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HENRYK MAKOWSKI

Some remarks on the ontogenetic development and sexual dimorphism in the Ammonoidea

ABSTRACT: The writer discusses the problem, suggested by some authors, of interpretation of small forms in Ammonoidea as neotenic ones. The classical conception of neoteny is connected with presence of a larval stage which in Ammonoidea was very tiny. It therefore appears that small forms in Ammonoidea are highly advanced in their ontogenetic development as compared with a larval stage of this group. Numerous examples are also known of the dimorphism, the large and small forms in which differ in their dimensions very indistinctly. The latter facts contradict a conception of a neotenic character of small forms. The writer discusses also the problem of systematics of the Ammonoidea against the background of the commonly being accepted theory of sexual dimorphism.

INTRODUCTION

Several papers and opinions on sexual dimorphism in the Ammonoidea have recently appeared in literature. The problems of systematics related to this phenomenon are dealt with by the authors who also discuss various concrete examples of dimorphism or certain biological interpretations of the essence of this phenomenon. The present writer's intention is to contribute some of his remarks concerning these problems.

SOME OF THE BIOLOGICAL INTERPRETATIONS OF SEXUAL DIMORPHISM IN THE AMMONOIDEA

Both within the framework of the theory of sexual dimorphism and apart of this theory, large forms of the Ammonoidea have been interpreted by many authors as normally developed and small ones as underdeveloped. The latter were considered by the followers of the theory of dimorphism as small, dwarfish, retarded and even neotenic males, while others saw in them symptoms of the phylogenetic ageing. L. F. Spath (1938) interpreted them as end forms of recessive side lines.

In his recent work on this problem, J. Guex (1970) expresses the supposition that the small forms are neotenic males. At the same time, he emphasizes that, as far as he knows, such a conception has for the time been expressed by H. Tintant (1963). In actual fact, however, the theory of this type has first been formulated by A. N. Ivanov (1960), which has already been mentioned before by the present writer (Makowski 1962b, pp. 36—38). Since A. N. Ivanov's (1960) work was published in a rather unattainable periodical, the writer's intention is to briefly present its fundamental contents.

First of all, it should be, however, explained that A. N. Ivanov's (1960) theory was developed on the basis of the example of the genera *Cadoceras* Fischer and *Pseudocadoceras* Buckman which occur abundantly and in a good state of preservation in the Callovian of Central Russia. Large forms, assigned to the genus *Cadoceras,* in mature stage reach considerable diameters (more than 100 mm) and have a completely smooth last body chamber. On the other hand, the development of small forms becomes arrested in the ribbed stage and, among other things, they differ from large forms in having their last whorl more flattened than the young specimens of large forms equalling them in diameter. Identical morphological conditions are recorded (Makowski 1962a, b) in the genus *Quenstedtoceras* Hyatt.

A. N. Ivanov (1960) believes that the development of small, more flattened offsprings of the genus *Cadoceras* might take place by dradigenesis, but that it also took place by neoteny, during which the underdeveloped descendant forms of the genus *Cadoceras* were arrested in their growth and thus produced dwarfish forms. Such an origin is precisely observed in the genus *Pseudocadoceras.* The characters of this genus presented above have already been noticed by S. S. Buckman (1919) who is the author of this genus and who emphasizes that the genus *Pseudocadoceras* includes form similar to the young individuals of the genus *Cadoceras* which, however, do not reach the typical stage of this genus, preceded by the appearance of the gerontic character, that is, the untwisting of the whorl spiral. At the same time, these forms remain flatter than the representatives of the genus *Cadoceras.*

Furthermore, A. N. Ivanov (1960) describes two species which occur together under the same conditions, that is, *Cadoceras tschefkini* (d'Orb.) and *Pseudocadoceras orbignyi* Maire. The former, *Cadoceras tschefkini* (d'Orb.) reaches 150 mm in diameter, has a smooth last body chamber and its aperture is provided with an elongate protuberance on the siphonal side. *Pseudocadoceras orbignyi* Maire grows only up to 30 mm in diameter and becomes arrested in this ribbed stage. Beginning with a diameter of 15 mm, there already starts the development of the last body chamber and further on, there takes place the untwisting of whorls. The last septa before the living chamber are strongly condensated. These characters leave no doubts that we have to do with adult forms. The sculpture consists of ribs which on the last living chamber become more and more widely spaced and prominent. The aperture has a protuberance on the siphonal side, but no lappets are observed.

It is also emphasized by A. N. Ivanov (1960) that the young development stages of the two species under study are, up to a diameter of 15 mm, quite similar to each other.

Further on, explaining the biological interpretation of this phenomenon, this author emphasizes that in literature there are many terms for defining various ways of morphological evolution in which the underdevelopment or the arrest of the ontogenic development take place. Here, the term neoteny may be used. According to a general interpretation of the phenomenon under study, the genus *Pseudocadoceras* is believed by him to be a neotenic form of the genus *Cadoceras*.

