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SOME DIFFICULTIES IN RECOGNITION OF SEXUAL DIMORPHISM IN JURASSIC PERISPHINCTIDS (AMMONOIDEA)

Abstract. — The recent studies on perisphinctids have shown repeated occurrence of peristomal modifications and thus their limited reliability as a sign of ceasing of shell growth. Moreover, they have shown a trend to disappearance of the lappets at larger shell diameters. New evidence for the occurrence of the lappets on small-sized "macroconchs" is given and the transition from "micro-" to "macroconchs" seems possible. It is concluded that the perisphinctids may represent a new type of dimorphism not encountered in other groups of ammonites and that the Makowski-Callomon hypothesis of the sexual dimorphism is not so universal as it was considered to be. The criterion of identity of inner whorls may be applied in the systematics of ammonites without making reference to the dimorphism as it was applied by Neumayr (1873) and Siemiradzki (1891).

INTRODUCTION

The hypothesis of sexual dimorphism in ammonites, put forward in the XIX c., revived and attracted much attention thanks to the papers by Makowski (1962) and Callomon (1963). The premise for differentiation of the dimorphism was the cooccurrence of two groups of ammonites differing in the ultimate shell size, ornamentation of outer whorl(s) and the type of peristomal modifications and displaying identical or practically indistinguishable inner whorls (Makowski, 1962; Callomon, 1963, 1969; and others). The dimorphism was interpreted as sexual in nature. Makowski (1962) interpreted smaller forms with more complex peristome as males, and larger — as females, whereas according to Callomon (1963, p. 47) "the question of which of a dimorphis pair should be identified with a particular sex... can never rise above speculation".

The dimorphism in perisphinctids, that is in the group most familiar to the authors, was studied by Callomon (1963, 1969), Enay (1966, in press), Cope (1967), Zeiss (1969), Mangold (1970) and others. Some authors made attempt to distinguish the dimorphism at the specific level or even to place dimorphs in the same species, while others found some difficulties even at the subgeneric level, related to the fact that "the initial development stages

are very similar to each other within a numerous taxonomic group" (of the family Perisphinctidae) (Makowski, 1971, p. 337). However, at present another problem seems to be the main obstacle in recognition of dimorphism in Perisphinctiadae, i.e. the recognition of the end of shell growth.

THE INDICES OF THE ULTIMATE SHELL SIZE AND MATURITY

According to the classic paper of Callomon (1963, p. 25) "the final stage in the ontogeny of ammonites was one of usually well-defined maturity" which is "usually easily recognizable, indicated by one or more of the following signs: (1) uncoiling of the umbilical seam..., (2) modification of sculpture near the peristome, usually a coarsening and re- or degeneration of ribbing but often with terminal constrictions, ventral collars, flares, horns, rostra, lateral lappets etc., (3) approximation and degeneration of the last few septal sutures". From the papers of Makowski (1963) and Callomon (1963, 1969) it would follow that the peristomal modifications of the type of lappets or horns were developed only once at the very end of the development of shell. However, soon afterwards Enay (1966) has shown the occurrence of "youthful peristomes" on several microconchs of the subgenera *Perisphinctes* (*Otosphinctes*) and *P.* (*Dichotomosphinctes*). These peristomes, perhaps somewhat less complex that the "final" (Enay, in press), do not mark the end of the development of shell as "during the shell growth they are built with the new part of the shell and the resorption is not needed" (for the elimination of them) (Enay, in press). Besides the „youthful peristomes" illustrated by Enay (1966, in press), subsequent analysis has shown that such feature is well-displayed by one of *Lithacoceras* (*recte Subdiscosphinctes*) *cracoviensis* (Siem.) figured by Brochwicz-Lewiński (1972, pl. 10) and it may be inferred in the case of another representative of that species (*ibidem*, pl. 11), less satisfactorily preserved and a bit overgrown by serpulids. It is admitted that subsequent growth of shell markedly obscures such "youthful peristomes" of the lappet type. But, when they are found on several specimens (Mangold, 1970, Gygi, pers. inf.) there arises a question how many "youthful peristomes" may be developed by a specimen till its growth ceases .Here the results of studies on another group of Late Jurassic perisphinctids, *Pectinatites* Buckman, 1922, are of much help. Cope (1967) has shown that the representatives of this group did not developed the lateral lappets as did their ancestors — *Propectinatites* Cope, 1968 — and close relatives, but ventral horns which are more difficult to obscure and which left behind a characteristic scar on the venter when shed off. The first horn is not developed until a diameter of at least 60 mm is attained, i.e. until a certain growth stage is reached, and further horns may be developed at various growth stages beyond this diameter. The maximum number of horns found on a single specimen is seven (Sylwester-Bradley, 1969) but there remains an open question whether or not

