

Sexual dimorphism in the virgatitid ammonites

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ABSTRACT - Microconchs of early Virgatitidae had unmodified terminal apertures and differed from corresponding macroconchs in more elevated ribbing of the last whorl. In the lack of lappets and the presence of a densely ribbed early stage in the microconchs, the virgatitids closely resemble *Pectinatites*. It is proposed thus to derive the earliest virgatitid *Pseudovirgatites* from some advanced *Pectinatites* instead of assuming complex parallel modification necessary to derive it from the lithacoceratids with lappeted and uniformly ornamented microconchs. The latest Jurassic perisphinctaceans lacking lappeted microconchs (*Pavlovia*, *Dorsoplanites*, and *Virgatites*) may thus share common ancestry in the *Pectinatites* lineage.

KEY WORDS: Ammonitina, Late Jurassic, sexual dimorphism, evolution.

INTRODUCTION

Sexual dimorphism is still rather poorly known in the virgatitid Late Jurassic ammonites. Makowski (in Kutek & Zeiss 1974: p. 529) identified an adult microconch about 100 mm in diameter among Michalski's (1890: Pl. 6:1) originals of *Zarajskites zarajskensis*. This has found support in a distinctly bimodal size distribution of presumably adult specimens of a somewhat older species from the black shales of Brzostówka in central Poland, the best preserved microconch being 107 mm, with a macroconch 217 mm in diameter (Dzik 1986: p. 80). The most interesting feature is an apparent lack of any lappets in microconchs despite aperturally modified ornamentation. However, the material from

Brzostówka is crushed and compressed so some uncertainty has remained regarding proper identification of adult specimens.

It was, therefore, of much importance to find in the museum collections of the Greifswald University (Sektion Geologische Wissenschaften, Ernst-Moritz-Arndt Universität; abbreviated EMAUG in the following text) several well preserved virgatitids from Pomerania, some of them being mature and with apertural modifications. In the present paper I shall analyze the morphology of these specimens and attempt to interpret their biological and evolutionary significance.

THE ŚWIĘTOSZEWO SAMPLE

The ammonite specimens from the disused quarry at Świętoszewo in West Pomerania are the best preserved Polish virgatitids (see Dzik 1986). Almost all the complete specimens collected there appear to represent adult conchs, even if the aperture is well preserved only in some of them. Three well preserved specimens are housed in the collections of Greifswald University, two being macroconchs and one a microconch.

The most completely preserved macroconch is that identified by Dohm (1925: p. 36, Pl. 2:3) as *Virgatites cf. quenstedti* Rouillier. It measures 210

mm in diameter (Dohm quotes 257 mm) and its aperture is complete, with some signs of termination of growth expressed by a slight lateral constriction preceded by some weakening of ornamentation (Pl. 1:1). The second of Dohm's (1925: Pl. 5:4) specimens from Świętoszewo, identified by him as *Virgatites scythicus* Vischniakoff, has not been traced in the collections, but it is clear from the published illustration that it also represented a macroconch, not quite completely preserved. According to Dohm's measurement it was 228 mm in diameter. Another specimen in the Greifswald collection is incomplete,

but it clearly represents a macroconch (Pl. 2). Its well preserved juvenile ornamentation appears to be closely similar to that of the specimen in the Zakład Paleobiologii PAN, Warsaw, collection (Dzik 1986). That macroconch has its living chamber only partially preserved, but its complete size was probably somewhat larger than both Dohm's specimens. Its whorls are slightly crushed, which precludes precise comparison.

The most interesting specimen in the Greifswald collection represents the microconch (Pl. 1:2a,b) with clear features of the conch maturation: an increase in evolution, then decrease in the whorl expansion rate, and finally a slight lateral constriction and disappearance of ribbing. There is no sign of lappets. The shell is 111 mm in diameter and although the phragmocone is rather poorly preserved, some signs

of approximation in sutures seem to be visible at its end. A little more than two-thirds of the last whorl is the living chamber.

The specimen from Świątoszewo in the collections of the Geological Survey in Berlin, named *Provirgatites pomerania* by Arkell (1935) (transferred subsequently to *Isterites* by Zeiss 1977), represents almost certainly the same population. This is a juvenile conch but, judging from its rather evolute appearance and prominent ornamentation, it is a microconch.

The new data on the Świątoszewo virgatitids fit thus well earlier identifications of both macro- and microconchs in collections from the Pilica valley in central Poland (Kutek & Zeiss 1974; Dzik 1986). The complete lack of lappets, as well as any other prominent apertural structures, in these ammonites (Fig. 1) seems now to be proven.