The described example of the phylogenetic change in the ammonites by neoteny clearly shows that neoteny, as phylembryogenesis (or, more accurately, phylontogenesis), differs from bradigenesis. In neoteny, the underdevelopment of the ammonites is expressed not only in falling--off of the last ontogenetic stages of the ancestors, but also in the arrest of growth, while in bradigenesis the slowing-down takes place in the rate of ontogenetic changes, concerning one or a few characters, which consequently do not appear in the last stages although the growth of the body takes place in principle quite normally. In neoteny, the ontogenetic development is heterochronous in character which is expressed in a relatively early development of sexual organs not recorded in the case of bradigenesis. The earlier sexual maturing of the underdeveloped representatives of the genus *Cadoceras* might take place as an adaptation caused by an increased rate of destruction of large individuals. Further on, A. N. Ivanov maintains that the neotenic forms are likely to live according to a different mode of life than that of large or normal forms. He also points out that the common occurrence of large forms of *Cadoceras tschefkini* (d'Orb.) and neotenic, dwarfish forms of *Pseudocadoceras orbignyi* Maire may be a basis for the supposition that this pair of species is an example of sexual dimorphism. Finally, this author recalls that the importance of neoteny to evolution was discussed by many other authors, including A. N. Severtsov (1939) and I. I. Schmalhausen (1939). Thus, we can state that the problem of neoteny, dealt with by A. N. Ivanov, has been presented in a fairly exhaustive manner as far as it was possible with the use of the single example. It may be also noted that the role of neoteny as an agent accelerating the evolution in Ammonoidea was already stressed by H. Schmidt (1926).

The next author, H. Tintant (1963), elaborating the Callovian ammonites of the family Cosmoceratidae, discusses the fact, known for many years, of the concurrence, within this family, of large and small forms which, within the framework of formal systematics, are assigned to various genera or subgenera. H. Tintant maintains that, not forejudging the nature of this phenomenon, small forms as the adults, in which juvenile characters have been preserved, bring to mind the phenomenon of neoteny.

A similar supposition is also presented by J. Mattei (1969) in his work on the new genus *Pseudopolyplectus* Mattei he erected and in which small forms appear as a result of neotenic processes being in their essence palyngenetic ones. This process of the development of small forms is also defined by J. Mattei as pedomorphosis, since juvenile characters distinct in their entire group have persisted in these forms.

J. Guex (1970) also tends to agree with such a biological interpretation of small forms in the ammonites. This author asks the question: is it possible to recognize small forms as neotenic ones? At the same time he explains that this term is used to designate the forms which have reached their reproductive capability prior to the completion of their ontogenetic development and he concludes that an affirmative answer may be given to this question if we consider the fact that the dimorphism of the ammonites is sexual in character.

Thus, according to this author, large forms may be considered as those developed as a result of a normally completed ontogenetic development, while their counterparts among small forms are neotenic ones, developed as a result of the arrest in the process of ontogeny and the speeding-up of the reproductive capability.

In comparing the views presented in the works discussed above, we can notice that A. N. Ivanov (1960), although not rejecting the idea that large, normally developed forms of *Cadoceras tschefkini* (d'Orb.) and small, neotenic forms of *Pseudocadoceras orbignyi* Maire, concurring in these same beds, may be a dimorphic pair, but examines neoteny as a creative evolutionary process which directly leads to the formation of a new strain of the ammonites, that is, a new taxonomic unit. The same was A. N. Severtsov's (1939) and I. I. Schmalhausen's (1939) view on the role of neoteny in the evolutionary proceses. The opinions of H. Tintant (1963) and J. Mattei (1969) may be also compared with such a presentation of this phenomenon. On the other hand, in regard to J. Guex's (1970) opinion, it should be stressed that, although the development of the dimorphic, neotenic form was bound to set in motion new evolutionary processes of the species comprised by this phenomenon, but — in his view — the role of neoteny in the evolutionary process was considerably smaller, as it did not directly lead to the formation of a new taxonomic unit.

Starting the discussion of the views and suppositions concerning the neotenic character of small forms in the ammonites, summarized above, we should begin with the explanations of the meaning of the term neoteny. Such an explanation may be found in nearly each of the more extensive textbooks of general zoology. Most authors maintain that this term is used for determining the phenomenon which occurs in various animals and which consists in reaching sexual maturity and reproductive capability by larval stages. This phenomenon is known in both vertebrates and invertebrates in which development stages occur determined by the name of larval stages and whose way to maturity leads through metamorphosis. The axolotl (*Ambystoma*), which reaches the sexual maturity, at the same time preserving its larval respiration organs, that is, the gills, is a typical example of neoteny most frequently cited in textbooks of zoology. In other amphibians, this organ disappears in the process of metamorphosis. In axolotl, it may also disappear as a result of an artificially evoked metamorphosis. In such an understanding of neoteny, this phenomenon is not accompanied by dwarfishness, since the neotenic forms may reach the size of normally transformed forms as is precisely the case of the axolotl. Likewise, the term of neoteny thus understood may be applied only in the cases in which the ontogenetic development leads through the larval stage.

However, there are also instances of the use of the term neoteny in a less precise meaning, namely to denote a general underdevelopment sometimes combined with dwarfishness and accompanied by an earlier sexual maturation. This is precisely the reason why the following two explanations of this term are given in R. W. Pennak's (1964) zoological dictionary: 1) Attainment of functional sexual maturity in an animal otherwise immature; 2) Retarded development of individual structures.

It should, however, be mentioned that several species whose males are small and dwarfish are observed among the Recent cephalopods. According to A. Naef (1922), the males of *Argonauta argo* L. may, in extreme cases, be 1,000 times (per body mass) smaller than the females and despite this fact they are not considered as neotenic forms. Likewise, the males of the Prosobranchia are in many instances considerably smaller than the females, sometimes even justifying the term dwarfish, but nevertheless they are not considered as neotenic forms, since in their ontogenetic development they have passed through the larval stage and regular metamorphosis. A review of such cases in the Prosobranchia has previously been given by the writer (Makowski 1962b).