it is really the maximum number. If the horns are actually ventral equivalents of the lateral lappets as Callomon (1963, p. 28) and others assumed and as it follows from *Propectinatites* — *Pectinatites* succession, then it is not excluded that the number of "youthful peristomes" of the lappet type could be equally high. On the basis of these still scarce data it is, however, possible to state that the peristomal modifications indicate maturity but do not guarantee that the growth of shell has finally ceased (see also Enay, in press) and that other criteria are necessary. Unfortunately, the majority of perisphinctids are characterized by a general trend in increase in evolutness of coiling of outer whorls. This results in the fact that the other criterion of maturity, i.e. the uncoiling of umbilical seam (Callomon, 1963), is difficult to apply alone. The last criterion, the approximation and degeneration of the last few septal sutures (*ibidem*, p. 25), would be of much help here. Unfortunately, the material of Cope (1967, p. 15) is insufficiently preserved. It is planned to test the material available whether or not the development of "youthful peristomes" is connected with some changes in sutures. It should be mentioned here that the recent studies have shown several cycles of approximation of septa in both "micro-" and "macroconchs" (Kulicki, 1974; and others) and it is debatable whether or not even the most severe approximation of sutures had any disturbing effect on the hydrostatic-apparatus function of ammonite shell (H. Mutvei, pers. inf.).

It may be concluded that the peristomal modifications are unreliable as an index of termination of growth. In that situation it seems reasonable to analyse eventual relationship between the repeated development of peristomal modifications and the phenomena of size changes and disappearance of lappets in evolutionary series of perisphinctids along with increase in shell size, inferred assuming that the peristomal modifications really indicate end of growth (Ziegler, 1959, 1962, 1972; Brochwicz-Lewiński & Różak, 1974, 1975). The phenomenon of the disappearance of the lappets with the increase in shell size is not in contradiction with the phenomenon of the repeated development of the lappets. The youthful peristomes of the lappet type are hitherto known from some *Perisphinctes* (*Otosphinctes*) attaining relatively small size and thus bearing usually small lappets or from *P.* (*Dichotomosphinctes*) and *Subdiscosphinctes* so large that the lappets are small again. The largest lappets found in *P.* (*Otosphinctes*) and *P.* (*Dichotomosphinctes*) measuring about 60—70 mm in diameter are so large (up to 48% of shell diameter) that either resorption or a drastic change in ornamentation would be necessary for the continuation of shell growth. In turn, the "youthful peristome" displayed by *Subdiscosphinctes cracoviensis* (pl. 1) seems to exort a distinct change in ribbing — a marked increase in spacing of ribs. It would be desirable to search through the collections to test whether it is a happenstance or a regularity.

The hypothesis of size changes (see Duong, 1974) is, of course, greatly imperilled when the above phenomena are confirmed and further studies are necessary.

It is, however, possible to follow Cope (1967) and accept the first peristome as the sign of maturity and to compare changes in size at which specimens reach maturity.

"LAPPETED MACROCONCHS" AND INTERSEXES

The phenomenon of repeated development of peristomal modifications makes it also necessary to revisit the hypothesis on the occurrence of macroconchs with the microconch-type peristome (Brochwicz-Lewiński & Różak, 1975). The analysis of the changes in lappets depending on shell size has shown that the lappets are being replaced by lateral lips at the diameter of over 100—120 mm and finally they seem to disappear at diameters exceeding 200 mm when there develops peristome of the macroconch type (simple, somewhat sinuous peristome). At the same time it was inferred that the macroconchs attaining less than 200 mm in size were lappeted. Further searching did not give any dwarfish macroconchs of *Perisphinctes* (*Perisphinctes*) nor *P.* (*Arisphinctes*) with sufficiently preserved peristome. However, there was found a perisphinctid assignable to *Idoceras* ex gr. *planula* (Hehl), with ornamentation of the macroconch-type and bearing a large lip-like peristome (see pl. XXXI, fig. 2) as well as another would-be macroconch of *Ringsteadia* sp. (see pl. XXXI, fig. 1) with a small lappet.

