POLSKA AKADEMIA NAUK

PALAEONTOLOGIA POLONICA

REDAKTOR

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No. 12 — 1962

PROBLEM OF SEXUAL DIMORPHISM IN AMMONITES

(ZAGADNIENIE DYMORFIZMU PŁCIOWEGO U AMONITÓW)

BY

HENRYK MAKOWSKI

(WITH 14 TEXT-FIGURES, 12 TEXT-PLATES AND 20 PLATES)

WARSZAWA 1962

PAŃSTWOWE WYDAWNICTWO NAUKOWE

PALAEONTOLOGIA POLONICA

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ACADÉMIE POLONAISE DES SCIENCES

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Warszawa 22, Al. Żwirki i Wigury Nr 6

Printed in Poland

Państwowe Wydawnictwo Naukowe — Oddział
w Krakowie

Nakład 850+150 egz. Ark. wyd. 13,50. Ark. druk.
$6^{3}/_{8}$+21 wkł. Papier ilustr. kl. III
100 g 61×86/8. Oddano do składa-
nia 16. XII. 1961. Podpisano do
druku 8. XI. 1962. Druk ukoń-
czono w lipcu 1963

Drukarnia Uniwersytetu Jagiellońskiego w Krakowie
Zam. 722/61

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PREFACE

In the course of studies started in 1945 on the Callovian fauna from Łuków (Makowski, 1952) the present writer repeatedly observed the simultaneous occurrence of the so-called large and small forms of ammonites whose young whorls are identical. The meagreness and the stratigraphic insufficiency of the material then available handicapped an investigation of the problems raised by this observation. However, from data in the literature and on evidence furnished by the Łuków material, it has now been ascertained that the phenomenon occurred with much similarity in a number of Mesozoic ammonite genera whose phylogenetic trends had diverged long ago. Sobolew's (1914) monographs on the Devonian goniatites from the Holy Cross Mountains (Góry Świętokrzyskie), as well as other works on goniatites from various areas and stratigraphic horizons (Demanet, 1943), suggest the occurrence of similar phenomena within this ammonoid group, too.

These interesting facts and the difference of opinion as regards their interpretation prompted the writer systematically to investigate this problem in groups of ammonoids that seemed conveniently accessible. Hence, in 1947, he started collecting ammonites from the Jurassic of the Cracow (Kraków)-Częstochowa Uplands and, in 1948, goniatites from the Upper Devonian of the Holy Cross Mountains. The task of collecting adequate material proved extremely slow since the studied dimorphism can only be properly observed in adult specimens of Mesozoic ammonites, in which the aperture is preserved. The aperture is on the whole very delicate, and therefore not often preserved. From 1951 the writer's search for ammonites in the Łuków brick-pits has been most successful, yielding a rich collection of ammonites. Very few faunal localities in the world yield fossil ammonites in such a perfect state of preservation, while equally well preserved specimens of the genera *Cadoceras*, *Quenstedtoceras* and *Cosmoceras* have probably never been obtained. Nevertheless, and in spite of the collecting being continued for so many years, in some cases it has not been possible to obtain more than two or three adequate specimens. In many cases the required material could not be secured among either the collected Mesozoic ammonites or the goniatites, and the work of collecting will still go on.

The purpose of this paper is to report the results of the writer's previous investigations. Although the number of species and genera exhibiting the same phenomenon is rather limited, they are so varied that it seems justifiable to draw more general conclusions.

*

The writer's cordial thanks are due to Professor A. Halicka, Director of the Muzeum Ziemi (Museum of the Earth) in Warsaw for financial aid in the work of collecting ammonites from the Jurassic of the Cracow-Częstochowa Uplands. The help of the Managing Board of the Geological Institute of Poland must also be here acknowledged. Its former director, late Professor Jan Czarnocki has made very valuable suggestions during the collection of goniatites in the Holy Cross Mountains. The late Professor JAN SAMSONOWICZ, Head of the Department of Geology of the Warsaw University, never tired in his efforts to obtain financial grants to cover the high cost of the writer's field work and was always ready to discuss the results obtained. Doc. Dr. S. SIEDLECKI and Mr. J. KOPIK kindly offered a number of their specimens. Other valuable specimens were obtained through the courtesy of the late Professor W. J. ARKELL. Very special thanks are due to Professor R. KOZŁOWSKI for reading the text of the present paper. His suggestions and remarks on some points have been of the greatest help.

The author also thanks Mrs. J. HUMNICKA for the English translation of this paper, Dr. A. PACKARD for a revision of the English text, and Mrs. B. DROZD for the photography.

All the drawings have been done by the writer.

Historical Geology Department
of the Warsaw University
Warszawa, June 1961

GENERAL PART

HISTORICAL REVIEW

AMMONOIDEA

The problem of sexual dimorphism in ammonoids, and more particularly in Jurassic ammonites, has been dealt with by numerous authors, but usually in rather brief notes and papers. Not all these publications will be commented upon here, only those containing a more comprehensive description of the studied problem, or those of major historical significance. Where necessary, others will be mentioned later. Literature dealing with the problem of sexual dimorphism in fossil nautiloids will also be reviewed, as being closely connected. Opinions on Mesozoic ammonites, goniatites and fossil nautiloids will be discussed separately and independently of the chronological order of publications for each group.

De Blainville (1840) was the first to advance suggestions on the subject of sexual dimorphism in ammonite shells. That author had studied sexual dimorphism in recent molluscs and his suggestions on this problem in respect to ammonites were probably influenced by these studies. De Blainville thinks that analogies furnished by the living *Nautilus* indicate that in ammonites the sexes were separate. Moreover, he associates the development and function of ovaries in ammonites with the greater convexity of the ventral side of the female shell and with the larger dimensions of females.

In his monograph of Jurassic ammonites d'Orbigny (1842-51) more than once touches on the problem of sexual dimorphism by which he interprets the variations observed within a group of forms considered by him as conspecific. Sometimes, e. g. in the description of *Ammonites bisulcatus* Brug. or *Ammonites variabilis* d'Orb., he only vaguely suggests that the observed variation may be an expression of the sexual dimorphism; in other cases, e. g. in the description of *Ammonites hecticus* Hartm. or *Ammonites spinatus* Brug. the presence of sexual dimorphism is firmly asserted. According to d'Orbigny, it is expressed by the presence of two groups of forms differing in whorl sections which are either convex or flat, while the character of ribbing is the same in both groups.

From the point of view, now held by palaeontologists concerning the morphology of the ammonite shell, d'Orbigny's suggestions, even though partly correct, are without major significance, since he mistook for young ammonites small individuals, in which the aperture is frequently provided with distinct lateral lappets.

In his widely known work Waagen (1869) was the first to determine two parallel phylogenetic — or at least two parallel morphological — lines among the Middle and Upper Jurassic ammonites belonging to the Oppeliidae. One of these lines consists of large forms, the other is represented by small, dwarf forms with the gerontic aperture provided with lateral appets. Waagen pairs those small and large forms that occur within the same beds and display distinct similarities of ornamentation in the inner whorls. That author is not, however, inclined to accept the theory of sexual dimorphism as an explanation of the difference in size chiefly on account of the far greater number of species in the line of larger forms than that in the line of small forms. Moreover, the numerical ratio of the large and small forms occurring side by side in the same strata, rather speaks against the theory of dimorphism. WAAGEN mentions e. g. that in one bed he collected 32 large specimens and only 6 small specimens. In another bed the large form was represented by as many as 150 individuals, the small form by one only. A certain section where one of the large forms is very common, did not yield a single one of the corresponding small forms. In other cases pairs of individuals, which may be regarded as conspecific but of different sex, occur in different beds of the same section. WAAGEN supposes this to be a result of the way of determining the thickness of the bed. He concludes that the problem presented by large and small forms could be cleared up by future studies.

REYNÈS (1879) asserts that there are two parallel ammonite groups displaying identical ornamentation and sutures. They differ however in that the adult stage of one group is larger and with more convex whorls, while the adults of the other group are smaller and with flatter whorls. REYNÈS is of the opinion that the former group represents female individuals, the latter male individuals.

In his description of a small, exceptionally well preserved ammonite, previously known as *Ammonites pseudoanceps*, DOUVILLÉ (1880) includes it within the genus *Morphoceras* established by him, and discusses the problem of sexual dimorphism in that genus. DOUVILLÉ supposes that *Morphoceras pseudoanceps* is the male form and *M. polymorphus* the female form of one species. According to him, *M. dimorphus* is the male and *M. defrancei* the female form of a similar conspecific pair. Pairs of the ammonites just mentioned are identical in the early stages of development.

In his monograph on the ammonites from the Dogger of Swabia QUENSTEDT (1886-87) more than once discusses the side by side occurrence of large forms and small forms with lappets, and with ribbing which is identical at least in the early stages. That author suggests that these may be conspecific forms of different sex. He is not, however, constant in his interpretation of that phenomenon since in certain cases he regards small ammonites provided with lappets as adult forms and in other cases as young individuals.

MUNIER-CHALMAS (1892) states that Jurassic sediments, from the *Ludwigia murchisonae* (SOW.) horizon to the Lower Neocomian, contain small ammonites with the last whorl more or less inclined. For these forms the generic name of *Oecotraustes* has been proposed by WAAGEN (1869). The genera *Oecoptychius* NEUMAYR and *Sutneria* ZITTEL were introduced later. All these forms are united by MUNIER-CHALMAS under the common name of scaphitoids and separated into the 6 following genera: *Oecotraustes*, *Oecoptychius*, *Sutneria*, *Cadomoceras*, *Horioceras* and *Creniceras*. Other genera, closely related in character of ornamentation, but attaining large dimensions, such as *Oppelia*, *Neumayria*, *Ochetoceras* and *Distichoceras*, are encountered in the same beds with the above named scaphitoids. Similarly we may observe two groups of forms among such genera as *Harpoceras*, *Ludwigia*, *Sonninia*, *Perisphinctes* and others. One of the groups has large dimensions and an aperture with a simple margin, while the other group is represented by small forms in which the gerontic aperture has lateral extensions (lappets). Moreover, MUNIER-CHALMAS mentions two groups of species assigned to two separate genera — *Cadomites* and *Normannites*. The former contains relatively large forms with the aperture lacking lateral extensions, the latter consists of relatively small forms in which the margin of the gerontic aperture is provided with lateral lappets, and stresses that the relationship between pairs of forms occurring within the same beds, but referred to two different genera, is one of specific characters. Quoting other similar examples he finally concludes that sexual dimorphism does actually occur in ammonites, and that the larger forms should be regarded as representing the females, while the smaller ones provided with lappets are the dwarf males. MUNIER-CHALMAS (1897) reverts once again to the question, which he believes to be a very important one, in connection with a paper of GLANGEAUD (1897) on a similar subject. He states that the probability of sexual dimorphism in ammonites grows continually though the evidence available is not yet conclusive. He also points out that the separation into large and small forms is to a certain extent reflected in their evolution. E. g. in the genus *Reineckeia* large forms attaining a diameter of 40 cm, are more progressive than the small forms not exceeding a 10 cm diameter. MUNIER-CHALMAS also mentions that analogies in this respect have been noted by GROSSOUVRE (1894) who was in possession of a rich collection of ammonites.

The possibility of sexual dimorphism in the closely allied ammonites *Sonninia* and *Witchellia* from the Dogger of France is suggested by HAUG (1893) in his description of these genera. He states that two groups of species may be distinguished in the genus *Sonninia.* To one belong such species as *Sonninia sowerbyi* (MILL.) whose ornamentation and suture characters should be regarded as typical and normal, while forms referred to the group of *Sonninia sulcata* (BUCK.) are abnormal. The initial evolutionary stages, 1-3 cm in diameter, are identical in the two groups and are thus indistinguishable. The later stages of ontogeny differ markedly in these groups. Group one develops the normal coil and attains considerable dimensions. In group two the growth is checked much earlier and the result is considerably smaller size; the ornamentation pattern changes and partly disappears; the whorls gradually become less involuted, while the umbilicus grows larger; the development of the suture ceases at an earlier stage, becoming much simplified, and some elements are atrophied; the adult aperture is characterized by the presence of lappets. The whole of this second group of species should be regarded as regressive, distinctly different from the normal forms which attain large dimensions. HAUG emphasizes the distinct parallelism in the evolution of ornamentation. We may indeed pick out pairs of forms from both groups, which occur in the same beds and display an identical ornamentation pattern in their early stages. Thus we are clearly dealing here with dimorphism analogous to that described by MUNIER-CHALMAS in various species from the genera *Cadomites* and *Normannites.* It is moreover maintained by HAUG that though small specimens without lappets do occur here, they should be regarded as young individuals which have not yet stopped growing, while the aperture with lappets is the full grown form. The following is an abbreviated diagnosis proposed by HAUG for the genus *Sonninia*: Sexual dimorphism strong. Females represented by medium-size and large shells, the males by all the small shells. The young stages of both forms display identical ornamentation. The female aperture is straight, with the margin parallel to the ribbing, the male aperture provided with lappets and sometimes preceded by a constriction. The relatively simple suture of the early stages of ontogeny persists in male individuals during the later stages, while in females it is subject to further development and grows strongly denticulated. Two lineages are similarly noted by HAUG in the genus *Witchellia,* analogous with those observed in the genus *Sonninia.* He characterizes the line with the large forms as normal and progressive, while the small forms are called recessive and degenerative. The paper ends with a new diagnosis of the genus *Witchellia* starting with the statement that the supposed sexual dimorphism is not conspicuous here.

It should be mentioned that the above quoted diagnoses of *Sonninia* and *Witchellia* are given by HAUG only in the summary of his paper and are not applied by him in the text.

At a later date, when reviewing the work of GLANGEAUD (1897), HAUG (1897) writes that similar dimorphism is observable among Triassic ammonites, as well as in other Jurassic ammonites such as *Oxynoticeras*, *Aganiceras*, *Arnioceras* and *Polynoplites*. This dimorphism varies in extent within the particular families and in many cases it is absent.

GLANGEAUD (1897) discusses, for a number of ammonites belonging to several genera, the importance of the adult aperture. In his discussion he compares two lines of forms at that time assigned to the genus *Morphoceras* established by DOUVILLÉ. Species such as *Morphoceras pseudoanceps* and *M. defrancei* consist of small forms whose adult aperture is provided with conspicuous lateral lappets; on the other hand, forms such as *M. polymorphus* and *M. dimorphus* attain far greater dimensions and their adult aperture has a simple margin and protrudes forward on the siphonal side. The four species just mentioned all occur within the same bed. GLANGEAUD makes references to the suggestions of D'ORBIGNY and DOUVILLÉ mentioned above, and he, too, interprets these phenomena as sexual dimorphism. At the same time he suggests that the diagnosis of the genus *Morphoceras* should be complemented by adding that this genus exhibits sexual dimorphism and that the males are small, flattened, with lateral lappets converging forward in the median line, while the females are represented by large forms, broad in section and with the aperture lacking lappets, but constricted and elongated forward on the siphonal side. Next GLANGEAUD similarly discusses the genus *Sphaeroceras*, postulating that *Oecoptychius refractus* is a male form, while *Sphaeroceras nux*, occurring in the same bed, is the female form of the same species. He also agrees with the view of MUNIER-CHALMAS (1892) regarding the occurrence of sexual dimorphism in numerous other cases.

In the present systematics, however, forms differing in sex are referred to separate genera. The assignment of forms of different sex to separate genera may be accounted for by the fact that their systematics are mainly based on the character of the suture. This is more conservative in the males and its development stops earlier than in the females which are more progressive. GLANGEAUD believes that methods thus far used in systematics should now be discarded and that a study of the adult aperture ought to prove more useful; it would probably furnish new evidence for that group of forms and the above conclusions may be applied to the whole ammonite group. By reducing species to half of their present number, this would distinctly simplify the systematics and lead to the elimination of a great number of unreliable species which are actually mere varieties only. GLANGEAUD proposes the introduction of nomenclature with the same specific name for both forms, and the use of the male and female symbols — ♂, ♀ respectively — as in zoology.

The problem of sexual dimorphism in ammonites is dealt with by ROLLIER (1913) in a comprehensive paper, which does not, however, contain any new information. He states that his long studies on ammonites have convinced him of the occurrence within the same genera, along with normal forms, of other, small, aberrant forms which may be regarded as males. Moreover, he mentions a number of large and small forms occurring in the same beds, which may be interpreted as different in sex but conspecific.

COËMME (1917) described two species of genus *Cadomoceras* from the Upper Bajocian of France. The genus *Cadomoceras* was established by MUNIER-CHALMAS who, as stated above, regarded this form as a dwarf male. *Cadomoceras* contains small forms, barely 2.5 cm in diameter, of a somewhat «scaphitoid» shape. The adult aperture is provided with prominent lappets which extend forward in a spade-like fashion and incline one to the other. COËMME is ready to agree with MUNIER-CHALMAS that these may be dwarf males and he points to analogies in respect of sex in such living cephalopods as *Rossia* and *Octopus*. He thinks that the rare occurrence of the small forms supports the supposition that they are males, since the numerical minority of males is observable in living cephalopods, also. E. g. in *Loligo* they represent 15 per cent of the population, in *Octopus* 25 per cent. Coëmme mentions another hypothesis that could explain the occurrence of these dwarf forms, namely: they may be degenerative, sterile hybrids of closely related species. Further, he supposes that ammonites, which had normally evolved at a slow rate, may at times have been subject to very rapid changes due to hybridization, invariably producing new forms. Though these new forms display a certain constancy, they would not be comparable with normal forms. Coëmme also reminds us of the opinion of some authors that the «scaphitoid-like» habitus expresses the decrepitude of a species nearing its extinction.

Djanelidzé (1922) remarks that the apertural extensions are characteristic of the adult, sexually mature stage, and hence may be reasonably associated with sexual functions. That author's observations of the genus *Spiticeras* from the Lower Cretaceous of southern France strongly support this hypothesis. Small forms with lappets and larger ones without lappets occur in the same beds. The ontogeny of the young whorls is identical. Transition forms are lacking between the two groups. Should it be accepted that changes affecting the last whorl of small forms express degeneration, then transitional forms connecting them with the normal forms must have existed, too. Djanelidzé also says that though the theory of sexual dimorphism in ammonites cannot be accepted without reservation, it is a very probable one. Forms supposed to be of different sex cannot as yet be described under a conspecific name, but they may be included into the same genus and for the time being this is the only practical consequence resulting from the application of the theory of sexual dimorphism in ammonites.

A very full description of the phylogeny of the genus *Cosmoceras* has been worked out by Brinkmann (1929). This work occupies an important place in the literature on sexual dimorphism in ammonites because the material available to the author, as well as his methods of collecting and of describing are unique. Brinkmann's collection permitted him to trace accurately the evolutionary stages of the genus *Cosmoceras* and to distinguish two parallel lineages of large forms and two of small forms, described by him as four separate subgenera. The near mutual resemblance, displayed by pairs in these two series, is by Brinkmann explained as convergence. The sexual dimorphism hypothesis is briefly discussed by that author on evidence from his own material. It is, however, rejected by him, chiefly on the grounds that the appearance and extinction of the large and small forms is not altogether synchronous. We shall return later to a critical analysis of Brinkmann's opinion.

When investigating the variability of the whorl section and of the number of ribs in *Inflaticeras varicosum* (Sow.), Jayet (1929) ascertained that the curve of variations in whorl section and pattern of ribbing shows two maxima which may perhaps express sexual dimorphism.

Gillet (1937) is undecided how to determine the role of the apertural extensions occurring in small forms only, whose function has been so much discussed. Some writers look on them as an attachment device for eggs, others as elements of ornamentation of the male shell. Gillet adds a suggestion that these extensions may not have been associated with sex at all, but were used as arm supports in swimming.

Davitašvili and Chimšiašvili (1954) published a paper with the aim — according to them — of furnishing a basis for the significance of apertural extensions in ammonites, but not claiming conclusively to solve this problem which needs to be treated in a separate work. These authors remind us that in molluscs the apertural extensions do not always mark the end of growth, but often only a temporary check. The siphonal and lateral extensions do not appear earlier than in the Jurassic ammonites. In older forms the corresponding parts display bends, but siphonal lips or lateral lappets are never produced. The authors emphasize that in some forms of ammonites, e. g. in *Phylloceras mediterraneum*, the apertural extensions may appear periodically, for a relatively short while, and disappear during further growth. The authors discuss this phenomenon and are ready to accept the occurrence of these extensions as associated with reproduction and sexual activities. The extensions may have served as an attachment for organs developing at periods of increased sexual activity or to attract individuals of different sex. They were too weak, however, to have served the male as weapons.

ARKELL, the author of numerous papers on ammonites, recognized the possibility of the occurrence of sexual dimorphism in this group of animals, as may be inferred from brief remarks in his publications. E. g. in a monograph of the Bathonian ammonites of England (ARKELL, 1952), while describing the genera *Cadomites* and *Polyplectites*, ARKELL states that they may possibly be congeneric forms of different sex. In the «Treatise on invertebrate paleontology» (ARKELL, KUMMEL et al., 1957) ARKELL expresses the following opinion: «There are some families in strata as high as the Middle and Upper Jurassic in which no lappets have been reported (e. g. Macrocephalitidae), and the theory of sexual dimorphism can only be shelved as unproved, until new evidence is forthcoming. Meanwhile lappets are regarded as of at least subgeneric rank in the present classification; an open verdict must be passed for the time being on their function, if any» (*l. c.*, p. L 90).

In his monograph of the Upper Jurassic genus *Glochiceras*, ZIEGLER (1958) also briefly mentions the possible occurrence of sexual dimorphism in species referred to that genus. It should be here stressed that the genus *Glochiceras* contains small, dwarf forms, attaining a diameter of 2-3 cm, and an aperture provided with prominent lappets extending forward. Within a group of specimens referred to the same species that author was able to distinguish small forms with a narrow umbilicus, and larger forms with a wide umbilicus. He writes that owing to insufficient data regarding the stratigraphic distribution of these forms, it is hardly possible to make inferences that would be conclusive. Nevertheless, the hypothesis explaining this phenomenon by sexual dimorphism cannot be altogether discarded.

In his discussion on the significance of apertural extensions in ammonites, DAVITAŠVILI (1961) is inclined to admit that these extensions represent secondary sexual characters which are due to sexual selection. That author believes, however, that the siphonal lips as well as the side lappets may appear and disappear more than once during the growth of the same individual.

The problem of sexual dimorphism has also been advanced in discussions on the origin of aptychi. SIEBOLD (1848) believed that aptychi might be the inner shells of dwarf ammonite males which thrived as parasites in the mantle cavity of females. This would explain the common occurrence of aptychi in the living chamber of ammonites, present in the females only. Another hypothesis is advanced by KEFERSTEIN (1866), who supposes that the aptychi occurred in females only and that they formed a capsule for the protection of nidamental glands.

Authors who also dealt with the problem of sexual dimorphism in ammonites are: BUCKMAN and BATHER (1894), POMPECKJ (1894), UHLIG (1903-10), DOUVILLÉ (1912), JEANNET (1951), BASSE (1952), as well as a number of others.

The problem of sexual dimorphism in goniatites was discussed for the first time in a paper by FOORD and CRICK (1897).

PERNA (1914) was the next to mention this subject in his description including, besides the typical species *Clymenia involuta* WED., the variety *Clymenia involuta* var. *frechi* TOK., which differs from the former in greater diameter and thicker whorls. He thinks that these may be conspecific forms of different sex.

A more detailed description of this phenomenon is presented by DEMANET (1943).

Considering the genus *Gastrioceras* from the Westphalian of Belgium that author asserts that two groups of forms may be distinguished within a group of specimens which on their suture are assignable to the same species. One of the groups has a wide umbilicus and low whorls, the other a narrow umbilicus with high whorls. Both these forms are by DEMANET described under one specific name of *Gastrioceras listeri* (MART.). Other authors describe such forms as separate species. DEMANET cites many cases of the simultaneous occurrence of both these forms within the same beds of Europe or America. The two forms mentioned exhibit certain morphological differences, but on the other hand, they occur together over vast areas independently of facies. DEMANET recognizes that these are conspecific forms of different sex and supposes that those with a wide umbilicus represent the females, while the males are represented by those with a narrow umbilicus. He also stresses that forms assigned to the genus *Homoceras* and described as *Homoceras beyrichianum* (KONICK) and *H. beyrichianum biplex* HAUG, constitute similar pairs.

NAUTILOIDEA

RUEDEMANN (1919, 1921) was the first to discuss sexual dimorphism in fossil nautiloids. When investigating the species *Oncoceras pupaeforme* RUED. from the Utica Shale of New York this author distinguished two forms among adult individuals with constricted aperture and showing a general resemblance. One is larger and wider, the other smaller and narrower. The former is supposed by RUEDEMANN to be the female, the latter — the male. According to the methods usually applied in systematics these forms should be regarded as two separate species (fig. 1). At the same time RUEDEMANN states that forms differing in the length of the living chamber, referred by BARRANDE (1877) to one species *Orthoceras culter* BARR., may also represent different sexes. In his next paper (1926) RUEDEMANN again describes the species *Oncoceras pupaeforme* RUED. applying the following nomenclature: „*Oncoceras pupaeforme* femina" and „*Oncoceras pupaeforme* mas" — for the female and male form respectively.

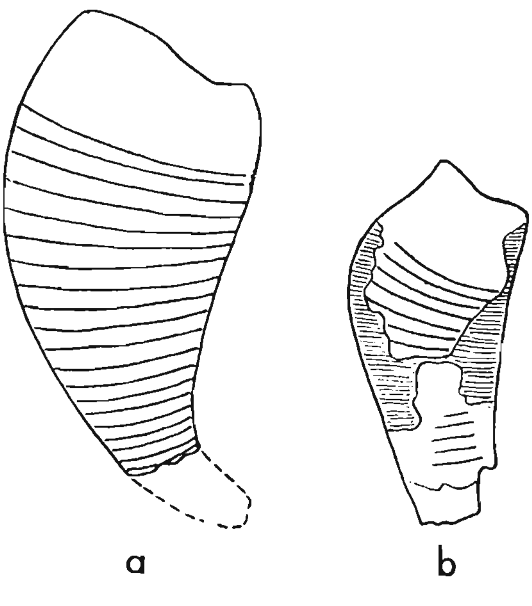


Fig. 1
Oncoceras pupaeforme RUD.: *a* female, *b* male; nat. size (after RUEDEMANN, 1921).

The theory of sexual dimorphism is discussed by FOERSTE (1926) to explain differences in the development of the dorsal collar in various forms belonging to the genus *Inversoceras*.

In his description of nautiloids from the Devonian of New York, FLOWER (1938) writes that two forms may be distinguished among specimens of *Ovoceras constrictum* FLOW. One is more slender, the other more convex. A similar occurrence has been noted by this author in the species *Verticoceras erectum* FLOW. FLOWER is of the opinion that the sexual dimorphism hypothesis can neither be discarded nor accepted merely on the evidence just mentioned. In order to give a clearer picture of the observed phenomena, the distribution of the supposed forms of different sex must in the first place be investigated with respect to their localities and stratigraphic horizons. In view of their extreme scarcity this will prove a difficult task.

Teichert (1940) ascribes to the species *Wadeoceras australe* Teich., from the Devonian of Australia, two types of forms, some of which are more convex, the others somewhat more slender. This author suggests that the former represent the females, the latter the males of one and the same species.

The historical review presented above shows that numerous authors, who recognized the presence of sexual dimorphism in ammonites, nevertheless interpreted it in various ways. They often used it to explain facts which they were not able to clarify. Hence their views on the problem frequently differ on cardinal points.

We see that small ammonites, with the aperture provided with lappets, are by d'Orbigny (1842-51) regarded as young individuals. Some authors, like Reynès (1879), Munier-Chalmas (1892), Haug (1893) and others, regard them as dwarf males. Ziegler (1958) likewise considers them as adults, at the same time discussing the possibility of sexual dimorphism within these forms.

The present writer believes that Reynès, Munier-Chalmas, Haug, Rollier and others followed the right course in their speculations and he will attempt to justify these views. The facts mentioned by them, however, were treated rather superficially, without going into ontogenetic details of the supposed forms of different sex, often on insufficiently reliable evidence. E. g. smooth ammonites are cited as examples though the relationship of the large and small forms cannot be readily demonstrated on them. These opinions have not, therefore, been generally accepted and have not given rise to further discussions.

SENILE (GERONTIC) FEATURES

When going into the problem of large and small forms in ammonites, it is essential to determine whether the forms considered, particularly the small forms do actually represent fully grown adults. As may be inferred from the historical review given in the preceding chapter, this problem has not as yet been fully cleared up. The important point is to ascertain the features that have for a long time been known in the literature as «senile» or «gerontic». A brief review of them, beginning with the most common ones, is not thought out of place here.

SUTURES

Increased density of septa, hence of the sutures too, is undoubtedly one of the most common gerontic features, both in ammonoids and nautiloids. This phenomenon is observable on shells of the living *Nautilus*, as well as on those of the Palaeozoic representatives of the genus *Orthoceras* or *Bactrites*. In such genera as *Nautilus*, *Orthoceras*, *Bactrites*, and *Agoniatites*, increased density of sutures does not produce any distinct changes in shape, since they are either quite simple or weakly differentiated. In such forms, however, as *Tornoceras* considerable shape changes do occur. Fig. 2 shows a small form of *Tornoceras acutum* (Frech), on which the sutures undergo a considerable reduction and their density gradually increases. Further development in this direction would lead to nearly complete simplification of the suture. Since further growth of such specimens and the eventual return of their sutures to the normal shape have never been observed, it is generally accepted that such a state characterizes the adult forms. In goniatites whose sutures have been very carefully analysed and described in palaeontological papers where they are considered as diagnostic classifying characters, an increase in density and simplification are treated as gerontic characters. In many cases, it is — practically speaking — the only character distinguishing the adult forms of *Orthoceras*, *Bactrites* and of many goniatites. The adult aperture in goniatites does not differ at all or only very slightly from the aperture in the growth stages, and, therefore, it does not furnish conclusive evidence.

In Mesozoic ammonites the phenomenon of increased density and regression of the sutures is occasionally very conspicuous in the gerontic stage. Frequently all the longer lobes are shortened and simplified. Fig. 3 shows part of a small form of the genus *Quenstedtoceras* with closely spaced and simplified suture. When ascertaining the distance between septa in the plane of symmetry, it may be seen that the height of the camerae after attaining a certain maximum gradually decreases, so that in the last chamber it is occasionally several times less than its maximum height.

While the occurrence of this phenomenon in goniatites has been carefully studied for a long time, its presence in Mesozoic ammonites, particularly of Jurassic or Cretaceous age, was not considered of first importance. This neglect was probably due to the wealth of other morpho-

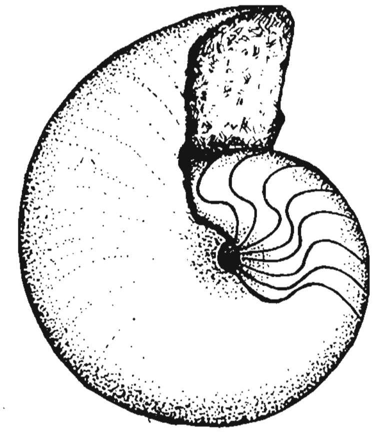


Fig. 2
Tornoceras acutum FRECH, Famennian, Janczyce. Small form, internal mould. The living chamber has been partly prepared, showing crowded and simplified sutures; × 2

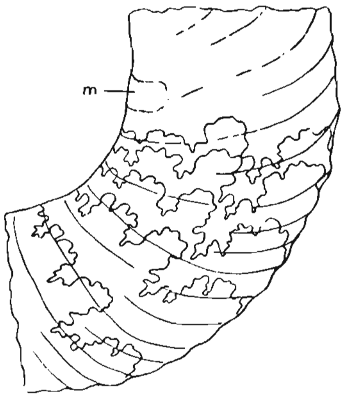


Fig. 3
Small form from the genus *Quenstedtoceras*, adult specimen. Last sutures. Sculpture schematically represented, *m* muscle scar. Callovian, Łuków; × 2

logical details, particularly in the sculpture of the shell, which effaced the undoubtedly intricate development of the suture.

Publications which have appeared thus far, do not show much concern with this problem when identifying adult Mesozoic ammonites. With respect to Jurassic and Cretaceous ammonites this neglect is methodologically unjustifiable since the body chambers, or at least their bases and sutures, are definitely preserved more often than the adult apertures which attracted the main attention of many palaeontologists. Adult ammonites, particularly among the small forms, are reliably distinguished on densely arranged septa and regression of suture. These two characters are on the whole more conspicuous in small forms than in the large ones. Pl. XIX shows sections in the plane of symmetry of adult individuals of the large and small form belonging to genus *Quenstedtoceras*. On the small forms we may observe that beginning with chamber 6-7 (from the end) the septa show a gradual increase in density. The height of the last air chamber is barely one fourth of that of the 6-7th chamber counting from the end. In the large forms this phenomenon is, as a rule, less pronounced.

This increase in density is most likely connected with the rigorous limitation of the growth of small forms to an established number of whorls, while in large forms the moment when growth ceases is subject much more to individual variations.

Having on hand a large collection of *Quenstedtoceras* specimens with preserved gerontic aperture from various stages of ontogeny, the writer was able to ascertain that the formation of the 3—4 last septa was preceded by a check in the growth of the shell and by the initial stage of the development of the final aperture. Hence the tendency to produce septa still persisted after the shell had stopped growing in length. This is reliably demonstrated by a certain shortening of the ultimate body chamber. At particular growth stages of all specimens belonging to various species of the genus *Quenstedtoceras*, the body chamber occupies one half of the whorl, while in adults it is often shortened.

All the observations indicate that the last septa were produced after the apertural margin had stopped growing. The resultant shortening of the final living chamber has been ascertained by the writer in goniatites, mostly in the genus *Tornoceras*. Individuals of that genus, displaying densely spaced septa and a regressive suture have the living chambers somewhat shorter (usually by about 1/10 of the whorl) than specimens which had not reached that stage.

This density of septal spacing and simplification of the suture is, as a rule, more prominent in small than in large forms, and is, most likely, associated with facts, to be described later, which indicate that the moment when growth ceased was more strictly held to in small forms than in large ones.

It should be mentioned, however, that in some cases densely spaced septa and the simplified suture are not conspicuously expressed. E. g. in the genera *Beloceras* and *Manticoceras* sharply pointed lobes overlap the lobes of the preceding sutures impeding any distinct reduction. In some Mesozoic ammonites, e. g. *Trimarginites* and *Pachydiscus*, strongly denticulated sutures are densely spaced even during the growth stages, overlapping one another so that the gerontic characters are poorly indicated and not readily distinguishable.

Moreover, it should be added that in nautiloids *(Orthoceras)*, in goniatites and in Mesozoic ammonites, septa may occasionally be produced at irregular intervals, resulting in local condensation of 2-3 septa. Such an increase in density, however, is never accompanied by simplification of the suture.

Special attention might be drawn to the fact that internal swellings in goniatites, constrictions at the beginning of the last whorl in the genus *Prolobites* and frequent constrictions in the young whorls of the genus *Perisphinctes* (s. l.) are never accompanied by densely spaced septa and simplified sutures.

Finally it may be asserted that the gerontic condensation of septa, together with the related simplification of sutures are characters most commonly preserved as evidence of the adult stage. Neither this fact, however, nor its significance have been widely enough recognized in the literature and used for the diagnosis of mature specimens whose growth had terminated.

APERTURE

During the last decades of the XIXth century and at the beginning of the XXth century, many authors regarded small ammonite forms with lateral apertural extensions (lappets) etc. as adult forms. In the small forms this type of aperture has been considered as a very reliable specific and even generic character. In some cases, e. g. in smooth forms, the aperture was the only character distinguishing them from related genera containing large forms. On the other hand, quite a number of authors postulate that the small forms with lappets and other extensions represent youthful individuals. These opinions will be illustrated here by stating the views of Siemiradzki, the author of the well known monograph of the genus *Perisphinctes*. In his handbook on palaeontology Siemiradzki (1925) writes that lateral lappets and other apertural extensions should not be regarded as gerontic characters. They are produced during periods of arrested growth and were resorbed during later growth. As an example of this supposed resorption of the aperture, Siemiradzki figures the well known specimen of *Morphoceras princeps*. Inconsistent with the above statement, is the acceptance in the literature of numerous small forms of ammonites with lappets and other extensions as species and genera which are mentioned as valid by Siemiradzki in the same handbook and his other papers.

Theories on the resorption of the aperture in ammonites have been advanced by many earlier writers such as Mojsissovics (1886), Bukowski (1887), Pompeckj (1894) [1]. Recently the problem has been critically discussed by Westermann (1956). This author categorically rejects any such possibility as not based on sound evidence, while many facts speak against the hypothesis.

Sazonov (1957) goes back to the opinion of Nikitin (1884) postulating that in the genus *Quenstedtoceras* the long extension on the siphonal side occurred in young specimens only, being subsequently reduced and rounded up in adult individuals with a smooth body chamber. This is an attempt to explain the disappearance of the aperture in small forms disregarding the concept of resorption.

On the whole, however, discussions concerning the interpretation of small ammonite forms with lappets and other extensions have been abandoned and it is now commonly accepted that they are adult forms whose growth is terminated.

The problem of the occurrence of constrictions and so-called parabolic nodes in *Perisphinctes* (s. l.) and *Phylloceras* calls for more detailed investigation. The writer's observations in this respect will be given in a later paper dealing with the problem of sexual dimorphism in these ammonites. At present it should be stated that observations carried out on very rich material show that these constrictions are never accompanied by increased density of septa or simplification of the suture. On the Łuków specimens, which have a well preserved outer surface of shell, it may be easily seen that the outline of the shell margin immediately after the constriction differs strongly from that of the definitive aperture provided with long lappets. Moreover, the constrictions just mentioned are not produced on the last body chamber either in large or small forms. The constriction preceding the gerontic aperture with lappets is an exception.