However, regardless of how we may understand the phenomenon of neoteny in general, it should be examined against the background of the ontogenetic development of a given taxonomic group and, therefore, if only a brief review of this phenomenon in the Ammonoidea and, for the sake of comparison, also in the Nautiloidea is presented below.

The ontogenetic development of both the Ammonoidea and Nautiloidea was the subject of very numerous works many of which are now of a merely historical importance.

Attention should first be attracted to the works of A. Hyatt (1872, 1894), who assumes that in the initial ontogenetic stages, a conchioline protoconch was formed in the Nautiloidea. In the forms with straight shells it might be preserved sometimes, but it always fell-off in twisted ones. A trace in the form of a cicatrix was left after the fallen-off protoconch on the beak of the shell of a nautiloid. These cicatrixes may be variously shaped, mostly they occur as a depression elongated in the plane of symmetry. A cicatrix of this type also occurs in the Recent nautili. Since the initial stages of ontogeny in the nautili have not been recognized, A. Hyatt gives a reconstruction of such a protoconch of the Recent *Nautilus* as a spherical vesicle. In the Ammonoidea, which descend from the nautiloids, the conchiolid protoconch became, on the other hand, calcified and permanently preserved at the beginning of the whorl of shell. In other words, this author assumes that the first chamber of the shell of a nautiloid (*e.g.*, the Recent *Nautilus*) is not homologous to the initial chamber of the shell of an ammonoid which represents a true calcareous protoconch and, consequently, the first chamber of a nautiloid would correspond to the second chamber of the Ammonoidea.

If a blindly terminating first chamber of the shell in the Ammonoidea was regarded unanimously by various authors as an initial stage of the ontogeny of shell, the fact of the existence of the cicatrix, mentioned above, on the beak of the shell of *Nautilus* and other fossil Nautiloidea aroused many discussions, which, in view of the ontogeny of the Recent *Nautilus* unrecognized so far, are still topical.

In earlier times, J. Barrande (1867—1877) believed that this cicatrix made up a trace of an aperture through which an embryo was connected with the yolk sac, or that this was an opening for the gill. Such views, due to their biological preposterousness, are now of course beyond any discussion.

In their monograph on the Nautiloidea from the Pennsylvanian of the U.S.A., A. K. Miller, C. O. Dunbar & G. F. Condra (1933) adopt A. Hyatt's theory of a falling-off protoconch. In his extensive work, devoted to this problem, O. H. Schindewolf (1933) concludes that the Recent *Nautilus* has not any falling-off protoconch and that no protoconch of such a type could occur in the fossil nautiloids, the cicatrix on shell beak being a trace of siphon attachment. According to the last named author, the first chamber of shell in the Nautiloidea is in this case an embryonal chamber quite homologous to the first chamber of shell in the Ammonoidea.

O. H. Schindewolf (1963) presents also a diagram of the phylogeny of the initial chamber of shell in the Tetrabranchiata. According to this diagram, the Orthoceratidae with a wide apical angle of shell and having a bowl-like initial chamber were initial forms, of which the Mesozoic Nautiloidea with a bowl-like initial chamber were evolved on the one hand and the Orthoceratidae with a narrow apical angle and a bulblike chamber on the other. The latter gave rise to the genus *Bactrites* Sandberger and they in turn to the goniatites and ammonites. On the basis of thin sections cut in the plane of symmetry, J. Böhmers (1936) studied the structure of initial whorls of numerous specimens of the Permian and Carboniferous goniatites assigned to the genera *Daraelites* Gemmellaro, *Pronorites* Mojsisovics, *Parapronorites* Gemmellaro, *Papanoceras* Hyatt, *Marathonites* Böse, etc. As follows from J. Böhmers' (1936), illustrations, no syphonal tubes have been preserved in the material studied, but the walls of shell were very well preserved and were not subject to recrystallization, which allowed him for an accurate observation of the structure of shell. As stated by this authors, he observed that the wall of shell (at the level of the 5*th* whorl) in the genus *Daraelites* was composed of three layers: 1) outer, darkcoloured, marked by black punctae and corresponding to the periostracum; 2) central, the thickest of them, light-coloured and most likely to correspond to the porcelain and 3) inner, mother-of-pearl in color and corresponding to the hypostracum. At the same time, he also states that sometimes he was able to notice that the wall of the initial chamber of the specimens, representing the genera *Pronorites* and *Parapronorites*, consisted near the first septum of two layers (ostracum and hypostracum). Further on, describing the initial chamber in the species *Papanoceras hameli* Smith, Böhmers states: „Die Wand der Anfangskammer ist kreisrund und geht ohne Unterbrechung in der Wand der Spirale über".

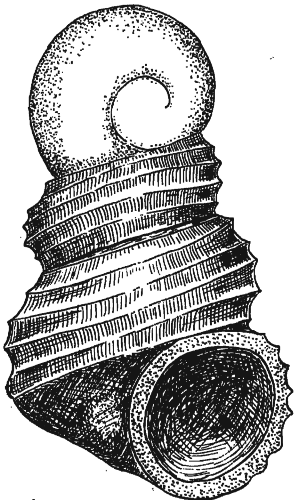
Thus, J. Böhmers' (1936) work discussed did not contribute anything new to previous works, since this author did not show a difference in the structure of the wall of shell which occurs between the first and the succeeding whorls.