The phenomenon of the repeated development of peristomal modifications makes it possible to approach that problem from another side: whether or not the further growth of shell lead to the appearance of sculpture of the type considered as characteristic of the macroconchs? Theoretically it is not excluded. For example, if *Perisphinctes* (*Dichotomosphinctes*) *buckmani* Arkell shown by Enay (in press, pl. 1, fig. 2) is immature and its excellently preserved peristome is "youthful", the subsequent whorl could be ornamented with the heavy ribbing typical of *P.* (*Perisphinctes*) or *P.* (*Arisphinctes*). Actually, there are some representatives of the latter, displaying "microconch-type" isocostate ribbing up to the constriction at the diameters of about 240—250 mm.

Other example is the above mentioned *Subdiscosphinctes cracoviensis* (Siem.), displaying onset of the ornamentation typical of the macroconchs at present assigned to subgenus *S.* (*Aureimontanites*) or *Larcheria* also considered as the macroconch, after a "youthful peristome".

It is also worth to refer to Cope (1967) as he described from a single fossiliferous horizon (bed) 32 microconchs, 34 macroconchs and 4 intersexes of *Pectinatites*. Three of these intersexes "appear to be normal

macroconchs, but have on their inner whorls structures resembling those of the horn of the microconch" and "the fourth... is intermediate in size between the two (micro- and macroconch) groups, has the typical microconch horn developed, but shows the beginnings of the macroconch type of ribbing" (Cope, 1967, p. 16). It would follow that the situation is similar in both Oxfordian *Perisphinctes* and Kimmeridgian *Pectinatites* faunas. On the other hand it is interesting whether or not the traces of earlier horns are marked on inner whorls of other macroconchs collected by Cope.

As far as the dimorphism is concerned it would follow from above that, contrary to the optimism of Callomon (1963, p. 39), the situation is not exceptionally clear in perisphinctids of the Oxfordian or any other age. We are afraid that similar is the case of other groups and at least other subfamily of Perisphinctaceae — the subfamily Aspidoceratinae Zittel, 1895. The lappeted small-sized *Euaspidoceras* (*Euaspidoceras*) *costatum* Dorn, figured recently by Enay (in press, pl. 3, fig. 4) indicates that not all the euaspidoceratids had peristomes of the macroconch-type and that the above phenomena may be also found in that subfamily.

IDENTITY OF INNER WHORLS OF MICRO- AND MACROCONCHS

To all those difficulties which seem to impede interpretation of the perisphinctids in terms of the dimorphism it should be added the above mentioned difficulty with applying the criterion of identity of inner whorls. However, the review of literature has shown that the phenomenon of similarity of inner whorls of forms differing in development of outer whorls was well-known to the XIXth c. researchers and it was explained in terms of "embryological principle". The principle was put forward by Neumayr (1873 and elsewhere) and precised by Siemiradzki (1891, p. 34) (translated from Polish): "forms apparently close but differing in their inner whorls cannot be considered as related; (2) forms differing in mature stage but having identical inner whorls belong to the same tribe; and (3) forms which retain features typical of only young whorls of geologically younger species in their senile age should be considered as ancestors of the latter". It follows from the analysis of Siemiradzki's (1891) paper that the tribe as used in the above definition was understood as of at least supraspecific rank. It may be concluded that despite of much smaller number of taxa recognized in these times, Neumayr and Siemiradzki considered identity of inner whorls as criterion for identification of tribes, i.e. they were familiar with several contemporaneous species displaying identical inner whorls. At the same time this may explain why they neglected the problem of sexual dimorphism.

Thus it may be concluded that the criterion of identity of inner whorls cannot be regarded as reliable and sufficient for identification of dimorphic

pairs. As it was noted above, a similar reservation was recently made by Makowski (1971, p. 337) for the case of Perisphinctidae and other well-known family Oppeliidae.

The present state of knowledge of the phenomenon of sexual dimorphism in Jurassic non-perisphinctid faunas also cannot be considered as satisfactory and several authors reported difficulties encountered in their work on that problem. They primarily reported troubles with too many taxa with identical inner whorls and the resulting "tri-" or "quadrimorphism" but, up to the present, not the repeatance of peristomal modifications.

CONCLUSIONS

It may be stated that at least in the case of Perisphinctidae the peristomal modifications alone cannot be used as a reliable sign of end of growth (see also reservations made by Enay, in press, and Mangold, 1970).