Detailed investigations do not confirm the supposition that the aperture with lappets is resorbed before further growth of the shell. Two new important observations speak against it. The first is that within large groups of ammonites the small forms attain an exactly defined

[1] The paper of Boone: Note sur la resorption chez les Ammonites et explication de divers accidents de leurs coquilles (*Bull. Soc. Géol. Min. Bretagne*, vol. 6, fasc. 1, 1925) was unfortunately inaccessible to the present writer.

number of whorls that is never exceeded, the other is that in small forms the last whorl, or at least its last half, develops along a different spiral than in the large forms. Therefore, were the small form to follow the evolutionary pattern of the large form, the process of resorption would have to be assumed to affect not only the aperture, but the major part or even the whole of the body chamber, too. This is, however, an unacceptable supposition. Text-pl. VII and VIII shows the ontogeny of small and large forms of the genus *Quenstedtoceras*, and draws attention to the differences between them from the stage of about $5^1/_2$ whorls onwards. This indicates clearly that small forms with an elongated extension on the siphonal side do not represent the young individuals of large forms with a smooth body chamber. This problem will be treated more at length later.

SCULPTURE

In the adult stage the sculpture is also subject to distinct changes. Above all, the individual features of ornamentation either vanish or become more densely spaced. In some ammonites, e. g. in representatives of the Cardioceratidae or the Parkinsonidae, the large forms are ribbed in the young stages, later the ribbing disappears so that the last whorl or last two whorls are quite smooth. In these cases the disappearance of ribbing is accompanied, as in the earlier stages, by a regular increase in the spacing of ribs which smooth out progressively. By contrast, in the gerontic disappearance of ornamentation all the features, such as ribs, nodes and spines, are not only reduced, but at the same time are more densely spaced. The situation is similar with constrictions. These, when occurring e. g. in the young stages of Perisphinctidae, are first densely spaced, later they become progressively spaced out to vanish completely on the last whorl. This can be observed both in small and large forms. In cases, however, where the constrictions occur not on the initial whorls only, but on the last body chamber, also, as in some representatives of the Litoceratidae, they become shallower, narrower and more closely spaced at the end of the last body chamber. Similar changes are noted in the so-called labial swellings of goniatites, marked on moulds as grooves. In the genus *Cheiloceras* it may be readily observed that in the adult stage of both small and large forms, these swellings are more densely spaced near the margin of the final aperture.

IMPRESSIONS OF MUSCLE ATTACHMENTS

In some ammonites the gerontic characters are occasionally represented by scars of the muscle attachment (muscle scars), occurring at the base of the last body chamber. They are produced after completion of growth by a thickening at the base of the last body chamber, just above the last suture, as the result of deposition of a supplementary prismatic layer. At the point of the muscle attachment the prismatic layer did not become additionally thickened and this area is distinctly depressed, while in moulds it appears as a node. This type of muscle impression is occasionally very prominent in small forms of the genus *Quenstedtoceras* (fig. 3). Similar ones are observable in small forms of *Tornoceras simplex* (Buch). In moulds they are indicated as a row of depressions just above the last suture. They resemble similar scars occurring on adults of some nautiloids.

NEW OBSERVATIONS CONCERNING DIMORPHISM IN AMMONOIDEA

On the basis of sex relations in living animals and of palaeontological facts usually explained by the hypothesis of sexual dimorphism in ammonites, and taking into account objections raised against it, four conditions are here advanced as reasonable pre-requisites for the acceptance of this hypothesis:

1) identical initial stages of ontogeny in both (small and large) forms, and identity of their phylogeny,
2) lack of intermediate forms in adult (gerontic) stages,
3) presence of both forms in the same strata,
4) numerical ratio of the two supposed sexes (sex ratio), comparable to that observed in living forms.

The requirements just listed call for at least some brief explanatory remarks.

Condition 1) must be accepted since a rational discussion on the theory of sexual dimorphism in these forms is justifiable only on the basis of a close alliance which has been ascertained at least in the early stages of ontogeny and, if possible, confirmed by phylogenetic lineages. This pre-requisite must be applied in order to eliminate cases of far advanced convergence, most commonly observable in the adult stages.

Naturally, possible errors and confusion in the study of dimorphism may be commited in relatively rare cases of far advanced convergence in the ornamentation and other characters of ammonites of the same age, occurring in the same strata. Indeed, such cases have long been known and described. E. g. Michalski (1890), in his well known work on ammonites of the Volga stage, writes that some of the ammonites he had studied, belonging to different species and, at the same time, to genetically different groups, show a strong resemblance in their adult stages. Occasionally this may impede even their specific differentiation, though the early whorls are completely different. The simultaneous occurrence in the same beds of large and small forms, displaying identical early whorls and a general resemblance of the adult stages, has by other authors been referred to convergence and parallel evolution. However, it will here below be demonstrated that this phenomenon may be explained by sexual dimorphism.

Condition 2) must be introduced chiefly because ammonites are extinct. In the presence of intermediates among the supposed male and female individuals, the theory of sexual dimorphism would hardly be acceptable or would at least give rise to serious objections. Such objections are even now raised by some authors and are responsible for this problem being generally shifted into the background of discussions on systematics.

Condition 3) was advanced already by the first authors who made suggestions on the subject of dimorphism in ammonites. This pre-requisite cannot be readily fulfilled since the meaning «of the same strata» is misleading. The accuracy of definition here may vary considerably, from very thin layers whose thickness does not exceed that of the ammonite shell, to much thicker beds. It is also rather difficult to determine the upper and lower boundaries of the stratigraphic range of the forms supposed to differ in sex. These boundaries may be determined solely within a continuous sedimentary series. The extinction of species is usually preceded by their progressive scarcity. Finally they become so rare that it is practically impossible to ascertain whether both these forms disappear simultaneously. This difficulty is increased by frequent differences in the numerical ratio of individuals referred to the two sexes. Therefore, the pre-requisite considered here will invariably raise certain doubts.

As regards condition 4), it should be pointed out that the mean sex ratio calculated for a large number of living species is approximately 1 : 1 and this figure may be regarded as representative. Often, however, the ratio differs notably. The deviation may either be primary, i. e. the difference is produced during the process of sex determination, or else secondary. The latter is chiefly observable in older individuals, possibly owing to the higher death rate among younger individuals of one sex, etc. Many examples of extreme variations in sex ratio have not so far been satisfactorily cleared up, none the less it is sometimes possible to correlate clearly between the extent of these differences in ratio and environmental conditions.

Numerous examples are now available to illustrate the important influence of climate in general and that of temperature in particular; therefore, even distinct deviations from the representative 1 : 1 numerical sex ratio in ammonites cannot be regarded as conclusive evidence for the rejection of sexual dimorphism in that group of animals. Even with a 1 : 1 sex ratio, the local distribution of the two sexes may be quite different (males may tend to stay together or have different feeding habits etc.). Special attention should be called here to possible changes in the numerical ratio of small and large forms caused by processes of fossilization and diagenesis in their broad meaning. The writer's own observations on the state of preservation and the processes of fossilization in Mesozoic and Palaeozoic ammonites have led him to the conclusion that the state of preservation of an ammonite shell may be greatly influenced by its absolute size. Hence, if the size differences were considerable, the processes of fossilization might have distorted the numerical ratio of fossil specimens representing conspecific individuals of different sex. In the Devonian of the Holy Cross Mountains the writer has observed within one bed that the large shells had been completely destroyed in the process of fossilization, while in an adjacent bed the preservation of both large and small forms was uniform. Such occurrences must also be taken into account when determining the numerical ratio of the supposed two sexes.

Detailed ontogenetic investigations of large and small forms of ammonites, displaying general similarities and by earlier authors regarded as congeneric, have been carried out for several years by the present writer with the aim of clearing up this problem in consistency with assumptions referred to above.

Comparative studies on the evolution of the sculpture and suture covered all the stages of ontogeny, starting with the earliest, i. e. the protoconch. They were greatly impeded by the scarcity of remains representing the protoconch and the first whorls. A long and laborious search had often to be made before discovering adequately preserved specimens of a given form. Moreover, it was necessary to prepare the young whorls in order to compare their ornamentation and suture.

Observations on the evolution of the sculpture and suture were a means of ascertaining the number of whorls on the specimens examined. This was achieved by admitting that the first whorl corresponds to the presumed larval stage ending at the first constriction. The larval stage consists of the protoconch and the completely smooth whorl surrounding it. The length of this whorl, from the proseptum to the first constriction, ranges from two thirds of a whorl *(Anarcestes, Agoniatites)* to one complete whorl (Jurassic and Cretaceous forms.). The first constriction is connected with the aperture of the supposed larval shell. In Mesozoic forms it is quite distinct, while in some Palaeozoic specimens it is either only faintly indicated or lacking. In its absence the determination of the boundary of the larval shell meets with difficulties. In some ammonites, e. g. in the genus *Cosmoceras* and *Garantiana*, the ornamentation characteristic of the full grown shell appears directly after the first constriction. This is very useful in determining the boundary of the larval shell. It is known that in Mesozoic ammonites and in goniatites a distinct swelling occurs just at the first constriction. This thickening is due to the fusion with and superimposition on the larval shell wall of the proper shell wall, and still more so of the prismatic layer which is notably thicker. The swelling is, as a rule, observable in slides made in the plane of symmetry and may be useful in determining the end of the first whorl. The objection that may be raised to this method of counting the whorls is that the larval shell does not always make up a complete whorl. This is essentially true. However, no matter what may be the opinion on this method of counting the whorls, we must accurately delimit the larval shell from the true shell. The important point here is the distinct structural difference between the two parts. It consists in the absence from the larval shell wall of the prismatic layer which appears suddenly at the point of fusion of the larval shell with the proper one. Colouration, lacking on the larval shell, appears with the prismatic layer. The analogy with conditions noted in gastropods is striking and may be explained by supposing that in ammonites the development of the proper shell was preceded by metamorphosis, as in recent gastropods. The number of whorls in the proper shell could, therefore, be counted ommiting the larval shell, but since in most ammonoids the larval shell consists of a complete or nearly complete whorl, the present writer accepts it as the first whorl.

The diameter of the first whorl, measured in the plane of symmetry, as ascertained on the writer's own observations and on data from literature, is as follows (in mm):

Manticoceras	1.20-1.30
Tornoceras	1.00-1.10
Cheiloceras	1.00-1.10
Mesozoic ammonites	0.50-0.75

In the study of shell ornamentation the supposed lack of conclusive evidence to clear up the relations between large and small forms, and the diversity of opinions on this question prompted the writer at the beginning of his research to investigate the suture. With time, however, as observations accumulated, he drew the conclusion that the development and character of the suture cannot furnish any essential criterion and that on the whole it is of much smaller significance than the character of ornamentation. E. g. a thorough study of the development and character of suture in the genera *Cosmoceras* and *Quenstedtoceras* does not contribute to a clarification of the phenomenon considered here. Congeneric species, differing strongly in sculpture and whorl section, have identical sutures, allowing for individual variations. The occasional clear differences in the symmetry and shape of the various elements are individual characters. Individual variations of the suture doubtlessly equal those of other characters, ornamentation and whorl section included, but they are not so easily distinguished and are relatively less known.

Moreover, in many cases the suture does not furnish reliable grounds for determining the systematic position and the phylogenetic relations of Mesozoic ammonites — particularly Jurassic ones — not only at the level of species and genus, but even at that of families or superfamilies. Certain genera of Jurassic ammonites have by some authors been placed in one family or superfamily, and by others in a different one, and frequently in such cases studies of the suture have failed to give a solution.

Observations concerning the ontogeny of large and small forms, involving the number of whorls, have been made on numerous species belonging to various Mesozoic and Palaeozoic genera, families and superfamilies of ammonites. These investigations have gradually made it clear that the number of whorls in the adult stage is, indeed, the most constant and conservative feature in ammonites. It is the writer's opinion that this feature is of great importance in clearing up the relations of large and small forms in all ammonoids. The phenomenon cannot be explained other than by sexual dimorphism.

Thus far it has been possible to ascertain the existence among ammonoids of two relevant kinds of dimorphism. One of them, let us say type «A», is characterized by the presence of 5-6 whorls in small forms, and of at least 7 whorls in large forms. In most species exhibiting this type of dimorphism the number of whorls in small forms is exactly six. In other species some of the small forms do not go beyond the stage of 5 whorls, some develop 6 whorls, while the rest halt at intermediate stages.

The large forms from the stage of $5\text{-}5^1/_2$ whorls onwards execute a different spiral from the small forms, the whorls being higher. Specimens of the two groups which have reached the 6 whorls-stage may thus be distinguished.

Some exceptions to this rule have been found by the writer both among small and large forms. E. g. some specimens of the large forms in the genus *Hecticoceras* do not go beyond the stage of $6^1/_2$ whorls. The same phenomenon, i. e. that some specimens of the large forms halt at a stage with less than 7 whorls, probably also occurs in the genus *Taramelliceras,* perhaps in *Scaphites*, too, but so far this supposition has not been reliably confirmed. They are, however, readily distinguished from the small forms on the character of their spiral. Moreover, large forms of Devonian goniatites from the genera *Tornoceras*, *Manticoceras* and others, rarely attain the 7 whorls-stage; most of them a little surpass the 6 whorls-stage. Among small forms, some specimens of the genus *Tornoceras* and certain Clymeniidae do not exceed the stage of about 4 whorls.

In the type «B» dimorphism, the small forms have 7-9 whorls, the large forms at least 8 whorls, and at least one complete whorl more than their associated small form. Rarely, some specimens of the small forms may halt at the stage with $6^1/_4$ whorls and, exceptionally, at the 6 whorls-stage. In the simplest cases of type «B» dimorphism the small forms have 7 whorls, the large forms 8 whorls. This is so in representatives of the genera *Sphaeroceras*, *Chondroceras*, *Cadomites* and others. In other cases, e. g. in some representatives of the genus *Perisphinctes* (s. l.) the small forms attain 7-8 whorls, the large forms at least 9 whorls.

Further studies will perhaps permit the differentiation within type «B» of smaller groups in which the morphological features of individuals of different sex are more conspicuous. At the present state of knowledge the writer considers it wiser to stop at the separation of the rather well differentiated type «B».

To sum up, the two morphological kinds of dimorphism in ammonoids may be concisely characterized merely on the number of whorls in small forms:

type «A» — small forms attaining 5 to 6 whorls,
type «B» — small forms attaining 7 to 9 whorls.

On present information it is hardly possible to make reliable conjectures about the occurrence of types other than those just mentioned. But even if other types do occur, the two cited above most likely predominate among Mesozoic as well as Palaeozoic ammonites.

A description of the material that provides evidence for the distinction of the two types of dimorphism, will be given below. Only some of the species investigated have been picked out as illustrative. It is the writer's intention to go into this problem by presenting those most common, well-known and frequently described species which at the same time are examples of different forms of ammonites, and illustrate various degrees of the dimorphism under consideration.

Dimorphism of type «A», which has been more fully investigated and is more easily presented, will be dealt with at length in the present paper. Type «B» will be illustrated by only a few very simple examples.

The characters of the suture and of ornamentation will not be described in detail as their evidence is inconclusive. The published drawings and photographs are thought reasonably reliable documentation for the conclusions made.

The systematics and nomenclature used in the following chapter are those commonly applied.

DIMORPHISM «A»

MESOZOIC AMMONITES

Genera **KEPPLERITES** NEUMAYR & UHLIG, 1892 and **COSMOCERAS** WAAGEN, 1869

(pl. I-V; text-pl. 1)

The genus *Cosmoceras*, together with the genus *Kepplerites* included within it as a subgenus, have been worked out in great detail by BRINKMANN (1929*a*, 1929*b*). BRINKMANN's paper is based on very rich and — to a certain extent — unique material. It is a valuable contribution to the general knowledge of ammonites and particularly to the problems discussed here. It demonstrates that lineages of large forms with simple aperture occur along with lineages of small forms which have an aperture provided with lappets, and that between them there are no intermediates. There is no other work — except for WAAGEN's paper published in 1869 — presenting a more illustrative picture of the side by side existence of large and small forms. Its value is enhanced in that this phenomenon is explained not only in individual pairs of forms, but also in a sequence of evolutionary lines.

BRINKMANN (1929*a*, 1929*b*) splits up the genus *Cosmoceras* into 5 subgenera. Those characters that are of bearing in the present paper are here briefly given after that author:

1. *Kepplerites* — large forms with simple aperture and small forms with short lappets,
2. *Cosmoceras* s. str. — large forms with simple aperture,
3. *Zugocosmoceras* — ,, ,, ,, ,, ,,
4. *Anacosmoceras* — smal forms with aperture provided with lappets,
5. *Spinocosmoceras* — ,, ,, ,, ,, ,, ,, ,,

According to BRINKMANN (1929*a*), lineages of the large forms of the subgenera *Cosmoceras* and *Zugocosmoceras* descend from an analogous form of the genus *Kepplerites*, while the origin of the small forms in the two remaining lineages is still an open question.

The present writer thinks that without discarding BRINKMANN's concepts the lines of small forms assigned to the subgenera *Anacosmoceras* and *Spinicosmoceras* may reasonably be traced down to an analogous form in the genus *Kepplerites*, the more convincingly so as the necessary small forms with lappets are described and figured by BRINKMANN himself (1929*b*).

The possibility of interpreting the side by side existence of lineages of large and small forms by sexual dimorphism is only rather briefly commented upon by BRINKMANN (1929*a*). His main objections for rejecting this theory are that:

1) the evolutionary line of *Cosmoceras* s. str. appears earlier and persists longer than a similar line of small forms of the subgenus *Spinicosmoceras*;

2) the evolution of *Cosmoceras* s. str. constitutes one evolutionary plexus, while the line of *Spinicosmoceras*, after a time, splits up into two parallel branches;

3) the evolutionary line of *Zugocosmoceras* persists longer than a similar line of small forms of the subgenus *Anacosmoceras*.

BRINKMANN's objections against the theory of sexual dimorphism in this particular case will be discussed later. Here the writer is presenting the results of his comparative studies on the ontogeny of large and small forms from the genera *Kepplerites* and *Cosmoceras*.

Kepplerites gowerianus (Sow.) is a rather common species in the Callovian deposits at Wieluń. Among the score or so of specimens found there, six have a complete last body chamber of 1/2 whorl. The last sutures are very closely spaced. The present writer had, moreover, the opportunity to study many similar specimens with preserved gerontic aperture from a number of Polish collections assembled from Wieluń and the Jurassic of the Cracow Uplands. The measured diameter of 26 adults ranged from 58 to 80 mm. The study of younger whorls was hardly possible. On the whole they were poorly preserved, with only fragmentary sutures. Nevertheless thin sections in the plane of symmetry distinctly indicated that the first whorl is 0.60-0.75 mm in diameter, whence it could be calculated that adults of this species have exactly 7 whorls. This was, however, detectable on two specimens only. Still, by comparing other specimens of the same species, it was observed that the pattern of spiral does not change and that nothing suggests a different number of whorls in other specimens.

Four specimens of *Kepplerites hexagonum* (LOEWE) from Wieluń have also been investigated. The writer is moreover in possession of a specimen of *K.* cf. *hexagonum* (LOEWE) from the Jurassic of Lithuania at Popielani. It differs from the typical forms of *K. hexagonum* (LOEWE) in having more flattened whorls and a more compressed siphonal side. The last whorl here is preserved as an impression only. The gerontic aperture, however, is excellently preserved and represented by a lappet, also the younger whorls filled with calcite. The diameter of these 5 specimens ranges from 32(?) to 43 mm. On one of the Wieluń specimens and on the Popielani specimen just mentioned it was ascertained that the shell of *Kepplerites hexagonum* (LOEWE) consists of exactly 6 whorls. The first whorl is 0.70 mm in both specimens. Up to the $5^1/_2$ whorls-stage the sculpture and the whorl section are identical in the two. Their sutures could not be accurately compared, but the fragments examined do not suggest differences. From the $5^1/_2$ whorls-stage on, some minor changes take place in the sculpture of the shell. Those in the whorl section, however, are conspicuous. In *K. hexagonum* (LOEWE) the section of the last half whorl housing the body chamber develops according to a different pattern. Namely, it gradually grows flatter and lower in relation to the section of the corresponding part of the same whorl in *K. gowerianus* (Sow.). Hence, even on the grounds of this scant material the affinities and differences in *K. gowerianus* (Sow.). and *K. hexagonum* (LOEWE) are enough to infer that the two are separated by a morphological hiatus of one whorl.

Large ammonites of more than 35 cm diameter from the Callovian of Alaska were described by IMLAY (1953) under the names of *Kepplerites (Seymourites) mclearni* IMLAY and *K. (Seymourites) rockymontanus* IMLAY. From the same beds, along with these, he described, under the name of *Cosmoceras (Gulielmiceras) knechteli* IMLAY, other relatively small ammonites, having a diameter of 55 mm only, provided with lappets (IMLAY, 1953, pl. 5,

TEXT-PLATE I

Former interpretation:	New interpretation:	Occurrence:
1 *Kepplerites gowerianus* (SOW.)	*K. gowerianus* (SOW.) ♀	Wieluń, Callovian
2 *K. hexagonum* LOEWE	*K. gowerianus* (SOW.) ♂	„ „
3 *Cosmoceras (Cosmoceras) spinosum* (SOW.)	*C. spinosum* (SOW.) ♀	Łuków, Callovian
4 *C. (Spinicosmoceras) annulatum* (QUENST.)	*C. spinosum* (SOW.) ♂	„ „

TEXT-PLATE I

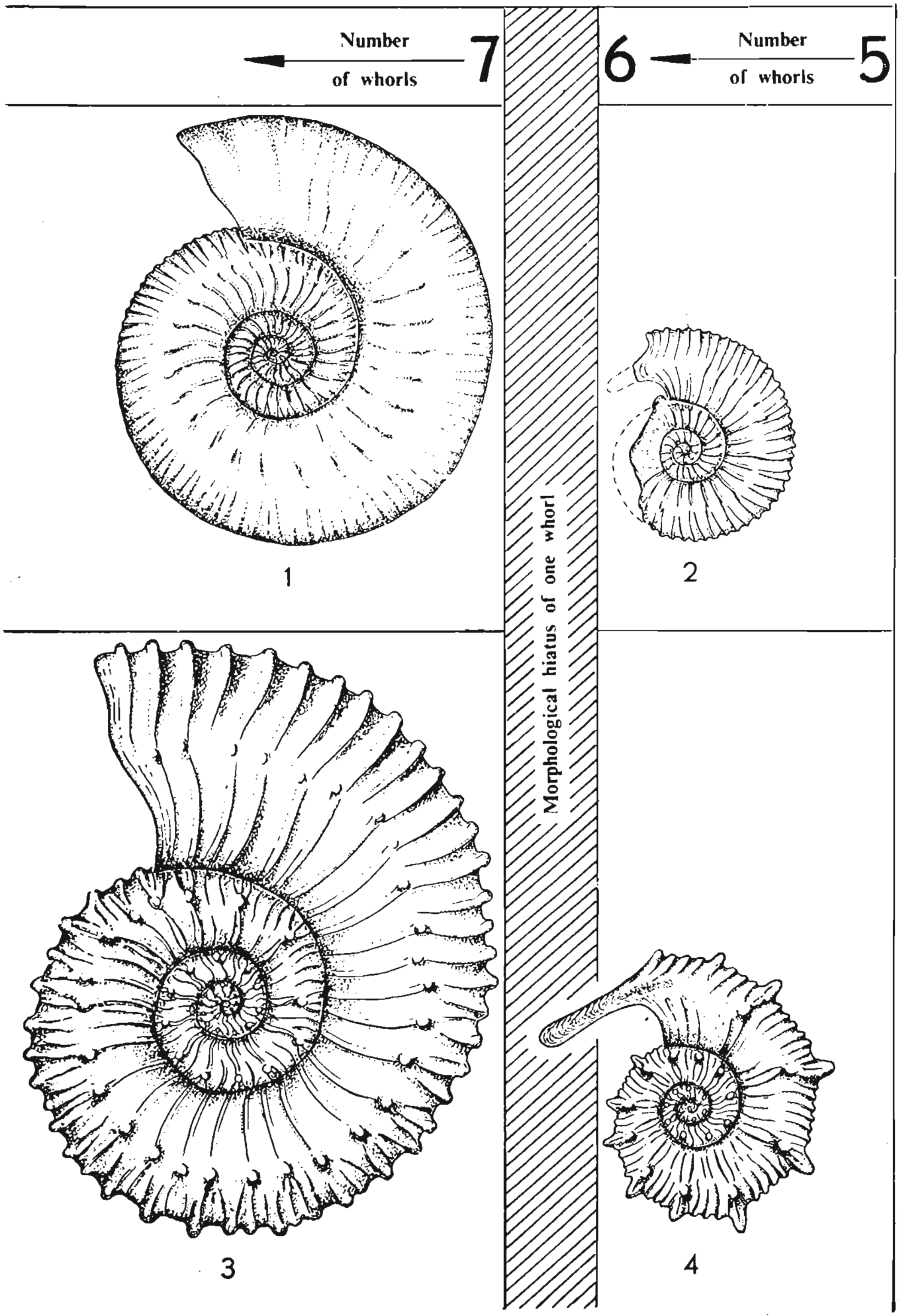

Number of whorls 7
6 Number of whorls 5
Morphological hiatus of one whorl
1
2
3
4

fig. 1-5). Both in ornamentation pattern and in their very characteristic trapezoidal section the latter forms resemble the young whorls of the big specimen of *K. (Seymourites) mclearni* IMLAY (IMLAY, 1953, pl. 14, fig. 1-6, 8). It should also be stressed that, judging from Imlay's excellent figures, the small individual of the genus *Kepplerites* from the Jurassic of Popielani, on which the number of whorls was determined, is identical in sculpture and section with the young whorls of *K. (Seymourites) mclearni* IMLAY.

As to the genus *Cosmoceras* there is a marked resemblance between the pairs of large and small forms in lines differentiated by BRINKMANN (1929*a*). These similarities are particularly conspicuous in forms belonging to the first pair of phylogenetic lines.

Large forms	Small forms
Zugocosmoceras BUCKMAN	*Anacosmoceras* BUCKMAN
Cosmoceras s. str. WAAGEN	*Spinicosmoceras* BUCKMAN

The line of *Zugocosmoceras* starts with the species *Cosmoceras (Zugocosmoceras) enodatum* NIKITIN. Eight specimens of that species, with the last body chamber complete, have been collected by the author from the Cracow Jurassic Uplands at Czatkowice and Filipowice. On one of these specimens a small constriction has been preserved, preceding the aperture whose margin is not preserved. These specimens were from 50 to 55 mm in diameter, while BRINKMANN (1929*a*) states that in this species the diameter ranges from 60 to 90 mm. Hence the specimens from the Cracow Jurassic seem to represent forms of relatively small diameter. The writer has studied the ontogeny and number of whorls on 5 specimens. Of these four have the first whorl preserved so that it was possible to ascertain that they had all developed exactly 7 whorls. In the remaining specimen the spiral is identical to those just mentioned. The writer was also able to examine 11 other specimens belonging to that evolutionary line and known as *Cosmoceras jason* (REIN.), *C. obductum* BUCK. and *C. proniae* TEISS. Most of them were fragmentary. The smallest complete specimen with a diameter of 56 mm belonged to the species *C. jason* (REIN.). In the other specimens the diameter probably ranged from 60 to 100 mm.

All these specimens had at least 7 whorls. On one specimen of *Cosmoceras jason* (REIN.) from the Swabian Jurassic of Gamelshausen, 7 nearly complete whorls were counted on the chambered part of the shell so that in all there must have been $7^1/_2$ whorls.

Two specimens only have been examined from the line of *Anacosmoceras*. One is from the Lithuanian Jurassic of Popielani and agrees fully with the form described by BRINKMANN (1929*a*) as *Cosmoceras (Anacosmoceras) gulielmi anterior* BRINKM. It is in an excellent state of preservation, 26 mm in diameter, with exactly 6 whorls. Up to the $5^1/_2$ whorls stage the ornamentation is identical with that observable on the same stage of young individuals of *C. jason* (REIN.). The other specimen of the species *Anacosmoceras* has been collected from the Cracow Jurassic at Czatkowice. It is 54 mm in diameter. The young whorls, up to the $5^1/_2$ whorls-stage, very closely resemble the young whorls of *Cosmoceras (Zugocosmoceras) obductum* BUCK. The thin section in the plane of symmetry shows that on this specimen, too, there were exactly 6 whorls.

The writer's observations of the *Cosmoceras* s. str. line are based exclusively on material from Łuków belonging to *C. (Cosmoceras) spinosum* (SOW.) and *C. (Cosmoceras) duncani* (SOW.). The adult shell diameter in these species ranges from 75 to 100 mm. On many specimens with such gerontic features as disappearance of ornamentation near the aperture, deviation of whorls from the normal spiral, greater density and simplification of the last septa, — it may reasonably be inferred that forms belonging to that subgenus developed at least 7 whorls.

Some big specimens of the two just named species, up to 15 cm in diameter, have $7^1/_2$ or even 8 whorls.

The group of *Spinicosmoceras* yielded the greatest number of specimens. They consisted of: one specimen of *Cosmoceras (Spinicosmoceras) ornatum* (Schloth.), and one specimen of *C. (Spinicosmoceras) pollux* (Rein.) — both from the Lithuanian Jurassic of Popielani; another specimen of the last named species from the Cracow Jurassic at Czatkowice; one specimen of *C. (Spinicosmoceras) aculeatum* (Eichw.) from Christian Malford in England with a complete aperture provided with a long lappet; and 60 specimens from Łuków of species *C. (Spinicosmoceras) transitionis* Nik. and *C. (Spinicosmoceras) annulatum* (Quenst.). In the Łuków material the diameter ranges from 25 to 42 mm. Most of the specimens are with a gerontic aperture provided with lappets. The young whorls, or at least their impressions, are here excellently preserved permitting a detailed examination. These specimens have from 6 to $6^1/_8$ whorls. Thus we see that individual variation is rather small. The same was also ascertained on the two above named specimens of *C. (Spinicosmoceras) pollux* (Rein.), 46 and 53 mm in diameter. Both these specimens which represent the lower stages of the *Spinicosmoceras* lineage, also have 6 and $6^1/_8$ whorls. The English specimen of *C. (Spinicosmoceras) aculeatum* (Eichw.) from Christian Malford is rather interesting in that it is the largest-sized among all the specimens of that lineage available to the writer. It is 65 mm in diameter, thus attaining twice the size of the average Łuków specimens. It also has exactly 6 whorls.

The Łuków material shows clearly that in young individuals of the *Spinicosmoceras* lineage — up to the $5^1/_2$ whorls-stage — the corresponding ontogenetic stages of large forms belonging to the subgenus *Cosmoceras* s. str. are exactly repeated. The individual variation range, as well as the range of ornamentation and whorl section, is identical in the two groups. The sutures in the small forms are distinctly more crowded, but relatively little simplified. Thus it may be seen that, contrary to what Brinkmann thought, the *Spinicosmoceras* lineage did not become extinct earlier than the *Cosmoceras* s. str., but survived quite as long. Its end link, i. e. *C. (Cosmoceras) spinosum* (Sow.) has its equivalent in *C. (Spinicosmoceras) annulatum* (Quenst.) which belongs to the small lineage.

The phenomenon of the splitting of the subgenus *Spinicosmoceras*, as compared with the unbranched development of large forms from the subgenus *Cosmoceras* s. str., still requires an explanation. On the basis of material investigated from Łuków and the Cracow-Częstochowa Jurassic Uplands, the writer thinks that this may reasonably be interpreted as follows. In the genus *Cosmoceras* (s. l.) all the changes in sculpture and whorl section (i. e. all new features) appear on young whorls and in the course of further phylogeny they are shifted on to successive whorls. These features are often modified or vanish so that they are absent from the end whorls. Hence we may note the side by side existence of large forms whose last whorls and particularly the last body chamber are identical, while their young whorls differ in section or in character of ornamentation. These differences, being not very striking, are not taken into account in the specific delimitation of large forms, they are, however, very readily discernible in small forms which repeat the character of the young whorls of large forms.

In the example presented by Brinkmann he emphasizes the outline of the whorl section which is different in two parallel lines of small forms from the subgenus *Spinicosmoceras*, i. e. *C. (Spinicosmoceras) castor* (Rein.) and *C. (Spinicosmoceras) pollux* (Rein.). In respect to large forms of the *Cosmoceras* s. str. line, Brinkmann supposes that *C. (Cosmoceras) pollucinum* Teiss. is chronologically similar to the two species just mentioned. From several, mostly incomplete specimens from the Cracow-Częstochowa Jurassic it was possible to ascertain that the young whorls of *C. (Cosmoceras) pollucinum* Teiss. display great variability. In some specimens they resemble the young whorls of *C. (Spinicosmoceras) castor* (Rein.), in others — those of *C. (Spinicosmoceras) pollux* (Rein.). In the systematic part a description of a case concerning the *pollucinum* — *pollux* forms and two similar examples from among the uppermost stages of these two evolutionary lines will be given.

The differences in stratigraphic range of the large forms of the subgenus *Zugocosmoceras* and the small forms of the genus *Anacosmoceras* emphasized by Brinkmann, still present an open question. These differences, however, are not important and the present writer thinks that they and other comparable facts do not furnish any conclusive evidence for clearing up the problem of the mutual relations of large and small forms.

The genus *Cosmoceras* (s. l.) is an ammonite rich in possibilities for the study and discussion of the problems being considered, particularly because of the wealth of ornamental details permitting the exact determination of relationship between large and small forms, and the profusion of palaeontological material from different regions of Europe, England in particular, on which Brinkmann's (1929*a*) work was based. A monograph of the genus *Cosmoceras*, with special reference to the problem of sexual dimorphism, would doubtless bring to light a number of interesting and valuable conclusions concerning the evolution and genetics of populations, etc. in ammonites. Its preparation, however, would require the assembly in one place of material from various parts of Europe.

Genus **HECTICOCERAS** Bonarelli, 1893

(pl. VI; text-pl. II, fig. 1, 2)

In his extensive monograph of the genus *Hecticoceras*, Lemoine (1932) differentiates approx. 55 species without subgeneric separation. In his diagnosis this author refers forms with the apertural margin provided with lappets to the genus *Hecticoceras*. From nearly 480 specimens which have been figured in Lemoine's paper, we find the description and illustration of apertures with lappets on only 5 (or 6) specimens belonging to four different species. They are small specimens, from 25 to 35 mm in diameter.

Jeannet (1951) described numerous species of *Hecticoceras*. In the diagnosis of the family Hecticoceratinae that author writes: «margin of aperture provided with lateral lappets». This would apparently suggest that all the species in this group are characterized by the presence of an aperture with lappets. This is not the case, however, since in the same paper Jeannet describes and figures a large specimen, 82 mm in diameter, with a simple aperture preceded by a distinct constriction. Near the aperture the shell is perfectly smooth. In the same description we read that the margin of the aperture is sinusoidal and without any traces of lateral lappets (fig. 4).

In the diagnosis of the family Oppeliidae given in the «Treatise on invertebrate paleontology» by Arkell et al. (1957), forms both with and without apertural lappets are assigned here. No mention, however, is made by these authors of the shape of the aperture either in the diagnosis of the subfamily Hecticoceratinae or in the description of genera. The genus *Hecticoceras* is split into 9 subgenera solely on the pattern of ornamentation. Most of these subgenera correspond to the genera distinguished by Jeannet (1951)

It will be to the purpose to add that approx. 800 specimens, from various species of the genus *Hecticoceras* (s. l.), are figured in the literature cited in the present Reference List covering a period of 110 years. Moreover, Haas (1955) writes that he discovered one only small specimen, having the aperture provided with lappets, among the 3300 specifically identifiable specimens belonging to 12 species, collected by him in Syria. 175 specimens of that collection have been figured by him. Thus among the approximately four thousand specimens cited in the relevant literature we find illustrations of only three large individuals (65-100 mm in diameter), having a simple aperture, the margin of which is straight and some 12 specimens 25-38 mm in diameter, in which the aperture is provided with lappets. Hence it may be concluded that the preservation of the aperture on specimens of the genus *Hecticoceras* is extremely rare. This may be due to the exceptional fragility of the shell in these ammonites. It is, indeed, the scarcity of material with preserved aperture that may account for the fact that in the systematics of the genus *Hecticoceras* this character was never ascribed any definite major significance.

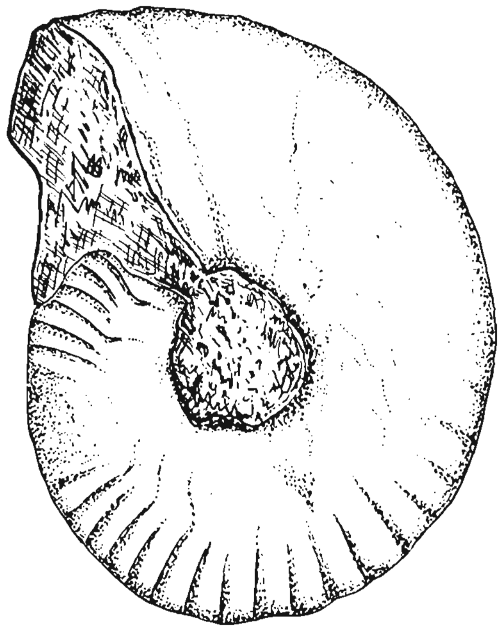


Fig. 4
Large form from the genus *Hecticoceras* with aperture, after JEANNET (1951)

The present writer has been able to assemble in his collection 5 specimens of the large *Hecticoceras* forms with preserved aperture, also 20 specimens of the small forms having the aperture provided with lappets. Of the large forms two are from Łuków, three from Cracow Jurassic at Czatkowice. Of the small forms 3 specimens are from Czatkowice, 1 from Wrzosowa, 1 from the Lithuanian Jurassic at Popielani, 15 from Łuków. The diameter of the small forms examined by the writer ranged from 18 to 40 mm. After treating the protoconch and the first whorl in 16 specimens it was seen that they all consisted of exactly 6 whorls and no individual deviation was observed.

The protoconch and the first whorl in all the 5 large specimens could be revealed. Two of them, having the aperture with a completely straight margin and preceded by a distinct constriction, consist of exactly 7 whorls each. The other three have $6^1/_2$ whorls each, their aperture is not quite simple, but is nearing that of the growth stages of large forms and provided with small broad lappets. However the spiral pattern followed is that of the large forms, completely different from the spiral in the small forms. Hence, they should be regarded as large forms whose growth halted at the stage with about $6^1/_2$ whorls.

Through the courtesy of the late Professor W. J. ARKELL the writer is also in possession of a large specimen of the genus *Hecticoceras* («*Hecticoceras hecticum*» HART.) collected at Coiffres (Sèvres, France) from Middle Callovian beds. This specimen is approx. 95 mm in diameter and has a straight gerontic aperture.