The explanation of the development of the initial ontogenetic stages of shells in the Tetrabranchiata was considerably advanced only by recent works, primarily those by V. E. Ruzhentsev & V. N. Shimanskij (1954), H. K. Erben (1964, 1968) and T. Birkelund (1967). These authors contributed to a considerable extent to the recognition of the ontogenetic development of the shells of the Ammonoidea and less so to the explanation of this problem in the Nautiloidea, but a new light was indirectly thrown also on this latter problem.

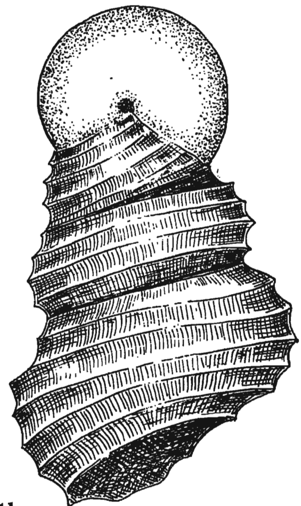
On the basis of H. K. Erben's (1964, 1968) and T. Birkelund's (1967) works referred to above, as well as on the basis of his own observations, the writer recognizes that three fundamental development stages may be distinguished in the ontogeny of the shells of ammonites. They may be distinguished concerning both their external morphology and the structure of the wall of shell. Stage *1* is formed by the initial chamber the wall of which is relatively simply composed of two layers. Stage *2* includes a tube forming about one whorl and terminating in a more or less strongly marked constriction. The wall of this tube, as could be found in several Mesozoic ammonites, displays a structure more complex as compared with the wall of initial chamber. In some of the older Devonian goniatites, the tube is more or less bent, but it does not yet form a whorl closely adhering to the initial chamber. Stage *3* already represents the shell proper; it starts directly under the constriction mentioned above and is characterized by the appearance of a quite new element in the structure of shell, that is, a prismatic layer, which appears simultaneously with growth lines, sculpture and colour.

The names of the ontogenetic stages of ammonite shells mentioned above are in principle derived from the analogy to similar development stages of other molluscs, distinguished before and considerably better recognized, primarily the Prosobranchia, in which there exists a districtly individualized larval stage (veliger), having a larval shell called a protoconch. The protoconch consists of a single, homogenous, calcareous layer and may have sometimes a characteristic sculpture. A further ontogenetic development leads through metamorphosis, which in the Prosobranchia results in the formation of, among other things, a pallial fold starting to produce the shell proper (final) called a teleconch. In contradistinction to protoconch, the teleconch consists of three principal layers. Growth lines, sculpture and colours of shell appear on the teleconch. If the protoconch has a sculpture, the sculpture of the teleconch is not its continuation, but has a different character and different pattern. In rare cases, the protoconch is rejected after metamorphosis, but usually it remains embedded on the apex of teleconch till its destruction (cf. Pl. 1, Fig. 1*a*, *b*).

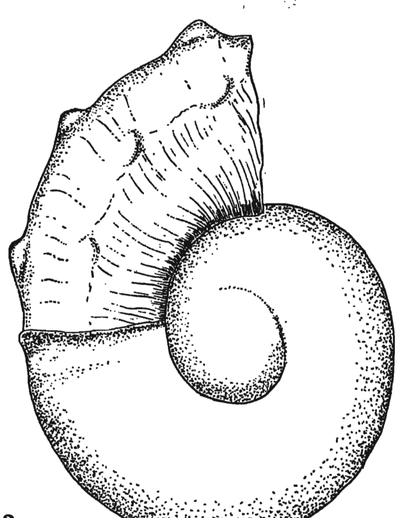
The term protoconch is, therefore, also applied to the initial development stages of the Nautiloidea and Ammonoidea. Regarding the Ammonoidea, some of the authors use the term protoconch to determine the initial chamber only (Erben 1964, 1968; Birkelund 1967 and others), while some others apply it to the entire first whorl, that is, to the first and second stages of those mentioned above (Ruzhentsev & Shimanskij 1954, Makowski 1962b). Both these interpretations are justified. The former by a simple structure of the wall of the shell of initial chamber in the



1a



1b



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PL. 1

1a, b — *Turritella krantzi* Roullier; Callovian, Łuków — protoconch and first whorls of the teleconch, × 50.

2 — *Cosmoceras* sp.; Callovian, Łuków — protoconch and a part of the first whorl of the teleconch (on the latter visible are the growth lines), × 80.

ammonites which in this respect displays a similarity to the protoconch of the Prosobranchia and the latter by the facts which indicate that a further growth of the shell in the ammonites and the formation of the shell proper, that is, the transition to stage *3* was preceded by a phenomenon strictly analogous to the metamorphosis in the Prosobranchia and deserving the name metamorphosis (cf. Pl. 1, Fig. 2).

Skeletal elements filling-up the upper part of the initial chamber and the lower part of the first whorl such as, protosiphon, prosepta and initial sector of siphon obviously belong to the second stage, but a further sector of siphon and septa which fill-up the first whorl visible inside larger specimens, were already formed after the metamorphosis and belong to the subsequent ontogenetic stage, that is, to stage *3*.

The facts discussed above lead to the conclusion that the ontogenetic development of the initial stages of shells in the Prosobranchia and Ammonoidea displays a far-reaching, although incomplete analogy. This analogy concerns only the wall of shell in the Ammonoidea and not inner elements, that is, siphon and septa, as no such elements occur in the Prosobranchia. Such analogies also occur in relation to other groups of molluscs such as, the Pteropoda and Lamellibranchiata, although they are more distant which, in the case of the Lamellibranchiata, is also expressed in a different terminology of these initial ontogenetic stages.