It seems that either the present state of knowledge of the Perisphinctidae is insufficient for recognition of the sexual dimorphism *sensu* Callomon (1963) and Makowski (1962) or this family represents type of dimorphism not encountered in other ammonites. If any direct or indirect sexual function is attributed to the peristomal modifications it would follow that both "micro-" and "macroconchs" of that family had several mating cycles. When the "macroconchs" are lager than "microconchs" it would follow that "microconchs" were giving rise to "macroconchs". Similarly, it may be argued whether or not the perisphinctids were sexually monomorphic. Thus, it follows that the Makowski-Callomon hypothesis of sexual dimorphism in ammonites is not so universal as it was considered to be.

Stephanov (1972, p. 22) stated: "Naturally, research work in this direction (i.e. on dimorphism in ammonites) is always welcome, but if we are realists, we should admit that sexual dimorphism in ammonites is only hypothesis for the time being. Its conclusions, therefore, should not be imposed in ammonite taxonomy before this hypothesis is proved".

The hypothesis of sexual dimorphism in ammonites was of great importance as it indicated the necessity of collecting highly complete material and it draw attention to gerontic features and inner whorls of ammonites studied. At the same time certain extremism resulted in some drawbacks and primarily in overcomplication of ammonite studies and thus in discouragement of some students and especially those having less-perfect material at their disposal. From the point of view of the taxonomy this hypothesis indicated the necessity of placing the forms with identical inner whorls in the same taxa, but, as it was shown above, it was nothing new in comparison with some of the ideas of Neumayr and Siemiradzki.

The inner whorls of several taxa of ammonites are practically indistinguishable as Callomon (1963) has stated, and thus the ammonites are difficult to separate on that basis. Therefore this phenomenon should be taken into account in the systematics at the specific, subgeneric or generic level, depending on the degree of similarity. However, it should be noted that it used to be a common practice in the past, without making a reference to the dimorphism.

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WOJCIECH BROCHWICZ-LEWIŃSKI & ZDZISŁAW RÓŻAK

TRUDNOŚCI W ROZPOZNAWANIU DYMORFIZMU PŁCIOWEGO U JURAJSKICH PERYSFINKTÓW (AMMONOIDEA)

Streszczenie

Najnowsze badania nad perysfinktami wykazały powtarzalność modyfikacji perystomalnych, a stąd ich znikomą wiarygodność jako wskaźnika zakończenia wzrostu muszli. Ponadto stwierdzono tendencję do zaniku uszek perystomalnych w przypadku okazów osiągających większe rozmiary, oraz zebrano nowe dowody na występowanie uszek u małych „makrokonch". Stwierdza się, że perysfinkty mogą reprezentować nowy typ dymorfizmu nie stwierdzony dotąd u innych grup amonitów,

oraz że dymorfizm płciowy w sensie Makowskiego (1962) i Callomona (1963) nie jest tak uniwersalny jak to uprzednio przypuszczano. Kryterium identyczności skrętów wewnętrznych może być stosowane w systematyce amonitów bez powoływania się na dymorfizm, jak to już uprzednio czynili Neumayr (1873) i Siemiradzki (1891).

ВОЙЦЕХ БРОХВИЧ-ЛЕВИНЬСКИ & ЗДЗИСЛАВ РУЖАК

ТРУДНОСТИ ВЫЯВЛЕНИЯ ПОЛОВОГО ДИМОРФИЗМА У ЮРСКИХ ПЕРИСФИНКТОВ (AMMONOIDEA)

Резюме

Новейшие исследования перисфинктов выявили повторимость перистомальных модификаций, следовательно, и их недостоверность в качестве показателя завершения роста раковины. Кроме того, констатировано, что у особей, достигающих крупных размеров, проявляется сокращение перистомальных ушек, а также получены данные о наличии ушек у мелких „макроконхов". Выявляется, что перисфинкты могут представлять новый тип диморфизма, не наблюдавшийся до сих пор в других группах аммонитов, и что половой диморфизм в понятии Маковского (1962) и Калломона (1963) не универсален настолько, насколько ранее предполагалось. Критерий тождественности внутренних оборотов может применяться в систематике аммонитов без прибегания к диморфизму, как это и осуществлялось ранее Неймайром (1873) и Семирадзким (1891).

EXPLANATION OF PLATES

Plate XXX

"Youthful peristome" displayed by *Subdiscosphinctes cracoviensis* (Siem.), from the upper Transversarium Zone of Olsztyn near Częstochowa (specimen no. Br 21/002); previously figured in Brochwicz-Lewiński, 1972, pl. 10; nat. size.

