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BRONISŁAW ANDRZEJ MATYJA

Developmental polymorphism in Oxfordian ammonites

ABSTRACT: A new interpretation of the variation in final diameter of the ammonite shell is presented and exemplified by several forms from the superfamilies Stephanocerataceae and Haplocerataceae, chiefly Oxfordian in age. These examples demonstrate occurrence of more than just two morphs differentiated by their final shell size, as well as occurrence of only one morph in other species. The new interpretation differs from the theory of sexual dimorphism in that the variation in final size of the shell is regarded as a result of intraspecific variation in time of the achievement of sexual maturity by individual specimens. This interpretation is supported by evidence from extant cephalopods.

INTRODUCTION

The present study is a result of the systematic investigation of the Lower to Middle Oxfordian ammonites of the Central Polish Uplands. The new concept of the ammonite polymorphism, which is here proposed, stems from an incompatibility of the empirical observations with the theoretical and practical consequences of the theory of sexual dimorphism as an explanation for the variation in final size of the ammonite shell. This new concept does not undermine the established relationships between micro- and macroconchs, but only leads to their new biological interpretation. This new interpretation, in turn, has considerable implications for ammonite taxonomy, stratigraphy, paleoecology, and evolutionary reconstructions.

THE THEORY OF SEXUAL DIMORPHISM IN AMMONITES

The theory of sexual dimorphism is widely accepted as the basis for any considerations of ammonite ontogeny, phylogeny, taxonomy, and even stratigraphy. The concept of sexual dimorphism in ammonites first appeared toward the end of the 19th century (MUNIER-CHALMAS 1892); it was intended to explain the common occurrence of two, more or less similar ammonite morphs which differed in their final size. In the 1960's, this theory was independently formulated by MAKOWSKI (1962, 1963) and CALLOMON (1963).

The main points of the theory of sexual dimorphism in ammonites are as follows:

1) Ammonites grew to a mature, final stage which can generally be recognized on the basis of shell morphology;
2) The final size of full-grown ammonite shells is a well-defined specific character;
3) Such apertural modifications as the lappets are indications of maturity instead of being transient features of the growing shell (MAKOWSKI 1962, 1963; CALLOMON 1963, 1969, p. 111).

According to MAKOWSKI (1963, p. 13), the following features are diagnostic of sexual dimorphism in ammonites:

(*i*) identical initial stages of ontogeny in both (small and large) forms and the identity of their phylogeny;
(*ii*) lack of intermediate forms at the adult (gerontic) stage;
(*iii*) presence of the both forms in the same strata;
(*iv*) numerical ratio of two supposed sexes (sex ratio) comparable to that observed in living cephalopods.

Several authors commented on the difficulties in practical application of these criteria. A review of these problems is given by DAVIES (1972), who noted that two sexes could present differential evolutionary patterns concerning the characters directly associated with the sexual identity of the organisms. Intermediate forms could occur owing to an overlap of the ranges of variability of the two morphs, pathological phenomena, hermaphroditism, etc. DAVIES also cited examples undermining the criterion of sex ratio (*cf.* COWEN, GERTMAN & WIGGETT 1972, p. 212) and the criterion of identity of the initial stages of ontogeny; he concluded that, "each criterion for the identification of sexual dimorphism can be open to serious doubt" (DAVIES 1972, p. 39).

Various authors differ also in identification of the characters of the ammonite shell which are supposed to exhibit sexual dimorphism. MAKOWSKI (1962, 1963) distinguished two types of dimorphism in Mesozoic as well as in Paleozoic ammonites. In type "*A*" dimorphism, small forms (males) always have 5—6 whorls, whereas large forms (females) have at least 7 whorls; in type "*B*" dimorphism, males have 7—9 whorls and females at least 8 whorls. GUEX (1968) added to this classification also type "*O*" dimorphism, with males having only 3—4 whorls. Under this concept, the main criterion of sex identification is the number of whorls, although there may be no other morphological difference, not even a difference in the final size of the shell (*cf.* MAKOWSKI 1971, p. 335).

CALLOMON (1963, 1981), in turn, takes into account several morphological features, such as the mode of shell coiling, the kind of shell ornamentation, and the modifications of the final peristome; a difference in shell size (diameter), however, is a necessary condition for recognition of micro- and macroconchs.

ZAKHAROV (1978) did not find any differentiation in the final size of the shell of Lower Triassic ceratites. In his opinion, their sexual dimorphism is expressed in the degree of shell coiling; hence, he distinguished between the so-called involuti- and evoluticonchs.

The question is still unresolved which of the morphs should be regarded as female and which as male. CALLOMON (1981) leaves the question open and consistently applies the terms micro- and macroconchs, which he introduced earlier (CALLOMON 1955). MAKOWSKI (1962, 1963) assumed that small forms were males, while large forms females. COPE & SMITH (*in:* CALLOMON 1969, p. 121) suggested that macroconchs could be males in some genera and females in other genera. ZAKHAROV (1978, p. 128) considered all evoluticonchs, to which he assigned also the Jurassic microconchs, as females and involuticonchs as males.

The state of empirical knowledge about dimorphism in ammonites widely varies between geological periods. This problem has been reviewed by CALLOMON (1981), and it is briefly summarized herein (Text-fig. 1). One can hardly resist the impression that the only, and classic, domain for discussion of the sexual dimorphism in ammonites is the Jurassic. Even for the Jurassic, however, some authors noted difficulties with its recognition (KENNEDY 1977, p. 269; HOWARTH 1977, p. 251), and expressed doubts if it can be demonstrated (HÖLDER 1975, p. 498), or even if it indeed occurs in the form postulated by the theory of sexual dimorphism (ZIEGLER 1972, p. 79, 1974; IVANOV 1975, 1983).

HETEROCHRONY AND ONTOGENETIC DEVELOPMENT IN AMMONITES

The present reappraisal of the concept of sexual dimorphism in ammonites has been prompted by the upcoming study of a large collection (several thousand specimens) of ammonites from the Lower and low-Middle Oxfordian of the Polish Jura. When compared to British and French collections, this fauna shows the expected similarities but also a clear distinctness in that it is strongly dominated by adult but small-sized forms. The problem has been only partly solved by the recognition of a relationship between ammonite shell size and habitat (MATYJA 1984). There still have remained the questions: *(1)* What are the abundant "miniconchs" smaller than typical microconchs? *(2)* What is their relationship to typical micro- and macroconchs *(3)* How do these three types of shells fit the postulates of the theory of sexual dimorphism in ammonites?

The problem of the relationship between mini-, micro-, and macroconchs touches, in fact, upon the basic question of the ammonite polymorphism, precisely the relationship between micro- and macroconchs. This question has been repeatedly discussed (see review by MAKOWSKI 1971). The variation in final size and ornamentation of the shell was referred either to a differentiation in individual growth rate, or in longevity, or in the relationship between shell size and morphology and the achievement of reproductive maturity. It appears that ammonites lack any clearcut correlations between these characteristics (IVANOV 1975, p. 9).

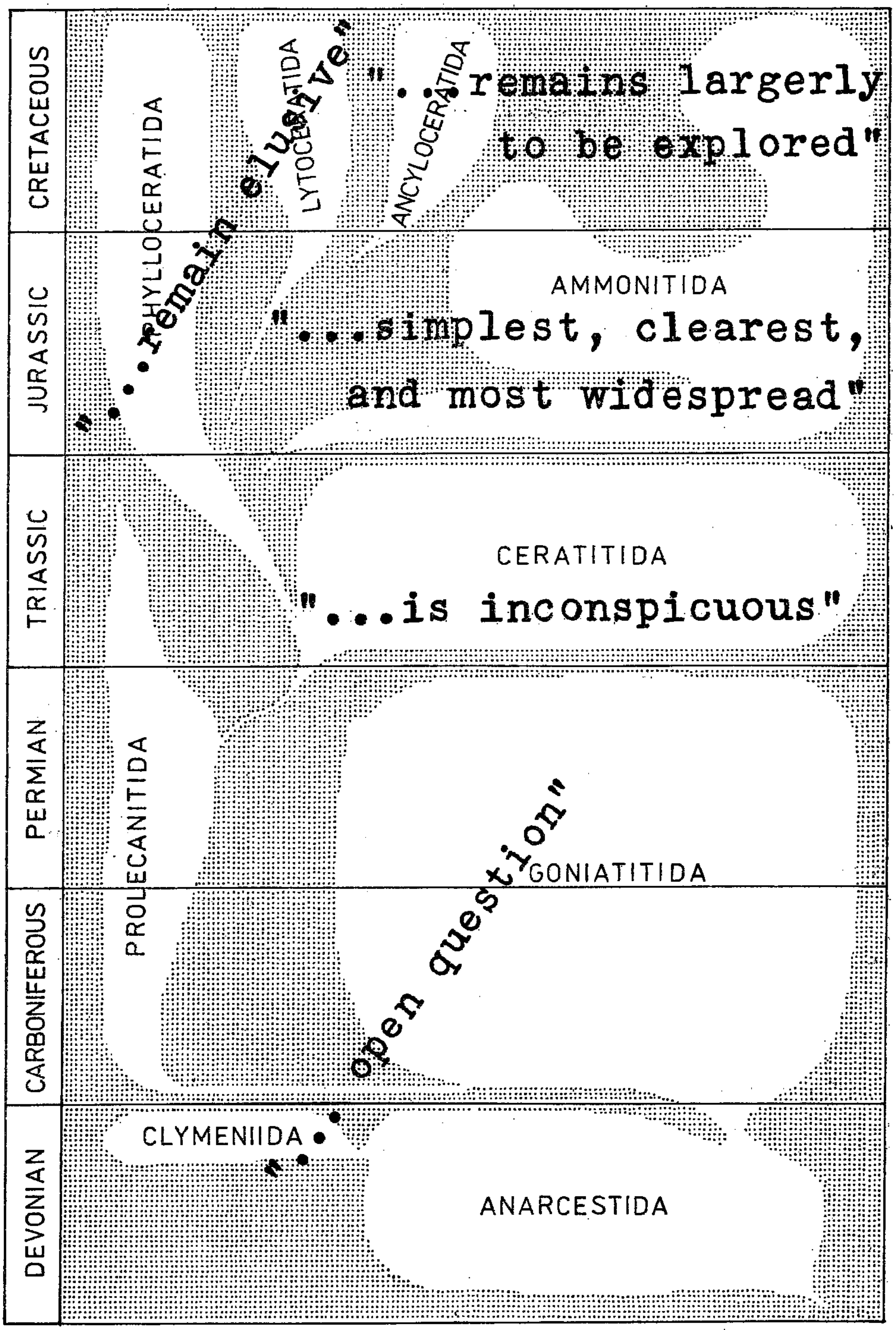

Fig. 1. State of recognition of sexual dimorphism in the Ammonoidea (*after* CALLOMON 1981)

In this paper, employed is the concept of the "clock of heterochrony" offered by GOULD (1977), to describe some relationships between the individual age, growth rate, stage of morphological development, and the achievement of maturity in ammonites (Text-fig. 2). It is to note that GOULD (1977) applied his concept to ancestor-descendant relationships, whereas the present consideration refers to the coeval forms.

The presented three cases (dwarfism, neoteny, progenesis) do not exhaust the alternatives. A simple reversal of the roles of the compared specimens leads to the other three categories of heterochrony as defined by GOULD (1977).

In any discussion of heterochrony, it is a crucial requirement to identify the considered features (individual age, growth rate, achievement of maturity, morphological stages) in the ammonites. This discussion will concern primarily the following aspects: final stage, morphological development, size and growth rate, and individual longevity.

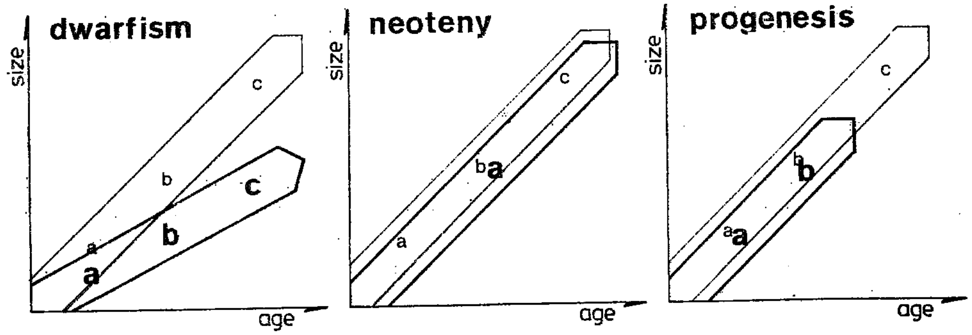

Fig. 2. Three cases of heterochrony

On the graphs, the normal ontogenetic development is marked by thin lines and symbols, whereas the various forms of heterochronic development are marked by thick lines and symbols.