In the Prosobranchia, the protoconch represents a skeletal larval element or a larval shell, produced and born by the larva, that is, veliger. A further development takes place as a result of metamorphosis, after which the animal begins to produce the shell proper, that is, teleconch. The proofs for the existence of such a metamorphosis in the Ammonoidea are quite obvious and the interpretation of this process, presented by H. K. Erben (1964) is sufficiently convincing. We should assume, therefore, that in the Ammonoidea there existed a larval stage displaying an anatomical and evolutionary individuality. The anatomical individuality was expressed in the lack of a capability of producing a prismatic layer characteristic of the shell proper. If this larval shell had an ornamentation, it may be only that typical of it, as is particularly well visible on the example of larval shells in the ammonites of the genera *Baculites* Lamarck and *Scaphites* Parkinson (cf. Smith 1901). Finally, we can notice that this stage terminates in a characteristic constriction strongly developed in most of the Paleozoic and Mesozoic Ammonoidea. It is also worth adding that this constriction is accompanied by a swelling formed on the inside in the process of continued growth. This swelling is formed primarily as a result of an internal superposition of the prismatic layer and is very well visible in sections cut in the plane of symmetry even in the case of the lack of the constriction and defines the boundary between the larval shell and last shell equally clearly as this constriction does. It is also worth mentioning that the larval shell of the Ammonoidea reaches only very small dimensions and, in the form the tube of which closely adheres to the initial chamber, its diameter amounts to 0.5 to 1.3 mm and, therefore, it is contained within dimension limits which only rarely are exceeded by the protoconch of the Prosobranchia. All these facts give ample evidence that the larval shell of the Ammonoidea may be also called the protoconch.

Since the smallest shells of the Ammonoidea ever found represent precisely the stage protoconch (data from literature and the writer's own observations were presented previously, Makowski 1962b), quite convincing seems to be V. E. Ruzhentsev's & V. N. Shimanskij's (1954) suggestion that the larval forms of this type were hatched of eggs, which, much the same as in the Prosobranchia, were very fine.

In contradistinction to the Ammonoidea, in the ontogenetic development of the Recent *Nautilus* there is no larval form and the development process of the initial ontogenetic stages becomes enclosed in the egg which reaches considerable dimensions. A young, completely developed form of *Nautilus* the shell of which comes to *c.* 25 mm in diameter is hatched of the egg. This was the point at which the larval stages disappeared and ontogeny started what is known as a simple development. Striking analogies are observed in the Pulmonata in which the larval stages also disappear, but the egg reaches considerable dimensions and a far-reaching ontogenetic development takes place within its shell. The form of a young gastropod, completely developed and having a final shell, represented by the initial whorls, is hatched of the egg. Studying the Permian Nautiloidea with coiled and bent shells, V. E. Ruzhentsev & V. N. Shimanskij (1954) conclude that these forms also had a simple ontogenetic development and their young individuals hatching of eggs reached 8 to 20 mm in length.

Consequently, we should assume that the cicatrixes, visible on the apex of shell in various representatives of the Nautiloidea, make up a trace left not by a fallen-off protoconch, but by a protoconch which disappeared during the phylogenetic development. The fissures, left in this place, are frequently filled-up with an amorphous calcareous substance, probably secreted by the disappearing shell gland. In the Pulmonata, at the end of the body, that is, in a place where a vestigial shell gland is located in the initial development stages, a grain also of amorphous calcareous substance is formed as a secretion of this gland.

The initial development stages of the larva of the Prosobranchia resemble a trochofore which surely leads to the conclusion that the ontogenetic development of the molluscs through the larval stages is a primary form of ontogeny inherited after the ancestors of this group. On the other hand, the simple development, observed in the Pulmonata, was formed secondarily as a result of the enclosure of younger and younger larval stages in the egg. At the same time, an increase was bound to take place in the amount of reserve substances in the egg and, consequently, in its size.

On the basis of the analogy, which here occurs, it should also be assumed that the ontogenetic development of the Ammonoidea through the stage of a free-living larva represents a more primary ontogenetic form inherited after the older Paleozoic Nautiloidea, which have shells with a narrow apical angle and very small initial chambers, resembling those in the genus *Bactrites* Sandberger. In this respect the Ammonoidea represent a conservative group as compared with the Nautiloidea whose evolution of the initial stages of ontogeny tended towards a simple development, in which, among other things, metamorphosis, that is, a process of the formation of a pallial fold capable of producing the final shell or teleconch, was shifted to earlier and earlier stages and, consequently, the larval form together with the larval shell were subject to reduction so that, finally, the larval shell was completely displaced by the final shell. The picture of the distal part of the body in early development stages of the Recent cephalopods of the order Dibranchiata may to a certain extent confirm these suppositions. A cicatrix, recognized by zoologists as a vestigial larval organ, that is, a shell gland which has already lost its capability of secreting the shell, is visible on the distal end of the body in these animals. The pallial fold begins to grow around this gland. It is easily imaginable that the cicatrix on the apex of shell of various Nautiloidea is a reflection of precisely such a system of soft parts.