Plate XXXI

Extremal differences in the "ultimate" shell diameter in the *Otosphinctes* → *Dichotomosphinctes* → *Dichotomoceras* series.

Fig. 1. Giant *Perisphinctes* (*Dichotomosphinctes*) *bedoensis* (Coll.) from the Pe-

risphinctes wartae & Amoeboceras alternans Zone of Zawodzie, described and illustrated in this journal by L. Malinowska (vol. 17, no. 2 for 1972); × 0.5.

Fig. 2. Dwarfish *Perisphinctes (Otosphinctes)* sp. from the Plicatilis Zone, Tenuicostatum-Antecedens junction beds of Prędziszów near Częstochowa; nat. size.

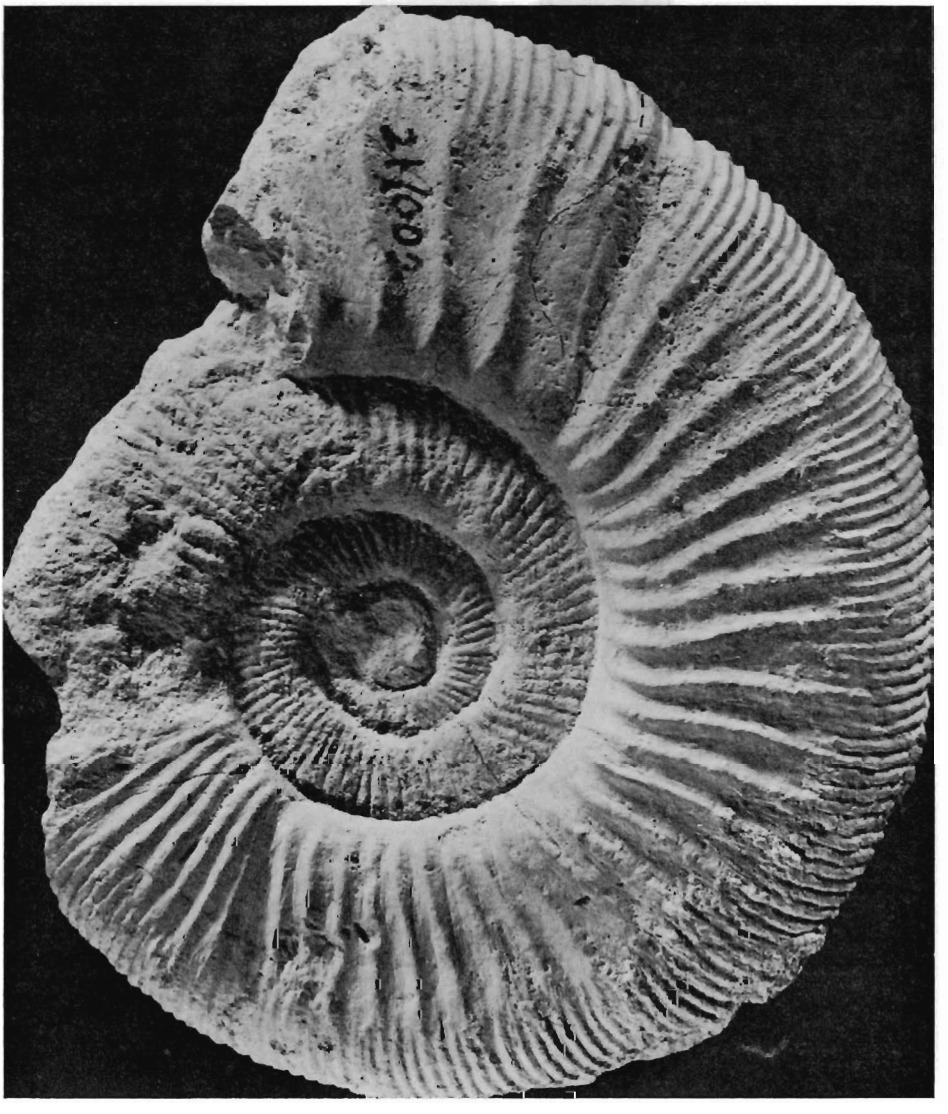
Fig. 3. Dwarfish *Perisphinctes (Dichotomoceras) bifurcatus* (Qu.) from the Bifurcatus Zone, Grossouvrei Subzone or Bifurcatus-Bimammatum junction beds of Biskupice near Częstochowa (Ha 24/7a); previously figured in Brochwicz-Lewiński & Różak, 1974, pl. 3, fig. 3; nat. size.