Dwarfism:

The rate of morphological transformation (individual stages marked by *a*-*c* symbols), the moment of final maturation (arrowlike ending of the bars), and the longevity (measured as the projection of the bars on the age axis) are identical in both the forms. The growth rate of the dwarfed form, however, is lower; hence, the slope of the thick bar is less steep.

Neoteny:

The growth rate, the longevity, and the moment of final maturation are the same in both the forms. The neotenic form, however, remains throughout its lifetime at an early (*a*) stage of the morphological transformation.

Progenesis:

The rates of growth and morphological transformation are the same in both the forms. The progenetic form, however, reaches its maturity earlier; hence, it is characterized by shorter longevity, smaller final size, and an earlier morphological stage at maturity.

FINAL STAG

There is some disagreement if such characteristics of the ammonite shell as the increased density and simplification of suture lines, the modification of shell ornamentation (*e.g.*, lappets, rostrum, increased density of ribbing), and the modification of shell shape are indicative of maturity, or if they rather define the gerontic stage.

MAKOWSKI (1963) regarded these characteristics as gerontic features. KULICKI (1974) considered the final increase in septal density as a gerontic feature; he considered earlier stages of increased septal density as indicative of consecutive sexual cycles. CALLOMON (1963, 1981), in turn, interpreted the discussed characteristics as diagnostic of maturity; in his opinion, ammonites did not continously grow until death but rather their growth rate declined rapidly to zero after the achievement of maturity (CALLOMON 1963, p. 25).

In the vast majority of ammonite shells, however, all these characteristics appear only once and always in the final part of the shell, thus indicating the ultimate stage of life. In the majority of living cephalopods, the moments of reproduction and death are very close to each other (WELLS & WELLS 1977). The apertural modifications (lappets, rostrum) may be related to the presence of reproductive organs (for review *see* DAVIES 1972). It seems, then, safe to assume that the morphological features indicative of maturity and gerontic phase of life are either identical or indistinguishable.

MORPHOLOGICAL DEVELOPMENT

Apart from the morphological modifications related to the achievement of the final stage, the patterns of morphological development are variable in various ammonite taxa, even in particular species. Hence, any generalization cannot be given. Some examples are presented below; the others from the Upper Jurassic were reported, for instance, by UHLIG (1881) and KNIAZEV (1975).

SIZE AND GROWTH RATE

Ammonite growth can be determined by measuring the shell. When coiled shells are considered, the shell size can be represented by either shell diameter, or the number of whorls. Shell diameter is more easy to measure, but it is reliable solely when the rate of coiling is the same. The number of whorls often cannot be determined because of the preservation state of shells, but it allows for comparing shells with different rates of coiling. This is well exemplified by a comparison of *Quenstedtoceras henrici* R. DOUVILLÉ and *Q. vertumnum* (LECKENBY). The microconchs of both these species have almost invariably 6 whorls each; *Q. henrici*, however, reaches maturity at 54 mm in diameter (MAKOWSKI 1963, Textpl. V), whereas *Q. vertumnum* already at 35.5 mm (MAKOWSKI 1963, Textpl. VI).

Septal density (*i.e.*, the number of septa per whorl) is a measure of individual growth rate. This conclusion follows from the identification of an increasing density of septa with decreasing growth rate at the final stage. There is a distinction between primary and secondary increases in septal density (HÖLDER 1975, p. 496). The secondary increase in septal density occurs at the final stage. The primary increase occurs earlier in ontogeny and is regarded as an indication of declining growth rate (HÖLDER 1955, p. 61; and 1975, p. 496; VOGEL 1959) leading to dwarfism.

INDIVIDUAL LONGEVITY

If septal density is a measure of growth rate, then the number of septa is a measure of ammonite longevity. This assertion does not imply that a comparison of the numbers of septa in phylogenetically distant groups of ammonites reveals the variation in longevities; though even such opinions have been expressed (IVANOV 1971, 1975; *see also* DOGUZHAEVA 1982). Nevertheless, the constancy of the relationship between the number of septa and the shell size in various species of *Quenstedtoceras* is indeed remarkable. Also, noteworthy are the data presented by KULICKI (1974, Fig. 2) to illustrate ontogenetic changes in distribution of septa in *Quenstedtoceras*; the changes in septal density he related both to the number of whorls and to the cumulative number of septa. There is a correlation between the number of whorls and the number of septa in several specimens; but it also seems that depressions and elevations of the curve are confined to intervals between particular septa, as if restricted to particular ontogenetic stages (*see* Text-fig. 12).

In practice, shell diameters may indeed be compared in order to get some indication of ammonite individual longevity, provided that: *(i)* the shells being compared have the same coiling rate, that is, the same index $\varrho = d_n/d_{n-1}$, where *d* is the diameter of n whorl (*cf.* CALLOMON 1969, p. 112); and *(ii)* the shells have no primary increase in septal density.

EMPIRICAL EVIDENCE

The evidence presented below comes from the Late Jurassic representatives of the superfamilies Stephanocerataceae and Haplocerataceae; the only exception is the Late Callovian genus *Quenstedtoceras*. The Jurassic age of all these ammonites is worth emphasizing in the context of the widespread conviction that sexual dimorphism is especially well expressed in Jurassic ammonites.

SUPERFAMILY STEPHANOCERATACEAE

All the examples come from the evolutionary sequence continuing *Quenstedtoceras* (Late Callovian — earliest Oxfordian), through *Cardioceras* (Early to Middle Oxfordian), to *Amoeboceras* (Middle Oxfordian through Late Kimmeridgian).

1. GENUS *QUENSTEDTOCERAS*

This genus is widely regarded as a classic example of sexual dimorphism (MAKOWSKI 1962, 1963; CALLOMON 1963; KULICKI 1974). Smooth and large (7 to 8 whorls) macroconchs have their partners in smaller (6 to 6.125 whorls; MAKOWSKI 1971, p. 334), strongly ribbed microconchs equipped with a rostrum. This dichotomy is obfuscated

(Text-fig. 3) by a few specimens which have only 4.5—5.0 whorls and no more than 13.5 to 18.7 mm in diameter (Pl. 1, Fig. 1a-d); these miniconchs come from the same outcrop at Łuków[1] which provided the majority of micro- and macroconchs described by MAKOWSKI. The miniconchs exhibit the final increase in septal density, whereas their inner whorls have the septal density typical of micro- and macroconchs. One miniconch also shows an increase in ribbing density at the end of the last whorl (Pl. 1, Fig. 1d-e). The existence or absence of rostrum cannot be established because of the preservation state. There are no intermediates between these miniconchs and typical microconchs.

2—4. GENUS *CARDIOCERAS*

The genus *Cardioceras* is highly variable morphologically, and the relationship between its micro- and macroconchs is more complex than in *Quenstedtoceras*. According to MAKOWSKI (1962, p. 51), microconchs attain precisely 6 whorls, but there is no strict correlation between sex and shell ornamentation.

2. SUBGENUS *SCARBURGICERAS*

According to the definition (ARKELL 1941, p. *LXVII*), this subgenus includes small to moderately sized forms with ribs continuing to the end or almost to the end of the shell. There also are some records of large (200—320 mm in diameter) ammonites with smooth outer whorl and with inner whorls having the ornamentation typical of *Scarburgiceras* (see, for example, MAIRE 1938, Pl. 7, Figs 1 and 4; CALLOMON 1985, Text-fig. 8S), and these are classic macroconchs corresponding to the microconchs of the subgenus *Scarburgiceras*. Among typical microconchs, however, there is a remarkable variation. For instance, the species *Cardioceras (Scarburgiceras) bukowskii* MAIRE and *C. (Scarburgiceras)* cf. *reesidei* (MAIRE) very closely resemble each other in shell shape, coiling, and style of ribbing at any given shell diameter (ARKELL 1946, p. 307). At the diameter of 22—25 mm, however, *C. (Scarburgiceras)* cf. *reesidei* achieves the final stage, whereas *C. (Scarburgiceras) bukowskii* at the diameter of approximately 30 mm enters the next stage of morphological development, and its ribs acquire small tubercles. The latter species archieves its final stage at the diameter of 45—51 mm.

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[1] The locality at Łuków (erratic mass of Jurassic clays in a Pleistocene ground moraine) does not yield paleontological material anymore, as this clay pit has been abandoned and completely filled with rainfall water. The present author has only a small collection, supplemented with specimens kindly donated by Dr. J. GŁAZEK, Professor A. RADWAŃSKI, and Dr. K. ŻAWIDZKA, all of the University of Warsaw.

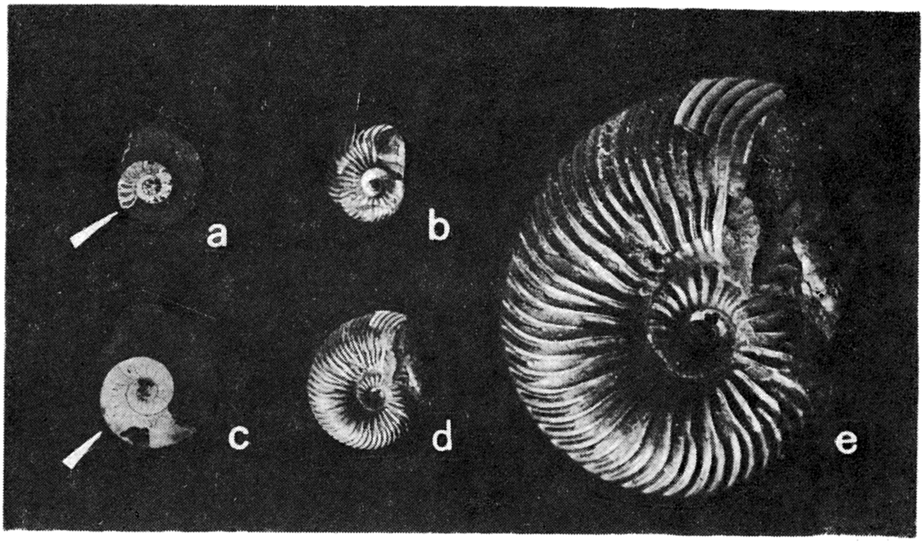

Fig. 1. Miniconchs of the genus *Quenstedtoceras* from Łuków

a — medial section of specimen *b* (arrow indicates last septum), **b** — lateral view of the sectioned specimen shown in *a* (both in nat. size); **c** — medial section of specimen *d* (arrow indicates last septum), **d** — lateral view of the sectioned specimen shown in *c* (both in nat. size); **e** — specimen shown in *d* (taken × 3), to show an increase in ribbing density at the dorsal part of aperture

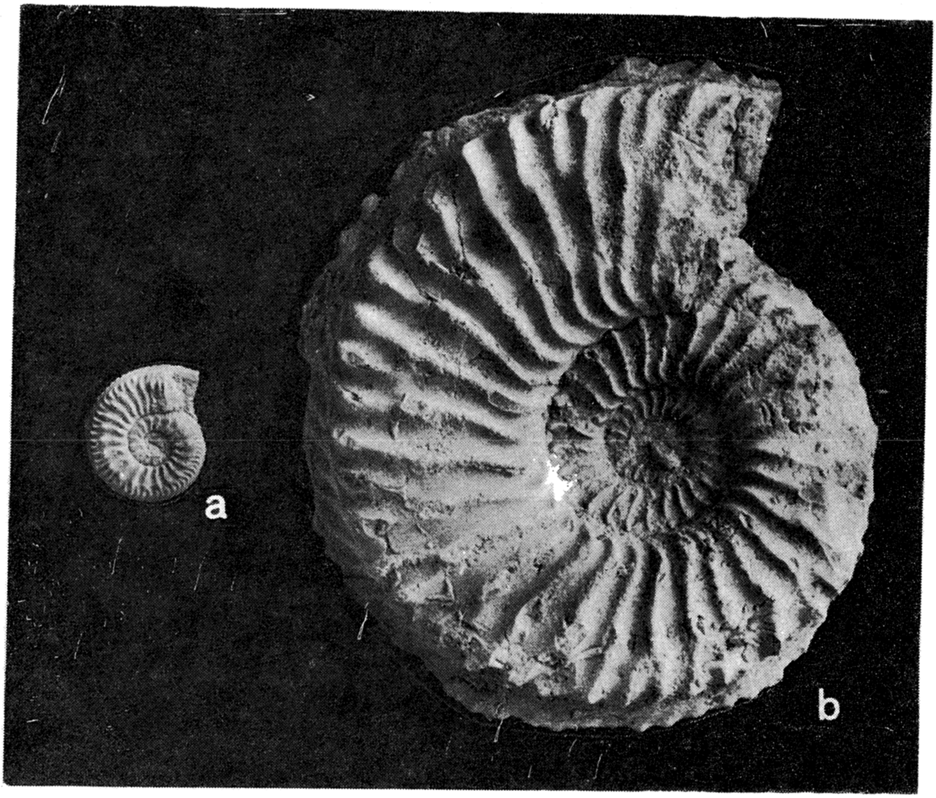

Fig. 2. Mini- and microconch of the genus *Cardioceras*

a — *Cardioceras (Subvertebriceras) sowerbyi* ARKELL — miniconch, **b** — *Cardioceras (Subvertebriceras) densiplicatum* BODEN — microconch; both in nat. size