Thus the diameter of all the large *Hecticoceras* specimens with preserved straight aperture that are known to the writer — including those figured in the literature — ranges from 90 to 125 mm. All the small forms having the aperture provided with lappets range from 18 to 40 mm in diameter.

When investigating the young whorls of large and small forms, in every case pairs of these two forms could be selected with identical early whorls. Starting from the $5^1/_2$ whorls-stage on, however, these forms become distinctly differentiated, particularly in respect to the character of the spiral. In small forms the height and width of the last whorl are considerably less than in the 6th whorl of the large forms.

Genera **LISSOCERATOIDES** SPATH, 1923 and **GLOCHICERAS** HYATT, 1900

(text-pl. II, fig. 3-5)

In the earlier literature species of the genera *Lissoceratoides* and *Glochiceras* were assigned to the genus *Haploceras*, with occasional differentiation of the large and small forms into separate subgenera. The problem of sexual dimorphism in these forms has also been discussed.

From the Lower Oxfordian strata of the Cracow-Częstochowa Jurassic the writer has collected 19 specimens of *Lissoceratoides erato* (D'ORB.) with a preserved last body chamber. In some of these specimens the gerontic aperture was also present. Their diameter ranged from 48 to 59 mm. Moreover the writer had on hand approx. 40 specimens of *Glochiceras cornutum* ZIEGLER in which the last body chamber was complete, while in some specimens the gerontic aperture was represented by complete or fragmentary lappets. The diameter here ranged from 12 to 25 mm.

As a rule, the protoconch and the first whorls are not preserved on these specimens. In the large forms referred to *Lissoceratoides erato* (D'ORB.) it required some pains to establish the presence of 7 whorls in the thin sections of the central part of the shell on two specimens only. In neither of these specimens was the first whorl preserved. Its supposed diameter was 0.6 mm. On one of the small specimens, 12 mm in diameter, the first whorl could be made out as having a diameter of 0.6 mm. This specimen had exactly 5 whorls. Similarly, in the thin section of several other specimens, 12-14 mm in diameter, the presence of 5-6 whorls was established by assuming that the first whorl was 0.6 mm in diameter. The shells of these species are perfectly smooth and their early stages and the sutures are identical. The problem will remain unchanged if another species with smooth whorls, such as occur in the same bed, is substituted for one of the partners in the paired two species just mentioned.

Genera **TARAMELLICERAS** DEL CAMPANA, 1904, **POPANITES** ROLLIER, 1909, **RICHEICERAS** JEANNET, 1951 and **ACANTHAECITES** ROLLIER, 1909

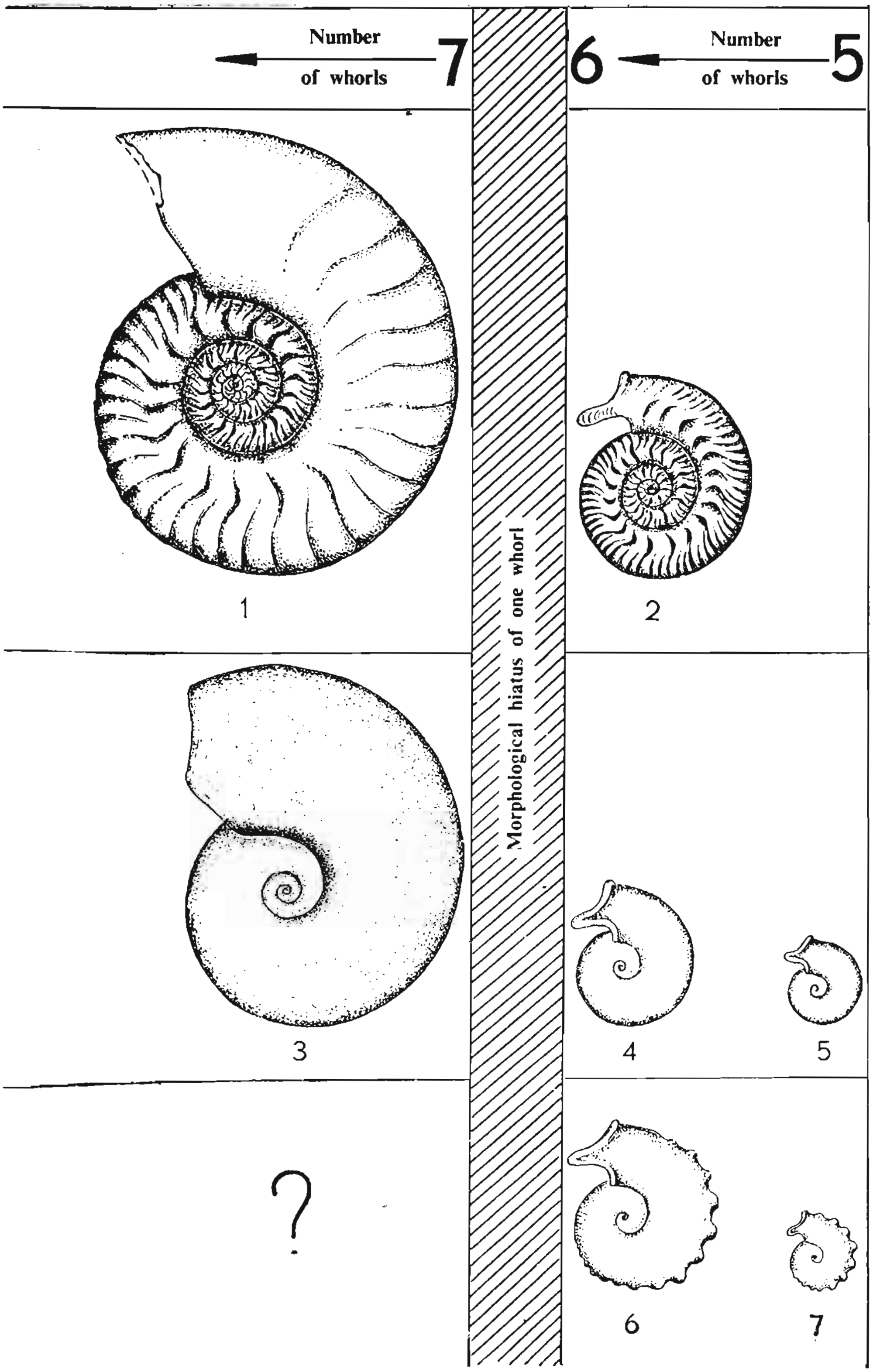
(text-pl. III, fig. 1-3; text-fig. 5)

Some attention will now be given to two species: *Taramelliceras minax* (BUK.) and *Popanites paturatensis* (GREPP.), recorded from the Częstochowa Jurassic and from several localities in Western Europe. They have been recently described by JEANNET (1951) from Lower Oxfordian beds at Herznach.

TEXT-PLATE II

	Former interpretation:	New interpretation:	Occurrence:
1	*Hecticoceras paulowi* TSYTOVITCH	*H. paulowi* TSYTOVITCH ♀	Czatkowice, Callovian
2	*H. hecticum* (REIN.)	*H. paulowi* TSYTOVITCH ♂	„ „
3	*Lissoceratoides erato* (D'ORB.)	*L. erato* (D'ORB.) ♀	Częstochowa, Oxfordian
4, 5	*Glochiceras cornutum* ZIEGLER	*L. erato* (D'ORB.) ♂♂	„ „
6, 7	*Creniceras renggeri* (OPPEL)	*C. renggeri* (OPPEL) ♂♂ (unidentified female form)	„ „

TEXT-PLATE II



From the vicinity of Częstochowa the writer has collected 7 specimens of *Taramelliceras minax* (Buk.) in which the body chamber is complete, and that has at least a partly preserved aperture. On one of the specimens the aperture was complete. The diameter here ranged from 43 to 55 mm. Their satisfactory state of preservation allows the earlier descriptions of this species to be completed.

Of the two, *Popanites paturatensis* (Grepp.) is far more common. 14 specimens with the body chamber complete have been found in the Jurassic deposits from the vicinity of Częstochowa; out of these quite a few had the gerontic aperture completely or partly preserved. In diameter they range from 18 to 22 mm.

It should be stressed that the aperture in these two species is identical and characteristic of the genus *Taramelliceras*. In *T. minax* (Buk.) the first whorls are perfectly smooth. At a diameter of approx. 10 mm ornamentation is encountered in the form of delicate ribs inclined forward. This ornamentation pattern first appears on the siphonal side. On some specimens the ribs are preceded by nodes on the siphonal side which may persist along with the ribs. An attempt to determine the number of whorls in this species was a failure since on four of the specimens examined the first 2-3 whorls were not preserved.This detail could not be checked owing to the scarcity of the otherwise valuable material. Accurate comparative measurements, however, indicate the presence in this species of one more whorl than in the largest specimens of *Popanites paturatensis* (Grepp.).

Among specimens of the latter species we encounter ones in which ribbing on the last body chamber is identical to that found in *Taramelliceras minax* (Buk.). Two of them were found to have 6 whorls. There are also smaller, quite smooth forms, with 5 or just a little more than 5 whorls. They seemed to be specimens that did not reach the stage in which ribs first appear. As will be shown later, appreciation of this fact is essential to the interpretation of some ammonite forms.

The same deposits of the Częstochowa Jurassic yield such species as *Taramelliceras pseudoculatum* (Buk.) and others of the genus *Richeiceras*. In *Taramelliceras pseudoculatum* the diameter ranges from 60 do 90 mm, while in the genus *Richeiceras* it is between 25 and 40 mm.

On the young whorls of *T. pseudoculatum* the ornamentation is identical or at least very similar to *Richeiceras*. The characteristic feature here is that in young whorls, from 10 to 20 mm in diameter, the nodes occur on the siphonal side only, arranged in a single row, while sickle-like ribs inclined forward appear later.

A painstaking quest failed to reveal even a single specimen of *T. pseudoculatum* in which the number of whorls was clearly distinguishable. Only on two specimens belonging to *Richeiceras* (*R. pichleri* (Oppel) and *Richeiceras* sp.), could the number of whorls be counted: they were $5^1/_2$ and 6 respectively. The first whorl is not present in either of these two specimens, and its diameter is only assumed to be 0.6 mm. A comparison of specimens of *Richeiceras* with *T. pseudoculatum* indicates that the latter almost certainly have one whorl more.

The illustration published by Jeannet (1951, pl. 30, fig. 2 a-b) is interesting in that it distinctly shows the gerontic aperture in *Richeiceras* to be identical with that of *Taramelliceras minax* (Buk.) or *Popanites paturatensis* (Grepp.). In the writer's specimens this aperture has been only partly preserved. Two specimens have been discovered in the material from the Jurassic of Częstochowa whose aperture closely resembles that of *P. paturatensis* (Grepp.) or of *Richeiceras*, figured by Jeannet *(l. c.)*. These specimens come from the same beds of the Lower Oxfordian as the species of *Taramelliceras* and *Popanites* mentioned above, and are 13 and 15 mm in diameter. The ornamentation of these specimens consists of one row of nodes on the siphonal side, which vanishes near the aperture. Thus it is identical with the ornament pattern noted on young whorls of *Taramelliceras* or *Richeiceras* up to the 10-20 mm diameter stage. One of these specimens is still complete, the other was used for preparing the thin section. It was then seen that the number of whorls on this specimen is 5 or just over ($5^1/_4$?). Hence it represents a small form and is the equivalent of small forms with 5 whorls from the genera *Glochiceras* or *Popanites*. In ornament it agrees with the young stages of representatives of the genus *Taramelliceras* or *Richeiceras*. Forms of this kind, long known from the Callovian beds of Germany, are now referred to the genus *Acanthaecites* Rollier in the subfamily Taramelliceratinae. The type species of this genus is *A. velox* (Oppel), recorded from the Callovian of Germany. This species has, i. a., been described by Quenstedt (1886-87) from the Upper Callo-

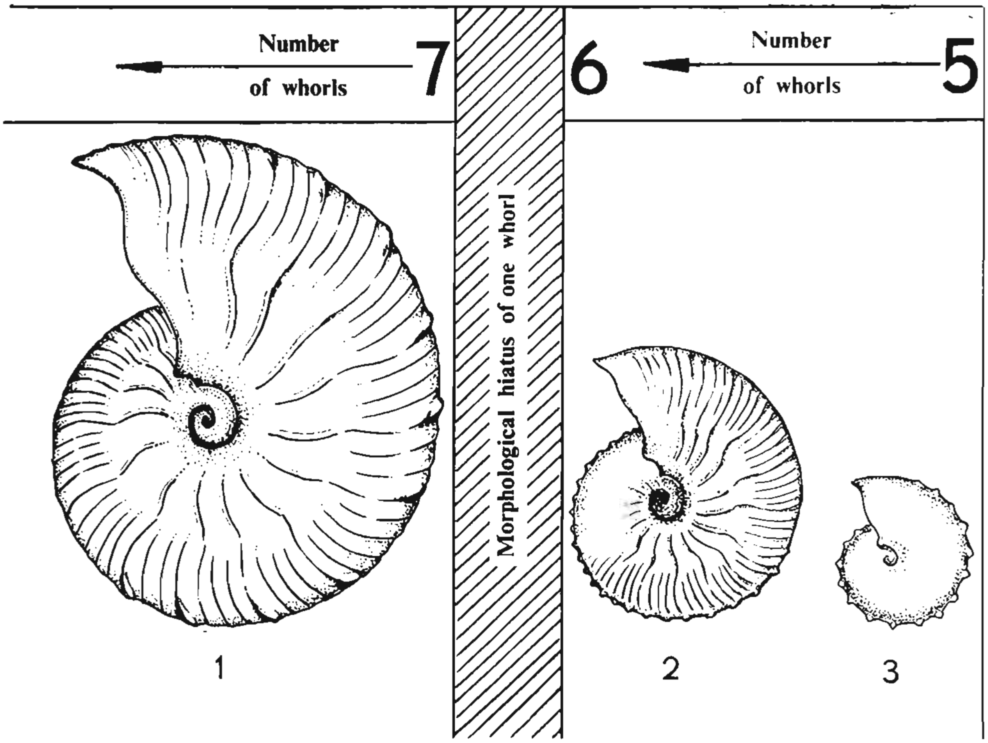


Fig. 5
Supposed inter-generic morphological relations: 1 *Taramelliceras*, 2 *Richeiceras*, 3 *Acanthaecites*.

vian beds at Gammelshausen in Germany, together with species at present assigned to the genus *Taramelliceras*. *Acanthaecites velox* (Oppel) is rather common, while the form from the Jurassic of Częstochowa considered here is doubtless extremely rare and its appearance was probably exceptional and sporadic. In other words, specimens of the genus *Richeiceras* only exceptionally stopped at the stage with 5 whorls.

The problem mentioned here requires more thorough investigation on larger collections of the genus *Acanthaecites* in order to ascertain its relation to representatives of the genera *Richeiceras* and *Taramelliceras*. The probable mutual morphological relations of the three genera are shown in fig. 5. We might therefore be dealing with small forms, having 5 whorls, referred to a separate genus owing to the occurrence of notable changes in ornamentation between the 5th and 6th whorls.

Genus **CRENICERAS** MUNIER-CHALMAS, 1892

(text-pl. II, fig. 6, 7)

It has been suggested many times that the genus *Creniceras* represents small dwarf males (MUNIER-CHALMAS, 1892; ROLLIER, 1913). The Lower Oxfordian deposits of the Cracow-Częstochowa Jurassic Uplands abound in *Creniceras renggeri* (OPPEL). These small forms often have the aperture preserved as lappets. The 40 available individuals of this species range from 13 to 25 mm in diameter. About 30 specimens have been studied, mainly in thin section, showing that they have 5-6 whorls.

This species and others referred to the genus *Creniceras* are characterized by the presence of denticles on the siphonal side of the last whorl. These denticles first appear at the beginning of the last whorl as tiny nodes which attain a considerable size on the last body chamber. This genus is assigned to the subfamily Streblitinae (BASSE, 1952) or Taramelliceratinae (ARKELL et al., 1957) within the family Oppeliidae. The following comments, however, should be made here: The internal whorls in *Creniceras renggeri* are smooth since the nodes and denticles just mentioned do not appear before the last whorl whatever the total number of whorls may be. They make their appearance at the beginning of the last whorl in specimens with 5 whorls, and the same happens in those with 6 whorls. It may be hence inferred that the denticles here are a character of this small form only and cannot be utilised as a criterion of relationship in the search for the corresponding large form. No conclusive evidence has been obtained from investigating the suture in this particular species and in other small species *(Scaphitodites, Glochiceras)*, or among the large forms existing side by side *(Lissoceratoides, Taramelliceras)*. According to JEANNET (1951) the suture in the genus *Creniceras* suggests a relationship with the family Oppeliidae, but in the same paper that author describes it as «incertae sedis».

Genus **LEIOCERAS** HYATT, 1867

(text-pl. III, fig. 4, 5)

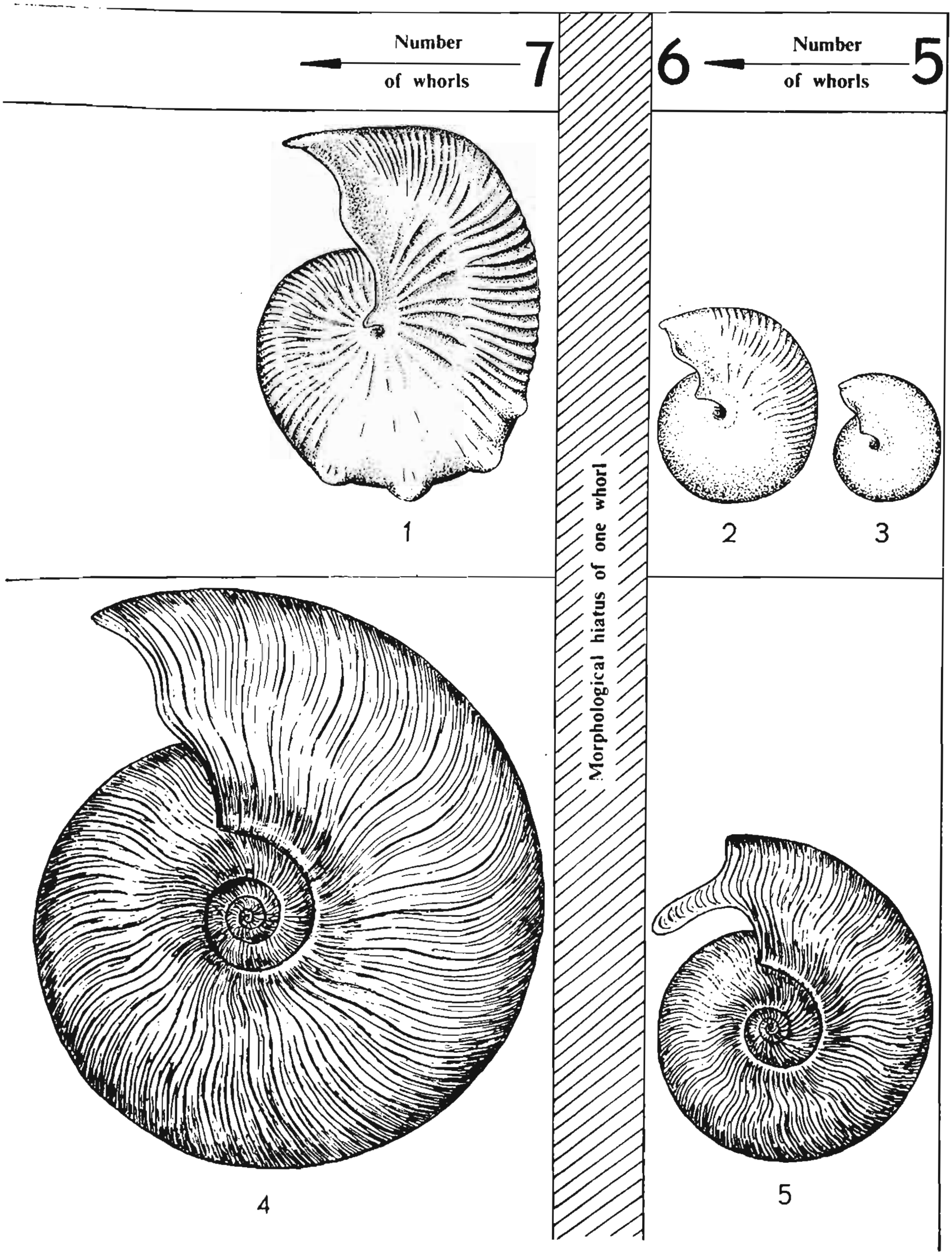
Of the genus *Leioceras*, *L. opalinum* (REIN.) is the best known species. BASSE (*in* PIVETEAU, 1952) and ARKELL et al. (1957) figure under this specific name a specimen with a prominent lappet, 58 mm in diameter. Similar specimens have been described in other papers. In the diagnosis of this genus by BASSE there is no mention concerning the shape of the aperture, but ARKELL, KUMMEL et al. state that the genus *Leioceras* is characterized by an aperture provided with a lappet.

Under the name *Ammonites opalinus*, QUENSTEDT (1886-87) presents two different groups of specimens. One contains 4 specimens, 15-58 mm in diameter, in which the aperture is provided

TEXT-PLATE III

Former interpretation:	New interpretation:	Occurrence:
1 *Taramelliceras minax* (BUK.)	*T. minax* (BUK.) ♀	Częstochowa, Oxfordian
2, 3 *Popanites paturatensis* (GREPPIN)	*T. minax* (BUK.) ♂♂	,, ,,
4 *Leioceras opalinum* (REIN.)	*L. opalinum* (REIN.) ♀	Ostenfeld, Bajocian
5 *Leioceras opalinum* (REIN.)	*L. opalinum* (REIN.) ♂	Schalksbach, Bajocian

TEXT-PLATE III



with lappets, the other consists of one single specimen, 120 mm in diameter, with a simple aperture. No mention of these facts has been found by the writer in recent literature. It seems that the picture which has been generally figured as an illustration of the species *Leioceras opalinum*, is that of a small form which has the aperture provided with lappets, and that the existence of large forms with simple aperture has been overlooked, even though one was figured by QUENSTEDT *(l. c.)*.

The writer was in possession of only one specimen of the large form, 125 mm in diameter, collected at Ostenfeld near Goslar from the so-called «Opalinuston». The margin of the gerontic aperture is damaged. It has been reconstructed in fig. 4 of text-pl. III on the basis of an illustration published by QUENSTEDT (1886-87, pl. 55, fig. 10). It was possible to prepare the protoconch and first whorl of this specimen which had $7^1/_4$ whorls.

One specimen of the small form, 52 mm in diameter, from the same beds at Ostenfeld, was also available to the writer. Its assignment to the small forms was made simply on grounds of the extremely crowded and simplified sutures. The body chamber consisting of half a whorl is preserved, but the apertural margin is lacking. The number of whorls was exactly six. A specimen from Schalksbach near Balingen, about 55 mm in diameter, came into the writer's possession through the courtesy of the late Professor W. J. ARKELL. Its last whorl was damaged, but the gerontic aperture in the form of a lappet was complete. Here also it was possible to establish that the number of whorls was exactly six. Moreover, the writer is in possession of a small form, 36 mm in diameter, collected at Zillhausen in Württemberg, last sutures of which are crowded, the body chamber occupying just a little more than half whorl, and with the apertural margin missing; in all, this specimen has 5 whorls. It may reasonably be supposed that this is a small form which halted in growth at the 5 whorls-stage.

So far the writer's observations on dimorphism in the genus *Leioceras* have been based on very scant material, they are nevertheless mentioned as presenting some interest. *Leioceras opalinum* exhibits a most characteristic ornament pattern consisting of strongly marked growth lines. This sculpture occurs even on very young whorls and does not change throughout the ontogeny. Thus the large and small forms fully agree in ornamentation and their close alliance cannot be doubted. Another reason for mentioning the above example is that finds of small forms with lappets are by no means rare, particularly so in Lower Bajocian deposits of Germany.

Genera **GARANTIANA** MASCKE, 1907 and **PSEUDOGARANTIANA** BENTZ, 1928

(text-pl. IV, fig. 1, 2)

The side by side existence of large and small forms with lappets, previously assigned in common to the genus *Garantiana*, is something that has been known for a long time. In 1928 the small forms with lappets were separated by BENTZ into the genus *Pseudogarantiana*.

The genus *Garantiana* includes forms attaining a diameter of up to 80-100 mm. *Garantiana garantiana* (D'ORB.) with simple aperture is the type species. The species of the genus *Pseudogarantiana* is *P. dichotoma* BENTZ, which is 30 mm in diameter, and has an aperture provided with 10 mm long lappets that expand forward. In other similar forms with lappets, known from literature, the diameter is up to 25-45 mm.

From the Bathonian deposits at Kamienica Polska, 3 specimens of *G. garantiana* (D'ORB.) have been collected, 85-98 mm in diameter, also 4 specimens of *Pseudogarantiana minima* BENTZ, 23-28 mm in diameter. The aperture, with its lappets, was at least partly preserved in the latter 4 specimens, and 6 whorls could be quite distinctly determined. In none of the large forms available was it possible to fix the number of whorls, since the first whorls are missing. From measurements it may be supposed that there were at least $7^1/_2$ or even 8 whorls.

The ornament pattern, so characteristic in these forms, is constant from the very early whorls and persists almost without modification through all the stages of ontogeny. Hence the identical sculpture pattern on the whorls of large and small forms, also the close resemblance of the adult stages, is very noticeable.

The dimorphism encountered in the genus *Garantiana* is particularly noteworthy in view of the uncertain systematic position of that genus. Some authors place it in the superfamily Stephanocerataceae, others in the Perisphinctaceae, and the study of dimorphism may possibly in time clear this up.

Genus **SCAPHITES** PARKINSON, 1811

(text-pl. IV, fig. 3, 4)

The original genus *Scaphites* has now been split up into a number of independent genera whose synonymics are not universally recognized. A species of this genus that is very common in the Upper Maestrichtian and now mostly referred to *Discoscaphites* (=*Hoploscaphites*) *constrictus* (Sow.), seems worth mentioning here. It is of considerable value for the problems being discussed since it is one of the last ammonite forms that survived till the Uppermost Maestrichtian. Moreover, typical normal-sized forms are known to occur together with small forms reaching barely one half of the diameter of the former. The small specimens are by some authors included in the same species with the large forms (GROSSOUVRE, 1894, 1908; NOWAK, 1911), while others (UHLIG, 1894) separate them into distinct species, though MICHAJLOV (1951) has recently identified the small forms as a variety. NOWAK (1911) figured 7 large forms from this species, with a diameter ranging from 47 to 53 mm, also 7 small forms, 22 to 34 mm in diameter. MICHAJLOV *(l. c.)* states that the large forms are 35 to 70 mm and the small ones 25 to 35 mm in diameter. According to NOWAK *(l. c.)* the two groups exhibit fairly strong but identical variability in the pattern of ribbing. This is excellently illustrated in figures published in that paper. Two varieties are hence differentiated: the coarse-ribbed *Hoploscaphites constrictus* var. *vulgaris* Now. and the fine-ribbed *H. constrictus* var. *tenuistriatus* Now. These two varieties contain both small and large forms. NOWAK makes speculations concerning the eventual assignment of the small forms to separate species, varieties or mutations, in the sense of WAAGEN. However, the side by side occurrence observed by that author of both forms within the same layer, that is less than 10 cm thick, speaks against such suggestions. Indeed, NOWAK finally draws the conclusion that these are merely dwarf individuals of the same species.

During his field studies on this species the writer has collected 22 large forms and 10 small forms from Upper Maestrichtian deposits in the vicinity of Kazimierz on the Vistula. The two groups ranged in diameter from 47 to 68 and from 22 to 35 mm, respectively. So far as size alone is concerned, these two distinct groups seem to be the same as those separated by NOWAK (1911). Only MICHAJLOV's data seem to indicate that there is no clear break between the two groups. This may possibly be explained by the great distance apart of the regions from which the material studied by MICHAJLOV had come, i. e. the vicinity of Lwów, the Crimea, northern Caucasus and Kopet-Dag. Hence, his collection may have contained different stocks of that species. It should also be borne in mind that the size («diameter») of scaphitoid ammonites is not controlled by the number and height of whorls only, but in a great measure also by the extent of separation of the last whorl. Both these characters are subject to individual variations. Therefore, the «diameter», i. e. the maximum dimension of ammonites of the genus *Scaphites*, is not a character of such comparative value as the diameter in ammonites with a normal spiral.

In specimens of *Discoscaphites constrictus* (Sow.) available to the writer the young whorls are on the whole poorly preserved, as in all Upper Cretaceous ammonites. The shells become wholly dissolved. Occasionally the shell walls and the septa may be silicified or the young whorls filled with calcite. Hence on thin sections of the central part of such a shell it has been possible to ascertain that the small forms have no more than 6 whorls. Measurements showed that the first whorl is 0.7 mm in diameter. The writer based his conclusions in this respect on data from the literature and on his own measurements of several specimens of the genus *Scaphites* from the Emscherian deposits of North Dakota. In these specimens the protoconch and the first whorl are excellently preserved. When determining the number of whorls it was accepted that the last body chamber corresponds to $^2/_3$—$^3/_4$ of a whorl.

Two specimens out of the writer's collection of small forms from Kazimierz were 22 mm in diameter. Thin sections of the adumbilical part did not supply any conclusive evidence since one and a half of the initial whorls had been silicified and any traces of the spiral were completely effaced. It is, however, probable that there were not more than 5 whorls. Their relatively great «diameter», i. e. the maximum dimension, is probably connected with their degree of evoluteness which is more marked than in other specimens.

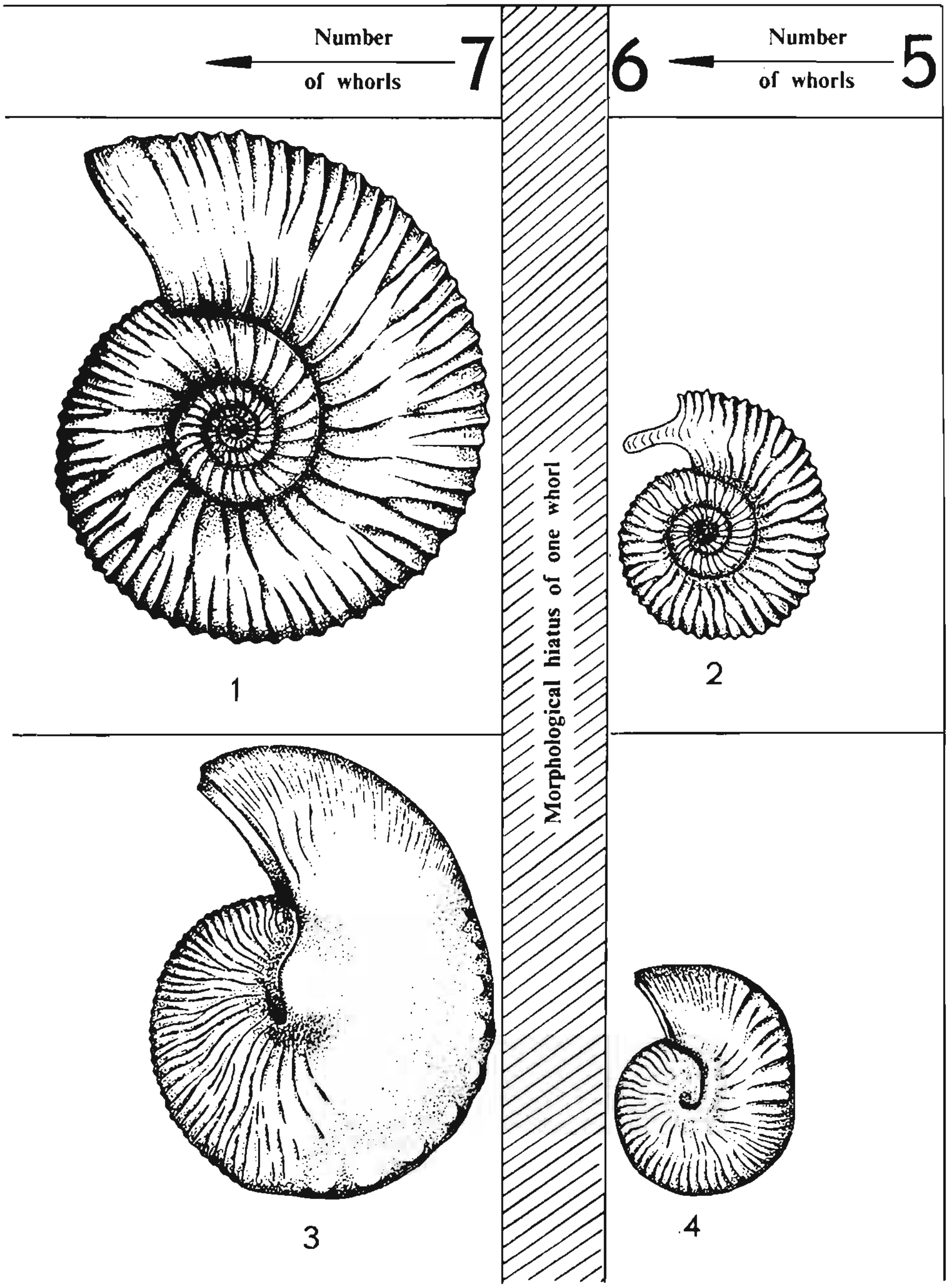
The early stages of the two groups coincide closely in character of sculpture and suture. Actually, both forms are by some authors regarded as conspecific, while a separate variety has been established by Michajlov (1951) for the small forms.

Two complete adult specimens of *Scaphites nodosus* var. *plenus* Meck, 62 and 68 mm in size, from the Emscherian deposits of North Dakota, have also been examined. The protoconch and the first whorl are there excellently preserved. They have 7 whorls each, or strictly speaking they are the morphological correspondents of forms having 7 whorls. When fixing these data the last body chamber was taken as equal to of at least $^3/_4$ whorl. This may be ascertained by comparing the number of ribs on the unrolled part with that on the normally coiled whorls. The writer did not have the opportunity to examine small forms from the Cretaceous of North America, but would like to turn the reader's attention to a paper by Cobban (1951). This is an extensive monograph on the Scaphitidae from the Upper Cretaceous deposits of North America, referable to the Colorado group (Turonian-Campanian). That author points to the wide size variability range within this family extending from 7.7 to 100 mm. In some cases the small specimens are by Cobban distinguished as varieties of species established on large forms, in others they are regarded as conspecific with the latter.

TEXT-PLATE IV

Former interpretation:	New interpretation:	Occurrence:
1 *Garantiana garantiana* (D'ORB.)	*G. garantiana* (D'ORB.) ♀	Kamienica Polska, Bathonian
2 *G. minima* WETZEL	*G. garantiana* (D'ORB.) ♂	,, ,, ,,
3 *Scaphites constrictus* (SOW.)	*S. constrictus* (SOW.) ♀	Kazimierz, Maestrichtian
4 *S. constrictus* var. *niedzwiedzkii* (UHLIG)	*S. constrictus* (SOW.) ♂	,, ,,

TEXT-PLATE IV



Some illustrative examples are given below. Figures alternately denote the maximum diameter of the large forms and the minimum diameter of the small forms (in mm):

Scaphites nigricollensis Cobban	65
,, ,, var. *meeki* Cobban	30
Scaphites impendicostatus Cobban	55
,, ,, var. *erucoides* Cobban	20
Clioscaphites vermiformis (Meek & Hayden)	60 and 22

Moreover, Cobban has described several minute species ranging in size from 7.7 to 15 mm. These are very poorly ornamented forms, that are occasionally even quite smooth, and in this respect they agree with the early stages of large forms. The writer's comparative measurements of the large specimens on hand show that these small forms cannot have more than $5^1/_2$ whorls. Very accurate cross sections of two such forms, namely *Scaphites coloradensis* Cobban and *S. auriculatus* Cobban, are given by Cobban. The sections are cut through the protoconch and clearly show that these small forms correspond to forms with 5 whorls (reduced to the normal spiral). According to Cobban these dwarf forms are a separate continuous evolutionary line, parallel to that containing medium sized and large forms. It may be conjectured that these forms are the equivalents of other small ammonite forms which halted at the 5 whorls-stage. A reliable confirmation of this supposition would once more argue strongly in favour of the rules already suggested for characterizing the types of dimorphism.

The final remark here is that the excellently preserved material of the genus *Scaphites* from North America is so profuse that any attempts at clearing up the problem of dimorphism in this ammonite group which ignores the North American material will be greatly handicapped.

Genus **QUENSTEDTOCERAS** Hyatt, 1877

(pl. VII-XX; text-pl. V, VI; text-fig. 3, 6, 11-14)

Quenstedt (1858, 1886-87) has figured small forms of the genus *Quenstedtoceras* whose gerontic aperture has an elongated ventral lappet (fig. 6). Quenstedt himself, however, and some other authors, too, used to regard these specimens as immature individuals. They believed

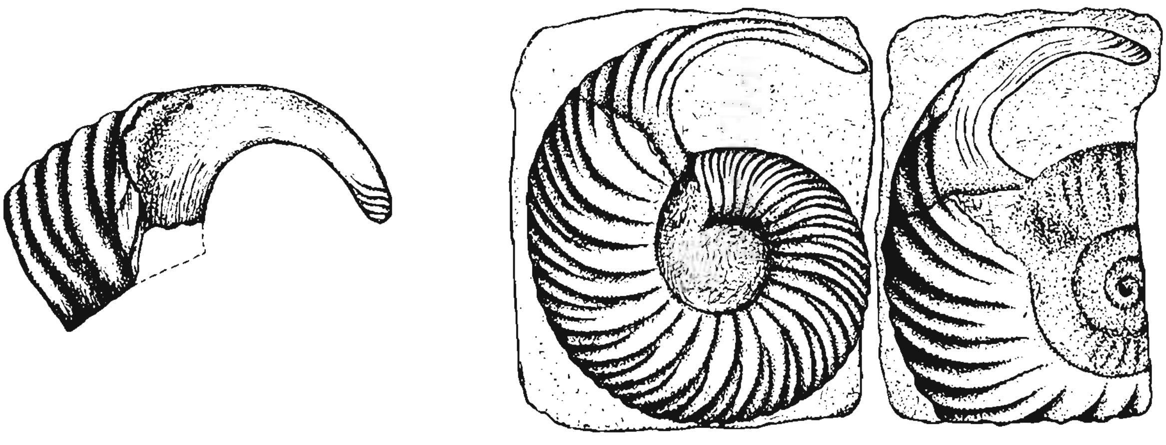


Fig. 6

Small forms from the genus *Quenstedtoceras* with apertures, after Quenstedt. Lext: «*Ammonites mariae*» (1858), right: «*Ammonites lamberti*» (1886-87) that all the *Quenstedtoceras* species attained large dimensions and had a smooth last body chamber. NIKITIN (1884) writes that the long ventral lappet is present on immature individuals only, being reduced and rounded up in adults which have the last body chamber smooth.