Returning to the problem of neoteny in the Ammonoidea, discussed at the beginning, we should state that neoteny, classically understood as a phenomenon, consisting in the attainment of sexual maturity by larval forms, cannot be applied to the interpretation of small forms. Even the smallest Ammonoidea of the small forms representing the adult individuals, at the same time represent very large forms undoubtedly far advanced in their development and in fact uncomparable in this respect with the presumed, tiny larval forms. The smallest forms assigned within the framework of formal systematics to the genera *Glochiceras* Hyatt and *Creniceras* Munier-Chalmas, reach 10 mm in diameter (Makowski 1962a). Slightly smaller are the smallest ever known forms of the Upper Devonian Tornoceratidae the diameter of which does not exceed 8.0 mm; such tiny forms of these goniatites were described by D. Sobolev (1913). Likewise, small forms of the genus *Harpoceras* Waagen only 8.2 mm in diameter and of the genus *Polyplectus* Buckman 9.5 mm in diameter were described by J. Guex (1968). Despite small dimensions, the volume of the final living chamber in these forms is several hundred times as large as that of the living chamber in the larval form, which depicts the degree of differentiation in the process of the ontogenetic development. This is precisely the reason why, applying the concept of neoteny to these small forms of the Ammonoidea, we can use it only in this broad and rather inaccurate sense of a general underdevelopment combined with an early arrest of growth, although this term is not applied to similar dwarfish forms of males in the Recent molluscs.

Since small forms in various taxonomic groups of the Ammonoidea represent, however, varying degrees of such an underdevelopment or dwarfishness and since the instances cited above concern precisely extreme cases, the question arises to what an extent we may justify the use of the concept of neoteny in the sense discussed above and with the consideration of a broader comparative back-ground. Taking into account several of the instances cited earlier (Makowski 1962b), we may conclude that small forms are sometimes arranged in series with a strongly varying degree of a differentiation in this underdevelopment, that is, that they were arrested when reaching various stages of ontogeny. These examples of very small but adult forms of the Ammonoidea represent — maybe as a whole, but at any rate in a predominant part (*Glochiceras, Creniceras,* Tornoceratidae) — the smallest, extreme forms of these series, compared with which, the most strongly grown individuals from the opposite end of such a series, might pass for „normally developed forms". As shown previously (Makowski 1962b), these differences in size, both in the series of small and large forms, are mostly caused by the attainment of a variable number of whorls. Small forms in, for instance, the genus *Glochiceras* reach five to six whorls, which, with a relatively small variability in the height of particular whorls, leads, however, to a considerable differentiation in the diameter of adult specimens. Instructive examples of such very series of variously developed small and large forms in a few species of the genus *Scaphites* Parkinson are figured by W. A. Cobban (1969).

In comparing with each other extreme individuals in a series of small forms, qualitative differences are mostly expressed in a varying degree of the development of the septal line. No substantial differences may be observed in the case of the Paleozoic Ammonoidea, in particular in the family Tornoceratidae cited above as an example. However, these differences are already clearly visible in the Mesozoic ammonites as, for instance, in the genera *Glochiceras* and *Creniceras* cited above, but other morphological elements characteristic of these forms, primarily the aperture do not display any differences in the degree of their developm-ent. In regard to the cases in which the aperture of small forms differs from that in large forms, this phenomenon may be explained as a symptom of a full sexual maturity of all individuals in a series of small forms with a simultaneous differentiation in the underdevelopment of some other organs. Such an explanation is, however, invalid when we examine this problem using the example of such genera as *Sphaeroceras* Bayle or *Chondroceras* Mascke, in which the apertures of small and large forms are identical. Similar is the case of most of the Paleozoic Ammonoidea, in which the apertures of small and large forms only rarely display some differences as, for instance, in the genus *Manticoceras* Hyatt. Thus analyzing the series of small forms, it is difficult to find a sufficient basis for the seggregation into groups of more and less underdeveloped individuals, despite the occurrence of obvious differences in size.

The differences in size, caused among small forms by the varying number of whorls, are observed only in some of both the Paleozoic and Mesozoic Ammonoidea. On the other hand, in some others as, for instance, in the genus *Quenstedtoceras* Hyatt, all individuals in the group of small forms attain six whorls (or, to be exact, 6 to $6^{1}/_{8}$) and the differences in their size result from a varying height of particular whorls, the same phenomenon being in fact recorded in large forms. We may, therefore, assume that in some of the groups there occurred a developmental stress of its kind, which caused that all small individuals reached the developmental limit, amounting, in the case of small forms of the family Cardioceratidae, to 6 whorls. In other Ammonoidea such as, for instance, the Oppellidae or Tornoceratidae, some developmental regulators were less precise in their activity, which deviated and caused the formation of several mature individuals, of which some only attained a maximum number of whorls, amounting, for the families mentioned above, also to six. Some other individuals were earlier arrested in their development, which need not necessarity be an evidence that their entire organization was marked by an underdevelopment.

Now, using one of the simplest examples of the dimorphism in the Mesozoic Ammonoidea, that is, in the species *Sphaeroceras brongniarti* (Sow.), in which all small and large forms are identical with each other in external morphology and differ only in the number of whorls and, consequently, in size, let us examine the relation between the small and large forms. In the collection of the specimens of this species studied by the writer (Makowski 1962a, b), the diameter of small forms fluctuated within limits of 18 and 24 mm and of large forms of 36 and 40 mm.