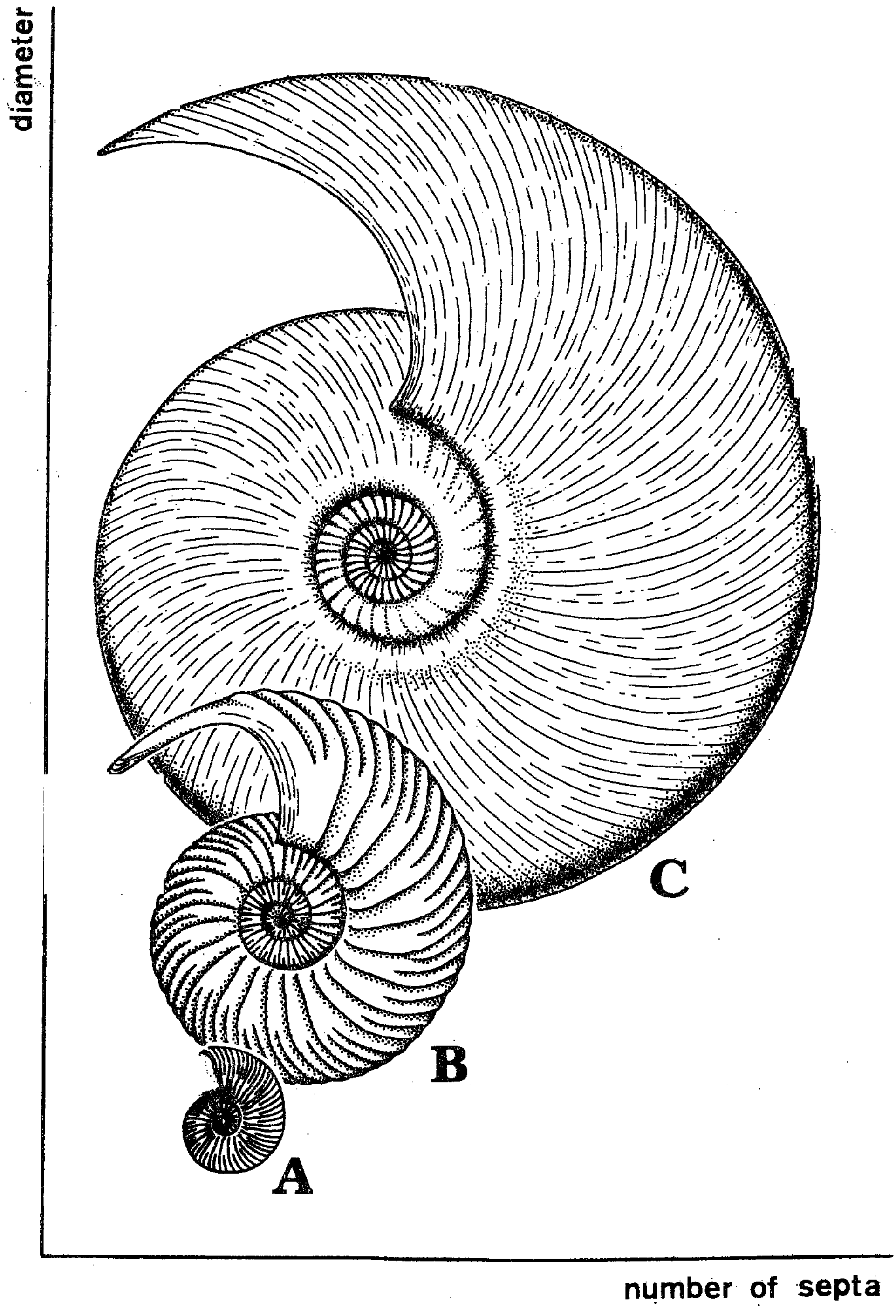

Fig. 3. Trimorphs of *Quenstedtoceras henrici* R. DOUVILLÉ

A — miniconch; **B** and **C** — micro- and macroconch (*B-C* after MAKOWSKI 1963, Text-pl. V)

3. SUBGENERA *SUBVERTEBRICERAS* AND *CARDIOCERAS*

The subgenus *Subvertebriceras* includes forms with strong ribs persisting to the end of the shell (ARKELL 1941, p. *LXXVIII*). Some of these forms are morphologically very close to each other, but with differential final sizes (Pl. 1, Fig. 2). For example, the species *Cardioceras (Subvertebriceras) sowerbyi* ARKELL reaches maturity at the shell diameter of 15—40 mm; *C. (Subvertebriceras) densiplicatum* BODEN, in turn, attains maturity at the shell diameter of 65—100 mm. These two species, however, cannot be regarded as sexual dimorphs, because there also is a typical macroconch with smooth ultimate whorl, described as *Cardioceras (Cardioceras) highmoori* ARKELL and once considered by CALLOMON (1963, Pl. 1) to constitute a dimorphic pair with *C. (Subvertebriceras) dinsiplicatum*. Recently, CALLOMON (1985, p. 70) regards however, another species with smooth ultimate whorl, *Cardioceras (Scoticardioceras) excavatum* (SOWERBY) as the macroconch in this dimorphic pair.

4. SUBGENERA *MITICARDIOCERAS, CAWTONICERAS,* AND *MALTONICERAS*

These three subgenera are characteristic of the Middle Oxfordian (upper part of the Antecedens Subzone and most, if not all, of the Parandieri Subzone). The subgenera *Cawtoniceras* and *Maltoniceras* are regarded as a dimorphic pair (CALLOMON 1963, Table 1); some representatives of *Miticardioceras* have been attributed to *Cawtoniceras* (ARKELL 1941, p. *LXXVIII;* MALINOWSKA 1981).

The shell ornamentation of *Maltoniceras* exhibits three distinct ontogenetic stages. At the first stage (up to 20—40 mm in shell diameter), the ornamentation is poorly developed, often confined to weak tubercles in the middle of the shell side. At the second stage (up to 70—100 mm), strong primaries develop, accompanied by more or less tuberculate, short secondaries. At the last stage, the ribs are gradually widely spaced and disappear, and the living chamber is smooth and a little flattened.

The subgenera *Miticardioceras* and *Cawtoniceras* have the first morphological stage identical to that of *Maltoniceras*, but *Miticardioceras* never passes beyond this stage; its final size only slightly exceeds 30 mm. The subgenus *Cawtoniceras* enters the strongly ribbed stage and, "unless the outer whorls are preserved, it is impossible to distinguish *Maltoniceras* from *Cawtoniceras*" (ARKELL 1941, p. *LXXIX*). The subgenus *Cawtoniceras* ends its ontogeny at this stage and acquires the final modifications. The subgenus *Maltoniceras* alone reaches the third stage of morphological development (Text.-fig. 4).

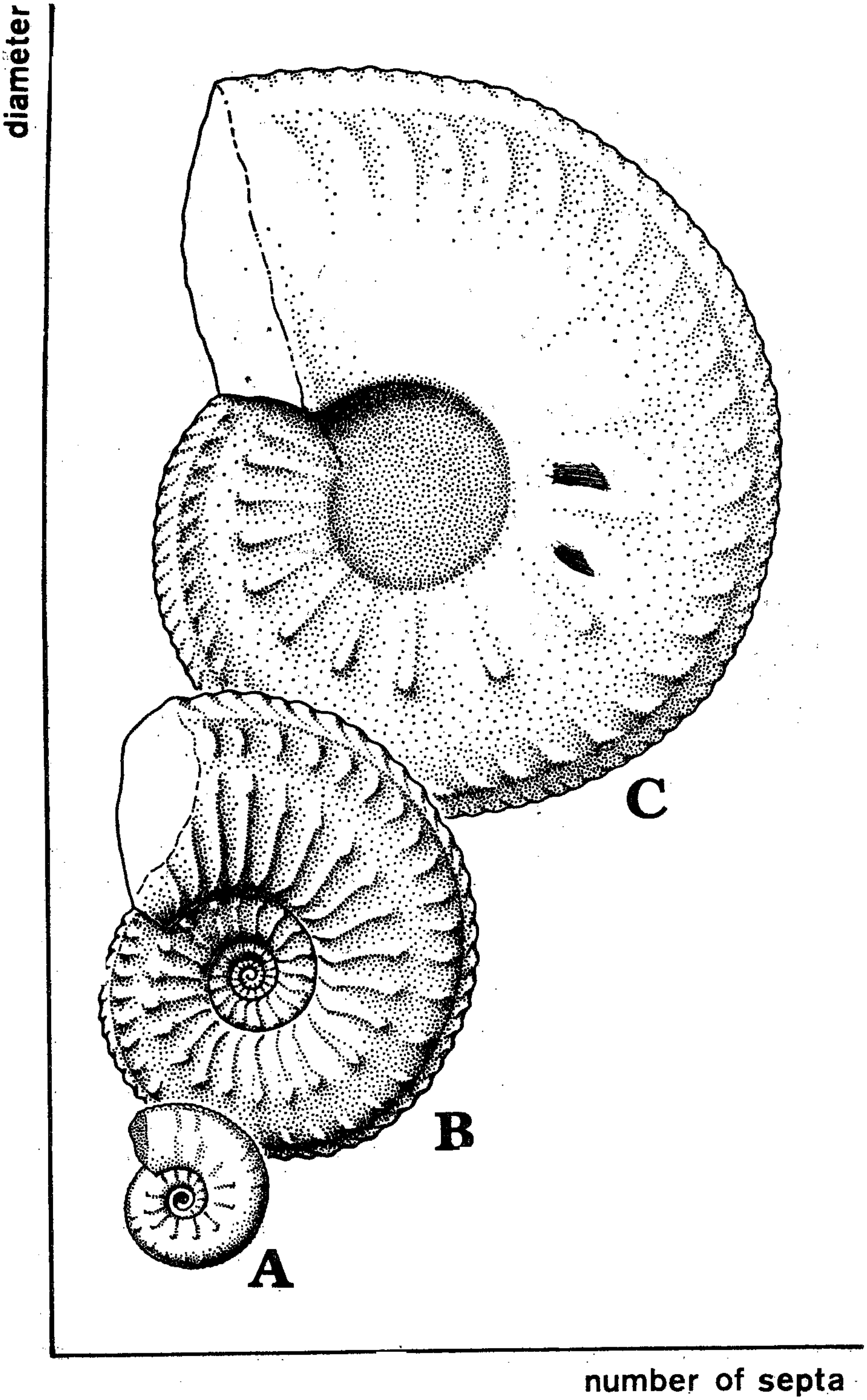

Fig. 4. Trimorphs among Middle Oxfordian *Cardioceras* subgenera
A — *Miticardioceras*, **B** — *Cawtoniceras*, **C** — *Maltoniceras*

5. GENUS *AMOEBOCERAS*

In this genus, dimorphism is expressed in the existence of smaller isocostate and larger varicostate or smooth forms; the adult peristome often is similar, although some macroconchs have a rostrum (*cf.* BIRKELUND & CALLOMON 1986, Pl. 3, Fig. 5).