ROMAN (1938) describes the aperture of a small specimen as it is figured by QUENSTEDT (1886-87), adding an explanatory remark that it is «the aperture of *Quenstedtoceras lamberti* SOW.» Elsewhere we learn from that author that this species reached large dimensions and had the last body chamber smooth. NIKITIN's opinion has lately been accepted by SAZONOV (1957). Different views have also been advanced. WEISSERMEL (1895) stresses that *Q. mariae* (D'ORB.) is never more than 6-7 cm in diameter and that none of the known specimens of that species display gradual smoothing out of the whorls, contrary to what has been observed in other representatives of the genus *Quenstedtoceras*. WEISSERMEL believes that *Q. mariae* (D'ORB.) may possibly be an evolutionary side branch from the main stock of that genus, represented by the species *Q. lamberti* (SOW.) which attained large dimensions. Under the name of *Q. mariae* (D'ORB.)[2] SOKOLOV (1913) described a specimen, 61 mm in diameter, stating that the ventral keel in this specimen extends into a rostrum protruding forward. This indicates an adult individual and suggests that a smooth body chamber was not typical for *Q. mariae* (D'ORB.), as had been supposed by NIKITIN (1878). ARKELL (1939) recognizes the side by side existence in the genus *Quenstedtoceras* (s. l.) of large and small forms, the latter making a halt at the ribbed stage. The small forms are by him (somewhat inconsistently) assigned to the subgenus *Quenstedtoceras* s. str., while the large forms are referred to several other subgenera. The species *Q. mariae* (D'ORB.), a typical small form, is however included by that author into the subgenus *Pavloviceras*, together with the large form *Q. pavlovi* R. DOUV.

KRIMHOLC, SAZONOV et al. (1958) consider the genus *Quenstedtoceras* sensu lato. According to their diagnosis, the ribbing dies out in the adult stage and the last body chamber is smooth. There is no mention of the occurrence of small forms. In the work of ARKELL et al. (1957) these authors split up the original genus *Quenstedtoceras* into 5 subgenera, again without mentioning the side by side existence of the large and small forms.

The writer's search for ammonites in Łuków and in the Jurassic Cracow Uplands has been pursued over a score of years. A total of 140 large forms with smooth last body chamber has been collected from Łuków. They range from 105 to 220 mm in diameter. About 300 specimens of small forms have also been collected with the gerontic aperture completely or partly preserved. These ranged from 24 to 65 mm in diameter.

A close examination of 72 specimens shows that all the large forms are made up of 7-8 whorls. Most of the small specimens attain the 6 whorls-stage, while some reach $6^1/_8$ whorls. These data come from nearly 180 specimens.

All the specimens examined have been prepared down to the protoconch, thus allowing the exact number of whorls to be counted.

It should also be mentioned that quite a number of the specimens were teratological, i. e. distorted. Owing to injuries at an early stage, some of the small forms were very asymmetrical, with the keel shifted to one side. In several specimens the injured aperture was abnormal, asymmetrical, and much reduced. But even in these damaged specimens the 6 whorls pattern was invariably maintained.

At Czatkowice and Racławice within the Cracow Jurassic Uplands large and small forms of the genus *Quenstedtoceras* were also found. Only one of the small specimens was found to have six whorls.

[2] The present writer believes that this specimen belongs to the genus *Cadoceras* (see p. 36.).

Up to the 5-5$^1/_2$ whorls-stage the ontogeny of large and small forms is identical. After that differences occur concerning whorl section, umbilical width and, to a certain extent, in the character of the ribbing. The specific and individual variability range is equal in large and small forms so that it is always possible to pick out several specimens identical in ontogeny up to the 5-5$^1/_2$ whorls stage.

All these facts will be accurately illustrated in the chapter on systematics.

Genera **CADOCERAS** Fischer, 1882 and **PSEUDOCADOCERAS** Buckman, 1919

(text-pl. VII)

Various species belonging to genus *Cadoceras* have, from early times, been repeatedly described and figured from the Jurassic beds of Russia. They attain considerable dimensions — 10-20 cm in diameter — and their last body chamber is smooth (Nikitin, 1881-85; Sazonov, 1957). One specimen of *C. tschefkini* (d'Orb.), which lacks the body chamber, but has the whorls gradually smoothening out, was described from Łuków in Poland (Makowski, 1952), though small forms have not so far been distinguished. Sokolov (1913) described and figured a specimen, 61 mm in diameter, referring it to *Quenstedtoceras mariae* (d'Orb.) with the remark that the ventral keel extends into an incurved rostrum which suggests an adult individual. The writer thinks that this is not a *Quenstedtoceras*, but a small form of *Cadoceras*. He bases his supposition on the fact that the body chamber here makes up about two thirds of a whorl, while the common rule for the body chamber in the genus *Quenstedtoceras* is to occupy not more than one half of a whorl, and sometimes even less. Moreover, in the pattern of ribbing this specimen is nearer to the genus *Cadoceras*. The secondary ribs are distinctly longer than in representatives of the genus *Quenstedtoceras*, but in agreement with those of the genus *Cadoceras*.

Under the name of *Cadoceras mundum* Sazonov, Sazonov (1957) described from the Lower Callovian of Elatma a small *Cadoceras* form, 35 mm in diameter, which had a gerontic aperture partly preserved as a constriction. Through the courtesy of that author, the present writer was offered an opportunity to study this specimen and to observe that it had 6 whorls.

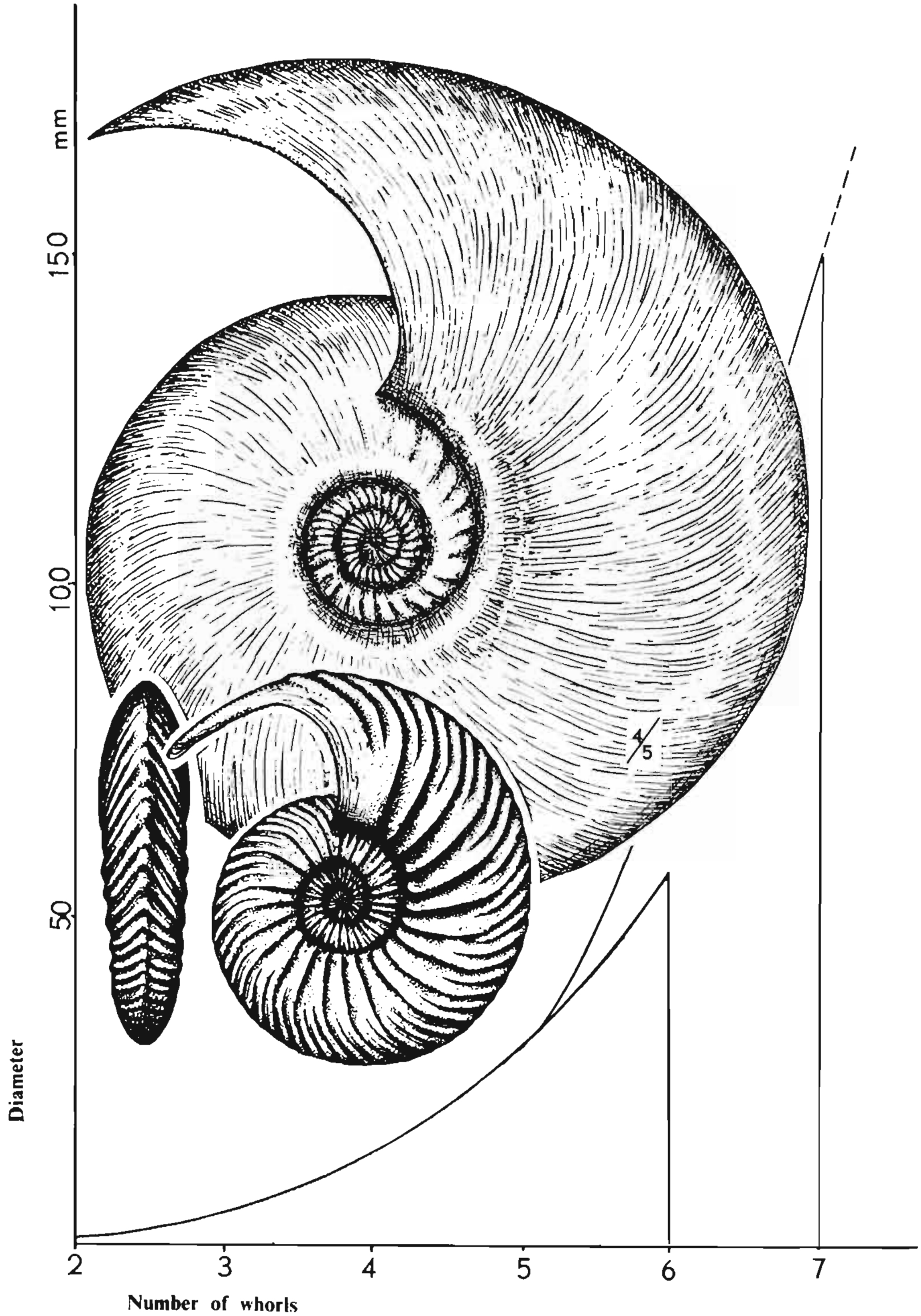
Under the name *Pseudocadoceras orbignyi* Maire, Ivanov (1960) described from the Callovian of Elatma small *Cadoceras* forms, with diameter not exceeding 30 mm, which exhibited gerontic characters. The ontogenetic stages of these forms, up to 15—16 mm in diameter, are identical with those in the large forms that are referred to *Cadoceras tschefkini*

TEXT-PLATE V

Ontogeny of the diameter of shell in genus *Quenstedtoceras*

Former interpretation:	New interpretation:	Occurrence:
large form:		
Quenstedtoceras (Bourkelamberticeras) henrici R. Douv.	*Q. henrici* R. Douv. ♀	Łuków, Callovian
small form:		
Q. (? Quenstedtoceras) macrum (Quenst.) (?)	*Q. henrici* R. Douv. ♂	,, ,,

TEXT-PLATE V



and which may be over 150 mm in diameter and have a smooth body chamber. IVANOV thinks that the genus *Pseudocadoceras* represents the neotenic *Cadoceras* form whose evolution halted at an early stage of ontogeny. Moreover, he supposes that side by side occurrence within one layer of large forms of *Cadoceras tschefkini* and the dwarfed neotenic forms of *Pseudocadoceras orbignyi* may be an expression of sexual dimorphism.

The present writer's observations on the genus *Cadoceras* from the Callovian strata at Łuków fully coincide with those made by IVANOV. The difference consists in the somewhat larger size of the small *Cadoceras* forms from Łuków and slightly different ornamentation of their body chamber, while the large forms referred to *Cadoceras tschefkini* are identical with specimens from Elatma which the present writer was able to study. When comparing small *Cadoceras* forms from Łuków with small *Cadoceras* forms from Elatma, it should be noted that the latter forms come from the Middle Callovian, while the Łuków deposits are Upper Callovian in age.

Several specimens have been described from Łuków by the writer (MAKOWSKI, 1952) under the name of *Cadoceras nikitinianum* (LAHUSEN). ARKELL (1956) suggested that these forms are referable to a new genus related to *Longaeviceras* BUCK. At first it was supposed that these specimens are young individuals of forms attaining large dimensions which have the last body chamber smooth. Two specimens of the same species found subsequently, however, had the gerontic aperture preserved as a ventral lappet, as in the genus *Quenstedtoceras*. Both these specimens had 6 and $6^1/_4$ whorls. Moreover, the same number of whorls (6) was to be found on two other specimens of the same species, lacking the aperture.

After these data had been obtained, young whorls were also examined and compared with the young whorls of the species *Cadoceras tschefkini* (D'ORB.) which occurs at Łuków, too, and has even been found in the same concretion together with *C. nikitinianum* (LAHUSEN). Examination showed that the whorls in these two species are identical up to about the 5 whorls-stage. Their sutures are also identical.

Accordingly we see that forms referred to the species *Cadoceras nikitinianum* (LAHUSEN) represent the small forms of the genus *Cadoceras*.

GONIATITES

Genus **TORNOCERAS** HYATT, 1884

(text-pl. VIII; text-fig. 2, 10*b*)

Tornoceras simplex (BUCH.) is one of the most common representatives of this genus. It is known from the Devonian beds of Europe and very similar forms occur in North America.

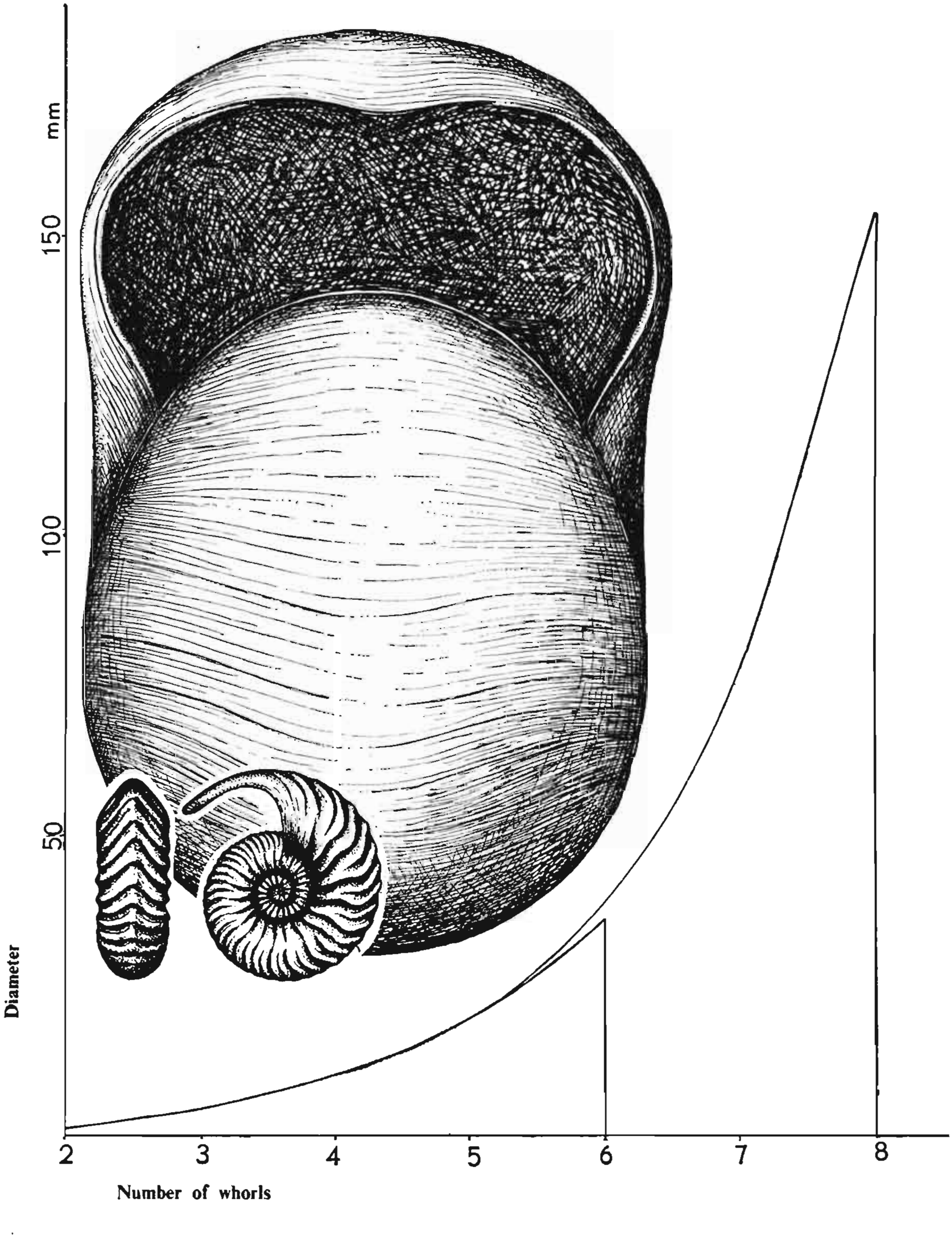
Three localities within the Holy Cross Mountains area, i. e. the «Kadzielnia» quarry near Kielce, Łagów and Janczyce, have yielded abundant specimens of *Tornoceras simplex.*

TEXT-PLATE VI

Ontogeny of the diameter of shell in genus *Quenstedtoceras*

Former interpretation:	New interpretation:	Occurrence:
large form:		
Quenstedtoceras (Bourkelamberticeras) carinatum (EICHW.)	*Q. vertumnum* (LECK.) ♀	Łuków, Callovian
small form:		
Q. (Quenstedtoceras) vertumnum (LECK.)	*Q. vertumnum* (LECK.) ♂	,, ,,

TEXT-PLATE VI



Everywhere small forms, reaching a diameter of 21-47 mm, with strongly crowded and simplified sutures, occur side by side with less numerous specimens that are up to 65-140 mm in diameter. The large forms are not only much fewer, but also less well preserved. The numerical ratio of the large and small forms varies considerably, sometimes being 1 : 10. The writer's collection contains 1600 small forms in which the living chamber is completely or nearly completely preserved, and the last sutures are very distinct. The body chamber here occupies about three fourths of a whorl. As has already been mentioned, the diameter ranges from 21 to 47 mm, the last sutures are crowded and simplified to a varying extent, sometimes very much so. The determination of the number of whorls and character of the spiral is handicapped by the fact that the young whorls are as a rule strongly re-crystallized and the line of spiral is completely obliterated. Nevertheless after examining about 180 specimens it has been found that the first whorl, ending in a faintly marked constriction, is 1 mm in diameter. There are 5-6 whorls in the small forms of this species. In specimens halting at the 5 whorls-stage, the diameter is somewhat greater than that in the 5 whorls stage of individuals which develop 6 whorls. Many intermediates occur in between forms with 5 whorls and those with 6 whorls.

160 large forms have been collected by the writer. On the outside they hardly differ at all from the small forms and the minute differences which will be considered below are not easily detected. The body chamber here, too, occupies about three fourths of a whorl. However an examination of the internal whorls shows considerable differences between large and small forms. From the $2^1/_2$ whorls stage on, the height of whorls in the large forms is greater and this difference increases progressively with growth. Thus the morphological separation between these two groups is already there at the 3 whorls-stage and increases gradually during further ontogeny. The majority, i. e. about 70 per cent of the large forms, stop just after passing the 6 whorls-stage, and only very few (10 per cent) attain the 7 whorls-stage. Those which do so appear in certain beds only, while in other beds large forms occur which reach or just pass the 6 whorls-stage; rarely, specimens attain $6^1/_2$ whorls.

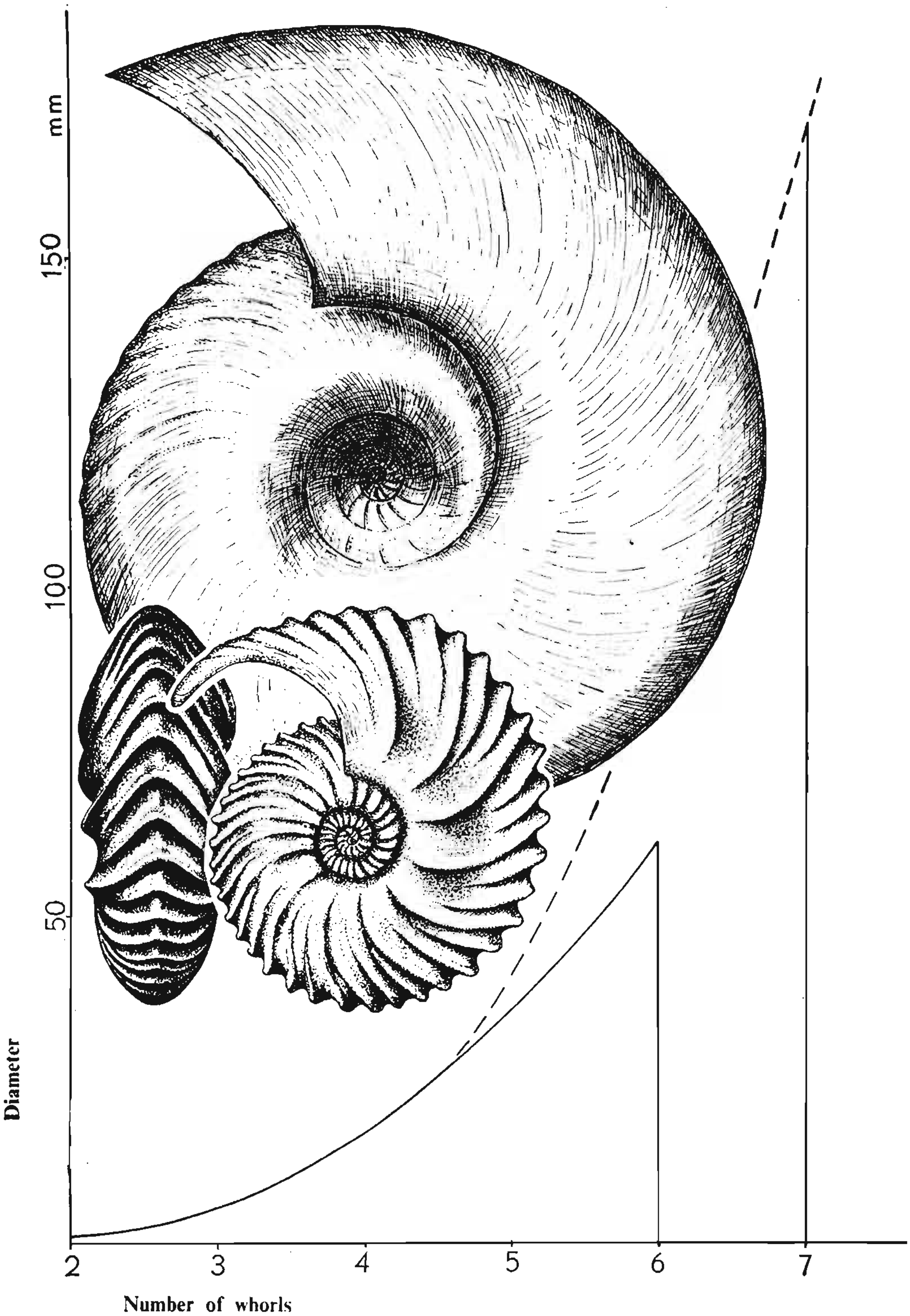
In external morphology the large and small forms are nearly identical and the younger the whorls the stronger the resemblance. Nevertheless, the character of the spiral makes them already distinguishable at the 3 whorls-stage, as is shown in text-pl. VIII. The difference is expressed by external morphology, as a greater increase in the height of whorls in large forms, demonstrable by statistical analysis. Similar dimorphism occurs in many other species belonging to the genus *Tornoceras* and family Tornoceratidae. The large forms do not, as a rule, attain 7 whorls; they halt at about the 6 whorls-stage, but can always be distinguished from the small forms on the character of the spiral.

TEXT-PLATE VII

Ontogeny of the diameter of shell in genus *Cadoceras*

Former interpretation:	New interpretation:	Occurrence:
large form:		
Cadoceras tschefkini (D'ORB.)	*C. tschefkini* (D'ORB.) ♀	Łuków, Callovian
small form:		
C. nikitiniatum (LAHUSEN)	*C. tschefkini* (D'ORB.) ♂	,, ,,

TEXT-PLATE VII



Genus MANTICOCERAS Hyatt, 1884

(text-pl. IX)

From the Upper Devonian of Timan, Holzapfel (1899) described the well known species *Manticoceras intumescens* (Beyr.), stating that the largest, incomplete specimen was 18 cm in diameter. A much smaller form occurs together with this species which that author identified as *M. ammon* (Keyser.). Two specimens have been figured and shown to be 45 and 63 mm in diameter. In the description the author mentions that shells of this species have 6 whorls.

In describing the species *Koenenites cooperi* Miller which belongs to the family Manticoceratidae, Miller (1938) states that adults of this species, up to 68 mm in diameter, just pass the 6 whorls-stage. Miller, Furnish et al. (1957) in «Treatise on invertebrate paleontology» publish the cross section of a mature *Manticoceras* sp., 70 mm in diameter. The section, cut through the protoconch, shows that this specimen has likewise 6 whorls.

Glenister (1958), in a description of several species of the genus *Manticoceras* from the Upper Devonian of Australia, mentions that some specimens are up to 210 mm in diameter. More than once he states that the adults attain about 6 whorls. A review of Glenister's paper does not clear up whether the data on number of whorls concern small forms or large ones which had halted at that stage of growth.

Thus it is seen that in describing the genus *Manticoceras* some value has been attached to the number of whorls. This is due to the shells being relatively weakly involute with the umbilicus open as far as the protoconch. Moreover, the protoconch and the first whorl here attain greater dimensions than in any other ammonoids, the first whorl being up to 1.3 mm in diameter.

From the *Manticoceras intumescens* horizon of the Holy Cross Mountains the writer has collected 6 adult specimens of *M. ammon* (Keyser.) 38-71 mm in diameter, also 5 incomplete mature specimens of *M. intumescens* (Beyr.) that are at least 15 cm in diameter (probably 18-21 cm). One specimen with a complete body chamber was 20.5 cm in diameter. On two specimens of *Manticoceras ammon* it was possible to ascertain the presence of exactly 6 whorls. One specimen of this species, 38 mm in diameter, probably has only 5 or just a little more than 5 whorls. This could not, however, be reliably determined as the first whorls were strongly re-crystallized and the outline of the spiral had become effaced. Descriptions of *M. intumescens* and *M. ammon* show that the latter species may be distinguished from the former on adult specimens only. Some authors, e. g. Foord and Crick (1897) considered these two forms as conspecific. After examining numerous young individuals in various states of preservation it

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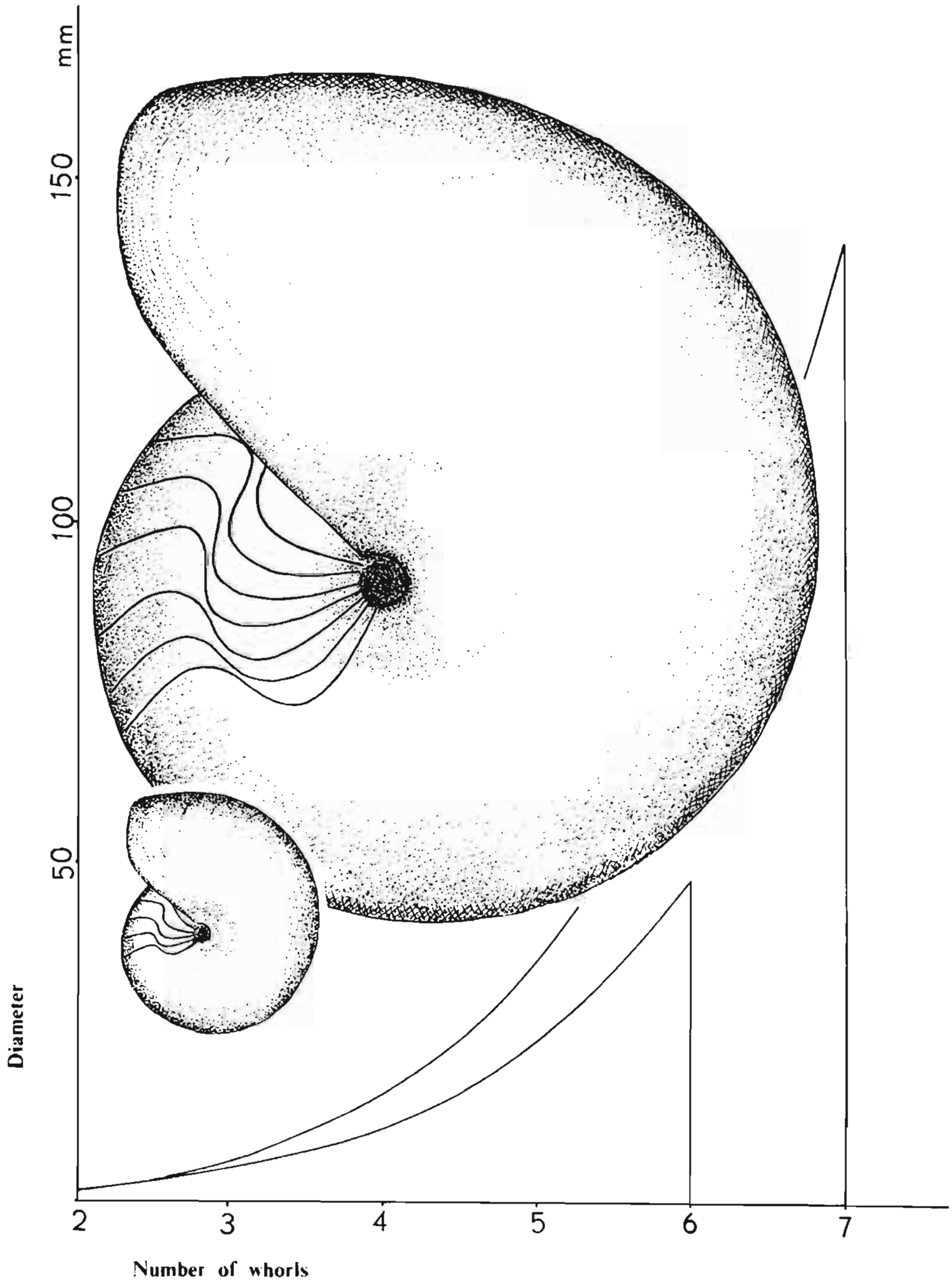
TEXT-PLATE VIII

Ontogeny of the diameter of shell in genus *Tornoceras*

Former interpretation:	New interpretation:	Occurrence:
large form:		
Tornoceras simplex (Buch)	*T. simplex* (Buch) ♀	Janczyce, Famennian
small form:		
T. simplex (Buch)	*T. simplex* (Buch) ♂	,, ,,

TEXT-PLATE VIII



was concluded that up to the 5-5$^1/_2$ whorls-stage they are identical in both species. *Manticoceras ammon* may be distinguished from *M. intumescens* only on the character of the last body chamber, which occupies half a whorl and is flatter and lower than the corresponding whorl in *M. intumescens*.

Genus **CHEILOCERAS** Frech, 1897

(text-pl. X*A*; text-fig. 2, 10*a*)

Cheiloceras subpartitum (Münst.), common in the Famennian deposits of Europe, is the genotype of the genus *Cheiloceras*. In the Holy Cross Mountains this species is fairly common in the Famennian deposits at Janczyce. From that locality the writer collected 46 small forms similar to those figured by Sobolew (1914, pl. 3, fig. 5-6). They range from 19 to 30 mm in diameter. The last sutures are very closely arranged and obviously simplified. The body chamber occupies one complete whorl or slightly less. The characteristic labial swellings, observable in moulds as constrictions, as a rule become more crowded on the last body chamber. Hence the angle between these constrictions is smaller near the aperture than at the beginning of the last whorl.

Much larger forms up to 53-70 mm in diameter occur side by side with these small forms, but are much fewer in number. In all 7 of these large specimens have been collected at Janczyce. By outward appearance they closely resemble the small forms. The only discernible differences, as in the genus *Tornoceras*, concern the increase in height of the whorls. Observations on ontogenetic stages of these forms indicate that the first whorl, ending in a faintly marked constriction, is about 1 mm in diameter.

It has been possible to examine the ontogenetic stages of approx. 25 small forms. The number of their whorls varies from 5 to 6, 70 per cent of the specimens attain 6 whorls, and about 10 per cent halt at the 5 whorls-stage, while the rest reach intermediate stages between 5 and 6.

One of the seven large specimens collected, that was 68 mm in diameter, had exactly 7 whorls. Another one, 70 mm in diameter, probably also had about 7 whorls, but this could not be quite accurately determined. Still another mature specimen, 53 mm in diameter, had about 6$^1/_4$ whorls.

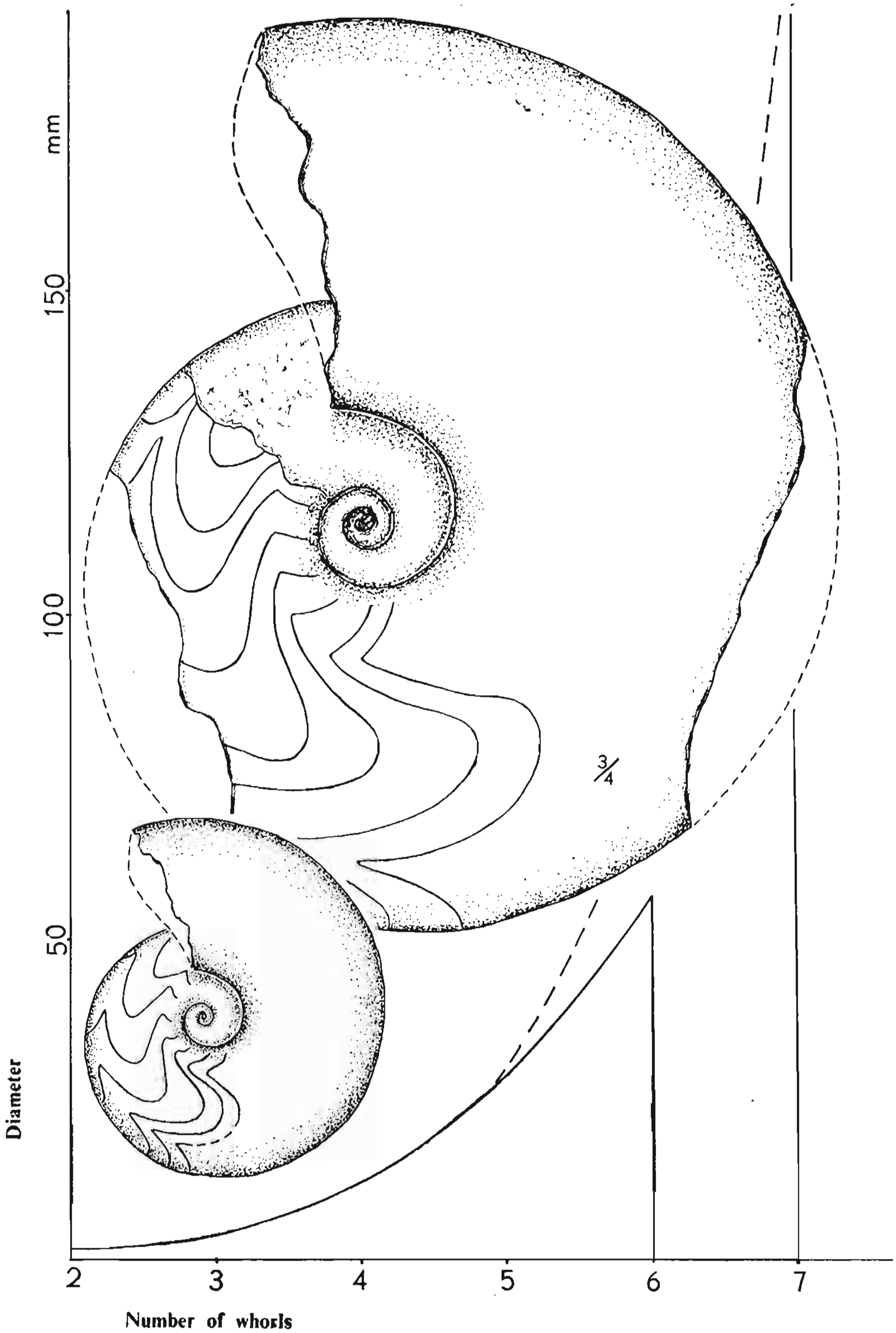
As in the genus *Tornoceras*, differences between large and small forms in the development of the spiral occur as early as the 2$^1/_2$ whorls-stage. The diameter in large forms increases more rapidly than that in the small forms, causing a morphological separation which increases with increasing growth. Thus we can see that dimorphism of type «A» occurs in the species *Cheiloceras subpartitum*, and in the genera *Tornoceras* and *Manticoceras*.

TEXT-PLATE IX

Ontogeny of the diameter of shell in genus *Manticoceras*

Former interpretation:	New interpretation:	Occurrence:
large form:		
Manticoceras intumescens (Beyr.)	*M. intumescens* (Beyr.) ♀	Płucki, Frasnian
small form:		
M. ammon (Keyserl.)	*M. intumescens* (Beyr.) ♂	,, ,,

TEXT-PLATE IX



Other numerous species, however, displaying dimorphism of type «B», are likewise assigned to the genus *Cheiloceras*. The presence in *Cheiloceras* of this type of dimorphism will be discussed later together with similar phenomena observable in Mesozoic ammonites (see p. 55.).

DIMORPHISM «B»

MESOZOIC AMMONITES

Genus **SPHAEROCERAS** BAYLE, 1878

(text-pl. XI, fig. 1, 2)

Specimens displaying identical morphological details, but with a wide range in diameter, have since long been grouped within the species known as *Sphaeroceras brongniarti* (Sow.). Such examples were given by QUENSTEDT (1886-87, pl. 64, fig. 1-2). The two individuals figured by him agree very closely in sculpture and aperture, but differ notably in size, being respectively 25 and 12 mm in diameter. A similar pair has been figured by ARKELL (1952-54, text-fig. 20-1, 2) consisting of two adults of *Sphaeroceras brongniarti* (Sow.), 35 and 19 mm in diameter. Fossil remains of this species are rather rare, but many of the available specimens have a gerontic aperture preserved. It is a fairly long-lived species (Upper Bajocian — Lower Callovian) and several varieties occur differing slightly in pattern of ribbing. These differences are most likely associated with different stratigraphic horizons and geographical regions. They are equally marked in large and in small forms.

Recently a very comprehensive paper was published by WESTERMANN (1956) on this species, based on 13 specimens from different localities of Western Europe. That author has very accurately analysed the ontogenetic stages of *Sphaeroceras* starting with the protoconch, also its stratigraphic distribution and phylogenetic relations. He has distinguished two subspecies on the character of ornamentation. WESTERMANN states that *S. brongniarti* is characterized by a considerable range in the diameter of the adult (from 8.5 to 40 mm). This species is of exceptional value in clarifying the problem of dimorphism insomuch as the morphological details of the large and small forms fully agree. Hence their assignment to the same species has never raised any objections.