The specimens of both groups, which are the closest to each other in dimensions are 24 and 36 mm in diameter and this difference of 12 mm departs not very far from the ontogenetic variability, observed, within the framework of formal systematics, in many such species, which include either large, or small forms only. Since both groups of forms are identical in external morphology and, within formal taxonomy, have hitherto been assigned to one and the same species, it would be difficult to find any justification for recognizing small forms as neotenic ones. Since small forms have 7 or, at most, $7^{1}/_{4}$ whorls and large forms have 8 whorls, they differ in the number of whorls and, to a certain, insignificant extent, in a dismembered septal line, which is more strongly developed in large forms.

Among the Paleozoic Ammonoidea, one may find many instances of dimorphism, in which large and small forms differ from each other only in size and only to an insignificant extent or in which small forms display on their final body chamber certain characters such as, a constriction which otherwise occurs on inner whorls of large forms (Makowski 1962a, b; Davis, Furnish & Glenister 1969). Using the example of *Manticoceras bickense* (Wedekind), one may observe (Makowski 1971) that despite the lack of a morphological gap between the group of small forms (10 to 15 mm in diameter) and a group of large forms (15 to 17 mm in diameter), such a gap may be found, however, if we pay attention to the number of whorls which in small forms amounts to 6 and in large ones to 7. In such cases, the interpretation of small forms as neotenic, that is, underdeveloped ones would be utterly groundless and certainly unacceptable to the specialists.

However, continuing the examination of several other, similar examples of dimorphism, we may also find such cases (*e.g.*, in the genus *Cheiloceras* Frech) in which small and large forms are quite similar to each other, but considerably differ in size. Here we face a possibility of quite different interpretation, viz., that the differences in size mentioned above arose not as a result of the underdevelopment of small forms, but as a result of a gigantism developed by large forms (Makowski 1962b).

In some of the genera of both the Paleozoic and Mesozoic Ammonoidea (*Tornoceras* Hyatt, *Hecticoceras* Bonarelli, *Scaphites* Parkinson), the phenomenon may be observed, in the process of which large forms are either in part, or — in some of the beds — as a rule, earlier arrested in their ontogenetic development, producing, as a result, several forms, compared to which small forms appear variously, sometimes being not much smaller. In such cases and concerning such large forms arrested in their development earlier than it may be expected from the rule based on many other examples, we might suggest a neotenic origin, but such speculations founded on single, isolated examples would be probably of a little use.

On the basis of the results of studies which have hitherto been conducted on sexual dimorphism in the Ammonoidea, we may conclude that this phenomenon occurs in the entire group throughout its history, but, at the same time, that it is too complex to allow us for constructing, on the basis of single instances, a sufficiently convincing biological interpretation of its essence.

The metamorphosis of the Ammonoidea has many times been discussed above as a process undergone by larvae and which led to the animal's attainment of a capability of producing the shell proper. The metamorphosis of this type is a fairly frequent phenomenon in fauna, known not only in the molluscs, but also in other groups. However, in some of the Ammonoidea and Nautiloidea, we encounter the phenomenon of a radical change in the shape of shell and, consequently, in the shape of body at the end of the ontogenic development just before the attainment of the final stage. In other words, these changes mostly involve only the final body chamber and less frequently start earlier, that is, in the chambered part of the shell. Among the Nautiloidea, the best known example of this phenomenon is the genus *Ascoceras* Barrande and among the Ammonoidea the genera *Prolobites* Karpinski, *Oecoptychius* Neumayr, *Scaphites* Parkinson, etc. This phenomenon is also a metamorphosis of its kind and in many cases, such as, for instance, that of the genus *Scaphites*, it is manifested simultaneously in the final stage of ontogeny in both large and small forms, which may indicate that the small forms are not inferior in their general development to their counterparts in the series of large forms, although in some cases as, for instance, in the genus *Oecoptychius*, this metamorphosis occurs only in small forms.

DIMORPHISM AND THE SYSTEMATIC PROBLEMS IN THE AMMONOIDEA

In connection with the acceptance of the theory of sexual dimorphism in the Ammonoidea, there arise certain new problems concerning their systematics. These are, on the one hand, purely formal matters and, on the other, certain difficulties resulting from the very nature of this phenomenon, primarily a confusion which follows the application of various taxonomic principles. These problems have recently been extensively discussed by many authors.

Within the framework of traditional, formal systematics, so far applied to the Jurassic and Cretaceous Ammonoidea, dimorphic forms were assigned to different subgenera. However, the instances were also recorded in which separate genera were erected for them depending not only on the degree of morphological differences between such dimorphic forms but also, to a considerable and, in addition, varying degree, on a subjective evaluation of these differences by individual authors concerning with the taxonomy of the Jurassic and Cretaceous Ammonoidea. At any rate, it may be stated that the number of subgenera distinguished in the Ammonoidea is the highest precisely for the Jurassic ones and quite low regarding the Paleozoic ones. This speaks much of the fact that the Jurassic Ammonoidea are frequently characterized by a rich sculpture, in which differences between small and large forms, as well as a frequent differentiation of the aperture, are more distinctly marked, while in the Paleozoic Ammonoidea, dimorphism is mostly expressed in size only, which usually leads to the assignment of both forms to one and the same species or, at least, genus, without distinguishing separate subgenera. Since, however, the degree of the differentiation of dimorphic forms was sometimes insignificant also in both the Jurassic and Cretaceous Ammonoidea or, as is the case of *Sphaeroceras brongniarti* (Sow.), both forms were identical, the approach to these facts, regarding external morphology, was strongly varying which caused that purely formal matters involved in this problem were strongly tangled and confused. New, in view of the fact that more accurate studies, based on a well preserved material, have covered only a small number of genera and species, the disentanglement of all this confusion seems to be impossible. In the writer's opinion, however, the principles of zoological systematics should be applied to all cases in which the quality of material allows one to establish dimorphic pairs. The application of this principles to the Ammonoidea, a completely extinct group, encounters certain difficulties, discussed below and which do not occur in the case of traditional taxonomy. Moreover, the adoption of the principle, according to which dimorphic forms should be assigned to different subgenera, will certainly be accompanied by yet greater difficulties. The matter is that the formal taxonomy of this type might to a certain extent be advantageous in regard to probably most of the Jurassic and some of the Cretaceous Ammonoidea. This is particularly true of the cases in which the initial development stages are very similar to each other within a numerous taxonomic group, *e.g.*, in the Perisphictidae and Oppeliidae, which poses considerable problems in attempts at the identification of dimorphic pairs, since sometimes it is only an accurate observation of the common occurrence in these same beds that may a really decisive factor. However, the Jurassic and Cretaceous Ammonoidea, referred to above, make up only part of this systematic group the practical taxonomy of which would be easier within the framework of a formal taxonomy of this type.