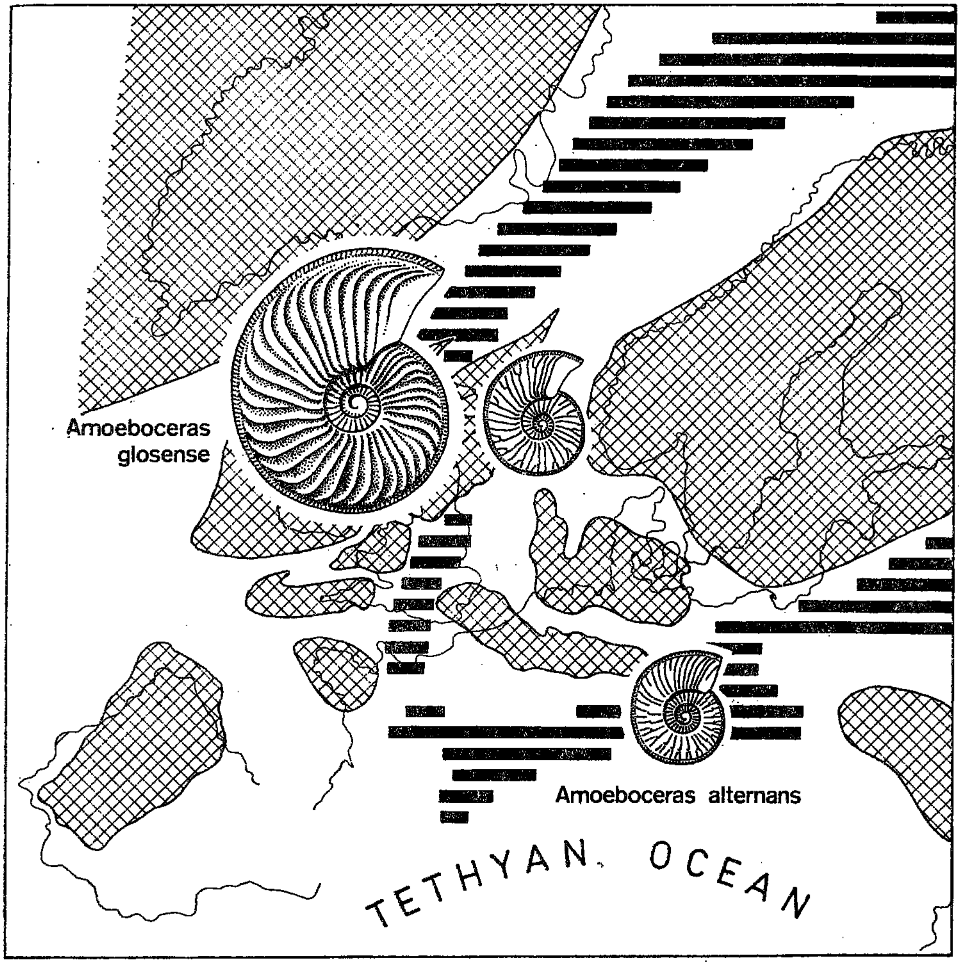

Fig. 5. Distribution and differentiation of morphs among Middle/Upper Oxfordian Boreal *Amoeboceras glosense* (BIGOT & BRASIL) and its Submediterranean morphological counterpart, *Amoeboceras alternans* (v. BUCH)

In the Bifurcatus and Bimammatum Zones of the Middle and Upper Oxfordian, two closely related species of *Amoeboceras* occur in Europe. The species *A. glosense* (BIGOT & BRASIL) occurs in the Boreal Realm, and *A. alternans* (v. BUCH) in the Submediterranean Realm. The Boreal form has both macro- and microconch (SYKES & CALLOMON

1979); the Submediterranean form, however, exists solely as microconch (Text-fig. 5). This is an example of a much more widespread phenomenon: macroconchs are extremely rare in the huge collections of *Amoeboceras* from Poland, West Germany, and France (*cf.* DORN 1931). Apparently, a single morph of the presumed dimorphic pair could exist alone in a considerable area.

SUPERFAMILY HAPLOCERATACEAE

The examples given below [2] come from the genera *Bukowskites, Creniceras, Glochiceras, Neocampylites, Ochetoceras, Popanites, Taramelliceras,* and *Trimarginites.* Both the phylogenetic and dimorphic relationships among these genera are dubious (*cf.* CHRIST 1961, MALINOWSKA 1963, PALFRAMAN 1966, ZIEGLER 1974). They represent, however, almost all the haploceratacean genera known from the Lower and Middle Oxfordian.

6. GENUS *TRIMARGINITES*

The Late through Middle Oxfordian *Trimarginites* includes smaller forms with lappets, *T. stenorhynchus* (OPPEL), and larger forms without lappets, *T. arolicus* (OPPEL) and *T. trimarginatus* (OPPEL). The range of the final shell sizes recorded in the author's collection spans from a little over 20 mm to more than 100 mm. As noted by MAKOWSKI (1963, p. 10), the recognition of the final stage is hampered in *Trimarginites* by the high complexity and density of suture lines achieved already at earlier ontogenetic stages. Because of this obstacle, and also because of the monotonous shell ornamentation, it is indeed difficult to determine how many morphs with differential final shell sizes actually occur in *Trimarginites.* The only applicable criterion refers the presence or absence of lappets.

When this sole criterion is applied, however, ZIEGLER (1974, p. 31 and Fig. 19) demonstrated that the stratigraphic ranges of micro- and macroconchs differ. The microconchs range to the top of the Bimammatum Zone, whereas the macroconchs range up to the top the successive Planula Zone. This implies that *Trimarginites* existed during one ammonite chron (that is, approximately 1 to 1.5 million years) in the form of one morph only, the macroconch, which must have included both the sexes.

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[2] All taxonomic considerations are deliberately left out of the scope of this discussion, even when the evidence presented herein suggests a particular taxonomic decision.

7. GENERA *BUKOWSKITES* AND *NEOCAMPYLITES*

The genus *Bukowskites* includes only one species, *B. distortum* (BUKOWSKI). MALINOWSKA (1965) assigned it to the subgenus *Glochiceras (Coryceras),* but ENAY (1966) to *G. (Glochiceras),* whereas ZIEGLER (1974) regarded it as a separate genus within the Glochiceratidae.

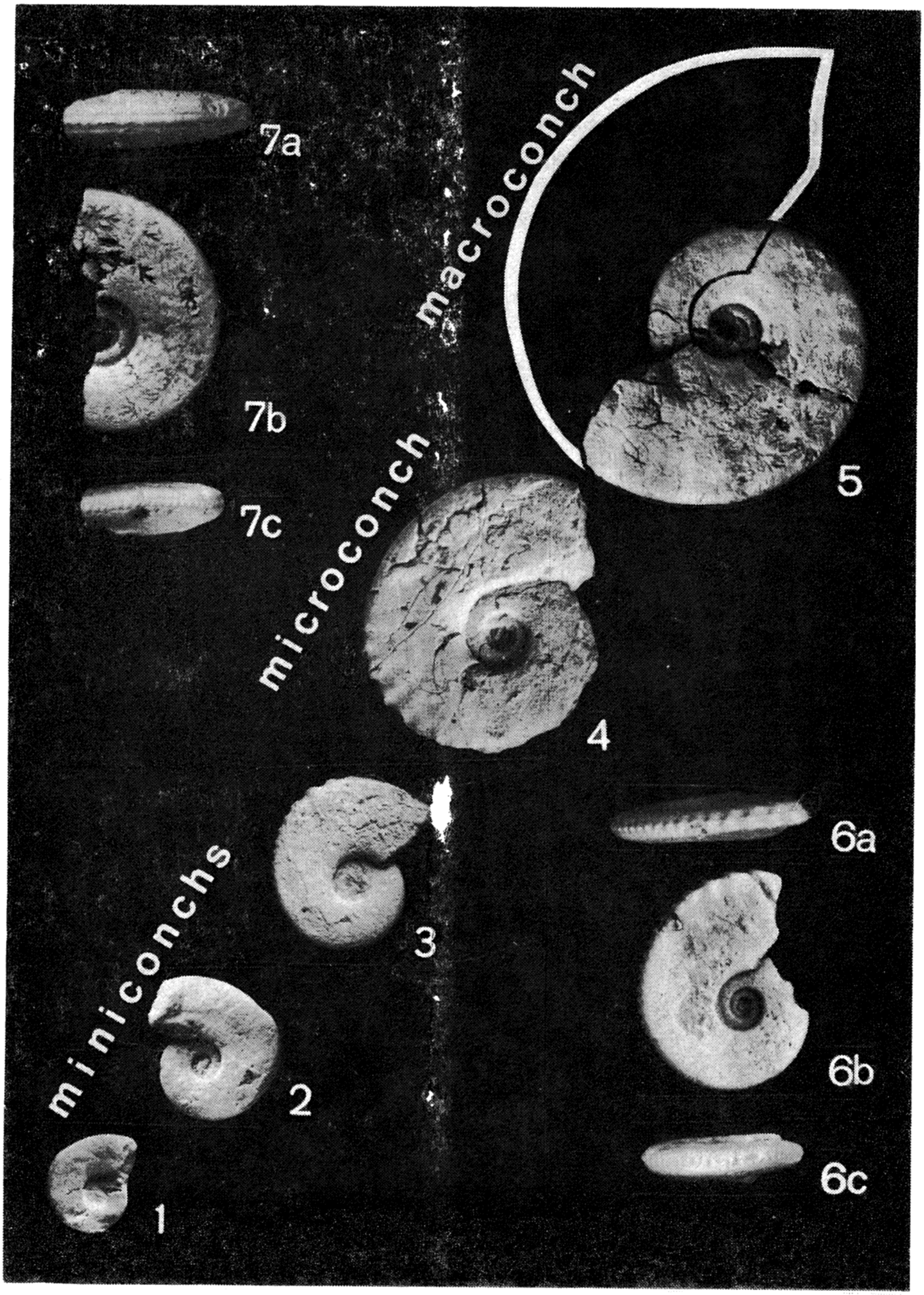
The species *B. distortum* passes through a number of morphological stages in its development. At first, the shell is entirely smooth. Beginning with the diameter of some 13 mm, numerous small and round tubercles appear at the ventral side. At approximately 25 mm, the tubercles are replaced with larger and asymmetric denticles. At the same time, ventrolateral rib-like swellings appear. On the last quarter of a whorl, denticles and swellings disappear; some specimens bear a shallow lateral groove at that stage. A geniculate change in shell coiling occurs on the last whorl, about one fourth of a whorl from the aperture, without any correlation with the stage of the morphological development. It is, however, correlated with the final increase in septal density, thus facilitating the recognition of the final stage.

In the author's collection, several specimens reach the final stage without passing through all the stages of morphological development: some specimens have a very short stage of small tubercles (Pl. 2, Fig. 1), but others have it much longer (Pl. 2, Fig. 2). The specimens which achieved maturity early in their morphological development are characterized by the shell diameter appropriate for their morphological stage. In spite of the variation in size and ornamentation, all these specimens fall within the range attributed to *B. distortum.* Some other specimens, however, acquire two ventrolateral keels toward the end of the stage of small tubercles (Pl. 2, Figs 5, 7a-c). The shell shape remains typical of *Bukowskites,* but the tubercles are then replaced by a third keel, and weak falciform ribs appear at the sides. According to the rigors of taxonomy, further developmental stages of these specimens must be regarded as *Neocampylites* aff. *girardoti* (de LORIOL).

The genus *Bukowskites* might, then, be considered as a microconch, with the corresponding macroconch reaching the *Neocampylites* stage of morphological development. Such a simple dimorphic scheme, however, would neglect the existence (*see* Pl. 2) of complex polymorphic relationships within *Bukowskites.*

8. *NEOCAMPYLITES DELMONTANUS* GROUP

This group of species occurs in the Lower to lowest Middle Oxfordian. Its characteristic features are: strong ribbing and three ventral keels. The morphology changes in ontogeny. At the first stage, the shell is smooth. Later, one keel apears at the venter, and soon the other two



Polymorphism among *Bukowskites distortum* (BUKOWSKI) and *Neocampylites* aff. *girardoti* (de LORIOL)

1-4 and **6a-c** — *Bukowskites distortum* (BUKOWSKI): 6a — ventral view, to show the stage of large denticles, 6b — lateral view, 6c — ventral view, to show the stage of small tubercles; all in nat. size

5 and **7a-c** — *Neocampylites* aff. *girardoti* (de LORIOL): 7a — ventral view, to show the three-keeled stage, 7b — leteral view, 7c — ventral view, to show the stage of small tubercles and the appearance of lateral keels; all in nat. size

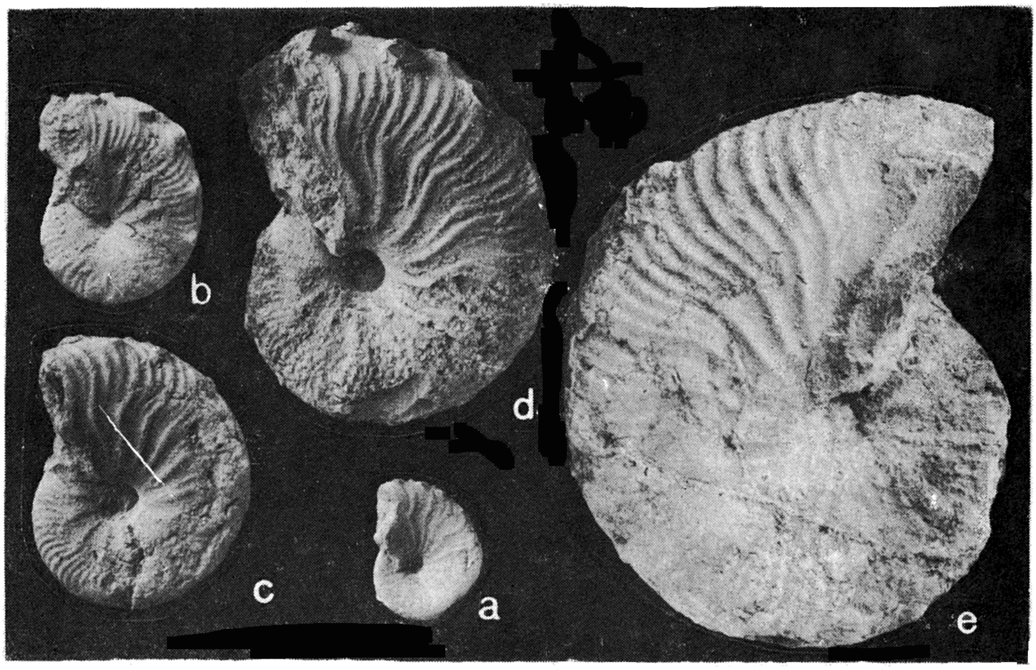


Fig. 1. Variability of final diameter amongst the Lower Oxfordian *Taramelliceras oculatum* group; all in nat. size