Sphaeroceras brongniarti occurs at Czatkowice and Racławice in the Cracow Jurassic Uplands. Over a period of several years the writer has collected 31 mature specimens there,

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TEXT-PLATE X

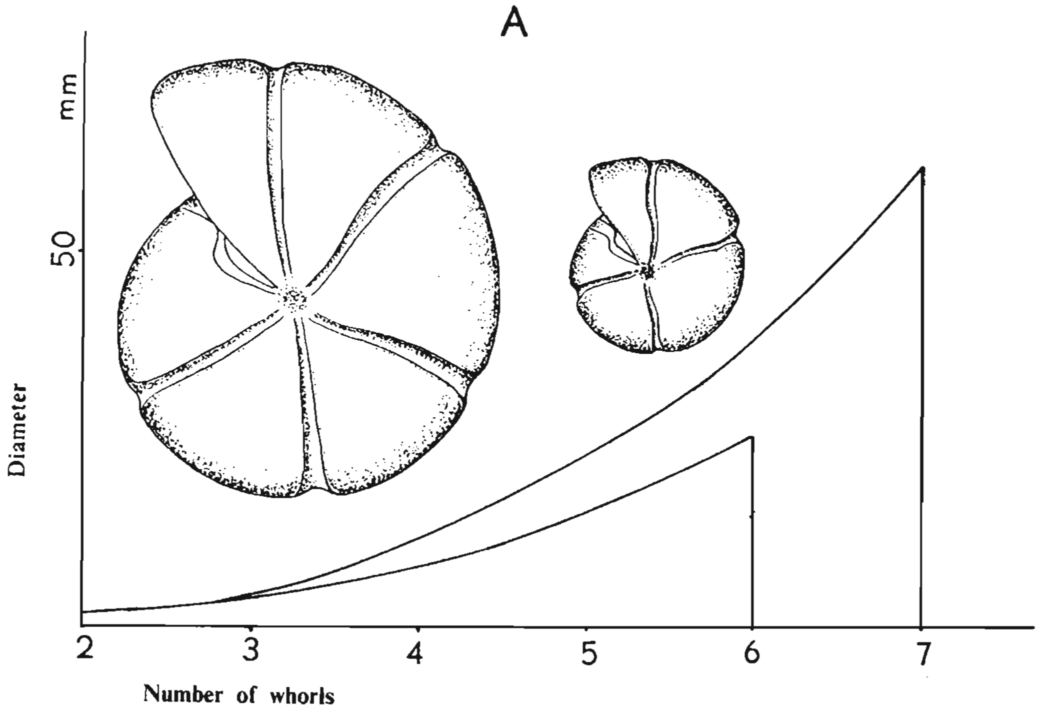
A. Ontogeny of the diameter of shell in genus *Cheiloceras*

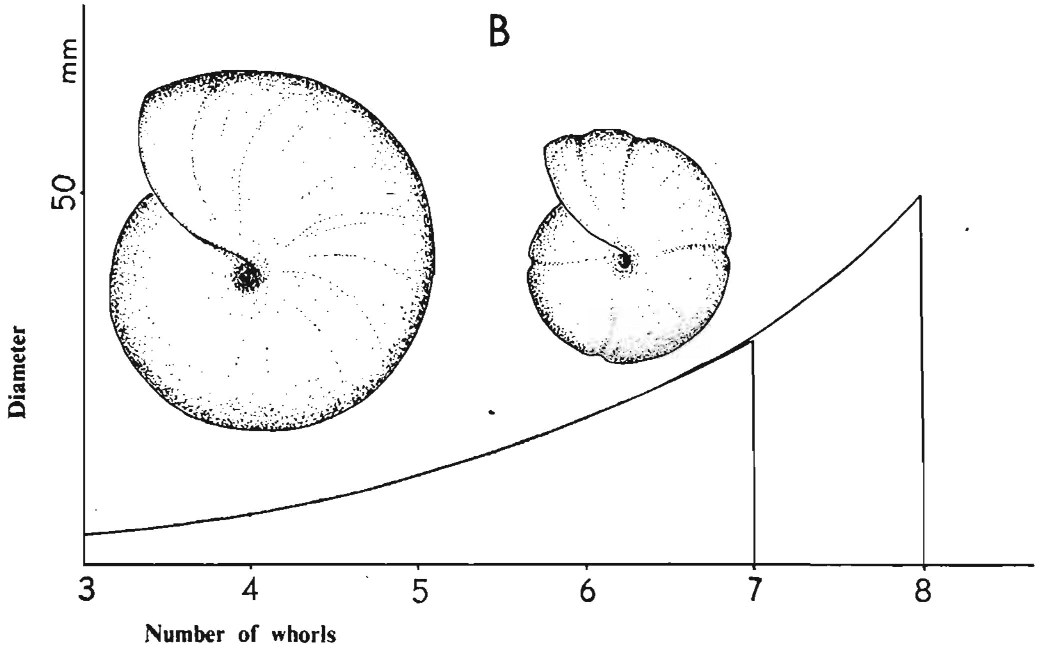
Former interpretation:	New interpretation:	Occurrence:
large form:		
?	*Ch. subpartitum* (MÜNST.) ♀	Janczyce, Famennian
small form:		
Ch. subpartitum (MÜNST.)	*Ch. subpartitum* (MÜNST.) ♂	,, ,,

B. Ontogeny of the diameter of shell in genus «*Cheiloceras*»

Former interpretation:	New interpretation:	Occurrence:
large form:		
Ch. globosum (MÜNST.)	«*Ch.*» *globosum* (MÜNST.) ♀	Łagów, Famennian
small form:		
Ch. praeglobosum SOBOLEW	«*Ch.*» *globosum* (MÜNST.) ♂	,, ,,

TEXT-PLATE X


A
mm
50
Diameter
2
3
4
5
6
7
Number of whorls


B
mm
50
Diameter
3
4
5
6
7
8
Number of whorls

in which the last body chamber is complete or nearly complete, and in some specimens the aperture is preserved. This collection contains 9 large and 22 small forms. In diameter they range from 36 to 40 mm and from 18 to 24 mm respectively, no intermediates have been found.

11 specimens of small forms were studied. Out of these, 8 had exactly 7 whorls, one had $6^3/_4$ whorls, two $7^1/_4$ whorls. Among the 5 large forms examined, four were seen to have exactly 8 whorls, and one had $8^1/_4$ whorls. On one small adult specimen from Bayeux (France), 15 mm in diameter, in which the protoconch and first whorl are preserved, it was possible to determine $6^1/_4$ whorls.

From these investigations it was also ascertained that the variability range of both the young whorls and the gerontic characters is similar in the two groups. The morphological hiatus between them is one whorl only. In his description of that species WESTERMANN (1956) publishes an accurate section ($\times$ 10 magnification) of a mature individual. Allowing for the magnification the individual represented is about 13 mm in diameter, thus belonging to the group of small forms. The seven whorls shown in that section have been numbered by the author. These data seem to agree with the writer's results; yet in the magnified figure just mentioned the first whorl is 3 mm, i. e. a natural size of 0.3 mm. On the other hand, WESTERMANN's text says that in *S. brongniarti* the protoconch is 0.3-0.4 mm in diameter and is encircled by the first whorl which together with the protoconch corresponds to the larval stage. In the illustration the protoconch has been blackened, showing it to be 2 mm in diameter, i. e. 0.2 mm in natural size, and this coincides with the writer's measurements. Thus there exists a slight discrepancy between the illustration and the accompanying text. If we accept the latter as correct, the figured specimen cannot have more than $6^1/_2$ whorls. However, it should be pointed out that among the great number of species and genera of Jurassic ammonites examined from this aspect by the writer, he never encountered a single protoconch with so large a diameter as 0.3 to 0.4 mm. The largest observed diameter of protoconch did not exceed 0.25 mm. If the present writer's dimensions of the protoconch are accepted, the first whorl would be 0.5 mm in diameter, thus suggesting at least 7 whorls in the figured specimen. These discrepancies may perhaps be due to the «partial reconstruction» of the figured specimen mentioned by WESTERMANN.

Genus **CHONDROCERAS** MASCKE, 1907

(text-pl. XII, fig. 1, 2)

This genus closely resembles the genus *Sphaeroceras* and many specimens are known with preserved gerontic aperture. The side by side existence of large and small forms, differing in size only, has been often reported. WESTERMANN's recent work (1956) contains a very detailed description of that genus, based on material from many localities of Western Europe, though

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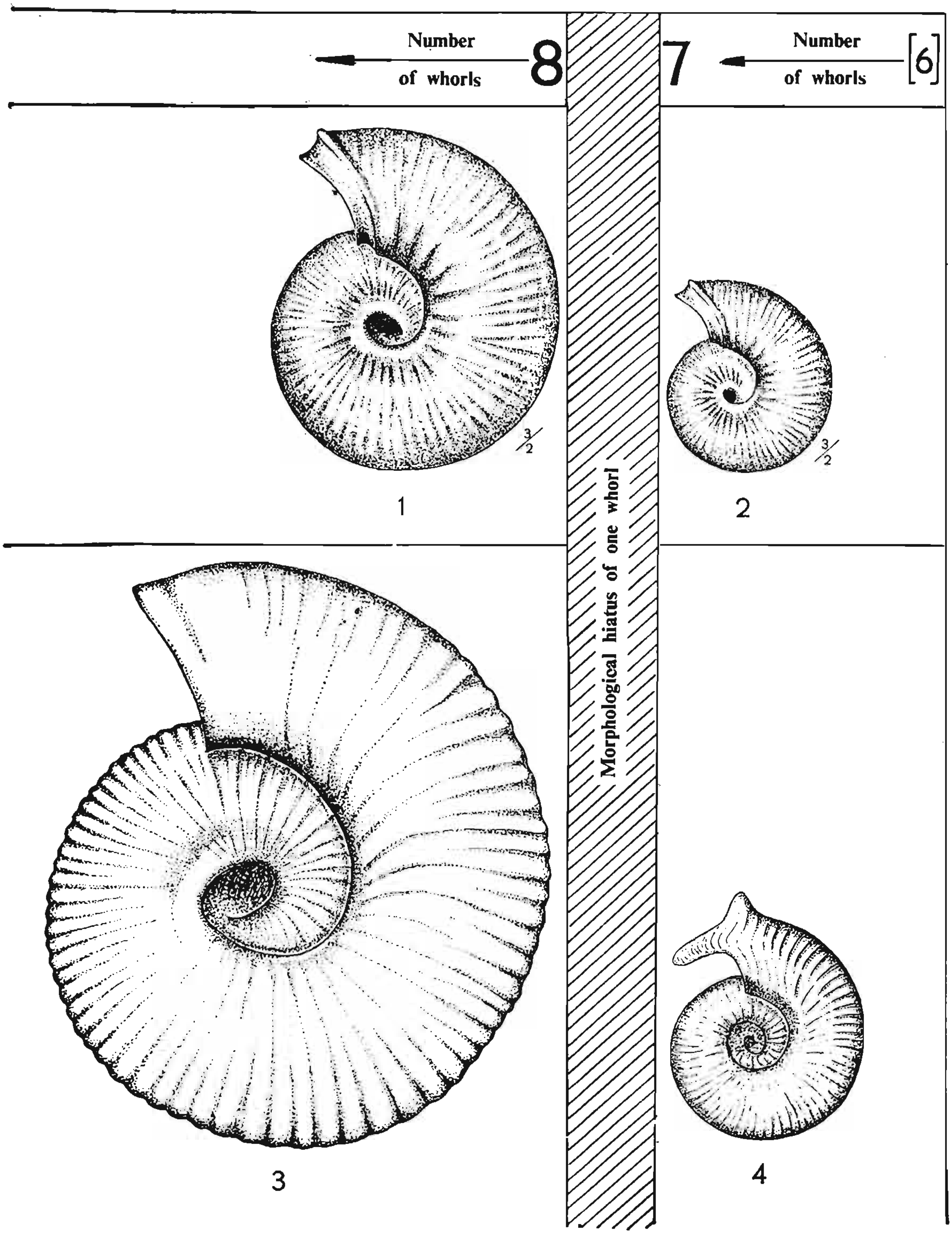
TEXT-PLATE XI

Former interpretation:	New interpretation:	Occurrence:
1 *Sphaeroceras brongniarti* (SOW.)	*S. brongniarti* (SOW.) ♀	Czatkowice, Callovian
2 *Sphaeroceras brongniarti* (SOW.)	*S. brongniarti* (SOW.) ♂	,, ,,
3 *Bullatimorphites bullatus* (D'ORB.)	*B. bullatus* (D'ORB.) ♀	Tatra Mts., Bathonian
4 *Schwandorfia marginata* ARKELL	*B. bullatus* (D'ORB.) ♂	,, ,, ,,

TEXT-PLATE XI



his interpretations of this phenomenon are not uniform. In one case, e. g. in his description of *Chondroceras gervilli* (Sow.), he assigns both forms to one species, in another case he differentiates them as separate systematic units. *Chondroceras wrighti* Buck. is an excellent example here. Westermann's statistical analysis of 20 individuals of this species separates them into two groups: one with diameter range of 30 to 45 mm (14 specimens) and the other 15 to 22 mm (6 specimens). There are no intermediary forms 22-30 mm in diameter. The two forms are described by Westermann as separate distinct subspecies.

Four specimens of that species were available to the writer. One large form and two small forms came from Oborne in Dorsetshire, England, and one large form from Germany (without accurate localization). The large forms were 36 and 42 mm in diameter, the small ones 17 and 24 mm. Since the protoconch and the first whorl were preserved on all the specimens, it was possible to count the exact number of whorls. The two large forms had nearly exactly 8 whorls. One small form had exactly 7 whorls, the other one slightly more, i. e. about $7^1/_8$ whorls. The ornament and suture were identical in both forms.

Both *Chondroceras* and *Sphaeroceras* are of the greatest value in confirming the theory of dimorphism. The evidence they supply is very convincing, since the two forms differ solely in size. A review of the literature suggests that large forms are rarely gigantic. The dimensions attained by large and small forms in the particular species show a range similar to that observed in the species *Chondroceras wrighti*. The genus *Chondroceras* contains about 20 species with a very wide geographical distribution. Hence, were the occurrence of similar dimorphism in a greater number of these species to be confirmed, it would supply conclusive evidence.

Genera **BULLATIMORPHITES** Buckman, 1921 and **SCHWANDORFIA** Arkell, 1951

(text-pl. XI, fig. 3, 4)

The genera *Bullatimorphites* and *Schwandorfia* are referred to the family Tulitidae (Basse, 1952; Arkell et al., 1957). Two groups of forms are included within this family. One contains such genera as *Tulites* Buck., *Bullatimorphites* Buck., *Rugiferites* Buck. and *Kheraiceras* Spath; the other consists of *Schwandorfia* Arkell, *Treptoceras* Enay, *Sphaeroptychius* Liss. and *Krumbeckia* Arkell.

Forms belonging to the first group are at least 80 mm in diameter, sometimes attaining 150 mm or more. The other group is made up of small forms, 20-40 mm in diameter. Some authors used to assign the large and small forms to the same genus. Their sexual dimorphism has also been a subject of discussion. Recently Enay (1959) described small forms belonging to the genus *Treptoceras* and *Schwandorfia*. He writes that the genera *Treptoceras*, *Sphaeroptychius*, *Schwandorfia* and *Krumbeckia* make up a characteristic group within the Tulitidae. These genera (or perhaps subgenera) contain small-sized forms with aperture provided with lateral processes. A counterpart of this group is formed by large forms with simple or slightly constricted aperture, always lacking the lateral processes. These forms are referred to the genera *Tulites*, *Bullatimorphites*, *Rugiferites* and *Kheraiceras*. The sutures, if known at all on small forms, resemble those on the large forms. Moreover Enay states that the problem of sexual dimorphism in the Tulitidae is particularly obvious.

The present writer was able to examine 4 specimens of the species *Schwandorfia marginata* Arkell. Three came from the Bathonian of the Tatra Mountains; one was from Germany (without accurate localization). On the two Tatra specimens the gerontic aperture was partly preserved, the two other specimens lacked the aperture but had the last body chamber nearly complete.

The diameter of these 4 specimens ranged from 21 to 40 mm. The first whorl was preserved on all of them allowing the exact number of whorls to be established. One of the Tatra specimens, with diameter of 40 mm, had $7^1/_4$ whorls. The other three specimens had exactly 7 whorls.

ENAY (1959) points out that this species comes very near to the genus *Rugiferites* (large forms). The writer did not have the opportunity of examining a specimen of that genus. However, in the Tatra Mountains, fossils have been found in a bed about 50 cm thick, together with *Schwandorfia marginata* ARKELL, that are doubtless referable to the genus *Bullatimorphites*. These specimens are characterized by an extremely narrow, nearly closed umbilicus on the penultimate whorl, which is a generic feature of *Bullatimorphites*, in distinction to the genus *Rugiferites* in which the umbilicus is wide open. The writer has collected two incomplete specimens, 67 and 72 mm in diameter, representing fragmented camerae of the shell without the body chamber. Two other specimens from the same bed were presented to him, one with a nearly complete gerontic aperture. This individual was 90 mm in diameter. Quite a number of complete specimens of *Bullatimorphites*, with preserved gerontic aperture, have so far been described and figured. Most of them have been referred to *B. bullatus* (D'ORB.), (LISSAJOUS, 1923; ARKELL, 1954; WESTERMANN, 1958). But some of these assignments and descriptions have been based on comparison with complete specimens without examining them, or at least without the figures of young whorls, comparable with the inner whorls of small forms. The writer had in his possession one incomplete specimen of *B. bullatus* (D'ORB.) collected from the Bathonian at Fuissé (France). It was possible to prepare the young whorls, which are 30 mm in diameter, and to examine them. The ornamentation here fully agrees with that figured by LISSAJOUS (1923, pl. 17, fig. 1, 2; pl. 18, fig. 1) on the specimens from Fuissé and Solutré. It consists of primary and secondary ribs which, running regularly on the siphonal side, characterize not only the penultimate adult whorl, but likewise young whorls 5-10 mm in diameter. The young whorls of two of the Bathonian specimens from the Tatra Mountains proved to be identical with the Bathonian specimen from Fuissé. On the other Tatra specimen the ribbing on young whorls, 5-30 mm in diameter, was slightly different. The ribs here are irregular, often discontinuous, forming a distinct ventral sinus. In this respect our specimen fully agrees with young whorls figured by LISSAJOUS (1923, pl. 21, fig. 2-4) for *Sphaeroceras (=Bullatimorphites) davaiacense* LISS. and *S. (=Bullatimorphites) angusticostatum* LISS. It is not out of the question that the irregular pattern of ribbing is due to damage suffered during the life-time of the animal. In any case some young whorls from the Bathonian of the Tatra Mountains, 5-30 mm in diameter, have the sculpture identical with that observed on a conspecific individual figured by WESTERMANN (1958, pl. 22, fig. 1) from the Upper Bathonian of Lechstedt near Hildesheim.

The young whorls of *Schwandorfia marginata* ARKELL from the Tatra Mountains, as well as on the writer's specimen from Germany, are identical with the young, regularly ribbed whorls of *Bullatimorphites bullatus* (D'ORB.). The suture could not be accurately compared, since it was impossible to trace its details on the specimens of *B. bullatus* examined. It has, however, been ascertained that on nearly analogous stages of the two species the general shape is identical. ARKELL (1952) and ENAY (1959) stress the close resemblance of the suture in *Schwandorfia marginata* to that in large forms of the genus *Rugiferites*. The writer supposes that the similarity of the suture and its individual variability in the forms studied reasonably exclude it as a proper basis for the discussion of affinities within the family Tulitidae. It should be added that, according to WESTERMANN (1958), the young whorls of *Krumbeckia* are the same as the young whorls of *Tulites mediolaris* (SMITH). That author publishes the photograph of a fairly well preserved specimen, 23 mm in diameter. He hesitates between its assignment to the genus *Tulites* or *Krumbeckia* (pl. 18, fig. 4), although the largest individual of *Krumbeckia* so far known is 30 mm in diameter (ARKELL, 1952-54, text-fig. 25).

The above suggestion that the first group of genera of the Tulitidae should contain forms at least 80 mm in diameter, does not seem very sound, since it means that mature individuals, less than 50 mm in diameter, are referred to the genus *Bullatimorphites*. Mature forms, 47 and 32 mm in diameter, are likewise assigned by ARKELL (1952-54) to *Bullatimorphites suevicus* (ROEMER) and *B. uhligi* (POP.-HATZ). WESTERMANN (1958) describes 3 analogous specimens, 30-47 mm in diameter, under the name of *(Bullatimorphites ?) Bomburites microstoma* (D'ORB.). We are dealing here with a species frequently described and discussed which until recently has been referred to as *Sphaeroceras microstoma* (D'ORB.). In most cases it has been described as occurring together with *S. (=Bullatimorphites) bullatus* (D'ORB.) which it very closely resembles. This resemblance is illustrated by LISSAJOUS (1923, pl. 17), who figures *S. bullatus*, with diameter up to 130 mm, together with a specimen of *S. microstoma* which is 45 mm in diameter, and has identical ornamentation. The problem of dimorphism in these species has often been discussed. *S. (=Bullatimorphites) microstoma* strongly resembles representatives of *Sphaeroceras* and *Chondroceras* in the present meaning of these genera. With reference to size this species is a «small form» as compared with the large forms of the genus *Bullatimorphites*, but it is a «large form» as compared with representatives of the genus *Sphaeroceras*.

The writer had the opportunity of examining two specimens of this species from France. One was found in the Bathonian of Fuissé, the other was labelled: «*Sphaeroceras microstoma* D'ORBIGNY. Callovien inférieur», without exact localization. In both, the gerontic aperture was partly preserved as a characteristic constriction which is observable e. g. in a figure of this species published by LISSAJOUS (1923, pl. 17, fig. 3). The aperture in this species, figured by D'ORBIGNY (1842-51, pl. 142, fig. 3-4), is characterized by the presence of short lateral lappets. No traces of such lappets could be detected on the writer's specimens. He has not indeed encountered any other mention of a similar specimen in the literature, except one called *Sphaeroceras microstoma* (D'ORB.) in a paper by RICHE and ROMAN (1921, pl. 7, fig. 11) which is accepted by ENAY (1959) as the genotype of a new genus *Treptoceras* (*T. laurenti* ENAY). Moreover, ARKELL (1952-54) writes that the above mentioned illustration of D'ORBIGNY was a combination of the young whorls of *Bullatimorphites* with the aperture of the genus *Schwandorfia*. Hence the exact shape of the aperture in this species has not been definitely determined. After a discussion of this feature WESTERMANN (1958) suggests that the aperture here comes closer to that characteristic of the genus *Chondroceras*.

The writer's specimens could be examined by gradually uncovering the whorls. It was thus seen that they had 7 whorls each. The young whorls here fully agree with the young whorls of *Bullatimorphites bullatus* (D'ORB.) and the suture displays no differences. Therefore, forms

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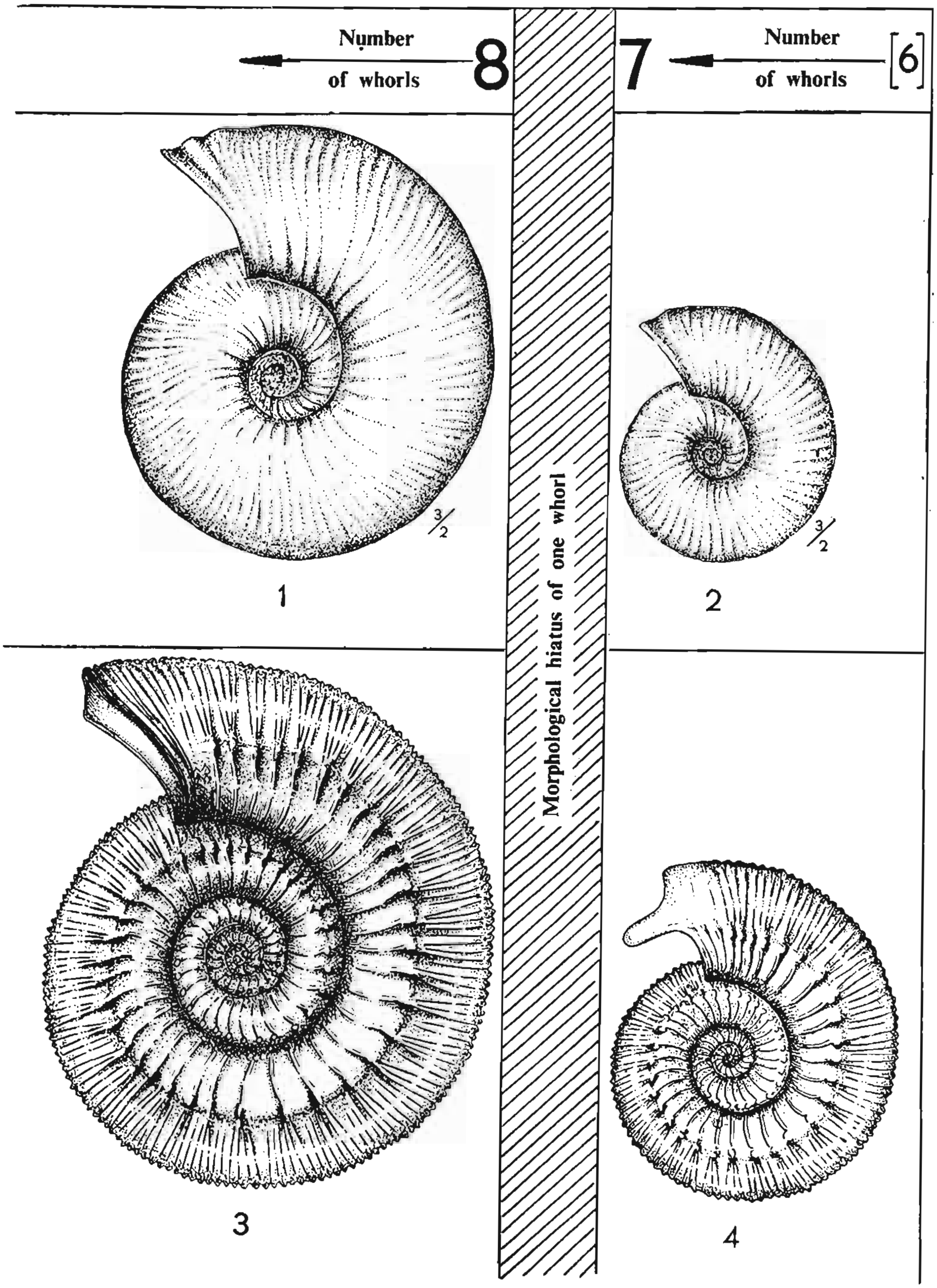
TEXT-PLATE XII

Former interpretation:	New interpretation:	Occurrence:
1 *Chondroceras wrighti wrighti* BUCK.	*Ch. wrighti* BUCK. ♀	Oborne, Bajocian
2 *Ch. wrighti minor* WESTERMANN	*Ch. wrighti* BUCK. ♂	,, ,,
3 *Cadomites deslongchampsi* (D'ORB.)	*C. linguiferus* (D'ORB.) ♀	Tatra Mts., Bathonian
4 *Polyplectites linguiferus* (D'ORB.)	*C. linguiferus* (D'ORB.) ♂	,, ,, ,,

TEXT-PLATE XII



described under the specific name «*microstoma* (d'Orb.)» and referred to the genus *Bullatimorphites* or *Sphaeroceras* and *Bamburites*, represent small forms. They differ, however, quite distinctly from the remaining small forms of the Tulitidae, usually referred to the genera *Schwandorfia* Arkell, *Krumbeckia* et al. Hence it may be recognized that the large forms assigned to the genus *Bullatimorphites* have their equivalents in two sets of small forms. One of these is commonly referred to the genus *Schwandorfia* Arkell, the other is described as identical with *Ammonites microstoma* d'Orb. The relationships existing between the particular large and small forms may be cleared up in the future by detailed investigation of adequately copious material.

Genera **CADOMITES** Munier-Chalmas, 1892 and **POLYPLECTITES** Mascke, 1907

(text-pl. XII, fig. 3, 4)

The close affinity of forms referred to these two genera is very striking and does not seem to call for an explanation. Their characteristic ornament, the details of which are already established on the earliest whorls, is the same as in large forms of *Cadomites* and in small forms of *Polyplectites*. These two genera differ only in size and shape of the gerontic aperture: in *Cadomites* the aperture is straight, in *Polyplectites* it is provided with lappets.

Arkell (1952-54, p. 79) writes: «*Cadomites* and *Polyplectites* (possibly females and males of single genus)...». That author also presents a genealogical tree of the family Stephanoceratidae demonstrating the common origin and identical stratigraphic distribution of the two genera. Westermann (1954) re-described the genus *Polyplectites* on excellently preserved specimens, the apertures of which are provided with lappets. *P. linguiferus* (d'Orb.) is among the most important and most frequently cited species. From the time of d'Orbigny (1842-51) the synonymics of that species involve 25 names and with one exception they are perfectly uniform. Hence it may be inferred that the species is well known. However, Westermann believes, unlike Arkell, that there are differences in the stratigraphic range of *Cadomites* and *Polyplectites* which mean that they cannot be linked together. On the well studied character of the suture and shape of aperture, the genus *Polyplectites* is even conditionally placed by that author into another family, the Otitidae, which contains forms having an aperture with conspicuous lappets. In a later paper, however, Westermann (1958) goes back to the commonly held view and includes the two genera into a new established subfamily Cadomitinae.

Cadomites deslongchampsi (d'Orb.) and *Polyplectites linguiferus* (d'Orb.) are among the most common species in these two genera. They are widely known and have been frequently described. The writer had on hand three specimens of *C. deslongchampsi* (d'Orb.). One came from an unknown locality in France, one from the Upper Bathonian of Calvados (France), the third from the Bathonian of the Tatra Mountains in Poland. They range from 75 to 86 mm in diameter. The first whorl has been preserved on the two French specimens and it was possible to ascertain that they each had 8 whorls, 4 Bathonian specimens of *Polyplectites linguiferus* (d'Orb.) have been examined, two from Calvados and two from the Tatra Mountains. They range from 31 to 50 mm in diameter. One of the Tatra specimens has $7^1/_4$ whorls; the other three have exactly 7 whorls. The two species considered above fully agree in sculpture and suture. Accordingly it may be concluded that the two forms differ in shape of aperture only and that they are separated by a morphological hiatus of one whorl.

GONIATITES

Genus «**CHEILOCERAS**» Frech, 1897

(text-pl. X, fig. *B;* text-fig. 10*a*)

As has already been stated (see p. 44) the species *Cheiloceras subpartitum* (Münst.), which is the genotype, exhibits dimorphism of type «A», while the dimorphism in numerous other species of the genus *Cheiloceras* is of type «B». However, the type «B» species should be recognized as typical representative of the superfamily Cheilocerataceae, since their sutures arch distinctly forward, while on the specimens of *Cheiloceras subpartitum* (Münst.) available to the author this is not so conspicuous. This problem will be dealt with again later (p. 63).

In his description of the genus *Cheiloceras* from the Devonian of the Holy Cross Mountains, Sobolew (1914) sometimes separates the small and large forms into different species. E. g. *Oma-monomeroceras (Cheiloceras) globosum* (Münst.) (large form), and *O. (Cheiloceras) praeglobosum* Sob. (small form).

From the *Cheiloceras* beds of Łagów and from the Kadzielnia quarry at Kielce some rich material has been collected, containing the various representatives of the genus *Cheiloceras* that have already been described by Sobolew *(l. c.)*. The writer was greatly handicapped in his investigation of these fossils, since in most specimens details of internal structure cannot be traced owing to re-crystallization. Nevertheless, after many attempts it has been discovered that in the genus *Cheiloceras* the first whorl, terminating in a faintly indicated constriction, is 1.0-1.1 mm in diameter. Also that the small forms halt at the 7 whorls-stage, while the large forms have at least 8 whorls. The suture is identical in the two forms. This also applies to the general shape of some species, as has been noted with the genera *Sphaeroceras* and *Chondroceras*. Where, however, the 7 whorls-stage in large forms differs from their adult stage, the same difference is noticed in the adult stage of the small form.

Because of the phylogenetic significance to be attached to sexual dimorphism in ammonoids, a revision of the systematics of the genus *Cheiloceras* and other goniatites from the Devonian of the Holy Cross Mountains cannot be attempted. Until the question has been clarified, it is thought wiser to retain the generic name of *Cheiloceras* in quotation marks for species with the «B» type of dimorphism.

* * *

Text-plates I—IX and X*A* illustrate the here decribed morphological relations in small and large forms that display the «A» type of dimorphism. Text-plates X*B*, XI and XII illustrating the «B» type of dimorphism, indicate for the sake of convenience 7 whorls as the maximum number accepted for small forms, even though $7^1/_4$ whorls are attained in some cases. In all these examples dual nomenclature is used, i. e. that followed in the present paper and that in common use to express the relation of recent systematics to the morphological phenomena figured.

The writer's conclusions drawn from the evidence cited above and its discussions may be summarized as follows:

1. Analogies occurring in the morphological relations of large and small ammonite forms cannot be accidental as they represent the most fundamental, constant and common features of that group of animals.

2. These morphological phenomena in ammonites require uniform interpretation and uniform consideration in systematics.

3. It is inadmissible to put forward a concept that large and small ammonite forms, identical in the early stages of ontogeny and separated by a morphological hiatus, may have originated independently as separate systematic units, by way of parallel evolution or by another mode.

4. The only reasonably acceptable interpretation of this phenomenon is the recognition that large and small forms are conspecific individuals of different sex.

The acceptance of the concept of sexual dimorphism in ammonites is not necessarily handicapped by the pre-requisites propounded on p. 13. The writer even thinks that the presence within the same bed of adequately preserved large and small forms is not always an indispensable test of this theory. Large and small forms, from diverse localities, belonging either to rare species, e. g. representatives of *Sphaeroceras*, or to common ones that are usually unsatisfactorily preserved (e. g. *Hecticoceras*), may constitute two separate groups differentiated on the basis of rules previously stated. In view of the facts discussed above, the side by side occurrence of paired forms in every locality does not seem strictly necessary.

Data concerning the stratigraphic range of large and small forms, their numerical ratio, etc., may not in some cases fully comply with the pre-requisites postulated on p. 13. The writer is, however, convinced that all these doubts should be discarded in view of the constant and uniform morphological characters that have been discussed.

SEX IDENTIFICATION IN AMMONOIDEA

The above historical review of the problem shows that, on the basis of analogies observable in the first place in living cephalopods, several authors suggested that large ammonite forms represent the females, small forms the dwarf males. When discussing this question, Arkell, Kummel et al. (1957) hint at the possibility that the small forms may be females, whose apertural extensions were used as supports for the egg-bearing cocoons. By now it has been shown that the apertural extensions are present in the small forms of certain ammonite groups only and that in many ammonoids the apertures of the large and small forms show no differences at all.

In a quest for appropriate analogies we may turn to sexual dimorphism in Gastropoda *(Prosobranchia)*. In this group the dimorphism, as seen in the shell, has not in fact been adequately investigated. The current opinion is that gastropod males are slightly smaller and more slender than the females, but careful observations show that this rule is more of a statistical character. And even in cases where sexual dimorphism is, statistically speaking, well expressed, some individuals may be sexually distinguished on the soft parts only. Nevertheless constant and well expressed dimorphism has often been noted.

Pelseneer (1926) shows that in the case of the gastropod *Lacuna pallidula* Da Costa (fig. 7) 2-3 small dwarf males are usually found resting on the female shell. Likewise e. g. in *Buccinum undatum* L. (Lamy, 1937) the males are smaller and in reef living colonies adult males attain half the size of female shells (fig. 8). In the Littorinidae the males are, on the whole, smaller and more slender than the females (Lamy, *l. c.*). This is well illustrated in *Littorina rudis*

MATON (fig. 9). SIMROTH (*fide* LAMY, *l. c.*) has investigated sexual dimorphism in the genus *Navicella* and has found that the females range in size from 17.5 to 26 mm, the males from 12.5 to 17.5 mm. Sexual dimorphism is similarly expressed in the parasitic species *Melanella*

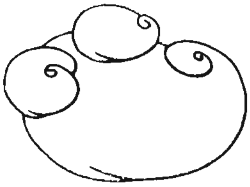


Fig. 7
Lacuna pallidula DA COSTA, a female with two dwarf males, after PELSENEER (1926)

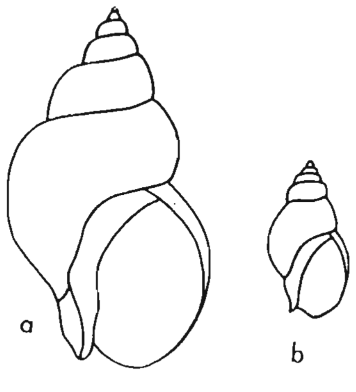


Fig. 8
Buccinum undatum L.: *a* female, *b* male; after LAMY (1937)

holothuricola (DOGEL, 1947). In certain parasitic gastropods the males are very much smaller, occasionally several hundred times smaller (in mass or bulk of body). Their function is that of complementary males as the females are hermaphroditic. Sometimes, e. g. in the species *Pelseneeria profunda* (DOGEL, *l. c.*) the males disappear and only hermaphroditic forms are produced.

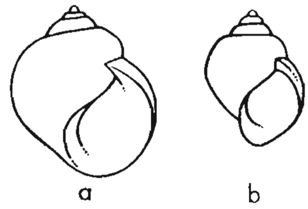


Fig. 9
Littorina rudis MATON: *a* female, *b* male; after LAMY (1937)

Accordingly it may be inferred that in the recent *Prosobranchia* there is a general tendency to express sexual dimorphism by smaller size and more slender shape of males as compared with females. A study of the evolution of this phenomenon would doubtless be very interesting, but unfortunately no such attempts seem to have been made.

In fossil *Prosobranchia*, all closely related forms, but of distinctly differing dimensions, are described as separate species, subspecies or varieties: it is just such differences (of size) that may express the separate sexes too. In descriptions of the recent *Prosobranchia* conspecific forms of different sex have indeed occasionally been referred to separate species (WAGNER, 1910).