Several genera such as, *e.g.*, *Psiloceras* Hyatt, *Aegoceras* Waagen, *Sphaeroceras* Bayle, *Chondroceras* Mascke, etc., in which the distinction of dimorphic subgenera is unjustified and would not be any facilitation are, however, met with even in the Jurassic. In such cases, the dimorphic forms should first be determined and only afterwards the dimorphic subgenera. As follows from these considerations, a cosistent adoption of the principle that dimorphic series belong to different subgenera is inadmissible even for many genera of the Jurasic and Cretaceous Ammonoidea. It is also unacceptable for the Paleozoic Ammonoidea. If we accepted such a principle, the taxonomy of the entire group would become more artificial than it is at present and, at the same time, the taxonomy of this type would become enriched with a vast number of absolutely unnecessary names to designate newly erected dimorphic subgenera. Thus, in the writer's opinion, undertaking certain attempts at a unification and settlement of taxonomy in connection with the adoption of the theory of dimorphism in the Ammonoidea, one must not restrict the discussion of this matter to so far best-known, expressive examples taken from the Jurassic and abounding in problems, since they represent only part of the phenomenon under study.

The present writer's nearly completed studies on the Devonian Ammonoidea of the families Tornoceratidae and Cheiloceratidae allow to conclude that the types of dimorphism (Makowski 1962a, b) may make up a fundamental criterion of distinguishing main development stocks of this group in the Devonian and of, at least partial, explanation of the origin of the Clymeniina, while other characters such as, the septal line, growth lines and a general shape of the shell may — due to frequent cases of convergence — be deceptive.

Returning to the subject of difficulties, encountered by the adoption of the principle of zoological taxonomy for establishing dimorphic pairs in the Ammonoidea as a completely extinct class, it should be emphasized that these difficulties are primarily due to an ununiform process of the evolution of small and large forms. As known for many years now, small forms are more conservative than large one, since they have not potential possibilities of developing all the characters which in large forms are formed on whorls. In small forms, some of these characters disappear in the process of the ontogenetic development. This phenomenon and, consequently, the problems of taxonomy are clearly visible precisely among the richly ornamented Jurassic forms, in which large forms develop, on their accessory whorls, the characters lacking in small ones. In this way, in one and the same stratigraphic member we may distinguish considerably more species in the series of large forms than in the series of small forms, which has already been pointed out by the present writer's work (Makowski 1962b) discussing the phylogenetic series of the Cosmoceratidae, described by R. Brinkmann (1929). Thus, identical small forms might be called by various specific names depending on the stratigraphic horizon. In this respect, so far it is difficult to find any formal solution. However, such formal problems of taxonomy, taking into account sexual dimorphism, do not appear in the case of the Paleozoic Ammonoidea or if they do, they concern only few cases of a distinct gigantism in large forms.

Institute of Geology
of the Warsaw University
Warszawa 22, Al. Żwirki i Wigury 93
Warsaw, April 1971

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H. MAKOWSKI

UWAGI O ROZWOJU ONTOGENETYCZNYM I DYMORFIZMIE PŁCIOWYM U AMMONOIDEA

(Streszczenie)

Przedmiotem pracy jest dyskusja podejmowanych parokrotnie w literaturze prób interpretacji form małych u amonitowatych (nadrząd Ammonoidea) jako form neotenicznych. Klasyczne pojęcie neotenii wiąże się z istnieniem stadium larwalnego, które u Ammonoidea było bardzo drobne, przy czym larwa podlegała metamorfozie. Tymczasem nawet małe formy Ammonoidea są daleko zaawansowane w rozwoju ontogenetycznym w porównaniu ze stadium larwalnym. Poza tym znane są liczne przykłady dymorfizmu, szczególnie wśród Ammonoidea paleozoicznych, gdzie formy duże i małe różnią się wielkością nieznacznie. Fakty te przemawiają przeciwko koncepcji o neotenicznym charakterze form małych.

Autor porusza także zagadnienie systematyki Ammonoidea w związku z coraz częściej przyjmowaną teorią dymorfizmu płciowego i wyraża opinię, że przy podejmowaniu decyzji w sprawach formalnych, należy brać pod uwagę charakter dymorfizmu w całej tej grupie.

Instytut Geologii Podstawowej
Uniwersytetu Warszawskiego
Warszawa 22, Al. Żwirki i Wigury 93
Warszawa, w kwietniu 1971 r.