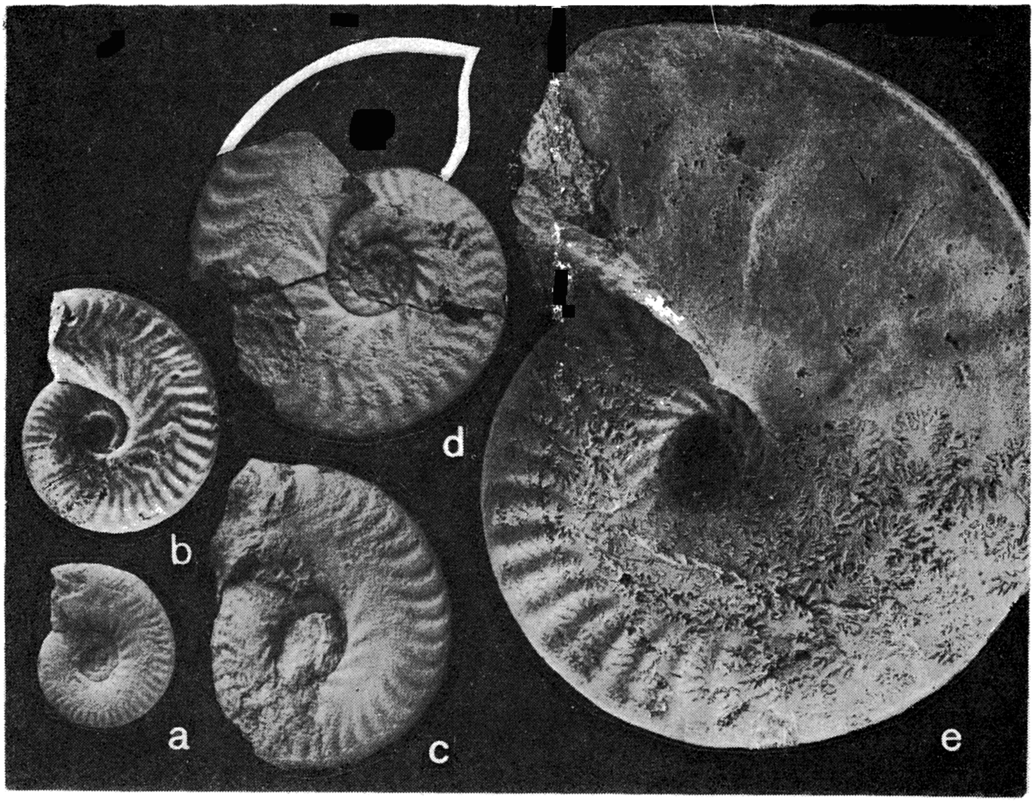


Fig. 2. Variability of final diameter amongst the Middle Oxordian *Neocampylites delmontanus* group; all in nat. size

keels. Ventral ribs appear earlier in ontogeny than dorsal ribs. The ontogenetic stage characterized by strong ribbing is long, but ribs disappear at the final stage.

The specimens illustrated herein (Pl. 3, Fig. 2) come from the Tenuicostatum Subzone of the lowest Middle Oxfordian. All of them are adult but the variation in the final shell size is very large. The smallest specimens have merely 21 mm in shell diameter, whereas the largest exceed 120 mm. In small specimens, the morphologic stage with three keels may encompass as little as a half of the last whorl, and the ribbing may cover only three fourths of the last whorl (Pl. 3, Fig. 2a). Moderately sized specimens exhibit strongly developed ribs up to the very end of the shell (Pl. 3, Fig. 2b-d). The largest specimens, in turn, have a part of the last whorl smooth (Pl. 3, Fig. 2c). The number of whorls ranges from 4.75 to 6.75 in this collection. The only gap observed is between 6.1 and 6.4; it may well reflect the relatively small sample size (70 specimens).

In some small specimens (*see* Pl. 3, Fig. 2c), the aperture is supplied with lappets, and a hood appears as a continuation of the venter; the adumbilical edge of the aperture is oblique. This morphology of the aperture resembles the subgenus *Glochiceras (Glochiceras)*. The resemblance may not be accidental, if considered in the light of morphological relationships in *Ochetoceras canaliculatum* (see below), which stems from the *Neocampylites delmontanus* group.

The occurrence of an almost continuous series of morphs which differ one from another in the final size and the stage of morphological development of the shell indicates that maturation could be achieved at various moments in ontogeny.

9. GENERA *OCHETOCERAS* AND *GLOCHICERAS*

The most common species of *Ochetoceras* in the Middle Oxfordian is *O. canaliculatum* (v. BUCH). It is a typical macroconch, with the final shell diameter averaging 91 mm but reaching even 140 mm (HOROLDT 1964, p. 38). On the last part of the shell, the lateral groove disappears; dorsal ribs, and later also ventral ribs, become weaker and then disappear as well.

ROLLIER (1913), and even earlier d'ORBIGNY (1850, Pl. 199), connected *O. canaliculatum* with a microconch, *Glochiceras (Glochiceras) subclausum* (OPPEL), which is a smooth form, with lateral groove, and with apertural lappets and hood. In addition to these two forms, however, the author's collection (*see* MATYJA 1977, Pl. 2, Fig. 8) also includes some specimens which are intermediate in size between these micro- and macroconchs but strongly ribbed up to the end of the shell.

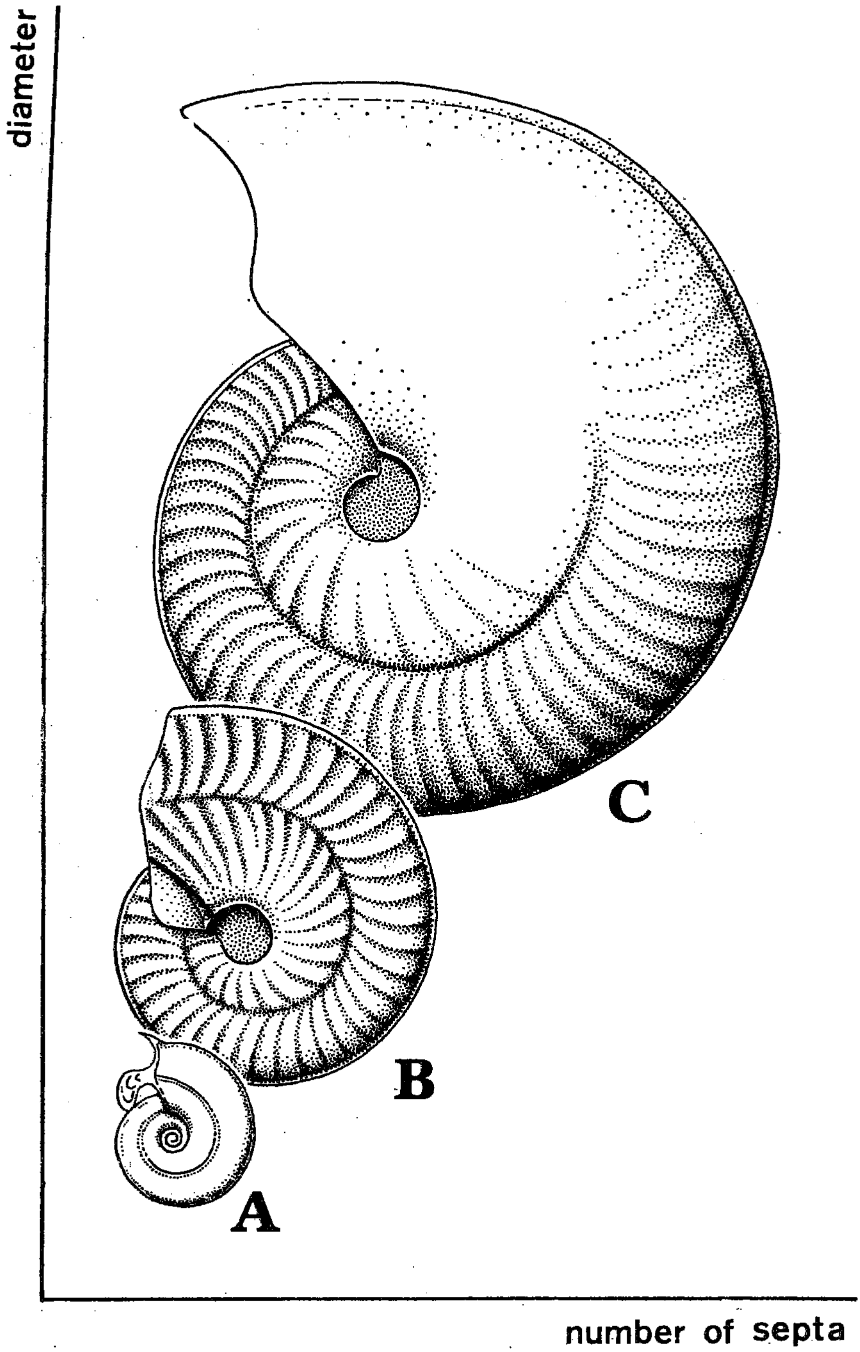


Fig. 6. Trimorphs of Middle Oxfordian *Ochetoceras canaliculatum* (v. BUCH)

A — *Glochiceras subclausum* (OPPEL) — microconch, **B** — *Ochetoceras canaliculatum* — small macroconch, **C** — *Ochetoceras canaliculatum* — big macroconch

As judged after the increasing septal density, and sometimes also the increasing density of adumbilical ribs, these forms have achieved the final stage. It is thought that HOROLDT (1964, p. 38) observed similar forms when he mentioned micro- and macrogerontic forms of *O. canaliculatum*; however, he did not give any more detailed description. The preservation state of the investigated specimens does not allow to determine the form of the aperture of these intermediate specimens. However, the lappets occur (*see* Pl. 3, Fig. 2c) in some representatives of the genus *Neocampylites*, from which *Ochetoceras* is derived. One may therefore suspect that lappets could occur also in the forms under discussion.

This is, then, one more example of three morphs (Text-fig. 6), instead of just two, as postulated by the theory of sexual dimorphism. It also shows that the number of distinguishable morphs may depend on distinctness of successive stages in morphological development.

10. GENERA *TARAMELLICERAS* AND *CRENICERAS*

According to MAKOWSKI (1963), *Taramelliceras* s. s. is a typical macroconch with more than 7 whorls; its sexual partners are *Richeiceras* and *Acanthaecites* which have 5 to 6 whorls (MAKOWSKI 1963, p. 27, Fig. 5). The genus *Taramelliceras* and its presumed microconchs have identical simple apertures. Concerning *Creniceras renggeri* (OPPEL), MAKOWSKI (1963), p. 29, Textpl. II) asserted that it was a microconch (5 to 6 whorls) but he could not identify its counterpart. PALFRAMAN (1966) studied in detail the ontogeny of *Taramelliceras richei* (de LORIOL) and *Creniceras renggeri* (OPPEL) and concluded that they were a dimorphic pair. The species *C. renggeri* attains 4.5 to 5.5 whorls[3] and has lappets, whereas *T. richei* has 6 to 6.75 whorls and a simple aperture.

In the Lower Oxfordian of the Middle Polish Uplands, strata a little younger than those containing *T. richei* and *C. renggeri* yield very abundant *Taramelliceras* and *Creniceras*. The latter genus is represented by "*C. crenatum*" (BRUGUIÈRE). Its specimens attain 4.125 to 5.125 whorls at the shell diameter of 11.5 to 25.5 mm. They are acccompanied by a number of "species" of *Taramelliceras*, among which the group of *T. oculatum* (PHILLIPS) is predominant. This group shows a very wide variation in the final shell size; its specimens attain 4.5 to 5.5 whorls at the shell diameters ranging from 19 to 73 mm, without any distinct gap (Pl. 3, Fig. 1). To identify any dimorphic relationships within this group

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[3] PALFRAMAN (1966) gave different figures because he regarded the protoconch as the first whorl, whereas MAKOWSKI (1963) viewed the nepionic constriction as the end of the first whorl. The number of whorls is given herein according to MAKOWSKI's method.

is hardly possible. On the other hand, no other group than *Taramelliceras* appears to be suitable as a potential macroconch for *Creniceras*.

The interpretation of *Taramelliceras* and *Creniceras* as a dimorphic pair was disputed by CALLOMON (1969, p. 117), who pointed out that many Early Oxfordian species of *Taramelliceras* cannot be assigned to any counterparts within *Creniceras*. This remark would be correct if paleontologists dealt indeed with biological species. Given the fact, however, that we deal here with morphospecies, the "species" are much more easily distinguished in richly ornamented *Taramelliceras* than in almost nonornamented *Creniceras*.