In recent cephalopods the males are smaller, even dwarfed. This is shown below by reference to 3 recent species of cephalopods on data taken from the literature:

	Length of body (in mm)	
	female	male
Ocythoe tuberculata	280 and more	30-50
Tremoctopus violaceus	120-150	20-25
Argonauta argo	100-180	15

NAEF (1923) states an extreme case where the weight of a male *Argonauta* is one thousand times smaller than that of its female counterpart. Analogous phenomena are common among all types of invertebrates and have been recorded in the Crustacea, Arachnoidea and Insecta. Among the Rotatoria, containing at least 1000 species, the males, with very few exceptions, are small, dwarfed and strongly simplified. They only have a vestigial oesophagus, are extremely short-lived and do not take any food. Similar facts have been noted even among vertebrates. In many fishes the males are smaller than the females. In the abyssal family of Ceratiidae the males are very much smaller, but their biology has not been thoroughly studied (SUVOROV, 1948). In body mass the males are at least many tens of times smaller than the females. They either lead an independent life or they are attached as parasites onto the body of the females. When this is so, their oesophagus and many other organs become atrophied.

To sum up our considerations concerning these interesting examples of sexual dimorphism, one conclusion may be made. In the organic world, wherever sexual dimorphism becomes strong enough to be expressed by notably smaller dimensions of one sex (occasionally many tens of times smaller), the dwarfism invariably affects the male individuals. Not a single case of opposite morphological conditions has so far been reported in this respect.

In ammonites sexual dimorphism varies widely in extent. E. g. in the genus *Sphaeroceras* the volume ratio of the last body chamber in the small and large forms varies from 1 : 3 to 1 : 5. In the genus *Quenstedtoceras* this ratio ranges from 1 : 8 to 1 : 800, while statistical data based on fragmentary specimens suggest that in many other genera the range of dimorphism is still greater. E. g. large forms of the species *Oppelia fusca* may attain some tens of centimetres in diameter. QUENSTEDT (1886-87) describes a specimen of «*Riesenfuscus*», not less than 50 cm in diameter, while probably conspecific small forms provided with lappets, referable to the same species, are from 20 to 40 mm in diameter. Here the extreme difference in the volume ratio of the last body chambers between large and small forms is 1 : 2000. Similar examples are supplied by the genus *Litoceras*.

On the grounds of the examples just cited, it is maintained that all these analogies in dimorphism within the living animal world supply conclusive evidence that small ammonite forms represent the males and that true gigantism occurs among the female forms only. This is a restatement of the concept advanced by DE BLAINVILLE one hundred and twenty years ago.

PROBLEMS OF NEW SYSTEMATICS

A summary is here given of the various standpoints from which the side by side existence of large and small forms is viewed in recent systematics. With regard to Devonian goniatites these differences are assigned a specific value at the most, as e. g. in the genus *Manticoceras*. Often both forms are referred to the same species. It should be stressed here that in recent systematics of the goniatites the authors rarely distinguished subgeneric taxa, while Mesozoic ammonites, particularly Jurassic, supply many examples of the separation of subgeneric units. In most cases new subgenera are established to accommodate the large and small forms. Among the Jurassic and Cretaceous ammonites the large and small forms are either assigned to different genera *(Lissoceratoides-Glochiceras, Cadomites-Polyplectites)* and subgenera *(Garantiana-Pseudogarantiana)*, or to different species of the same genus *(Kepplerites)*. Sometimes one of the forms is regarded as a separate variety (*Discoscaphites constrictus* (Sow.)) or both forms may be regarded as conspecific — as is done in goniatites — if the morphological differences are not conspicuous and concern the size only, as e. g. in the genus *Sphaeroceras* or *Chondroceras*.

The abundance of finds has a bearing, often quite important, on the taxonomic value attached to the differences considered. E. g. the establishment of the new genus *Glochiceras* to accommodate small forms with lappets may probably be explained by the abundance of the remains. Without doubt these are the commonest ammonites yielded by the lower Malm deposits in which the aperture is still preserved. Their abundance was so striking to the eye that palaeontologists were prompted to establish a separate genus for these forms. This fact is mentioned in order to emphasize that the differences used to separate small forms into the genus *Glochiceras* and large forms into the genus *Lissoceratoides* are much less important than those by which large and small forms have been assigned to separate species in the genera *Kepplerites* and *Hecticoceras*, or split up into varieties of the same species as in the case of *Discoscaphites constrictus* (Sow.). Of the genus *Kepplerites*, however, no more than 2 or 3 specimens with preserved aperture are recorded. The same extreme scarcity of specimens is true of the genus *Hecticoceras*. As has already been mentioned above, of about 4000 specimens cited in the literature, only 3 specimens of the large forms and 8 of the small forms are known with preserved gerontic aperture. In such genera as *Trimarginites* and *Ochetoceras* the situation is very similar. Using the same generic examples their modern diagnosis will here be approached from the writer's standpoint.

In their diagnosis of the Cosmoceratidae published in «Osnovy Paleontologii», Krimholc, Kamyševa-Elpatevskaja et al. (1958) mention the «aperture with lateral lappets». By now it has been shown that this is not correct, at least as far as concerns *Cosmoceras* s. str. which is here treated sensu lato. On the basis of copious and reliable material it has been demonstrated beyond doubt by Brinkmann (1929*a*) that only some species have an aperture provided with lappets, while the majority have a simple aperture without lappets. In the diagnosis of the genus *Cosmoceras* (s. l.) there is no mention of lappets though representatives of this genus have exceptionally long apertural extensions, sometimes reaching two thirds of the diameter of the shell, and there are many illustrations of this in various earlier and recent publications. On the other hand, the diagnosis by the same authors for the genus *Kepplerites* mentions «aperture simple or with small lappets»; it is true that the lappets are developed, but they are small and only 2 or 3 specimens with lappets have so far been actually recorded. The genus *Garantiana* (s. l.) is also cited and *Garantiana garantiana* (d'Orb.), with simple gerontic aperture, has been figured as the genotype. Forms with lappets are not mentioned at all although many specimens with them have been described (e. g. Bentz, 1924, 1928).

These examples seem to be good illustration of the confusion about the systematics of ammonites prevailing in the literature. This is observable both in original works and in comprehensive syntheses which strongly influence the trend of investigations and exaggerate current misleading notions. This confusion also has some bearing on the etymology of generic and subgeneric names. Some authors when erecting separate genera or subgenera to accommodate the large and small forms give to these taxonomic units names stressing the striking affinities between them. The following are examples of this practice in both types of dimorphism:

Large forms	Small forms
Cadoceras Fischer	*Pseudocadoceras* Buckman
Garantiana Mascke	*Pseudogarantiana* Bentz
Reineckeia Bayle	*Reineckeites* Buckman
Wedekindia Schindewolf	*Parawedekindia* Schindewolf

Even this very brief review and the accompanying examples indicate that in modern systematics the side by side existence of large and small forms of ammonites is treated with wide disparity, casually and inconsequentially. In Devonian goniatites the two forms are either regarded as conspecific or as separate species. In the more strongly differentiated Mesozoic ammonites, where dimorphism is expressed by sculpture and the gerontic aperture, the two forms are referred, according to the writer, to different genera, subgenera, species, subspecies or varieties. Only seldom are they regarded as conspecific individuals without subdivision into minor systematic units. Every possibility not in disagreement with the nomenclatorial rules has been here explored and its application conditioned by the extent of dimorphism in each particular case and by the subjective appraisal of the present writer.

The frequency of occurrence, making identification of forms more or less easy, also plays a certain role here. If the findings are common, any differences are usually treated as higher systematic categories, than if the findings are meagre, when no great significance is attached to the differences. Systematics is not an abstract method for the classification of forms of life, but must be in accordance with the actual forms which life takes.

Opinions differ widely as to what should be the proper criteria of systematics in the field of palaeontology. Some authors claim that in palaeontology systematics should take into consideration the scientific information on contemporaneous living organisms. Others think that convenience in the assignment and identification of fossil remains is the only reasonable criterion for the establishment of taxonomic units. According to the writer, there should at least be uniform treatment in ammonite systematics irrespective of the standpoint taken on this question.

It could, for instance, be conventionally accepted that the large and small forms will be consistently assigned to separate genera, species or other taxonomic categories. The writer, however, does not consider this solution to be sufficiently clear and convenient, since it would necessitate the introduction of a number of new names into each given systematic category in which that type of subdivision was still lacking. Moreover, the already existing etymological confusion would produce an extremely strange picture of such systematics in the taxonomic categories already established.

Therefore, it is probably better to retain the old generic names sensu lato so that they would embrace the phenomenon of dimorphism. There would then be no formalistic or real handicaps since the separation of the old original genera into new genera or subgenera to accommodate the large and small forms, has not been generally recognized and many recent authors still use the old traditional generic names. The author proposes the retaining of the original generic names, regardless of whether their genotypes had been large or small forms, with the supplementation of their diagnosis by a characteristic of the dimorphism.

The question of systematics on the level of species is more complicated. It has been ascertained that the morphology of small forms is not equivalent to that noted in their larger partners. The small forms display only some features and recapitulate some processes such as occur on a strictly limited early segment of the large form. Other features and processes subsequently expressed on the later whorls of the large forms are not present at all in the small forms. An exception here are the gerontic apertures which may be similar or even identical in both forms *(Sphaeroceras, Taramelliceras)*.

Moreover, among small forms there are individuals which have halted at various stages of ontogeny. E. g. among species affected by type «A» dimorphism, some individuals halt at the 5 whorls-stage, while others attain the 6 whorls-stage. If this occurs in forms that are smooth

(Lissoceratoides-Glochiceras) or whose ornamentation is constant from the earliest whorls *(Leioceras)*, the only discernible difference is that of size. If this halt occurs in species exhibiting distinct changes in sculpture between whorl 5 and whorl 6 *(Taramelliceras)*, specimens may be encountered differing both in size and in sculpture. Specimens which have halted at the 5 whorls-stage, naturally have a suture less differentiated than those that have attained the 6 whorls-stage and which consequently have about 10 more septa. All these remarks concerning the size, sculpture and development of the suture are likewise applicable to the large forms. Some of these, affected by type «A» dimorphism, halt at the 7 whorls-stage, while others may attain 8 or more whorls.

If a new character first appears on the earliest whorls and, during further evolution, passes onto the next whorls, this process embraces simultaneously both the small and the large forms. If, however, a character makes its appearance on the last whorls of the large forms, subsequently passing onto the earlier whorls, it will not appear in the small forms until it reaches the ontogenetic stage attainable by them. Hence there arises an understandable increase in the number of species differentiated according to traditional systematics among the large forms as compared with small ones. Up to a certain stage of ontogeny both forms have the same characters. Toward the end of ontogeny these characters may be diversely modified or even vanish. In addition, the small forms may also have their own features which evolve independently. E. g. special apertures and ornamentation occurring on the last body chamber.

The recognition of dimorphism also produces certain more specific systematic problems. The most serious of these will probably be encountered in the systematics of Jurassic species of ammonites which display strongest sexual dimorphism due to the range and ontogenetic variability of details in ornamentation. In the majority of the Triassic and Cretaceous ammonites, on the other hand the ornament pattern becomes stabilized on the early whorls and does not greatly change during later ontogeny. In palaeozoic ammonites sexual dimorphism is expressed only by the size and the relatively unimportant changes in the development of the suture.

Difficulties in systematics with regard to dimorphism at the species level increase with the narrowing of species, while conversely their formal clarification becomes easier when the species is considered broadly. The same difficulties are encountered in modern systematics. Much confusion and a lack of consequence prevail here encumbering ammonite literature with a heavy ballast of argument. The discussion is concerned mostly with the value to be attached to the side by side occurrence of large and small forms, and the examples cited represent only an insignificant part of the discussions on the genera and species in question. In some generic descriptions discussion on this particular problem predominates and the value attached to each character varies according to the author. Numerous tentative solutions have been put forward not always showing full awareness of the existence of large and small forms.

Personal bias cannot be completely eliminated from ammonite systematics, as with the systematics of any group of animals. This factor, however, at times becomes so paramount in the interpretation of the phenomena studied in ammonites as to deprive some of the publications on systematics of their scientific character. The recognition of the theory of dimorphism would render groundless the discussion quoted above and eliminate the ballast of generic and specific differentiation of large and small forms.

Hence the writer proposes to apply the same specific name to large and small forms, using the symbols accepted in zoology for the male and female forms (♂, ♀). Young specimens in which sex cannot as yet be determined may be referred to by adding the abbreviation «juv.» after the name.

FINAL REMARKS

PHYLOGENETIC PROBLEMS

Two types of ammonoid dimorphism have so far been distinguished and both are already discernible among the Devonian ammonoids. Type «A» is observed in the genus *Tornoceras* and in the species *Cheiloceras subpartitum* (Münst.). Other species of *Cheiloceras*, e. g. *Ch. lenticulare* Sob., *Ch. tenue* Sob., *Ch. globosum* (Münst.) belong to type «B». Here the small forms attain at least the seven whorls-stage, as in representatives of the Middle Jurassic family Stephanoceratidae *(Sphaeroceras, Cadomites)*.

The writer has long searched for intermediates between these two types among the above mentioned goniatites. This quest, however, has not met with success and no such forms have been found.

According to Wedekind (1917) and Ruzhencev (1960) the shape of the growth lines is the only diagnostic character distinguishing the superfamily of Tornocerataceae from that of the Cheilocerataceae. In representatives of Tornocerataceae the growth lines form a sinus on the ventral side and on the flanks, while in Cheilocerataceae they form a sinus on the ventral side only arching forward on the flanks (fig. 10). On most of the specimens of *Cheiloceras*

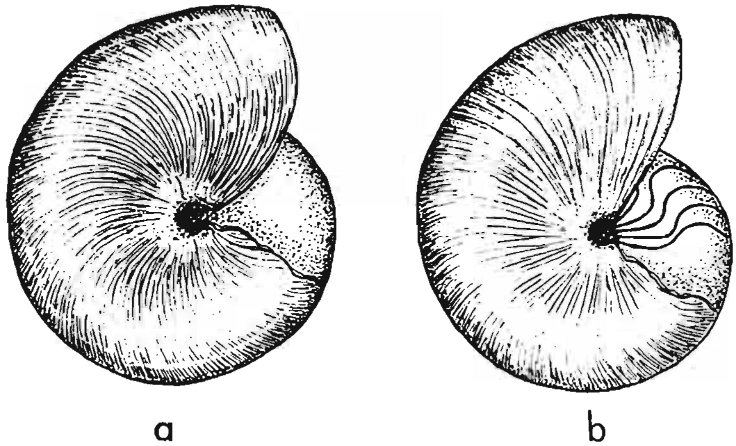


Fig. 10
a Cheiloceras globosoides Sob., Famennian, Łagów; *b Tornoceras acutum* Frech, Famennian, Janczyce. Course of growth lines

subpartitum (Münst.) from the Holy Cross Mountains the growth lines do not actually form a lateral sinus, some specimens showing only a tendency thereto. On specimens of *Tornoceras simplex* (Buch.) the sinus is sometimes only faintly indicated, while on other species of the genus *Cheiloceras* mentioned above the growth lines arch forward very distinctly. The primitive suture in *Cheiloceras subpartitum* (Münst.) does not supply any good evidence to indicate that this species is more nearly related to other species of *Cheiloceras* exhibiting type «B» dimorphism than to representatives of the genus *Tornoceras*. It is possible that the Devonian specimens from the Holy Cross Mountains referred to the species *Ch. subpartitum* (Münst.) both by Sobolew (1913) and by the present writer, are not identical with the German specimens on which this species has been described and which the writer has not been able to examine.

Several small forms of *Tornoceras simplex* (Buch.), just under the 6 whorls-stage, have been collected by the writer from beds with *Manticoceras intumescens* (Beyrich) which has a dimorphism of type «A». The large forms here are fragmentary. Accordingly it may be concluded that dimorphism of type «A» occurs in goniatites as early as the *Manticoceras intumescens* horizon. It has not as yet been cleared up whether type «B» appeared before the *Cheiloceras* horizon or whether it existed earlier along with type «A».

Both types of dimorphism occur also in Clymeniida. Type «A» is observed in some species of *Kosmoclymenia* Schind., type «B» in the genus *Wocklumeria*. This suggests that Clymeniida is polyphyletic and that the descent e. g. of the genus *Wocklumeria* is from the Cheiloceratidae. It is noteworthy that Basse (1952) actually includes the genus *Wocklumeria* into the Cheiloceratidae.

The question now arises as to the systematic value to be attached to these differences in the dimorphism occurring in representatives of goniatites assigned to the genus *Cheiloceras*. The writer thinks that these differences can be justly estimated only by studying a large number of Palaeozoic genera. At present it may only be conjectured that the basic traits of ammonoid morphology, so conservatively retained in Mesozoic ammonites, appeared as early as the Devonian, maybe even earlier.

Investigations of the dimorphism in Palaeozoic ammonoids, particularly in Cheiloceratidae and Clymeniida, have been pursued further by the writer and the results obtained will be published separately. An attempt will now be made to discuss the same problem against the wider background of a greater number of genera of Mesozoic ammonites. In this connection a table I is given correlating some of the genera so far investigated, and indicating the type of dimorphism involved. On this table are mentioned only those genera in which the type of dimorphism is based on evidence of at least one of the species in the genus, while it disregards other genera, assigned by particular authors to the superfamilies described by them, but for which the direct evidence of dimorphism is lacking. For the sake of clarity the subdivision into minor subgenera has been disregarded. In a few cases subgeneric names have been treated as generic, if this does not conflict with the theory of dimorphism. Actually these changes and apparent inconsistencies are of no consequence here. Indeed, in view of the strong diversity of opinions, a compilation of this kind can hardly be expected to be consistent.

The systematic arrangement of genera in this table is that followed in the three most up-to-date syntheses on systematics:

1952. Traité de Paléontologie, ed. by J. Piveteau, vol. II;

1957. Treatise on Invertebrate Paleontology, ed. by R. C. Moore, Part I;

1958. Osnovy Paleontologii, ed. by J. A. Orlov, Molluski-Golovonogie, II.

The above table shows that according to some authors the major systematic units, such as families or superfamilies, constitute uniform groups as far as concerns dimorphism, while according to others they are more or less mixed. Certain characteristic connections are, however, discernible even among these mixed groups, e. g. between the genus *Garantiana* and genus *Parkinsonia*. Basse (1952) and Arkell, Kummel et al. (1957) refer the genera *Garantiana* and *Parkinsonia* to the superfamily Perisphinctaceae, while Krimholc, Kamyševa-Elpatevskaja et al. (1958) place these genera within the superfamily Cosmocerataceae, where *Garantiana* together with *Kepplerites* and *Cosmoceras* make up the single family of Cosmoceratidae. The genus *Reineckeia* and *Morphoceras* are associated by Krimholc with the genus *Cosmoceras*, while Basse (1952) and Arkell, Kummel et al. (1957) place them into the superfamily of Perisphinctaceae.

The phylogenetic scheme of Jurassic ammonites given by ARKELL (1957, p. L106-L107) suggests that during the Middle Jurassic such families as the Cosmoceratidae, Clydoniceratidae, Oppeliidae etc., displaying dimorphism of type «A», descended, independently from each other, from forms having type «B» dimorphism. The phylogenetic schemes of other authors (e. g. BASSE 1952) differ in many points from ARKELL's scheme although they also present the problems that are being considered here.

Two logical explanations of these facts may be advanced:

1. During the evolution of ammonites, forms with dimorphism «A» repeatedly and independently originated from type «B», or vice-versa.

2. Some of the polygenetic connections have been determined incorrectly and accidentally.

The first explanation seems hardly likely from a general biological standpoint. It is inconceivable that forms «A» could have arisen from forms «B», or vice-versa, at different times and in various ammonite groups, and that within each type the forms should always be the same. More attention should be focussed on the uncertain and diversely interpreted systematic position of genera that are most often inconsistently united together, thereby disturbing the uniformity of families or superfamilies.

Hence the above mentioned mixture of the two types of dimorphism, at the family or superfamily level, may be accounted for by the misinterpretation of phylogenetic relations and by erroneous taxonomic assignment. This is a consequence in the first place of the strongly convergent ornament and suture. E. g. the constant practice of uniting the genus *Garantiana* with *Parkinsonia* which represent two different types of dimorphism, is doubtless due to the extremely strong convergence of the ornamental details which even on the youngest whorls are so similar as to be almost identical.

The establishment of the superfamily of Cosmocerataceae by KRIMHOLC, KAMYŠEVA-ELPATEVSKAJA et al. (1958) represents a rather isolated opinion since in none of the more recent synthetic works are such genera as *Cosmoceras*, *Reineckeia* and *Morphoceras* assembled into one superfamily.

In this connection LUPPOV, KIPARISOVA et al. (1958) state, in the same volume, that this new superfamily unites such ammonite groups as are referred in the systematics of other authors to different superfamilies, but which display nevertheless certain peculiar characters suggesting their affinity.

Though not explicitly stated by the authors, it may reasonably be assumed that peculiarities of ornament constituted the basis for the establishment of the superfamily Cosmocerataceae. If suitably selected forms are compared from among such genera as *Cosmoceras*, *Garantiana*, *Reineckeia* and *Parkinsonia*, the resemblance here can be very striking. But, their sexual dimorphism indicates, on the contrary, a different genetic ancestry. A reconstruction of the higher systematic units so that each embraces only one type of dimorphism does not require supplementary argumentation outside that applied in traditional systematics.

An attempt to reorder the higher systematic units, such as family or superfamily, into groups according to the type of dimorphism, will obviously consistently involve us in similar rearrangement of their phylogenetic connections. We are thus led to the problem of a choice of methods for the establishment of phylogenetic relations in ammonites.

There is ample literature on this problem, beginning with the classical papers by KARPIŃSKI (1890) and HYATT (1894) up to the most recent publications. Many authors on the whole support HYATT's views. He differentiated 5 main ontogenetic stages in Tetrabranchiata: 1) embryonic, 2) nepionic, 3) neanic, 4) ephebic and 5) gerontic, claiming that the neanic (youthful) stage is of marked significance in the interpretation of the phylogenetics below the family level. No ontogenetic or phylogenetic value is attached by that author to the gerontic stage. In the introduction to a volume of the «Osnovy Paleontologii» concerned with ammonites, Luppov, Kiparisova et al. (1958) point to the lack of generally accepted systematics of the ammonoids. Indeed, the classification schemes drafted by various authors disclose fundamental differences and none of them meets the requirements of natural (phylogenetic) classification, primarily because of the lack of adequate knowledge of the early ontogenetic stages of most Mesozoic ammonites. They claim that fuller information about young stages should form the basis for the reconstruction of phylogenetic relations.

The value of a method based on similarities or differences in the early stages of ontogeny has undeniable advantages. Its general and logical application may in many cases be of help for the elaboration of systematics and phylogeny, particularly within families or superfamilies. The writer is inclined, however, to attach greater importance to the method, based on the types of sexual dimorphism, since it is very reliable when assigning genera to major systematic groups. This method necessitates the examination of mature individuals which alone allow a determination of the type of dimorphism.

The presence of both types of dimorphism as early as the Devonian suggests the side by side existence of the two types throughout ammonite history from the Devonian to the Cretaceous. In view of the extremely conservative character of the phenomenon, it may be that the two types of sexual dimorphism distinguished in ammonites will prove an important clue to their phylogeny.

SOME EVOLUTIONARY PROBLEMS

Ammonite history supplies ample material for the study of evolutionary problems. Hence literature contains many descriptions and incidental remarks on diverse evolutionary questions, illustrated by examples from ammonite history. Among them are parallel evolution, convergence, homeomorphism, biogenetic law, rate of evolution etc. Some of these theories have a purely speculative character. It may not be out of place to point here to certain opinions and theories which should be critically evaluated with reference to dimorphism.

1. In works on ammonites the small forms are frequently rated as degenerative or retrogressive. Such definitions are due to the erroneous belief that they arose in each case from normal forms, as the last links of recessive evolutionary side lines (the «end forms» of Spath, 1938). With recognition of the existence of dimorphism and of the extremely conservative laws controlling it, such an explanation of small forms is inadequate and seems a distortion of the biological meaning of their existence. Often small forms, indeed, are pygmies, but their dwarfism represents a fundamental character of an entire group, probably transmitted by whole assemblage of genes. Moreover, the relative dwarfism of the small forms is in particular cases enhanced as a result of the progressive development of gigantism in the large forms. The growth to the large and the small forms was most likely controlled by some hormonal processes. Hence it is supposed that a close analysis of the growth and the associated hormonal processes in recent cephalopods exhibiting such strong sexual dimorphism may prove the only correct clue to a better understanding of this phenomenon in ammonoids. Once the theory of sexual dimorphism has been accepted, speculations suggesting that the small forms have been affected by degeneration, phylogenetic gerontism, processes of iterative evolutions etc., become groundless.

2. Ammonites furnish numerous illustrations for the discussion of parallel evolution and convergence. Doubtless in many cases conjectures on that problem are groundless since the

SYSTEMATIC ARRANGEMENT OF GENERA AND TYPES OF DIMORPHISM

TRAITÉ DE PALÉONTOLOGIE

E. Basse, 1952

	Type of dimorphism
Superfamily STEPHANOCERATACEAE	
Family Stephanoceratidae	
Cadomites	B
Family Otoitidae	
Otoites	B
Family Sphaeroceratidae	
Sphaeroceras	B
Family Tulitidae	
Bullatimorphites	B
Family Macrocephalidae	
Macrocephalites	A
Family Cosmoceratidae	
Cosmoceras	A
Kepplerites	A
Family Cardioceratidae	
Cadoceras	A
Quenstedtoceras	A
Pachyceras	B
Cardioceras	A
Superfamily PERISPHINCTACEAE	
Family Perisphinctidae	
Leptosphinctes	B
Perisphinctes	B
Ataxioceras	B
Proplanulites	B
Virgatites	B
Family Parkinsonidae	
Parkinsonia	B
Garantiana	A
Family Morphoceratidae	
Morphoceras	B
Oecoptychius	B
Reineckeia	B
Family Aspidoceratidae	
Peltoceras	B
Aspidoceras	B
Family Craspeditidae	
Craspedites	B
Kashpurites	B

TREATISE ON INVERTEBRATE PALEONTOLOGY Part L

W. J. Arkell, B. Kummel & C. W. Wright, 1957

	Type of dimorphism
Superfamily STEPHANOCERATACEAE	
Family Otoitidae	
Otoites	B
Family Stephanoceratidae	
Cadomites	B
Family Sphaeroceratidae	
Sphaeroceras	B
Family Tulitidae	
Bullatimorphites	B
Family Macrocephalidae	
Macrocephalites	A
Family Oecoptychiidae	
Oecoptychius	B
Family Pachyceratidae	
Pachyceras	B
Family Cosmoceratidae	
Kepplerites	A
Cosmoceras	A
Family Cardioceratidae	
Cadoceras	A
Quenstedtoceras	A
Cardioceras	A
Superfamily PERISPHINCTACEAE	
Family Parkinsonidae	
Parkinsonia	B
Garantiana	A
Family Morphoceratidae	
Morphoceras	B
Family Reineckeidae	
Reineckeia	B
Family Perisphinctidae	
Leptosphinctes	B
Proplanulites	B
Perisphintes	B
Ataxioceras	B
Virgatites	B
Family Aspidoceratidae	
Peltoceras	B
Peltoceratoides	B
Euaspidoceras	B
Family Craspeditidae	
Craspedites	B
Kashpurites	B

OSNOVY PALEONTOLOGII

G. J. Krimholc, N. T. Sazonov et al., 1958

	Type of dimorphism
Superfamily STEPHANOCERATACEAE	
Family Sphaeroceratidae	
Sphaeroceras	B
Otoites	B
Bullatimorphites	B
Family Macrocephalidae	
Macrocephalites	A
Family Pachyceratidae	
Pachyceras	B
Family Cardioceratidae	
Cadoceras	A
Quenstedtoceras	A
Cardioceras	A

G. J. Krimholc, V. G. Kamyševa-Elpatevskaja et al., 1958

	Type of dimorphism
Superfamily COSMOCERATACEAE	
Family Parkinsonidae	
Parkinsonia	B
Family Cosmoceratidae	
Garantiana	A
Kepplerites	A
Cosmoceras	A
Family Reineckeidae	
Reineckeia	B
Family Morphoceratidae	
Morphoceras	B
Oecoptychius	B

N. G. Chimšiašvili, V. G. Kamyševa-Elpatevskaja et al., 1958

	Type of dimorphism
Superfamily PERISPHINCTACEAE	
Family Perisphinctidae	
Leptosphinctes	B
Perisphinctes	B
Proplanulites	B
Ataxioceras	B
Virgatites	B
Family Aspidoceratidae	
Peltoceras	B
Aspidoceras	B
Craspedites	B
Kashpurites	B

examples quoted actually refer to phenomena of dimorphism. Nevertheless the recognition of the theory of dimorphism does not in the least diminish the importance of parallel evolution in ammonite history, on the contrary, it is constantly growing. The main issue here is that the separation of certain allied phylogenetic lineages is shifted by the method of the reconstruction of phylogenetic relations into a past far more distant than has so far been supposed. It has already been shown here that in the important branch of the Perisphinctaceae the evolution of sculpture strongly resembles, and the evolution of the suture is nearly identical with that noted in forms from the stock of Litoceratinae. This occurs to such an extent that suggestions have been advanced regarding the Lower Dogger origin of the Perisphinctaceae from groups derived from the Litoceratinae, while dimorphism only indicates their very distant connection with that shoot. Should these suggestions be confirmed by future investigations, the importance of the phenomena here studied will increase accordingly. As has, however, been stated, the small forms have some features of their own not encountered in large forms. Some of them, e. g. the aperture with lateral lappets, appear in various phylogenetic lines. Regardless of the biological function ascribed to this apertural type, this character must be recognized as having evolved in connection with that part of the animal's genetic constitution strictly associated with sex.

3. It has often been asserted that certain processes known as isomorphism or homeomorphism can sometimes be so strong that forms affected by them have been included within one genus or family, although their origin was actually quite different. Now, these processes may be used as evidence of either apparent relationships, as in parallel evolution and convergence, or apparent polyphyletism, thus masking the actual phylogenetic relations in ammonites as much as in other groups of animals. An analysis of the particular examples of homeomorphism, with special reference to dimorphism and the establishment of characters associated with one or other sex, would be most interesting. The morphological characters connected with sex and their respective value in systematics could thus be determined.

4. In a paper dealing with the significance in systematics of parabolic nodes in the genus *Perisphinctes* (s. l.) Teisseyre (1889) introduced the concept of tachygerontic (rapid ageing) and bradygerontic (slow ageing) forms. The bradygerontic forms are claimed to attain huge dimensions, while the tachygerontic forms derived from them by way of mutation are one third the size. The writer had an opportunity of examining some of Teisseyre's specimens housed in the Museum of the Polish Academy of Sciences in Cracow, and some topotype material from the same beds in the Cracow Jurassic Uplands. From this material it was possible to ascertain that tachygerontic, i. e. rapidly ageing forms, are nothing else but the small forms in which the aperture is provided with lappets, while the bradygerontic forms represent those of larger dimensions with a simple aperture.

A number of other authors have advanced similar theories. The tachymorphism and bradymorphism discussed by Schmidt (1935) in relation to differences of umbilical width in specimens of *Reticuloceras reticulatum* having the same diameter, probably also are expressions of sexual dimorphism.

BIOMETRIC METHODS

Practically every one of the more comprehensive works on ammonite systematics contains certain statistical data from biometric analysis. A few remarks will, therefore, be here devoted to that subject.

Biometric studies may prove very helpful in analysing the lower systematic units (species, subspecies, variety), although they obviously cannot fully explore the subject. In using biometric methods for the detection of a biological phenomenon they must be so appropriately chosen that, to a certain extent, they envisage the phenomenon itself. Knowledge of certain biological facts acquired in this fashion may, in turn, contribute to the improvement of the biometric methods. It should be noted that objective numerical values (dimensions) worked out by a certain recognized method invariably produce a numerical result. It does not follow, however, that the obtained result always represents a biological reality.

Some examples are analysed here. For example, if the required measurements are made of a collection of *Tornoceras simplex* (Buch), up to 3 cm in diameter, and the height of whorl to the diameter ratio during ontogeny is computed, a result will be obtained expressed by a curve, which however does not coincide with the line of development of any one specimen.

Wenger (1957) states that species of the genus *Ceratites*, described by him, have from $6^1/_2$ to $8^1/_2$ whorls [3]. This assertion is only formally correct, since actually we are dealing with two groups of forms: one with 6 whorls, the other with 7 to 8 whorls, separated by the morphological hiatus of one whorl.

It is known that within the one species *Sphaeroceras brongniarti* (Sow.) there are included large and small forms separated by a morphological hiatus of one whorl. As a result the two forms, owing to differences in the diameter of the shell, constitute two quite separate groups. Accordingly, if we work out the mean diameter for a group of conspecific specimens, consisting of large and small forms in approximately even numbers, the mean diameter figure will occur within the morphological hiatus and not correspond to any existing biological reality.

Hence the dimorphism studied here should be taken into consideration in biometric studies of the ammonites.

THE APTYCHI

If the aptychi are really ammonoid opercula, they may also be expected to display sexual dimorphism. From the description of dimorphism given here it is seen that up to a certain stage or size the section of the shell of both forms develops according to the same pattern. Subsequently they are differentiated according to constant rules. On the surface of the aptychi the growth striae are readily discernible; they record the development of their shape and reproduce the outline of the shell section.

Therefore, if two groups of forms can be distinguished within an assemblage of aptychi from one bed, differing merely in size and development of outline, as the sections of shells of supposedly different sex, this would be a reliable hint to their systematic position.

According to certain authors, it may be supposed that some small ammonite forms had no aptychi, since opercula of this kind could not function in view of the shape of the aperture, e. g. in the case of incurved lappets. On the other hand, in the corresponding large forms, with simple aperture, the functioning of this kind of operculum is not handicapped. Nevertheless, aptychi have sometimes been assigned to forms with extremely big apertural extensions, e. g. *Normannites* and *Germanites* (Westermann, 1954).

[3] Wenger counts the number of whorls in a different way from that accepted by the writer and as a result there is a difference of half a whorl.

SYSTEMATIC PART

GENERAL REMARKS

The recognition of sexual dimorphism in ammonites necessitates the elaboration of new diagnoses of genera, families and higher taxonomic units. The different morphological features of dimorphism vary in importance depending on the taxonomic level being diagnosed. It is supposed that the types of dimorphism described above have a high systematic rank, while other features, such as shape of aperture, can characterize families and genera. The elaboration of new diagnoses calls for uniformity and for appropriate estimation of the rank of the taxonomic value of each particular character. This task is closely connected with the previously discussed revision of phylogenetic relations based on the highly conservative phenomenon of dimorphism and the two problems relating to systematics and phylogeny must be considered together.

Nevertheless the elaboration of new diagnoses, even for some families only, would still be premature and should be delayed until the significance of the above described types of dimorphism for phylogenetic systematics has been finally determined. This may be achieved through investigation of the distribution and evolution of the various characters concerned in dimorphism.

Below are given new generic diagnoses. Such diagnoses should naturally be regarded as only tentative. The morphological details of dimorphism embraced by them may not only bear generic significance, but also characterize the higher taxonomic units.

As far as possible the most up-to-date publications are referred to in the synonymics. Most of the species given here are well known and have frequently been described, hence only brief synonymics are given now, supplemented by some data concerning dimorphism.

EXAMPLES OF TYPE «A» DIMORPHISM

MESOZOIC AMMONITES

Genus **KEPPLERITES** NEUMAYR & UHLIG, 1892

New diagnosis. — Sexual dimorphism strong. Females attain at least 7 whorls and have a simple aperture. On the young whorls the ornamentation consists of straight ribs, 2 or 3 of them joining on the flanks of whorls. On mature whorls numerous ribs assemble in bundles with one primary thick rib, running from each bundle to the umbilical seam. Males halt at the 6 whorls stage and have an aperture with small lappets.

Kepplerites gowerianus (SOWERBY, 1826)

(text-pl. I, fig. 1, 2)

1883. *Cosmoceras Gowerianus* SOWERBY; I. LAHUSEN, Fauna..., pl. 6, fig. 5-7 (♀), fig. 8 (♂?).
1929b. *Kosmoceras (Kepplerites) hexagonum* LOEWE; R. BRINKMANN, Monographie..., p. 24-29, 35-36, pl. 1, fig. 1 a-b, 2-4 (♂).

A detailed description of this species is given by BRINKMANN (1929*b*) on the pages quoted above. Data from the literature confirmed by the writer's observations indicate that the male forms are very rare.

Genus **COSMOCERAS** WAAGEN, 1869

New diagnosis. — Sexual dimorphism strong. Females attain at least 7 whorls. Ornamentation consists of numerous straight ribs converging at the lateral tubercles from which one well pronounced primary rib runs to the umbilical seam. Ventral side flattened. Tubercles present on the ventro-lateral margin. Aperture simple. Males have 6 whorls and an aperture with a large lappet.

Cosmoceras pollucinum TEISSEYRE, 1884

(pl. I)

1884. *Cosmoceras pollucinum* n. sp.; L. TEISSEYRE, Ein Beitrag..., p. 579, pl. 4, fig. 31 a-b; pl. 5, fig. 30 a-b (♀♀).
1915. *Cosmoceras Pollux* REINECKE var. β; E. KRENKEL, Die Kelloway-Fauna..., p. 270, pl. 22, fig. 4 (♂).

Descriptions are given by the above named authors and by BRINKMANN (1929*b*, p. 67-70 and 87-90). The sex ratio seems to be about 1 : 1.

Cosmoceras duncani (SOWERBY, 1817)

(pl. II)

1952. *Cosmoceras (Cosmoceras) duncani* (SOWERBY); H. MAKOWSKI, La faune callovienne..., p. 36-37, pl. 3, fig. 8, 8a; pl. 4, fig. 13 (♀♀).
1952. *Cosmoceras (Spinicosmoceras) arkelli* n. sp.; H. MAKOWSKI, *Ibid.*, p. 40-41, pl. 4, fig. 10, 10a, 11 (♂♂).

A description of this form is given by the above named author and by BRINKMANN (1929*b*, p. 90-94). The writer's observations during collection at Łuków suggest a nearly even sex ratio (16 ♀♀, 13 ♂♂).

Cosmoceras spinosum (SOWERBY, 1826)

(pl. II, fig. 3; pl. III-V; text-pl. I, fig. 3, 4)

1952. *Cosmoceras (Cosmoceras) spinosum* (SOWERBY); H. MAKOWSKI, La faune callovienne..., p. 35, pl. 3, fig. 5-7 (♀♀).
1952. *Cosmoceras (Spinicosmoceras) annulatum* (QUENSTEDT); H. MAKOWSKI, *Ibid.*, p. 38-39, fig. 2-8 (♂♂).

