznano obecność poziomych elementów szkieletowych odgradzających proksymalne części szkieletu od ciała u większości tych korali.