It appears that either both MAKOWSKI (1963) and PALFRAMAN (1966) were right and *Taramelliceras* s.s., *Richeiceras*, and *Creniceras* represented a trimorphic group; or *Creniceras* did not have any macroconch counterpart, and its males and females had the same shell-size distribution.

11. *TARAMELLICERAS (PROSCAPHITES) MINAX* AND *POPANITES PATURATTENSIS*

The species *Taramelliceras (Proscaphites) minax* (BUKOWSKI) and *Popanites paturattensis* (GREPPIN) were regarded by MAKOWSKI (1963, p. 24, Textpl. III) as a dimorphic pair.

The author's collection of bed-by-bed collected 30 specimens of *T. minax* and more than 100 specimens of *P. paturattensis* indicates, however, that these two forms have different stratigraphic ranges: *T. minax* occurs in the Bukowskii and Costicardia Subzones, whereas *P. paturattensis* appears only in the upper part of the Costicardia Subzone and disappears within the Tenuicostatum Subzone. Furthermore, there exist forms intermediate between *T. minax* and *P. paturattensis*. These data corroborate a suggestion presented by MAŁECKI & TARKOWSKI (1982) that *T. minax* is ancestral to *P. paturattensis*.

In the context of the present work, another aspect of phenotypic variation in these two species is important. A decrease in shell size and whorl number through geological time is apparent in the evolution of this stock. The oldest representatives of *T. minax* have 5.5 whorls and up to 45 mm in shell diameter (= 32.5 mm in phragmocone diameter). The youngest representatives of *P. paturattensis* have only a little more than 4 whorls and no more than 11 mm in diameter (= 6.5 mm in phragmocone diameter). This decrease in shell size (Text-fig. 7) is accompanied by the waning ornamentation, so that the youngest representatives of *P. paturattensis* are almost entirely smooth at maturity and resemble (*cf.* MAKOWSKI 1963, p. 28) the early morphological stages in development of *T. minax*.

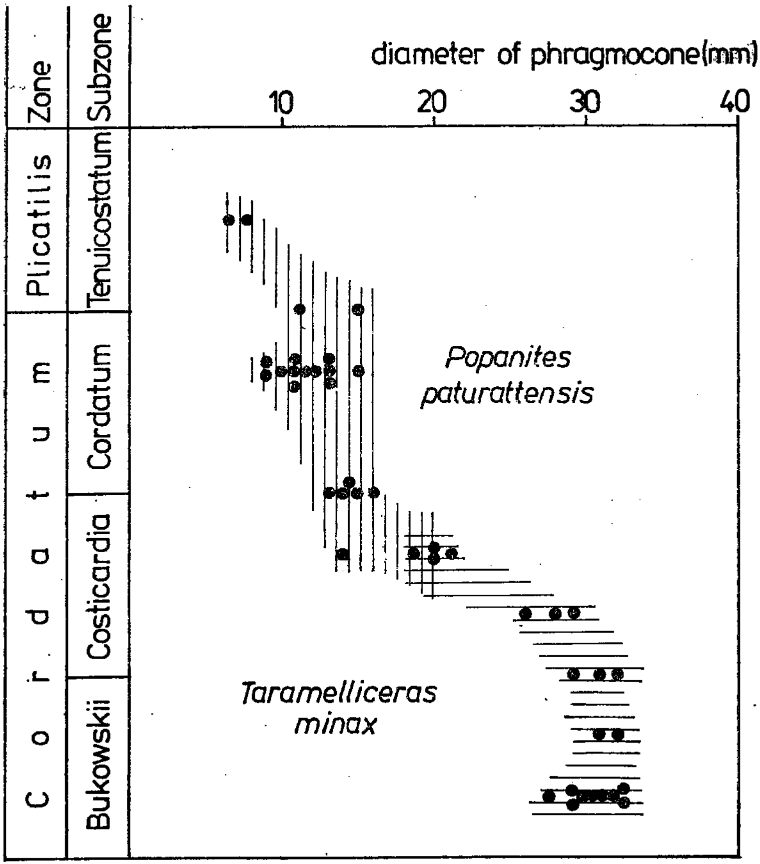


Fig. 7. Decrease in phragmocone diameter of *Taramelliceras minax* — *Popanites paturattensis* phyletic lineage

This is, then, a case of progenesis, that is, the achievement of maturity at progressively earlier stages of ontogenetic development. This example strongly undermines the claim that the number of whorls is diagnostic of a particular sex. The group of *T. minax* and *P. paturattensis* represents a continuum of forms filling the "gap" between presumed micro- and macroconchs.

EVIDENCE FROM LIVING CEPHALOPODS

Recent studies on living cephalopods have brought much new information on their development, growth rate, sexual maturity, and reproduction. This information cannot be directly extrapolated to the fossil record, but it nevertheless is suggestive of some striking analogies with the observations discussed above.

The following observations of WELLS & WELLS (1977) are significant in the context of the present discussion: *(i)* the sexes are separate in all cephalopods, which, unlike some other mollusks, never change sex in the course of their lifetime; *(ii)* individual longevity of cephalopods ranges from a few months to 3 years; *(iii)* it appears that death typically is the consequence of mating and egg-laying in cephalopods.

Sexual dimorphism in body (or shell) size does not seem to be well expressed in living cephalopods. DEAN & WILEY (*fide* HAVEN 1977) observed that shell size is unreliable as an indicator of sex in adult *Nautilus*. SAUNDERS & SPINOSA (1978) showed that the male shell is, on the average, 5.5% larger and 9% wider than the female shell of *Nautilus*. Among squids in the Indian Ocean (Text-fig. 8), the size differences between the two sexes often are minute and variable even within one genus (ZUEV 1971). A variation in size difference between the two sexes has also been recorded in the Atlantic squids *Loligo pealei* and *L. opalescens* by ARNOLD & WILLIAMS-ARNOLD (1977). It appears that, "in most species males and females are rather alike in form, (...) but there are exceptions among secondary pelagic octopods, and of these *Argonauta* shows extreme sexual dimorphism, with minute males" (WELLS & WELLS 1977, p. 293).

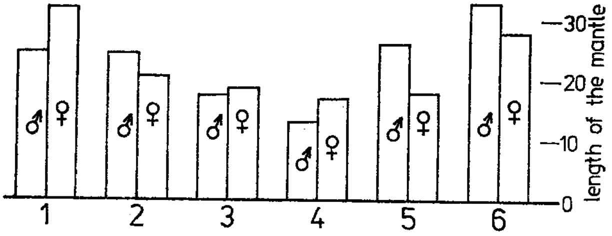


Fig. 8. Maximum size of males and females of some recent cephalopod species from the Indian Ocean (based on the data presented by ZUEV 1971, Table 12)

1 — *Symplectoteuthis oulaniensis*, 2 — *Loligo* sp. *A*, 3 — *Loligo duvauceli*, 4 — *Loligo edulis*, 5 — *Sepioteuthis lessoniana*, 6 — *Sepia pharaonis*

In both the Octopoda and the Decapoda, however, a considerable variation in body size (or to be more precise, mantle length) within a single sex has been observed. In *Octopus vulgaris*, for instance, two cohorts of females were found: one cohort lived 15 months, the other 18—24 months; the difference in longevity had clear effects on variation in size (WELLS & WELLS 1977). This difference was caused by differential timing of hatching and breeding, with egg-laying always leading to death. Females that hatch in spring, breed and die in the summer of the following year; females that hatch in late summer, in turn, breed only during their second year. Similar observations on this species were reported by MANGOLD & FROESCH (1977) from the Catalonian Sea;

these authors found immature females 4 kg in weight, but also mature females only 0.5 kg in weight.

In the squid *Sthenoteuthis pteropus* from the tropical Atlantic, ZUEV (1976) found three groups of mature females different in body size (Text-fig. 9). This variation is due entirely to differential rates of attaining maturity: early maturing females attain maturity at the mantle length of 17—30 cm, and their final size does not exceed 35 cm; small late maturing females attain maturity at 33—40 cm and do not exceed 45 cm; big late maturing females reach at least 40 cm in mantle length before maturation, and their final size ranges up to 50—60 cm. In the same squid species in the east-central Atlantic, small and big mature females can be distinguished (ZUEV & *al.* 1979). The growth rate is the same in both the groups, but small females more rapidly attain sexual maturity. There is a correlation between the rate of maturation and surface water temperature. Big mature females comprise the entire population at the temperature of 18—22° C. At higher temperatures, however, small mature females also appear, and they predominate the population at the temperature of 26—30° C.

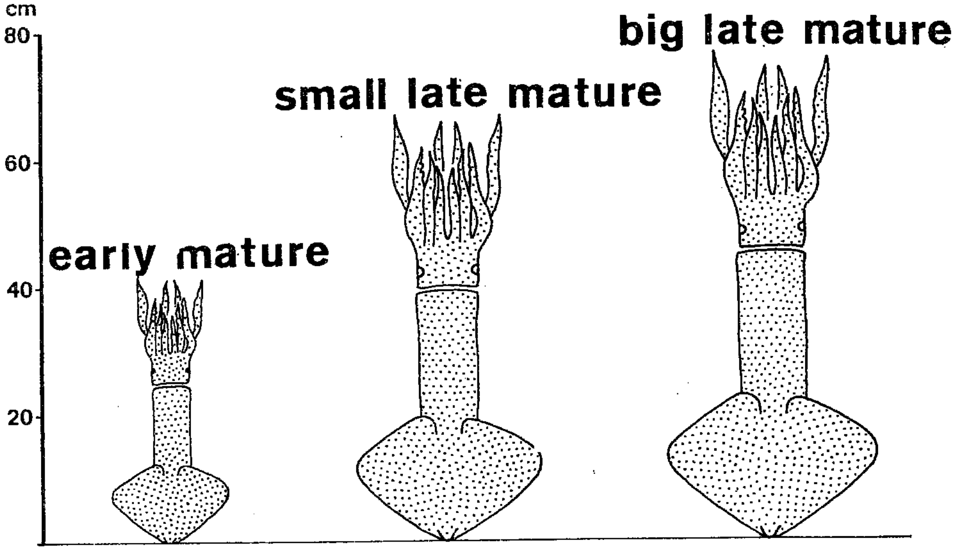


Fig. 9. Three-sized mature females of *Sthenoteuthis pteropus* from the tropical Atlantic (based on the data presented by ZUEV 1976)

In the squid *Ornithoteuthis antillarum*, the maximum body size is 125 mm for tropical Atlantic forms, 168 mm for individuals living off the shore of Uruguay, and even 188—196 mm for individuals in Bermuda. NESIS & NIGMATULLIN (1979) explain this variation by a decrease in the rate of sexual maturation in cooler waters at the margins of the geographic range typical of this species; in conjunction with continuous growth of the animal, this slowdown leads to larger body sizes.

In an Indo-Pacific squid, *Sthenoteuthis oualaniensis*, NESIS (1977) found early and late maturing forms among both males and females. They differ in the final body size, and the early maturing forms are restricted to the warmest-water part of the geographic range typical of the species. NESIS (1977, p. 25) also gives several other examples of sympatric populations of the ommastrephids which differ in the timing and location of breeding and in the rate of growth and sexual maturation.

The effect of environmental factors on the rate of maturation is illustrated by the phenomena observed by ZUEV (1971, p. 53) in the squid *Loligo duvauceli*. Two allopatric populations of this species (one in the Persian Gulf, the other in the Sonmiani Bay) differ not only in the occurrence of either early or late maturing females, but also in the consequent reversal of the size relationships between males and females (Text-fig. 10).

In summary, the size differences between females and males are negligible in the majority of living cephalopods. Within a single species,

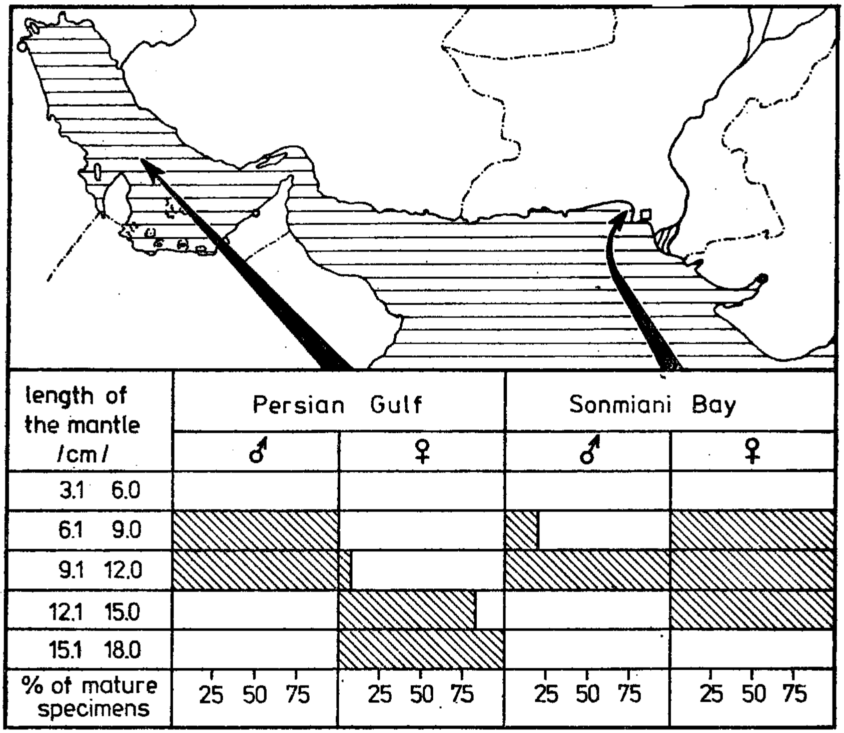


Fig. 10. Percentage of mature males and females of the squid *Loligo duvauceli* versus length of their mantle in two different regions of the Indian Ocean (based on the data presented by ZUEV 1971, Table 3)

however, several populations of one sex may occur which differ in body size. This variation is related to differential rates of sexual maturation, which appear to be controlled by environmental factors.