This form has been described in the paper quoted and by BRINKMANN (1929*b*, p. 102-106.) Over a period of some years the writer has collected numerous specimens of this species indicating a nearly even sex ratio (43 ♀♀, 36 ♂♂).

Genus **HECTICOCERAS** BONARELLI, 1893

New diagnosis. — Sexual dimorphism expressed mainly by size of shell and by shape of aperture. The females have 7 or more whorls; occasionally they halt at the $6^1/_2$ whorls-stage, and then the shape of the aperture approaches that of the growing margin, while in specimens attaining 7 or more whorls it is simple. The males have 6 whorls and an aperture with lappets. Ornament consists of falcate ribs and, occasionally, lateral tubercles.

Hecticoceras lunuloides KILIAN, 1889

(pl. VI, fig. 3 *a*, *b*, fig. 4 *a-c*)

1951. *Lunuloceras lunuloides* KILIAN; A. JEANNET, Stratigraphie u. Paläontologie..., p. 58-59, pl. 13, fig. 3 (♂), fig. 4-6 (♀♀); pl. 12, fig. 10-11 (♀♀?).

A detailed description of this species is given in the above mentioned work and in a paper by LEMOINE (1932, p. 360-376). The writer's findings from the Jurassic Cracow-Częstochowa Uplands and from Łuków reasonably suggest a marked predominance of the females.

Hecticoceras paulowi TSYTOVITCH, 1911

(text-pl. II, fig. 1, 2)

1886. *Ammonites hecticus* REINECKE; A. J. ZAKRZEWSKI, Die Grenzschichten..., p. 31, pl. 1, fig. 6 (♂).
1951. *Orbignyceras paulowi* TSYTOVITCH; A. JEANNET, Stratigraphie u. Paläontologie..., p. 45-47, pl. 9, fig. 12-16; pl. 10, fig. 1-2; pl. 16, fig. 1; pl. 21, fig. 10 (♀♀).

An accurate description of the female forms is given in JEANNET's work (1951). ZAKRZEWSKI's figure represents a male form with a complete aperture. The males are probably extremely rare.

Hecticoceras ferrugineus SPATH, 1928

(pl. VI, fig. 1 *a-e*, fig. 2 *a-d*)

1951. *Kheraites ferrugineus* SPATH; A. JEANNET, Stratigraphie u. Paläontologie..., p. 51, pl. 11, fig. 5-7 (♀♀).

An exhaustive description of this species, contained in the above cited paper by JEANNET, refers to females only. In the available literature the writer was not able to find a figure that could be interpreted as a male. Males are probably extremely rare.

Genus **LISSOCERATOIDES** SPATH, 1923

New diagnosis. — Sexual dimorphism expressed mainly by size of shell and by shape of aperture. The females attain at least 7 whorls and have a simple aperture. The males halt at the 5-6 whorls-stage. The male aperture is pro /ided with strong lateral lappets. The umbilicus is narrow, open. The shell smooth.

Lissoceratoides erato (D'ORBIGNY, 1850)

(text-pl. II, fig. 3-5)

1951. *Lissoceratoides erato* (D'ORBIGNY); A. JEANNET, Stratigraphie u. Paläontologie..., p. 103-104, pl. 31, fig. 6 (♀).
1958. *Glochiceras (Coryceras) cornutum* n. sp.; B. ZIEGLER, Monographie..., p. 117-120, pl. 11, fig. 5-10 (♂♂).

The above named papers contain detailed descriptions of this species. Data from the literature and the writer's own observations indicate that the males predominate. The female/male sex ratio of specimens from the Jurassic Cracow-Częstochowa Uplands is 1 : 2 (19 ♀♀, 40 ♂♂).

It should be noted that the interpretation of the male form recognized here is but one among several reasonably probable ones since various male forms with smooth whorls occur in the same beds. ZIEGLER (1958) assigns to the genus *Glochiceras (Coryceras)* forms characterized by strong denticles on the ventral side of the last body chamber, but which are usually referred to the genus *Creniceras* (e. g. *Creniceras crenatum* (OPPEL)). These forms should also be taken into consideration in discussing the male forms of the species *Lissoceratoides erato* (D'ORB.). Because of these doubts the generic name *Lissoceratoides* is retained here for this species, although the name *Glochiceras* has the priority.

Genus **TARAMELLICERAS** DEL CAMPANA, 1904

New diagnosis. — Sexual dimorphism either strong or insignificant. The females have 7 or more (?) whorls and occasionally display the scaphitoidal type. Ornament consists of falcate ribs. The males halt at the 5-6 whorls-stage. The aperture is identical in both sexes. It is characterized by the presence of a keel on the venter and of a serrate ridge near the umbilicus. The umbilicus is narrow or completely closed.

Taramelliceras minax (BUKOWSKI, 1886)

(text-pl. III, fig. 1-3)

1887. *Oppelia minax* n. sp.; G. BUKOWSKI, Über die Jurabildungen..., p. 105-108, pl. 25, fig. 1 a-c (♀).
1951. *Popanites paturattensis* (GREPPIN); A. JEANNET, Stratigraphie u. Paläontologie..., p. 102-103, pl. 30, fig. 9; pl. 31, fig. 12-15 (♂♂).

Detailed descriptions of this species are contained in the works quoted above. Females with preserved aperture, however, had not been recorded previously. The aperture here is characterized by the presence on the venter of a keel, extending as a short lip, and of a short denticulate extension near the umbilical edge. This kind of aperture has been observed previously in other representatives of the genus *Taramelliceras*. Males with apertures of the same type as the female are also known from the literature. Within the Jurassic Cracow-Częstochowa Uplands males predominate distinctly (7 ♀♀, 14 ♂♂).

Genus **CRENICERAS** MUNIER-CHALMAS, 1892

New diagnosis. — Males belonging to the family Oppeliidae have 5-6 whorls and an aperture with lappets. Strong denticles on the last body chamber. No female forms have been identified.

Creniceras renggeri (OPPEL, 1862)

(text-pl. II, fig. 6, 7)

1939. *Creniceras renggeri* (OPPEL); W. J. ARKELL, The ammonite succession..., p. 150-151, pl. 9, fig. 15-17 (♂♂).

The male forms abound in the Lower Oxfordian deposits of the Jurassic Cracow-Częstochowa Uplands.

Genus **LEIOCERAS** HYATT, 1867

New diagnosis. — Sexual dimorphism expressed by size of shell and by shape of aperture. The female forms have 7 whorls and a simple aperture. The male forms halt at the 6 whorls-stage (5-6 whorls?) and have an aperture with lappets. Ornament consists of falcate, strongly pronounced growth striae or faint ribbing.

Leioceras opalinum (REINECKE, 1818)

(text-pl. III, fig. 4, 5)

1886-87. *Ammonites opalinus* REINECKE; A. QUENSTEDT, Die Ammoniten..., p. 610-611, pl. 55, fig. 10 (♀), fig. 1-4, 13, 16 (♂♂).

The meagre information obtainable from the literature suggests the predominance of males.

Genus **GARANTIANA** MASCKE, 1907

New diagnosis. — Sexual dimorphism strong. Female forms reach at least 7 whorls with a simple aperture. Ornament consists of strongly pronounced ribs, forking at midlength of whorl. On the venter the ribs are discontinued. The male forms have 6 whorls, the aperture is provided with lappets.

Garantiana garantiana (D'ORBIGNY, 1846)

(text-pl. IV, fig. 1, 2)

1924. *Garantia Garanti* D'ORBIGNY; A. BENTZ, Die Garantienschichten..., p. 152-154, pl. 5, fig. 1 (♀).
1924. *Garantia minima* WETZEL; A. BENTZ, *Ibid.*, p. 171-172, pl. 7, fig. 8-9 (♂♂).

A detailed description of this species is given in the above mentioned work. From the literature and from his own observations the writer supposes that the male forms are less frequent than the females.

Genus SCAPHITES PARKINSON, 1811

New diagnosis. — Sexual dimorphism expressed mainly by size. The body chamber partly or completely unrolled. Ornament consists of falcate, somewhat irregularly running ribs. Aperture simple, constricted. Females have 7 whorls, the males have 5-6 (?) whorls. Umbilicus closed.

Scaphites constrictus (SOWERBY, 1817)

(text-pl. IV, fig. 3, 4)

1951. *Discoscaphites constrictus* (SOWERBY); N. P. MICHAJLOV, Verchnemelovye ammonity..., p. 90-92, pl. 17, fig. 77-80 (♀♀).
1951. *Discoscaphites constrictus* var. *niedzwiedzkii* (UHLIG); N. P. MICHAJLOV, *Ibid.*, p. 93-94, pl. 15, fig. 65; pl. 17, fig. 81, 82; pl. 18, fig. 85 (♂♂).

A detailed description of this species is given in the paper of MICHAJLOV mentioned above and in an article by NOWAK (1911). Information from the literature suggests the predominance of females. The sex ratio of specimens collected by the writer over a number of years from the Upper Maestrichtian deposits near Kazimierz on Vistula is 2 : 1 (22 ♀♀, 10 ♂♂).

Genus QUENSTEDTOCERAS HYATT, 1877

New diagnosis. — Sexual dimorphism strong. The females have at least 7 whorls. Ornamentation consists of falcate ribbing; in female forms it vanishes at the 6-7 whorls-stage. The last whorl entirely smooth. The aperture with a hood pushed forward on the venter. The males halt at the ribbed 6 whorls-stage. Their aperture is characterized by the presence of a long lip on the venter.

Ontogeny. — Up to the $5\text{-}5^1/_2$ whorls-stage the ontogenetic stages in the male and female forms are identical. The normal pattern of ribbing is often disturbed after the $5^1/_4$ whorls-stage is attained, the long ribs being discontinued. This disruption of the ribbing pattern commonly affects one quarter of a whorl and occurs at the stage when the male and female shells can first be distinguished from each other.

Females. From the $5^1/_4\text{-}5^1/_2$ whorls-stage on the shell becomes more involute and this character is retained until the middle of the last whorl. Thereafter involution gradually decreases, more markedly so near the aperture. From the 6-7 whorls-stage on, the ribbing gradually dies out. The last whorl is quite smooth, marked by growth striae only. The umbilical seam disappears near the gerontic aperture, then the aperture becomes constricted and develops an elongated hood on the venter. The diameter is up to 105-220 mm.

Males. In the male forms the degree of involution decreases slightly near the gerontic aperture. The whorl section, however, is modified conspicuously, i. e. the last half of the whorl is less thick and slightly less high than the corresponding female stage. The ribs are more strongly curved forward. The ribbing vanishes near the aperture. A long extension (lip), in the form of a gutter opening inwards, is produced on the venter. This extension is often slightly asym-

Fig. 11
Posterior parts of the living chambers in small forms from the genus *Quenstedtoceras*. Internal moulds. Muscle scars in form of nodules, and extinction of ribbing due to internal thickenings of the shell. Callovian, Łuków; × 2

metrical. The shell wall at the base of the last body chamber becomes thickened, particularly around the muscle scars near the umbilical seam. On the muscle scars the shell wall does not thicken, so that the muscle scars are discernible as well-marked pits or corresponding nodes in moulds (fig. 11). The male shell ranges from 24 to 65 mm in diameter. Up to the $5^1/_2$ whorls-stage the development of the suture is identical in both sexes. The number of septa ranges from 65 to 85 in females, while in males it is from 40 to 55. Accordingly, the last septa in female forms are markedly more differentiated than those in the male specimens. On data from the literature and from the writer's observations of the Łuków specimens it is reasonably concluded that most of the individuals of the genus *Quenstedtoceras* must have perished during the early stages of ontogeny. From specimens of the various *Quenstedtoceras* species obtained from Łuków, where they are very abundant and where most specimens have the body chamber preserved, the writer was able to calculate that adults constitute not more than 0.0001 per cent. Out of the total number observed, the majority had perished before reaching the $5^1/_2$ whorls-stage. Hence it may be inferred that this was the critical stage during the development of these forms. It is the very stage during which sexual differentiation of the shell occurs.

Evolution of the genus Quenstedtoceras. — The writer's description of the genus *Quenstedtoceras* is based on the Łuków material collected from the dump, and on that from the Cracow

Jurassic Uplands. In the last named area, beds yielding representatives of the genus *Quenstedtoceras* are extremely thin (10-30 cm) so that the stratigraphic sequence of species occurring there cannot be accurately established. Moreover, the higher evolutionary links of the genus *Quenstedtoceras* are missing at Łuków. Hence only a very rough sketch of the evolutionary process can be attempted on the writer's own material. In the first place it will be concerned with the pattern of ribbing.

In forms displaying the simplest morphology, one secondary rib occurs between two primary ribs, or else, a pair of primaries separated from the next primary by one secondary. The primary pairs occur either regularly or sporadically, at very varied rates of frequency. In morphologically higher forms two secondaries are present between two primaries, while three or even four secondaries may be observed between two primaries in forms that have reached the highest degree of evolution. The sequence of this evolutionary pattern is such that the new scheme of ribbing appears at the close of the preceding ribbing stage, and passes on to the early ontogenetic stages of the next. As a result the different ribbing patterns may be observed on the same specimen. The Łuków material contains specimens of flat forms on which two secondary ribs intervene between two primaries, but there are no forms of higher evolutionary stage. In the Jurassic Cracow Uplands, on the contrary, forms have been encountered with three or even four secondary ribs occurring between two primaries. Two or three secondaries may occur side by side either according to a regular pattern, or else sporadically, and this handicaps the separation of systematic units based on the above described scheme of ribbing.

The systematics of the genus *Quenstedtoceras* is extremely intricate since the majority of species have been described on young individuals which it is often impossible to compare with adult specimens. Moreover the meaning of large and small forms had not previously been properly taken into consideration.

Quenstedtocera henrici R. Douvillé, 1912

(pl. VII-XII; text-pl. V)

1912. *Quenstedticeras Henrici* n. sp.; R. Douvillé, Etudes, p. 55-56, pl. 4, fig. 24-31 (juv.), fig. 32-33 (♀♀)
1912. *Quenstedticeras Henrici* var. *Brasili* n. var.; R. Douvillé, *Ibid.*, p. 56-57, pl. 4, fig. 1-8 (juv.), fig. 9 (♀)
1939. *Quenstedtoceras (?Quenstedtoceras)* cf. *macrum* (Quenst.); W. J. Arkell, The ammonite succession... p. 169 (♂).

Ornament characterized by the presence of one secondary rib between two primaries. The side by side occurrence of two primary ribs is either regular or sporadic.

In the writer's collection from Łuków the sex ratio is 1 : 3 (82 ♀♀, 230 ♂♂).

Quenstedtoceras praelamberti R. Douvillé, 1912

(pl. XVII; text-fig. 12)

1912. *Quenstedticeras Henrici* var. *praelamberti* R. Douvillé; R. Douvillé, Etudes..., p. 57-58, pl. 4, fig. 34-38 (juv.).

Ornament characterized by the presence of two secondary ribs between two primaries. The writer is in possession of 3 females and 7 males found at Łuków.

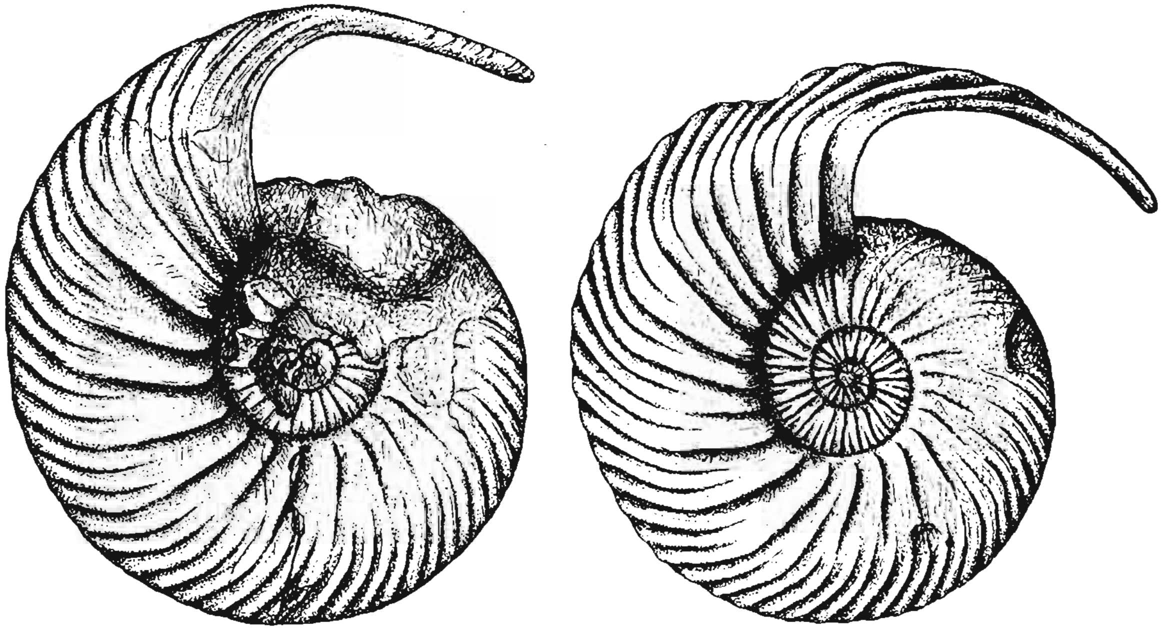


Fig. 12
Quenstedtoceras praelamberti R. DOUV., males with completely preserved apertures. Callovian, Łuków; × 1.5

Quenstedtoceras lamberti (SOWERBY, 1819)

(pl. XX, fig. 4 *a-c*, 5)

1912. *Quenstedticeras Lamberti* SOWERBY; R. DOUVILLÉ, Etudes..., p. 58-62, pl. 4, fig. 39-48 (juv.).

Ornament characterized by the presence of three or four secondary ribs between two primaries.

8 female and 3 male specimens have been collected by the writer at Krzeszowice, Czatkowice and Racławice in the Cracow Jurassic Uplands.

Quenstedtoceras mariae (D'ORBIGNY, 1848)

(pl. XIII-XVI; text-fig. 13)

1952. *Quenstedtoceras (Quenstedtoceras) mariae* (D'ORBIGNY); H. MAKOWSKI, La faune callovienne..., p. 29, pl. 7, fig. 1, 1a, 2, 2a (♂♂).
1952. *Quenstedtoceras (Bourkelamberticeras) rybinskianum* (NIKITIN); H. MAKOWSKI, *Ibid.*, p. 30, pl. 6, fig. 4, 4a, b (♀).

Ornament consists either of single primary ribs and secondaries, or of regularly occurring pairs of primaries.

11 female and about 20 male specimens have been found at Łuków. The sex ratio is thus 1 : 2.

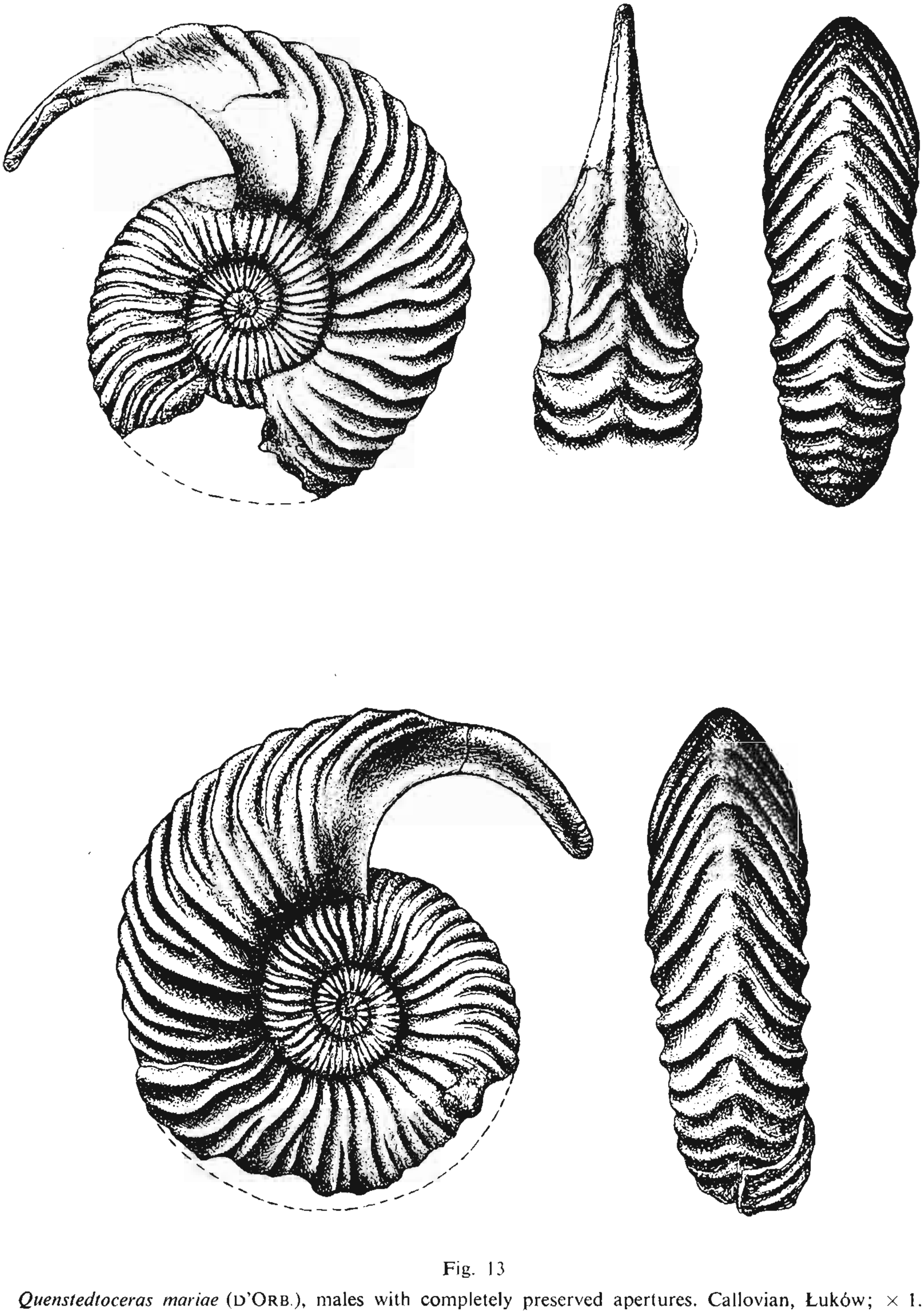


Fig. 13

Quenstedtoceras mariae (D'ORB.), males with completely preserved apertures. Callovian, Łuków; × 1.5

Quenstedtoceras vertumnum (LECKENBY, 1859)

(pl. XVIII, XIX; XX, fig. 1 *a-e*, 2 *a-b*, 3; text-pl. VI; text-fig. 14)

1952. *Quenstedtoceras (Quenstedtoceras) vertumnum* (LECKENBY); H. MAKOWSKI, La faune callovienne..., p. 29, pl. 3, fig. 2, 2a (♂).
1952. *Quenstedtoceras (Bourkelamberticeras) carinatum* (EICHWALD); H. MAKOWSKI, *Ibid.*, pl. 7, fig. 3, 3a-b((♀).

Pattern of sculpture as in *Quenstedtoceras mariae* (D'ORB.). The specimens collected at Łuków represented 40 female and 40 male specimens, so that the sex ratio is exactly 1 : 1.

Genus **CADOCERAS** FISCHER, 1882

New diagnosis. — Sexual dimorphism strong. The females have at least 7 whorls. Ornamentation consists of arched ribs, disappearing in the 6-7 whorls-stage. The last whorl is perfectly smooth. The aperture in the shape of an elongated hood on the venter, extending forward. The living chamber occupies three fourths of a whorl. The umbilicus is funnel-like. The males halt at the 6 whorls ribbed stage and have an aperture with lip-like extension on the venter.

Cadoceras tschefkini (D'ORBIGNY, 1845)

(text-pl. VII)

1952. *Cadoceras tschefkini* (D'ORBIGNY); H. MAKOWSKI, La faune callovienne..., p. 27-28, pl. 7, fig. 4, 4a-b (♀).
1952. *Cadoceras nikitinianum* (LAHUSEN); H. MAKOWSKI, *Ibid.*, p. 26-27, pl. 3, fig. 1; pl. 6, fig. 1-3 (♂♂).

In this species ornament distinctly resembles that in some species of the genus *Quenstedtoceras*, two or three secondary ribs occurring between two primaries. Three female and eight male specimens have been found at Łuków. As far as may be judged from the literature, male individuals are in other areas extremely scarce, e. g. in the Jurassic of Russia.

GONIATITES

Genus **TORNOCERAS** HYATT, 1884

New diagnosis. — Shell completely or almost completely involute. Growth lines form a sinus on the flanks of whorls. Sexual dimorphism pronounced or weak, expressed by size only. The females attain 7 whorls, the males 5-6 whorls.

Tornoceras simplex (BUCH, 1832)

(text-pl. VIII)

1899. *Tornoceras simplex* BUCH; E. HOLZAPFEL, Die Cephalopoden..., p. 14-15, pl. 8, fig. 1-6 (juv.), 7 (♀?), 8 (♀).

Females commonly halt at the stage just above 6 whorls being then 65-70 mm in diameter. Specimens that attain 7 whorls are about 140 mm in diameter. The males rarely reach the 6 whorls-stage. They range from 25 to 45 mm in diameter. The sex ratio ranges from 1 : 4 to 1 : 10.

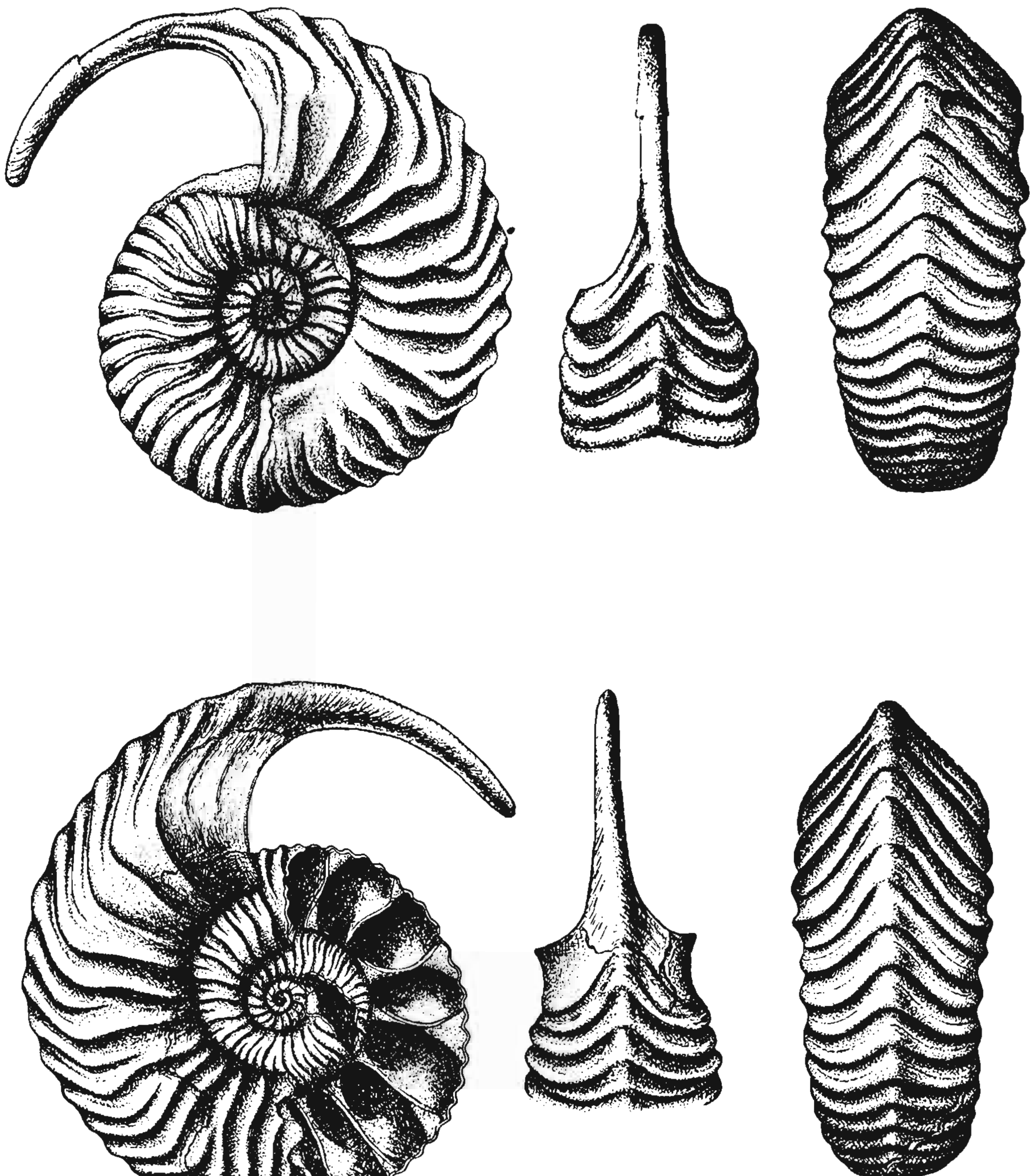


Fig. 14
Quenstedtoceras vertumnum LECK., males with completely preserved apertures. Callovian, Łuków; × 2.

Genus **CHEILOCERAS** Frech, 1897

New diagnosis. — On flanks of whorls the growth lines run nearly straight, curving gently forward in an arch. Shell completely involute, umbilicus closed. There are 1-5 labial swellings on each whorl. Sexual dimorphism weak, expressed in size only. The females attain the 7 whorls-stage, the males have 5-6 whorls.

Cheiloceras subpartitum (Münster, 1839)

(text-pl. X, fig. *A*)

1902. *Cheiloceras subpartitum* Münster; F. Frech, Über devonische Ammoneen, p. 69, pl. 3, fig. 1 a-c (juv.?).
1914. *Oma-monomeroceras (Cheiloceras) subpartitum lativaricatum* n. nom.; D. Sobolew, Skizzen..., p. 36, pl. 3, fig. 5 (♂).
1914. *Oma-monomeroceras (Cheiloceras) subpartitum angustivaricatum* n. nom.; D. Sobolew, *Ibid.*, p. 37, pl. 3, fig. 6 (♂).

Female specimens very rare and probably as a rule not attaining the 7 whorls-stage. Those that have 7 whorls are up to 70 mm in diameter. The males range from 19 to 30 mm in diameter. Near the gerontic aperture the labial swellings become more crowded in both forms. The numerical ratio of the females to the males is about 1 : 7 (7 ♀♀, 46 ♂♂).

Genus **MANTICOCERAS** Hyatt, 1884

New diagnosis. — Lateral saddle very high. Ventral lobe divided by a secondary saddle. Umbilicus narrow, open. Sexual dimorphism commonly rather strong but expressed by size only. The females attain considerable dimensions. The males halt at the 6 whorls-stage.

Manticoceras intumescens (Beyrich, 1837)

(text-pl. IX)

1899. *Manticoceras intumescens* Beyrich; E. Holzapfel, Die Cephalopoden..., p. 21-23, pl. 1, fig. 1-3, 9 (juv.); pl. 2, fig. 1 (♀), 5 (juv.).
1899. *Manticoceras ammon* (Keyserling); E. Holzapfel, *Ibid.*, p. 23-25, pl. 1, fig. 4-7 (juv.), 8, 10 (♂♂).

Females probably seldom reach the 7 whorls-stage, those that do are about 20 cm in diameter. Some males perhaps halt at the 5 whorls-stage, those that attain the 6 whorls-stage are about 70 mm in diameter. Data from the literature and from the writer's own observations suggest an almost equal numerical ratio of the two sexes.

EXAMPLES OF TYPE «B» DIMORPHISM

MESOZOIC AMMONITES

Genus **SPHAEROCERAS** Bayle, 1878

New diagnosis. — Sexual dimorphism weak and expressed by size of the shell only. The females have 8 (or more?) whorls, the males 7 at the most. Shell spherical, strongly involute, umbilicus closed. Aperture simple, constricted. Ornamentation consists of fine ribs converging into bundles near the umbilical seam.

Sphaeroceras brongniarti (Sowerby, 1818)

(text-pl. XI, fig. 1, 2)

1952-54. *Sphaeroceras brongniarti* (Sowerby); W. J. Arkell, The English Bathonian..., p. 76-77, text-fig. 20, 1 (♀), 2 (♂).
1956. *Sphaeroceras brongniarti* (Sowerby); G. Westermann, Monographie..., p. 28-34, pl. 14, 1, 2, 4, 6-7 (♂♂), 3 (♀?).

An exhaustive description together with a discussion of other problems concerning this species are given by Westermann (1958). Data from the literature indicate the preponderance of males. In the Jurassic Cracow Uplands the sex ratio is 1 : 2 (9 ♀♀, 22 ♂♂).

Genus **CHONDROCERAS** Mascke, 1907

New diagnosis. — Sexual dimorphism weak and expressed by size of the shell only. The females have 8 whorls (or more ?), the males 7 whorls at the most. The shell is globose, strongly involute, the umbilicus narrow. The aperture simple, constricted. Ornamentation consists of fine ribs converging into bundles near the umbilical seam.

Chondroceras wrighti Buckman, 1923

(text-pl. XII, fig. 1, 2)

1956. *Chondroceras (Chondroceras) wrighti wrighti* Buckman; G. Westermann, Monographie..., p. 60-61, pl. 2, fig. 3-4; pl. 3, fig. 1 (♀♀).
1956. *Chondroceras (Chondroceras) wrighti minor* n. subsp.; G. Westermann, *Ibid.*, p. 61, pl. 3, fig. 2-3 (♂♂).

A detailed description of that species together with a discussion of the problems concerning it are given in the above mentioned paper of Westermann. That author's work is based on a collection of 20 specimens found at a number of localities in Western Europe. It contained 14 females and 6 males.

Genus **BULLATIMORPHITES** Buckman, 1921

New diagnosis. — Sexual dimorphism strong. The females attain more than 8 whorls. In the young stages ornamentation consists of fine straight ribs. In the adult stage the ribbing smoothes out and vanishes. The aperture simple, constricted. The umbilicus narrow in the early stages, often closed on reaching maturity. The males halt at the 7 whorls-stage. The aperture is constricted, provided with short broad lappets. The umbilicus narrow.

Bullatimorphites bullatus (d'Orbigny, 1846)

(text-pl. XI, fig. 3, 4)

1958. *Bullatimorphites bullatus* (d'Orbigny); G. Westermann, Ammoniten-Fauna..., p. 64-65, pl. 20, 21; pl. 22, fig. 1-2 (♀♀).
1959. *Sphaeroptychius (Schwandorfia) marginatus* Arkell; R. Enay, Note..., p. 255-257, pl. 7b, fig. 1, 2 (♂♂).

The above mentioned works contain detailed descriptions of this species. The males are probably far rarer than the females.

Genus **CADOMITES** MUNIER-CHALMAS, 1892

New diagnosis. — Sexual dimorphism expressed by size of shell and by shape of aperture. The females have 8 whorls and a simple, slightly constricted aperture. The males reach 7 whorls and are characterized by an aperture with lappets. The ornamentation consists of numerous thin ribs converging at midheight of whorl into a node. One thick rib extends from that node to the umbilical seam. The umbilicus is broad.

Cadomites linguiferus (D'ORBIGNY, 1846)

(text-pl. XII, fig. 3, 4)

1952-54. *Cadomites deslongchampsi* (D'ORBIGNY); W. J. ARKELL, The English Bathonian..., p. 79-80, text-fig. 21, fig. left (♀).
1952. *Polyplectites linguiferus* (D'ORBIGNY); W. J. ARKELL, *Ibid.*, p. 80, text-fig. 21, fig. right (♂).

An accurate description of this species is given in the above mentioned paper of ARKELL. It also gives the synonymics corresponding to the female form. A detailed description of the male form together with full male synonymics are contained in WESTERMANN's paper (1954). The specific name *linguiferus*, applied by D'ORBIGNY (1846) to a male form of this species, has the priority in relation to *deslongchampsi*, applied in the same paper to a female form. According to data in the literature the numerical ratio of the males in relation to the females is probably even.

GONIATITES

Genus «**CHEILOCERAS**» FRECH, 1897

New diagnosis. — Growth lines arching forward on the flanks of whorls. The shell completely involute, the umbilicus closed. Labial swellings common. Sexual dimorphism weak. The females attain at least 8 whorls, the males stop at the 7 whorls-stage.

«**Cheiloceras**» **globosum** (MÜNSTER, 1831)

(text-pl. X, fig. *B*)

1914. *Oma-monomeroceras (Cheiloceras) praeglobosum* n. nom.; D. SOBOLEW, *Ibid.*, p. 42, pl. 4, fig. 3, 4 (♂).
1914. *Oma-monomeroceras (Cheiloceras) globosum* MÜNST.; D. SOBOLEW, Skizzen..., p. 42, pl. 4, fig. 5 (♀).

SOBOLEW (1914) writes that *O. (Cheiloceras) praeglobosum* SOB. occurs within the upper Łagów beds and in the *Clymenia* limestone, while *O. (Cheiloceras) globosum* (MÜNST.) also in the upper Łagów beds and possibly in the *Clymenia* limestone. On his observations the writer has found that the former is encountered more frequently in the upper Łagów beds, the latter in the *Clymenia* limestone, while their stratigraphic range coincides.

These forms are characterized by labial swellings not reaching to the umbilicus. In large forms the swellings occur only on internal whorls, while the last body chamber is without them. In small forms the swellings become crowded on the last body chamber. The females attain a diameter of 50-75 mm, the males — 23-33 mm. The numeral ratio of the females to the males is about 1 : 3.

GENERAL CONCLUSIONS

1. Large and small forms of Palaeozoic and Mesozoic ammonites, whose young whorls are identical, often occur side by side in the same beds. These forms differ not only in size, but also differ markedly in the development of the aperture. In the small forms the aperture is frequently provided with characteristic extensions (lappets) which are absent in the large forms. The simultaneous occurrence of the two different forms is regarded by the writer as a manifestation of sexual dimorphism.

2. Presence in ammonites of gerontic features, characteristic of all Tetrabranchiata, is decisive in determining whether the small forms under consideration are mature individuals, or young specimens of large forms. In the writer's opinion, the increased density of the last sutures, disappearance of some sculptural details and their crowded arrangement, are all gerontic characters.