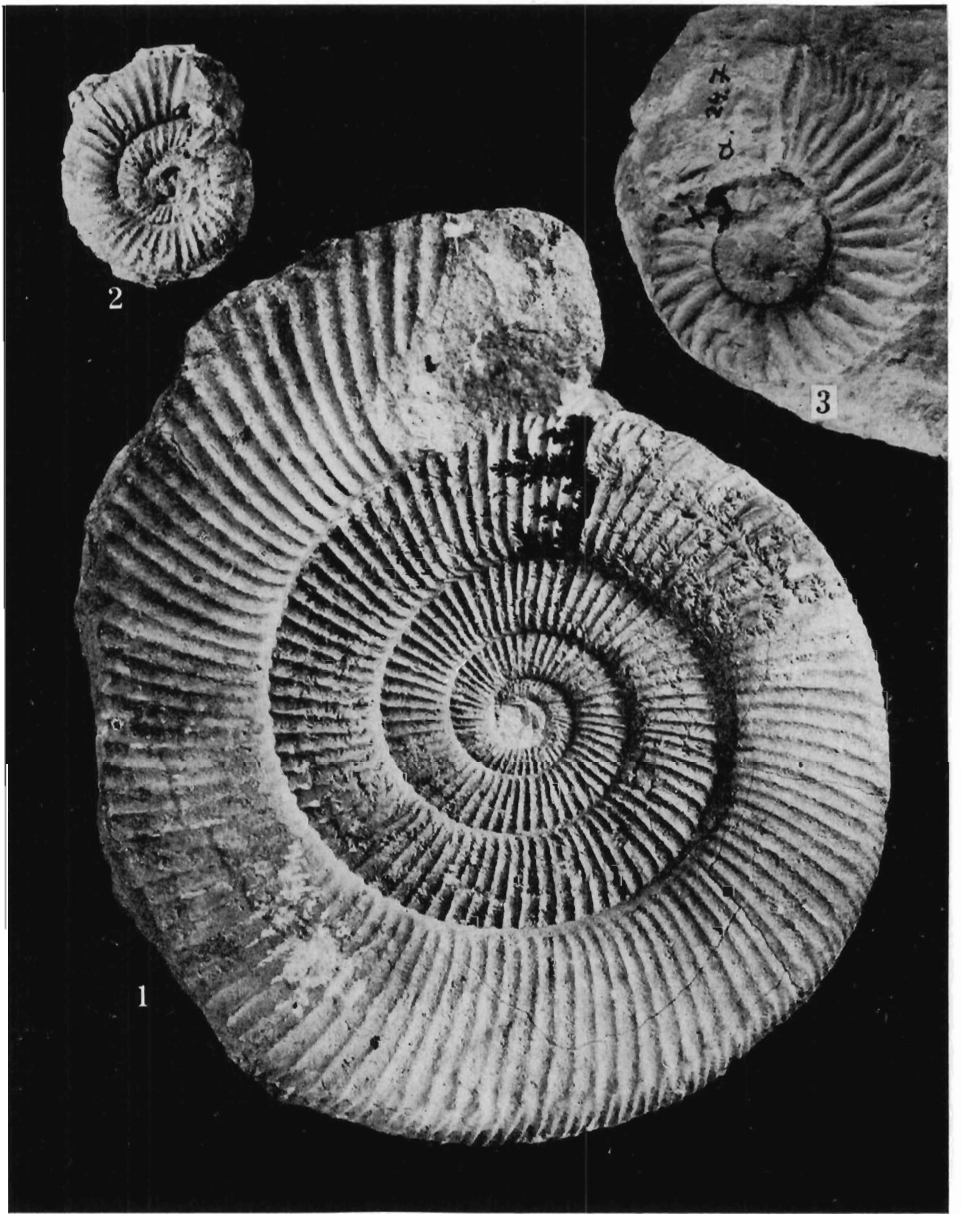
Plate XXXII

"Lappeted macroconchs"

Fig. 1. *Ringsteadia* sp.; lower part of the Bimammatum Zone, ?Hypselum Subzone of Biskupice; 103 mmD.

Fig. 2. *Idoceras* ex gr. *planula* (Hehl) originally described as *Perisphinctes* cf. *acer* Neumayr by Siemiradzki (1891); Krzemionki, ?Idoceras planula Zone; Geol. Mus. PAN, Cracow, A-I (2) 238; c. 150 mmD.

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