DEVELOPMENTAL POLYMORPHISM IN AMMONITES

According to the theory of sexual dimorphism in ammonites (MAKOWSKI 1962, 1963; CALLOMON 1963), the growth rate and the morphological development were identical at the early ontogenetic stages of both micro- and macroconchs. Recognition of the identity of such early ontogenetic stages makes, then, the basis for identification of the corresponding micro- and macroconchs. At later stages, however, ontogenetic development differed between micro- and macroconchs. The microconch attained sexual maturity, which was manifested by modifications of shell morphology and a decline in growth rate down to zero. The macroconch, however, continued to grow and reached further stages of morphological development. Finally, the macroconch also attained sexual maturity, stopped to grow, and acquired morphological modifications. The difference in time necessary for conspecific males and females to attain maturity was equivalent at least to the time needed to grow one full whorl of the shell (MAKOWSKI 1963).

The theory of sexual dimorphism thus implies that the microconch sooner reached the final stage, lived shorter (*e.g.*, KULICKI 1974, p. 219), and hence, attained only a smaller shell size and earlier stages of morphological development. Such a relationship between the micro- and macroconch corresponds to progenesis (*see* Text-fig. 2).

It is worth noting that such relationships among Middle Jurassic perisphinctids were discussed already in the 19th century by TEISSEYRE (1889), who described large-sized individuals as "slowly aging forms" (*"langsam alternde Formen"*) as compared to smaller-sized „quickly aging forms" (*"rasch alternde Formen"*). Three years later, MUNIER-CHALMAS (1892) interpreted such a relationship in terms of sexual dimorphism.

It is the fundamental premise of the theory of sexual dimorphism that, in each case where the theory is applicable, two morphs exist which constitute "a couple". The examples *1—11* discussed above suggest, however, that *(i)* more than two morphs commonly exist, instead of only the micro- and macroconch; *(ii)* a single morph can exist in a wide geographic area or over a considerable time interval. It is to note that the three-sized assemblages of the morphs were already stated by IVANOV (1975), who recognized not only the micro- and macroconchs, but also the megaconchs. The existence of mono- and trimorphic systems undermines the theory of sexual dimorphism and, thus, suggested herein is an alternative hypothesis of the developmental polymorphism in ammonites. It states that occurrence of various numbers of ammonite morphs which differ in shell size and morphology is due to a variation in time needed for sexual maturation of individuals hatched in particular spawns.

This hypothesis is consistent with observations on living cephalopods and accounts for phenomena observed in the fossil record. Ammonites have a number of characteristic stages of shell development, which are all present in ontogeny of the largest in a group of related morphs. The maturation and the gerontic stage account for additional morphological modifications (CALLOMON 1969, p. 111). The maturation is marked by interruption of the normal morphological development and by the appearance of these additional modifications. Each completely preserved ammonite shell represents, then, either a part of, or (in the case of the largest morph) the entire sequence of morphological development (Text-fig. 11) characteristic of a given group plus its final stage (*i.e.*, mature and gerontic stages).

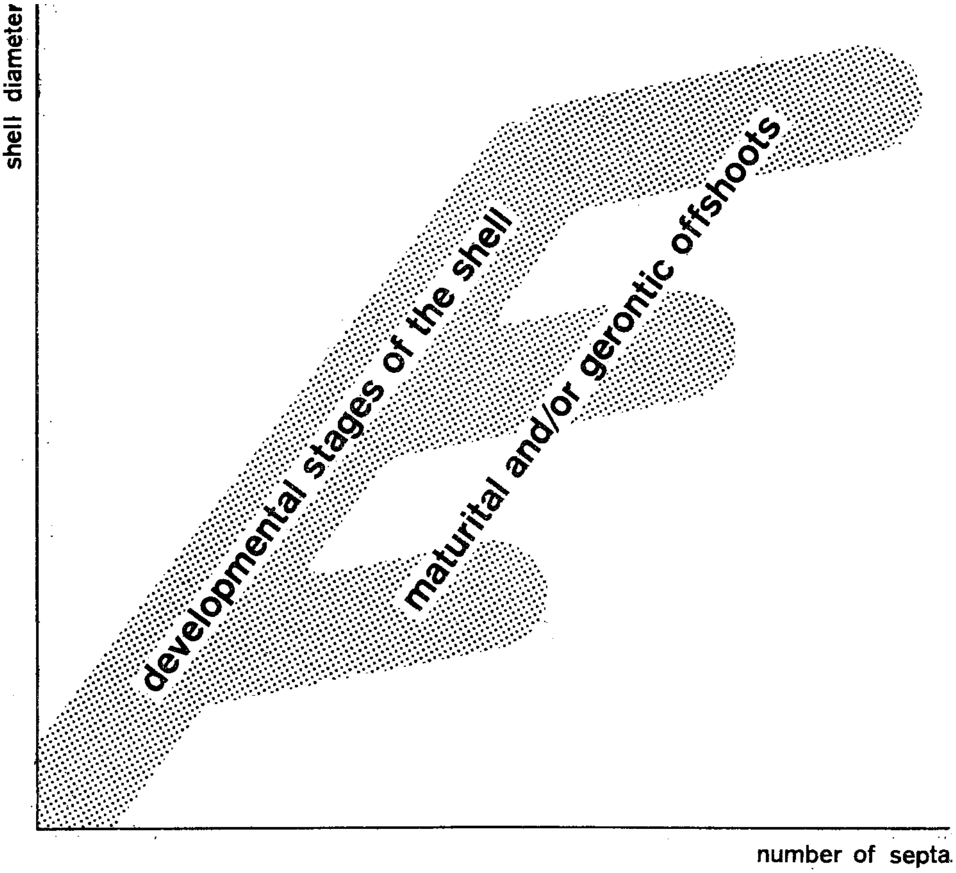


Fig. 11. Idealized sketch of the origin of a trimorph species

This component of the theory of developmental polymorphism is fully consistent also with the concept of sexual dimorphism. According to the latter, however, two distinct ages of maturation are specific for each ammonite species. Microconchs attain maturity first and macroconchs later. According to the theory of developmental polymorphism, in turn, there may be a whole variety of ages (*e.g.* three in Text-fig. 11) at which maturity is attained in a population; this variety is reflected by the variation in shell size and morphology. If there is only one specific age of maturation, it may be either early or late in ontogeny; in the former case, the only morph is the mini- or microconch, whereas it is the macroconch in the latter case. Megaconchs, as interpreted by IVANOV (1975), escape from the assemblage of morphs which reflect developmental polymorphism; they realized another life strategy to grow continously until their death, and not displaying any final stage, but having a lowered breeding potential all that time. According to IVANOV (1975, p. 50), a differentiation of the population into small, quickly maturing (micro-), median (macro-), and larger, long-growing forms (megaconchs) results from diverse ways of "acquiring biological progress and from adaptative radiation".

It is difficult to speculate about the reasons for existence of only one, or two, or more morphs within a single population. Biological evidence suggests some environmental factors. Some paleontological observations are consistent with this suggestion. For instance, some particular facies in the Upper Jurassic sponge megafacies (Lochen Facies in West Germany, Jasna-Góra Beds in Poland, area of Poitou in France) appear to be predominated by early maturing forms. Contrarily, the examples presented by IVANOV (1975) clearly indicate that the Late Jurassic environment of the Volga Basin has prefered the long-growing forms (megaconchs).

In the case of the genus *Quenstedtoceras* from Łuków, the three morphs have evidently been stated. KULICKI (1974) when describing irregularities in relative density of septa in such specimens from Łuków, distinguished 5 phases of the septal crowding, and called them the depressions; the three last depressions he attributed to the sexual cycles (depression *III* in males, versus *III* and *IV* in females) and to the terminal stages (depression *IV* in males, and *V* in females). All three depressions fall into narrow intervals between successive septa (Text-fig. 12), and, what is more important, the final stage in the investigated miniconchs of the genus *Quenstedtoceras* coincides with the depression *III* which KULICKI (1974) interrpreted as the beginning of the sexual cycles.

Consequently, it seems resonable to state that in the discussed *Quenstedtoceras* specimens from Łuków the three last depressions reflect the three sexual cycles, and the mini-, the micro-, and the macro-

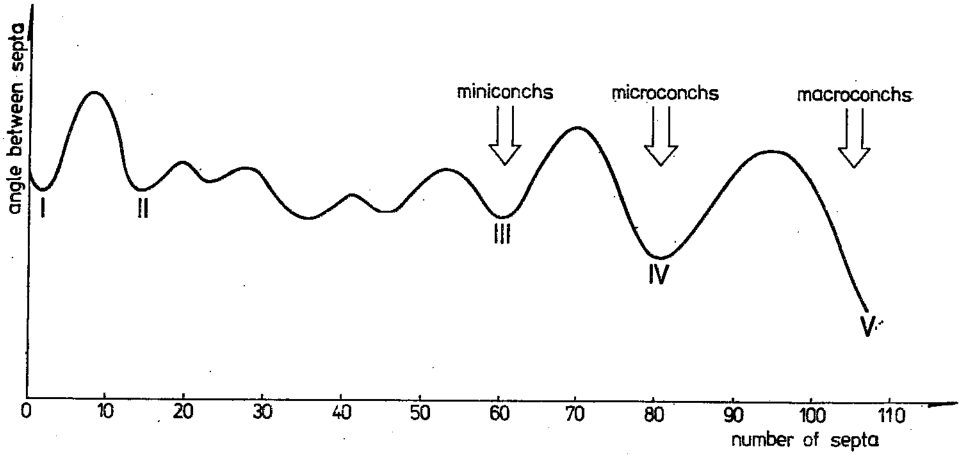


Fig. 12. Distribution of mini-, micro- and macroconchs of *Quenstedtoceras henrici* R. DOUVILLÉ plotted on an idealized sketch presenting the curve of relative density of septa (data reinterpreted *from:* KULICKI 1974, Fig. 8)

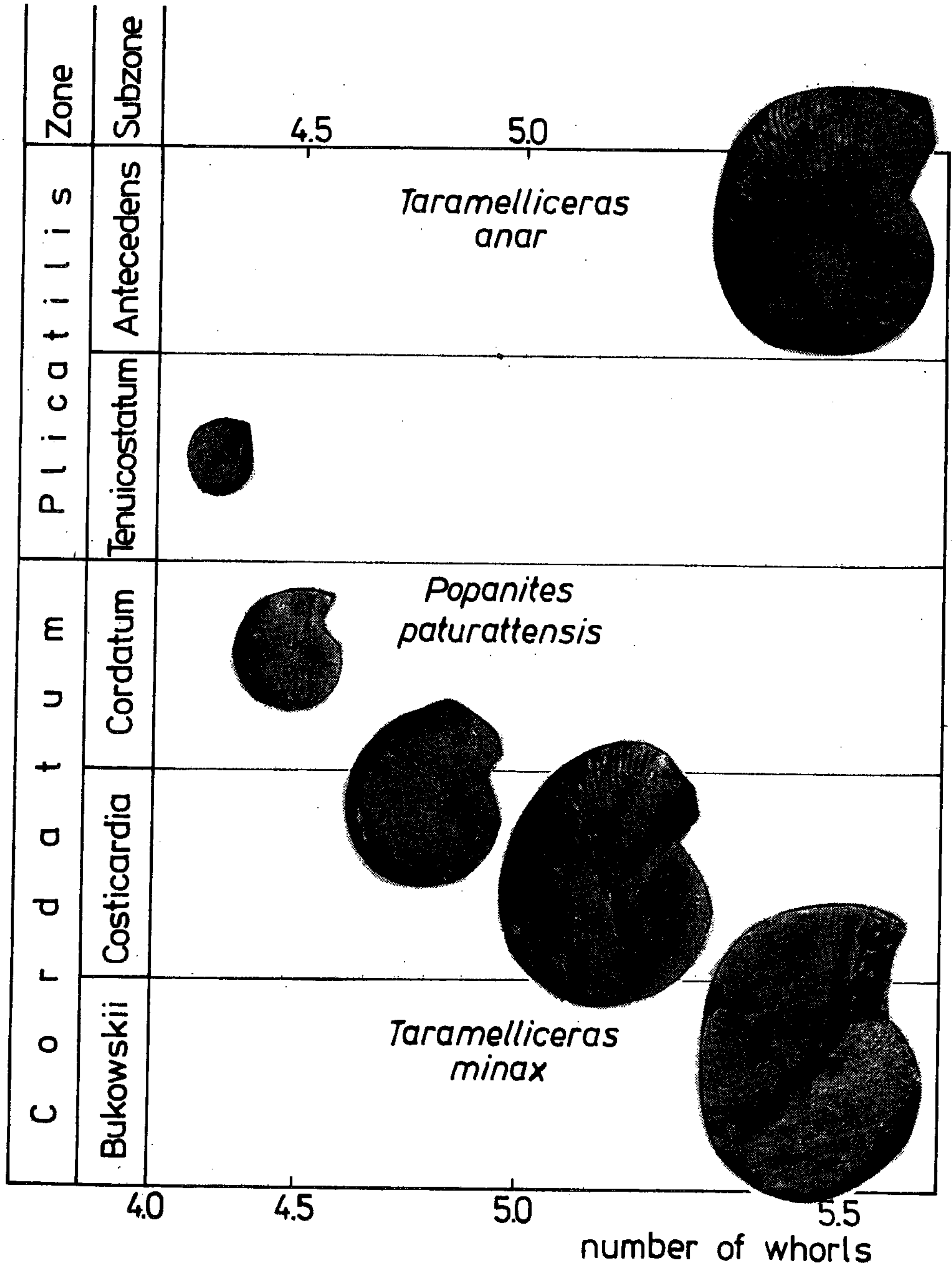
conchs represent these subpopulations which attained the sexual maturity and the gerontic stage in three different spans of their growth time.