3. Two types of dimorphism have been observed by the writer among ammonites. In one of them, called type «A», the small forms always have 5-6 whorls, and the large forms at least 7 whorls. The other type, called type «B», is characterized by the presence of 7-9 whorls in the small forms, and at least 8 whorls in the large forms. According to the writer, the number of whorls is the most constant and conservative ammonite character which has persisted throughout the history of this group. Mesozoic ammonites belonging to type «A» descend from the same type of Palaeozoic ammonites, while Mesozoic ammonites of type «B» have Palaeozoic ancestors of type «B».

4. Great significance is attached to the lack of intermediates between large and small forms within one definite type.

5. Considerations on the occurrence of sexual dimorphism in various groups of recent molluscs, particularly in gastropods and cephalopods, lead the writer to the conclusion that the small forms of ammonites most probably represent males, the large ones females.

6. Recognition of sexual dimorphism in ammonites puts their phylogenetic relations in a new light and allows a new classification to be introduced. Major systematic units (superfamilies), based chiefly on the «A» and «B» types of dimorphism, on the whole agree with the hitherto prevailing classification based mainly on the sculpture of the shell.

7. In some cases the types of dimorphism will also permit the systematic assignment of groups so far referred to as *incertae sedis*. Recognition of the concept of sexual dimorphism calls for a revision of the classification of minor systematic units (genera and species), since the conspecific large and small forms differing in sex have, up to now, been assigned to separate species, or even genera.

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II. PALAEONTOLOGICAL INDEX

Systematic names cited only are indicated by *italic*, and names accompanied by description are indicated by roman letters.

Numerals which indicate the page, on which the species is cited only, are standart; numerals, which indicate pages with description, are **bold**.

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PLATES

H. MAKOWSKI: PROBLEM OF SEXUAL DIMORPHISM IN AMMONITES

PLATE I

Fig. 1. Preparations of inner whorls of a female specimen, 11 cm in diameter, consisting of just a little more than 7 whorls.
a-c Preparation of 6 1/2 inner whorls, nat. size.
d-e Preparation of 6 inner whorls, nat. size.
f-g Preparation of 5 1/2 inner whorls, × 2.

Fig. 2. *a* Male specimen, 6 whorls; nat. size.
b-c Preparation of 5 1/2 inner whorls, × 2.


1b


1a


1c


1f


1g


2b


1d


1e


2a


2c

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PLATE II

Page

Cosmoceras duncani (SOWERBY) 69

(Łuków, Callovian)

Fig. 1. *a-c* Female specimen consisting of 7 whorls, nat. size.
d-e Preparation of 6 inner whorls, nat. size.
f Preparation of $5^1/_2$ inner whorls, $\times$ 2.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c Male specimen, $\times$ 2.

Cosmoceras spinosum (SOWERBY) 69

(Łuków, Callovian)

Fig. 3. Male specimen, 6 whorls; $\times$ 2 (see fig. 2 on pl. III).

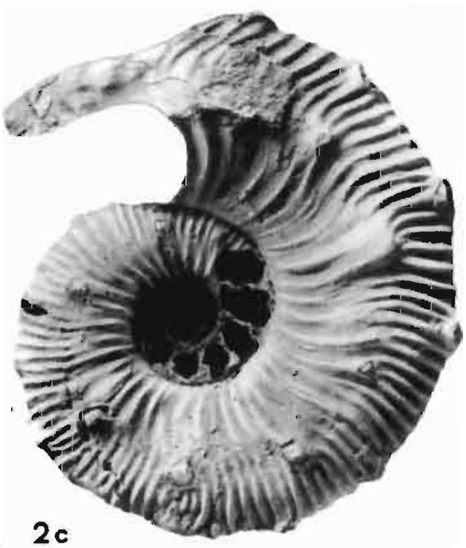
(See also pl. III, IV and V)

2a

1d

1e

1f



2c

2b

3

1a

1b

1c

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PLATE III

Fig. 1. *a-b* Female specimen consisting of 7 whorls, nat. size.
c-d Preparation of 6 inner whorls, nat. size.
e-g Preparation of $5^1/_2$ inner whorls, × 2.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c-d Preparation of $5^1/_2$ inner whorls, × 2.

Fig. 3. Male specimen, 6 whorls; nat. size.

(See also pl. II, IV and V)


2a


2b


2c


2d


3


1e


1f


1g


1a


1d


1c


1b

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PLATE IV

Female specimen consisting of 7³/₄ whorls, nat. size.

(See also pl. II, III and V)

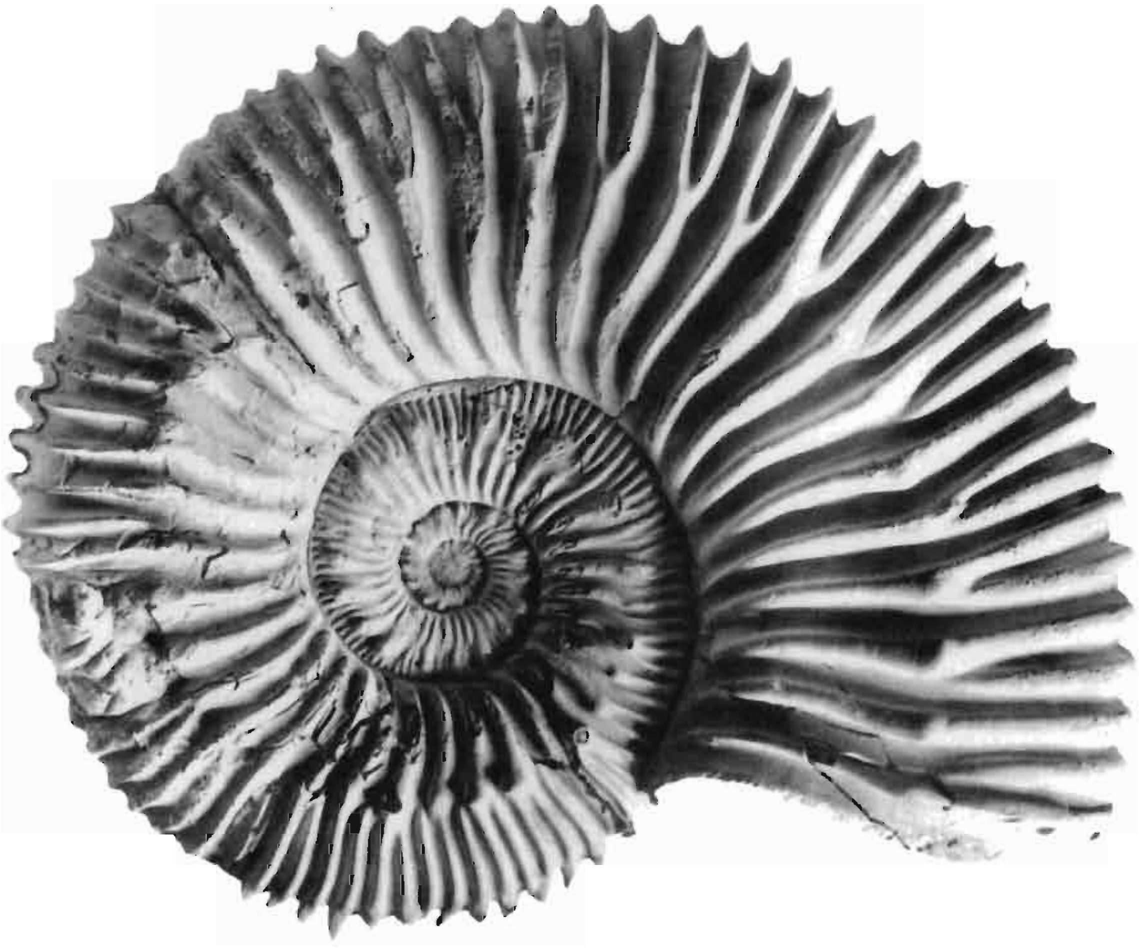

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PLATE V

Fig. 1. *a* Specimen from pl. IV, apertural view; nat. size.
b-c Preparation of 7 inner whorls of the above specimen, nat. size.
d-e Preparation of $5^1/_2$ whorls, × 2.

Fig. 2. Male specimen, 6 whorls; nat. size.

Fig. 3. Male specimen, × 2.

(See also pl. II, III and IV)

1 d

2

1 e

1 a

1 c

1 b

3

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PLATE VI

(Wrzosowa, Callovian)

Fig. 1. *a-b* Female specimen consisting of 7 whorls, nat. size.
c Preparation of 5 inner whorls, nat. size.
d-e Preparation of 5 inner whorls, × 2.
Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c-d Preparation of 5 inner whorls, × 2.

(Łuków, Callovian)

Fig. 3. *a-b* Female specimen consisting of 7 whorls, nat. size.

Fig. 4. *a-b* Male specimen, 6 whorls; nat. size.
c Male specimen, × 2.

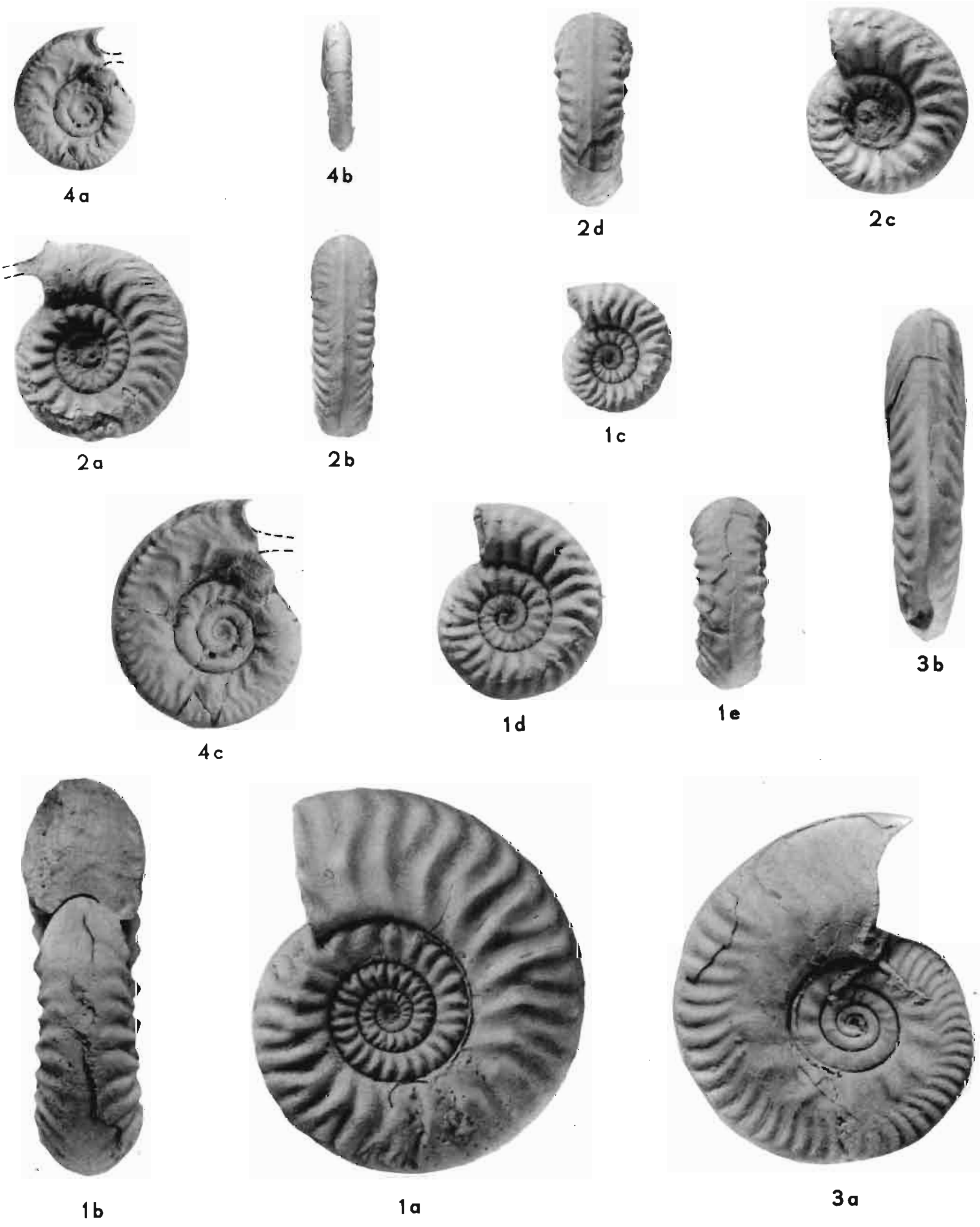

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PLATE VII

(Łuków, Callovian)

Fine-ribbed form

Fig. 1. *a* Female specimen consisting of 8 whorls, nat. size.
b Preparation of 6 inner whorls, nat. size.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.

Fig. 3. *a* Suture at base of living chamber, nat. size.
b Female specimen consisting of 6 whorls, nat. size.

Fig. 4. *a-b* Male specimen, 6 whorls; nat. size.

Fig. 5. *a-b* Male specimen, 6 whorls; nat. size.

(See also pl. VIII-XII)


2a


1a


2b


5a


5b


1b


4b


3a


3b


4a

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PLATE VIII

Page

Quenstedtoceras henrici R. Douvillé 75

(Łuków, Callovian)

Fine-ribbed form

Fig. 1. Female specimen consisting of 8 whorls, nat. size.

Fig. 2. Male specimen, 6 whorls; nat. size.

Fig. 3. Male specimen, 6 whorls; nat. size.

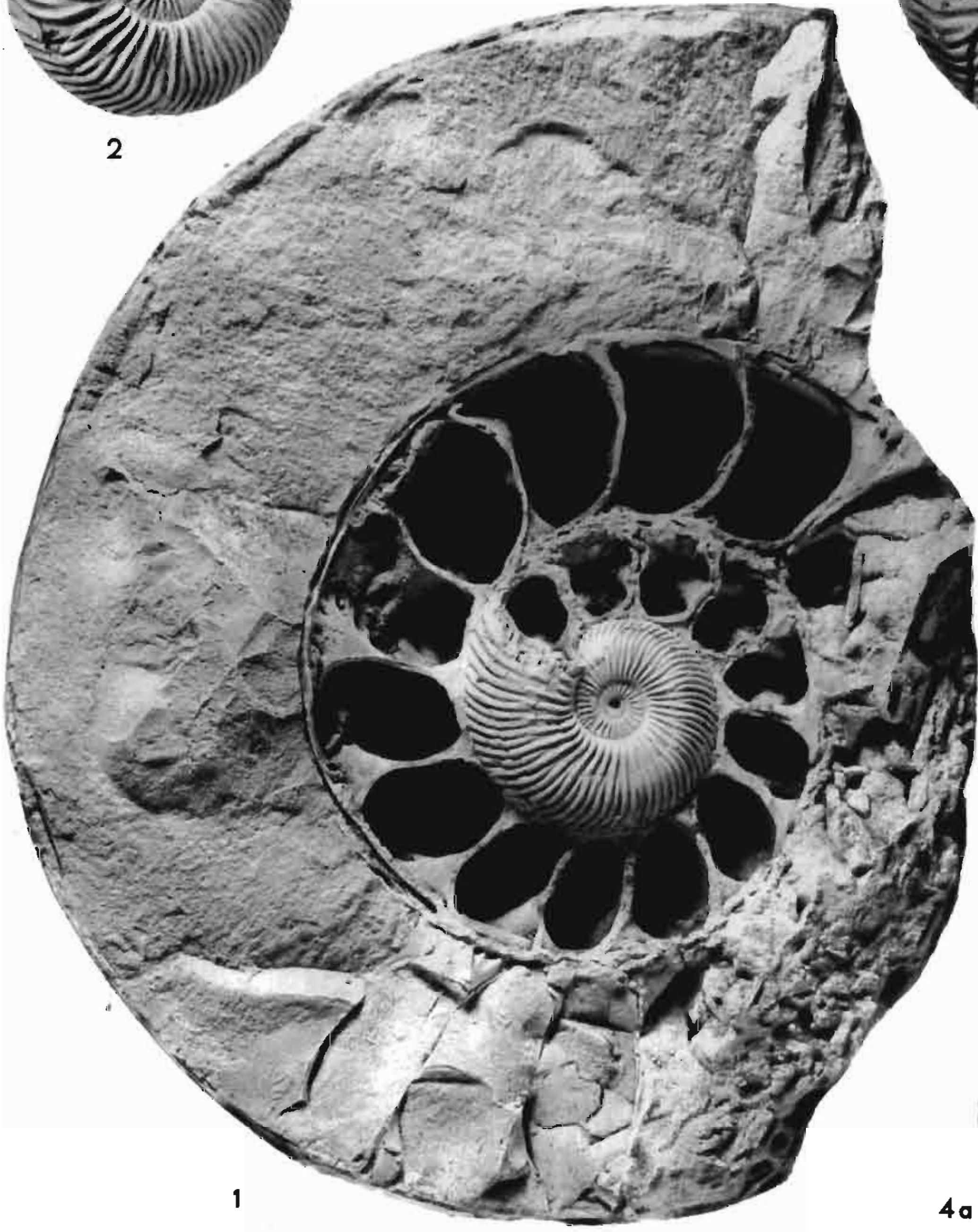
Fig. 4. *a-b* Male specimen, 6 whorls; nat. size.

(See also pl. VII, IX-XII)

2

3

4b



1

4a

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PLATE IX

Typical form

Fig. 1. *a* Female specimen consisting of 7 1/2 whorls, nat. size.
b-c Preparation of 6 inner whorls, nat. size.

Fig. 2. Male specimen, 6 whorls; nat. size.

Fig. 3. Male specimen, 6 whorls; nat. size.

Fig. 4. Male specimen, 6 whorls; nat. size.

Fig. 5. *a-b* Male specimen, 6 whorls; nat. size.

(See also pl. VII, VIII, X-XII)

1b

1a

1c

2

3

4

5a

5b

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PLATE X

Page

Quenstedtoceras henrici R. Douvillé 75

(Łuków, Callovian)

Typical form

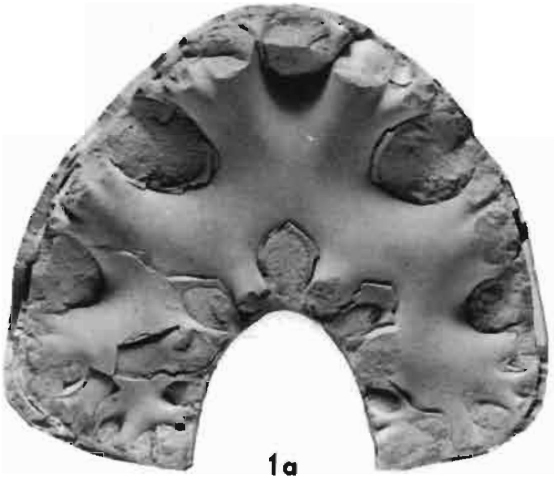
Fig. 1. *a* Suture in female specimen composed of 8 whorls, nat. size.
b-c Preparation of 6 inner whorls, nat. size.
d Preparation of 5 inner whorls, nat. size.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c Latex cast of 5 whorls of specimen fig. 2*a*, nat. size.

Fig. 3. *a-b* Male specimen, nat. size.

(See also pl. VII-IX, XI and XII)

3b



1a

2c

1c

1b

1d

3a

2b

2a

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PLATE XI

(Łuków, Callovian)

Coarse-ribbed form

Fig. 1. *a* Female specimen consisting of $7^1/_2$ whorls, nat. size.
b-c Preparation of $5^1/_2$ inner whorls, nat. size.
d Preparation consisting of just a little more than 5 whorls, nat. size.

Fig. 2. *a-b* Male specimen, nat. size.

Fig. 3. *a-c* Male specimen, 6 whorls; nat. size.

Fig. 4. Male specimen, nat. size.

(See also pl. VII-X)

1a

1b

1c

1d

2a

2b

3a

4

3b

3c

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PLATE XII

(Łuków, Callovian)

Coarse-ribbed form

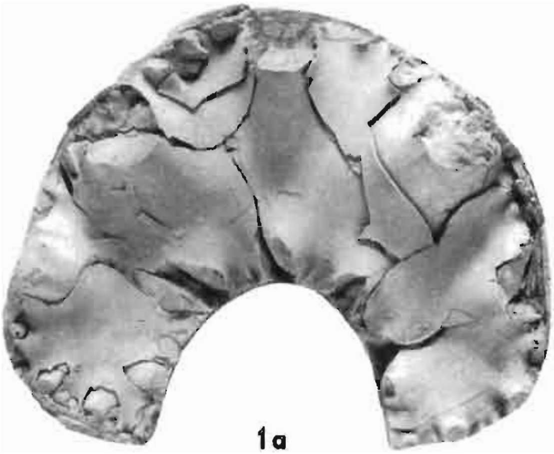
Fig. 1. *a* Suture in female specimen composed of 8 whorls at base of living chamber, nat. size.
b-c Preparation of 6 inner whorls, nat. size.
d-f Preparation of 5 inner whorls, nat. size.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c Preparation of $5^1/_2$ inner whorls, nat. size.

Fig. 3. Male specimen, nat. size.

(See also pl. VII-XI)

3



1a

2b

1c

1b

2a

1e

1d

1f

2c

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PLATE XIII

(Łuków, Callovian)

Form with high whorls

Fig. 1. *a* Female specimen consisting of 8 whorls, nat. size.
b Preparation of $6^1/_2$ inner whorls, nat. size.
c-e Preparation of $5^1/_2$ inner whorls, × 2.

Fig. 2. *a* Male specimen, 6 whorls; nat. size.
b-d Preparation of $5^1/_2$ inner whorls, × 2.

(See also pl. XIV-XVI)

1a

1c

2a

2b

2c

1e

2d

1b

1d

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PLATE XIV

(Łuków, Callovian)

Form with high whorls

Fig. 1. *a-c* Male specimen, nat. size.

Fig. 2. *a-c* Male specimen, 6 whorls; nat. size.

Fig. 3. *a-b* Male specimen, nat. size.

Fig. 4. *a-b* Male specimen, 6 whorls; nat. size.

Typical form

Fig. 5. *a-b* Male specimen, 6 whorls; nat. size.

(See also pl. XIII, XV and XVI)

1c

1b

1a

2a

3a

3b

2b

2c

4b

4a

5a

5b

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PLATE XV

Typical form

Fig. 1. *a* Section through the living chamber and the previous whorl of a female specimen composed of $7^1/_2$ whorls, nat. size.

b-c Preparation of $6^1/_2$ inner whorls, nat. size.

d-e Preparation of $5^1/_2$ inner whorls, nat. size.

f-h Preparation of $5^1/_2$ inner whorls, $\times$ 2.

Fig. 2. *a-b* Male specimen, nat. size.

c-e Preparation composed of slightly less than $5^1/_2$ whorls, $\times$ 2.

(See also pl. XIII, XIV, XVI)


2a


2b


2d


2c


2e

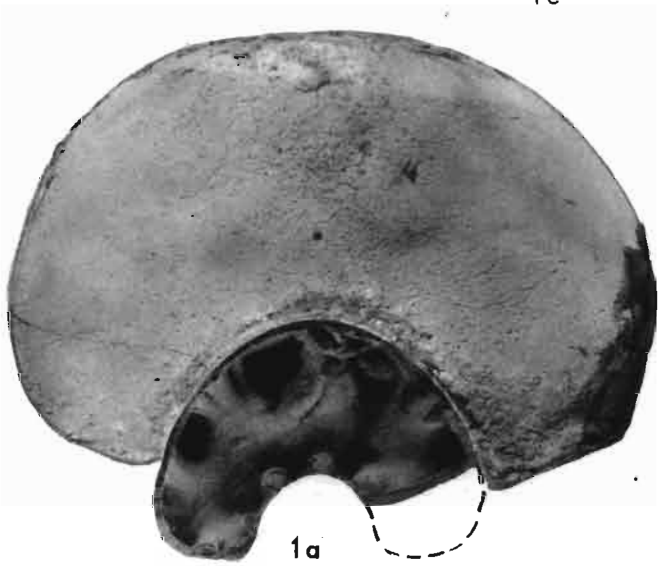

1g


1b


1c


1f


1h


1a


1d


1e

H. MAKOWSKI: PROBLEM OF SEXUAL DIMORPHISM IN AMMONITES

PLATE XVI

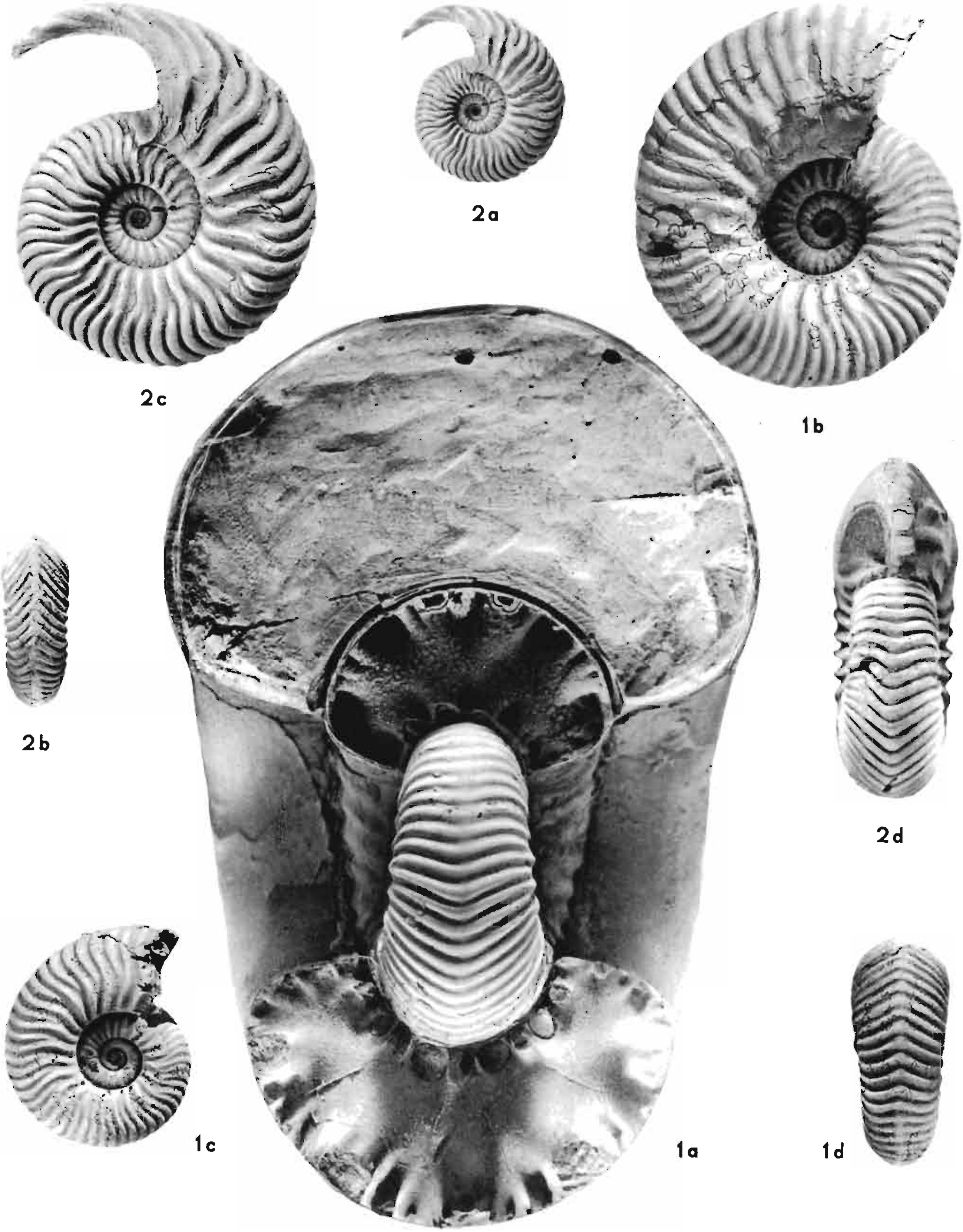
(Łuków, Callovian)

Form with low whorls

Fig. 1. *a* Female shell with undetermined number of whorls, nat. size.
b Preparation of young whorls, nat. size.
c-d Preparation of whorls younger than above, × 2.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c-d Male specimen, × 2.

(See also pl. XIII-XV)



H. Makowski: Problem of sexual dimorphism in ammonites

Palaeontologia Polonica, No. 12, 1962

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PLATE XVII

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Quenstedtoceras praelamberti R. DOUVILLÉ 75

(Łuków, Callovian)

Fig. 1. *a* Section of female shell composed of $7^1/_2$ whorls, nat. size.
b-c Preparation of young whorls, nat. size.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.
c Preparation of $5^1/_2$ inner whorls, nat. size.

2b

1a

1b

2c

2a

1c

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PLATE XVIII

Page

Quenstedtoceras vertumnum (LECKENBY) 78

(Łuków, Callovian)

Fig. 1. *a* Female shell composed of 8 whorls, nat. size.
b-c Preparation of 6 inner whorls, nat. size.

Fig. 2. *a-c* Male specimen, 6 whorls; nat. size.

Fig. 3. *a-b* Male specimen, nat. size.

Fig. 4-6. Small male specimens, 6 whorls; nat. size.

(See also pl. XIX and XX)

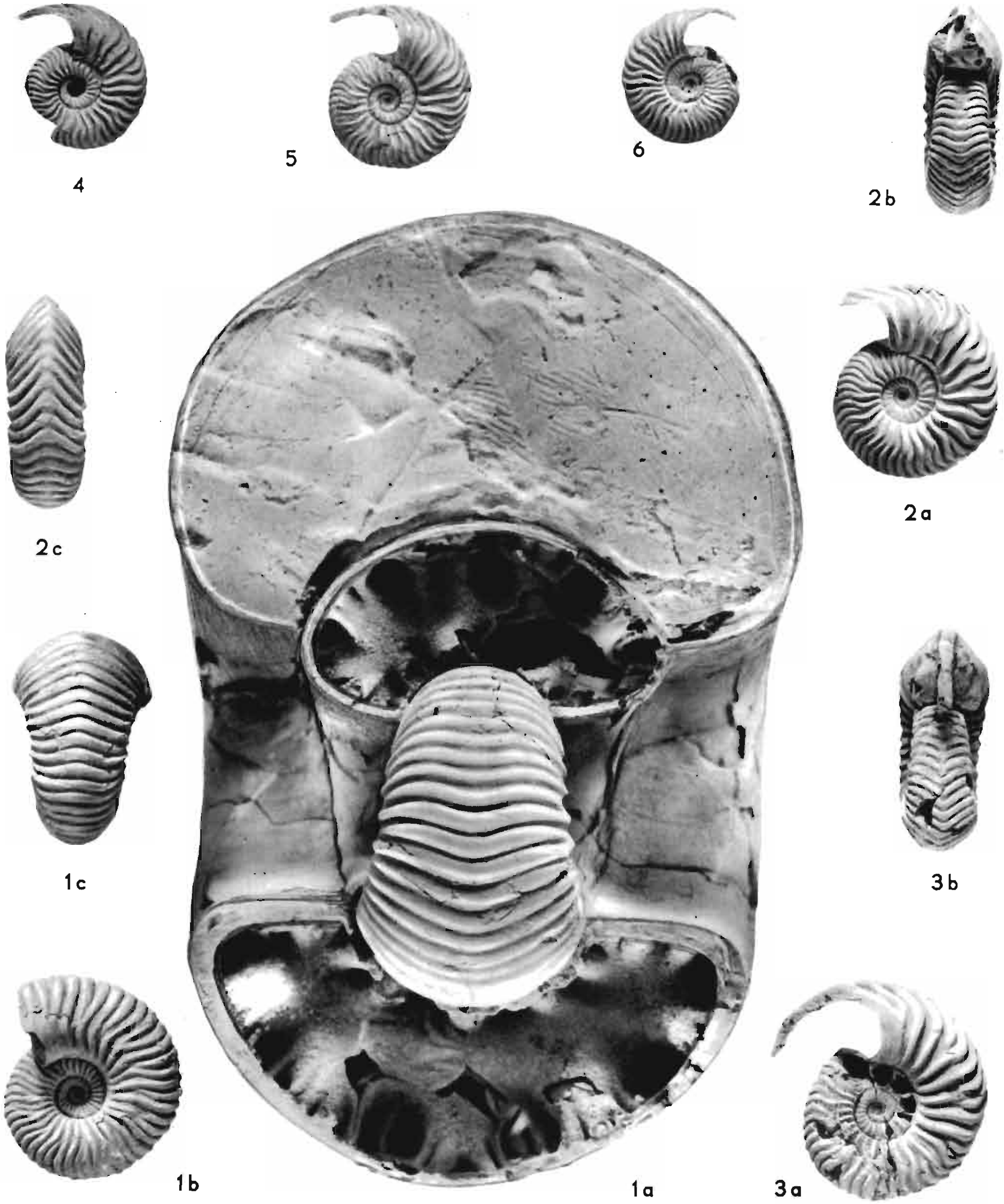

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PLATE XIX

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Quenstedtoceras vertumnum (LECKENBY) 78

(Łuków, Callovian)

Fig. 1. Female shell with partly preserved last living chamber, nat. size.

Fig. 2. Female shell with nearly 6½ whorls preserved, nat. size.

Fig. 3. Section of male shell through symmetry plane, showing crowded arrangement of last sùtures, 6 whorls; nat. size.

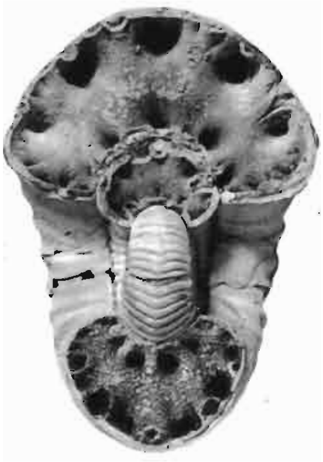
Fig. 4. Male specimen, nat. size.

Fig. 5. *a-b* Male specimen, nat. size.

Fig. 6. *a-b* Male specimen, 6 whorls; nat. size.

(See also pl. XVIII and XX)

4

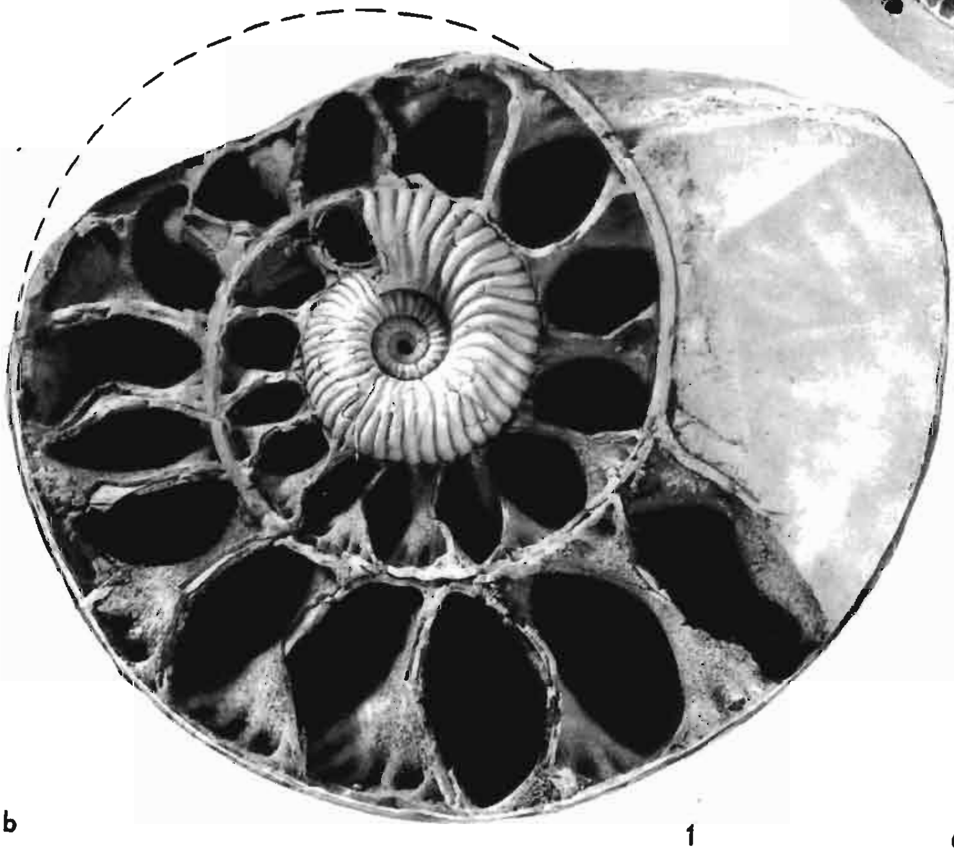


2

6a

5a

3



1

5b

6b

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PLATE XX

Page

Quenstedtoceras vertumnum (LECKENBY) 78

(Łuków, Callovian)

Fig. 1. *a* Female shell consisting of 7 whorls, nat. size.
b-c Preparation of $5^1/_4$ inner whorls, × 2.

Fig. 2. *a-b* Male specimen, 6 whorls; nat. size.

Fig. 3. Male specimen, nat. size.

(See also pl. XVIII and XIX)

Quenstedtoceras lamberti (SOWERBY) 76

(Czatkowice, Callovian)

Fig. 4. *a* Section of the last living chamber of female specimen, nat. size.
b-c Part of the shell ribbing of female specimen, nat. size.

Fig. 5. Male specimen with partly preserved gerontic aperture, nat. size.

2a

1a

3

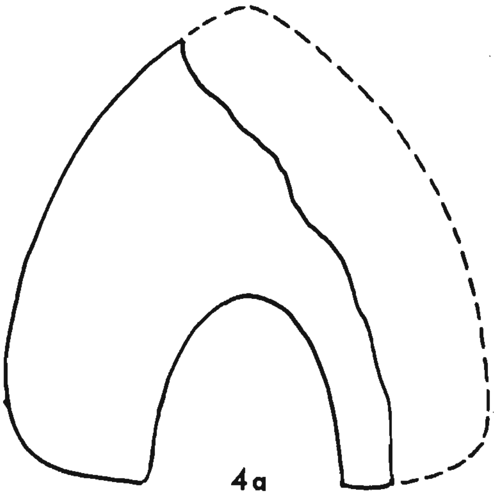
2b

1b

1c

5

4b



4a

4c

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