The interpretation of ammonite polymorphism as caused by a variation in the age of maturation has implications for phylogenetic reconstruction, taxonomy, and even stratigraphy. These problems can be illustrated by the two forthcoming examples.

TARAMELLICERAS MINAX AND *TARAMELLICERAS ANAR*

The species *Taramelliceras (Proscaphites) minax* (BUKOWSKI) occurs, as given above, in the Lower Oxfordian Bukowskii and Costicardia Subzones. In the upper part of the Middle Oxfordian Plicatilis Zone, there appears *Taramelliceras (Proscaphites) anar* (OPPEL), very similar to *T. minax* in shell size, shape, and ornamentation. The two forms are separated by two ammonite subzones; hence, they were not linked with each other, and the ancestry of *T. anar* was regarded as puzzling (ZIEGLER 1974, Fig. 6).

The two subzones that separate *T. minax* from *T. anar* contain, however, *Popanites paturattensis* (GREPPIN) which is an early maturing descendant of *T. minax*. It is very likely that the phyletic link between the late maturing *T. minax* and *T. anar* is represented by the early maturing *P. paturattensis*. Speaking in other terms, one might say that two macroconchs are phyletically linked through a microconch (Pl. 4).



Phyletic lineage *Taramelliceras (Proscaphites) minax* (BUKOWSKI) → *Popanites paturattensis* (GREPPIN) → *Taramelliceras (Proscaphites) anar* (OPPEL)

Late maturing morphs, *Taramelliceras minax* (BUKOWSKI) and *Taramelliceras anar* (OPPEL), are linked by the early maturing morph, *Popanites paturattensis* (GREPPIN)

GENUS *CRENICERAS*

The genus *Creniceras* ranges from the uppermost Callovian to the Upper Kimmeridgian. In the lower part of its range, in the Lamberti Zone through the Cordatum Zone, it is represented by *C. renggeri* (OPPEL) and "*C. crenatum*" (BRUGUIÈRE). The next successive representative of the genus, *C. lophotum* (OPPEL), appears only in the lower part of the Upper Oxfordian. The last form of this genus, *C. dentatum* (QUENSTEDT), appears in the Hypselocyclum Zone and ranges into the Eudoxus Zone (ZIEGLER 1958, 1974). The gaps in the stratigraphic record of *Creniceras* were initially explained by iterative evolution (ZIEGLER 1958). Subsequently, ZIEGLER (1974) interpreted all these forms of *Creniceras* as a single phyletic lineage which sometimes had decreased in abundance to become invisible in the fossil record.

When interpreted in the light of the theory of developmental polymorphism, *Creniceras* does not represent a separate biological entity. It includes early maturing forms of another ammonite group, most likely some representatives of *Taramelliceras.* The appearance of *Creniceras* marks periods and areas with ecological circumstances that favored early maturation. In other times and areas, the evolution of this ammonite group took place entirely (Text-fig. 13) within the limits of the late maturing *Taramelliceras.*

FINAL REMARKS

The developmental polymorphism concept, herein presented, is based on observations of the two superfamilies of the Oxfordian ammonites. It concerns neither an exceptional case nor special groups of ammonites. The examples of the superfamily Perisphinctaceae from the Jurassic and Cretaceous, described by IVANOV (1975), seriously enlarge the range of this phenomenon. All the herein discussed examples indicate that the interpretation of the size diversity by the theory of sexual dimorphism does not embrace the whole pattern of relations observed amongst the recognizable morphs.

The commonly reported couples of morphs (micro- and macroconchs) appear, in the light of the developmental polymorphism concept, to be only one of the possibilities realized by the ammonites. It is not, however, possible to judge how this commoness is natural, or how it reflects either the theory of sexual dimorphism or the non-recognition, or even non-recognizability of a greater number of the morphological stages. This question may be answered by a careful survey on the occurrence of all the morphs which are present in deposits of a definite area or a definite spantime.

The existence of merely one morph throughout a certain spantime (examples *5*, *6*, *11*) is entirely consistent with the concept of developmental polymorphism, even in a group that yields several morphs in other times. Therefore, the temporal differences in the appearance or disappearance of the corresponding micro- and macroconchs, which have undermined (as stated already by BRINKMANN 1929, p. 212) the theory

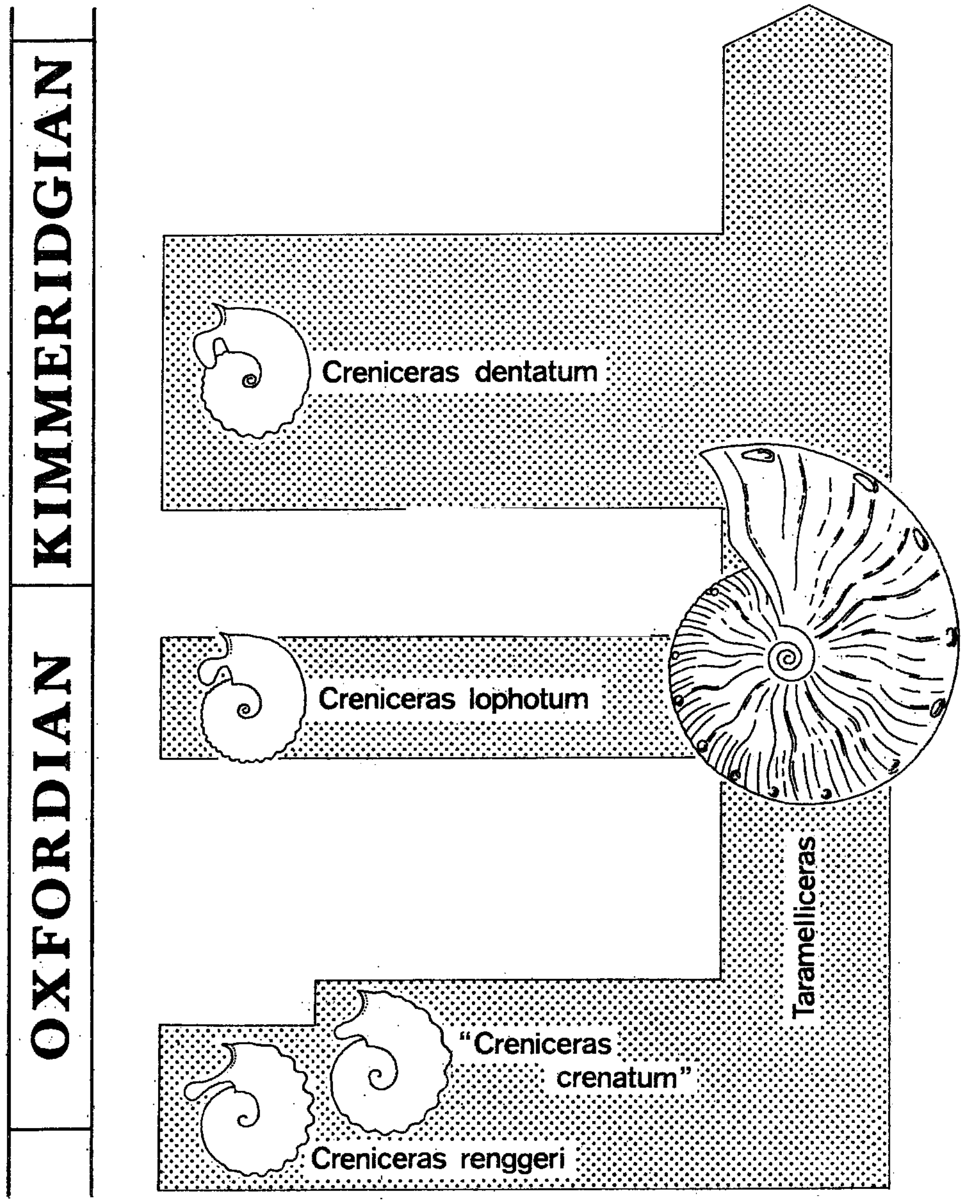


Fig. 13. Interpretation of an interrupted occurrence of the genus *Creniceras* as the early mature morphs of the genus *Taramelliceras*

of sexual dimorphism, become now an important line of inquiry to recognize when the one-sized and very often early mature morphs appear in the phylogenetic lineage — at its beginning, as results from the data presented by MARCHAND (1985), or at its end, as results from the data presented by GLENNISTER (1985) and CALLOMON (1985, Fig. 8 Ω).

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Institute of Geology
of the University of Warsaw,
Al. Żwirki i Wigury 93,
02-089 Warszawa, Poland

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B. A. MATYJA

POLYMORFIZM ROZWOJOWY U AMONITÓW OKSFORDZKICH

(Streszczenie)

W pracy niniejszej przedstawiono odmienną od teorii dymorfizmu płciowego koncepcję dotyczącą zróżnicowania wielkości muszli amonitów. W swej klasycznej formie dymorfizm płciowy rozpoznany jest głównie wśród amonitów jurajskich (fig. 1). Na amonitach jurajskich oparto również prezentowaną tu koncepcję.

Rozpatrzono szereg przykładów dotyczących przedstawicieli oksfordzkich nadrodzin Stephanocerataceae i Haplocerataceae, u których w relacji jaką zarezerwowano dla samca i samicy pozostają więcej niż dwie morfy, bądź też gdy na pewnym obszarze lub w pewnym przedziale stratygraficznym istnieje tylko jedna morfa (fig. 3—7 oraz pl. 1—3). Przykłady te dowodzą, że przypadek współwystępowania dwóch morf, eksponowany przez teorię dymorfizmu płciowego, nie wyczerpuje wszystkich możliwości istniejących wśród amonitów.

Zjawisko współwystępowania w obrębie jednego gatunku wyraźnie wyodrębnionych subpopulacji różniących się wielkością końcową obserwuje się u współczesnych głowonogów, tyle tylko, że nie odzwierciedla ono różnic pomiędzy płciami (fig. 8). Obserwowane jest ono bowiem u przedstawicieli jednej płci i wiązane ze zróżnicowanym tempem dojrzewania płciowego (fig. 9). To ostatnie z kolei wydaje się być uwarunkowane wpływem środowiska (fig. 10).

Przykłady z materiału kopalnego wsparte obserwacjami u głowonogów współczesnych pozwoliły sformułować koncepcję polymorfizmu rozwojowego. Przyjmuje ona, że relacje w jakiej pozostają do siebie powiązane wczesnym etapem rozwoju morfologicznego, a różniące się wielkością morfy (mini-, mikro-, czy makrokonchy), wynikają z zatrzymywania rozwoju muszli (jej wielkości i stadiów rozwoju morfologicznego) w wyniku osiągania przez amonity stadium dojrzałości płciowej, tak jak to jest przyjmowane w procesie progenezy (fig. 2). Różny czas osiągania tego stadium przez różne osobniki powoduje powstanie szeregu morf różniących się wielkością końcową (fig. 11 i 12). Podano interpretacje (fig. 13 oraz pl. 4) powiązań filogenetycznych łączących formy wczesno- i późnodojrzewające wśród górnojurajskich Haplocerataceae.