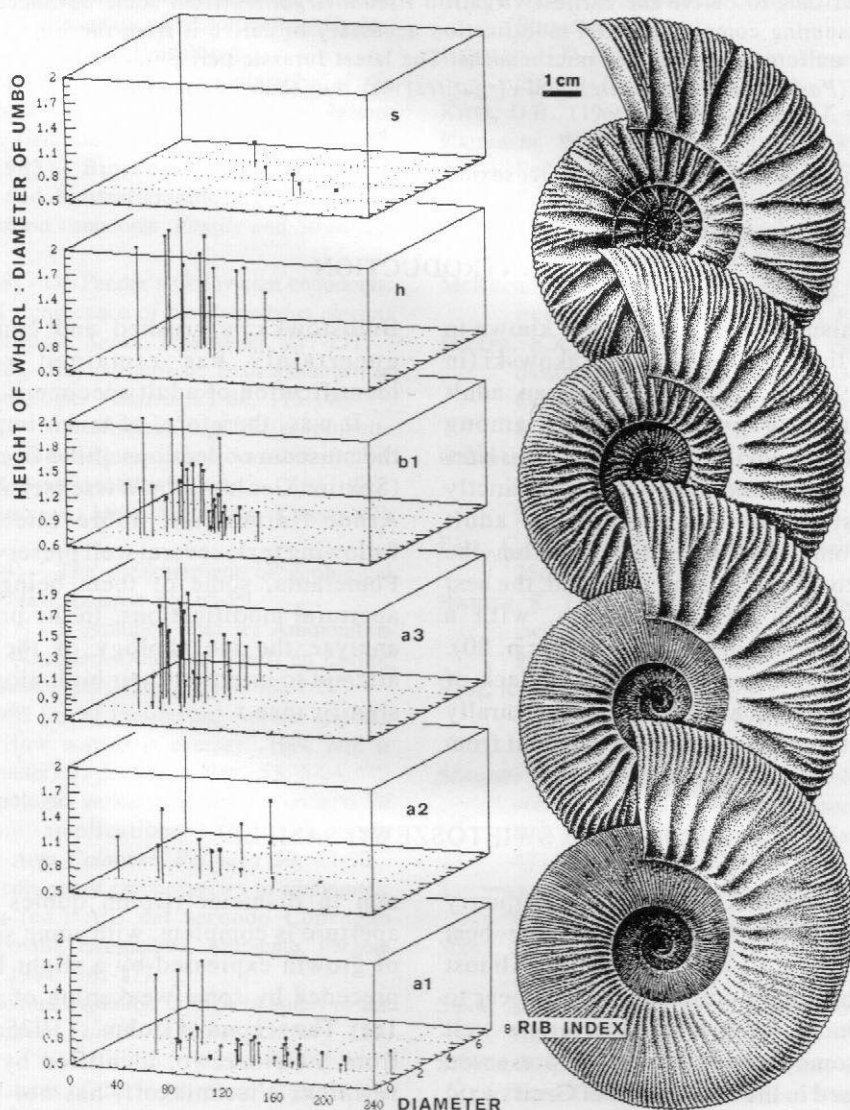


Fig. 1 - Modifications of conch ontogeny along the section at Brzostówka (Tomaszów Mazowiecki) in the Pilica Valley of central Poland (see Dzik 1986, 1990). Three-dimensional scattergrams of conch involuteness (diameter of umbo to conch diameter) and rib index (ratio between number of external and internal ribs) against diameter (as a measure of ontogeny) given for each sample, drawings represent reconstructed appearance of mature microconchs in successive populations.

From the topmost beds of the Brzostówka section some specimens of *Zarajskites zarajskensis* have been described that very closely approach the Świetoszewo microconch in size, a slight uncoiling close to the aperture and prominent ornamentation of the living chamber (see Lewiński 1923: Pl.11:2; Kutek 1967: Pl.1). It appears thus that the basic features of sexual dimorphism were rather stable in the virgatitids.

THE CZARNOGŁOWY SAMPLE

In the early 1940's Konrad Richter of the Greifswald University assembled a good collection of nineteen specimens of virgatitid ammonites from the Czarnogłowy quarry, located in the proximity of the Świetoszewo one. The specimens occur in a black marly mudstone, almost certainly coming from bed 53 at the top of the section of Wilczyński (1962) who described from it fragmentary ammonites identified as *Zarajskites scythicus* (Vischniakoff), *Z. pilicensis* (Michalski), and *Pavlovia pavlovi* (Michalski). Richter (1931: p. 14) on the basis of earlier collections of poorly preserved ammonites from the mudstone identified there *Provirgatites compressodorsatus* (Fiebelkorn) and a bifurcate species with an indistinct ventral furrow at early stages. There are some inconsistencies in published measurements of this part of the section. According to Richter (1931) the bed with *Provirgatites* occurs about 3.2 m above the very characteristic glauconitic sandstone bed 38 of Wilczyński (1962) with a fauna of *Aulacostephanus*. However, Wilczyński (1962; see also Dmoch 1970) reported several marly beds with *Aulacostephanus* and *Aspidoceras* up to 7.2 m above the glauconitic sandstone, then a 0.7 m thick bed of marly sands, and finally the black mudstone mentioned above.

The specimens from the mudstone are generally crushed but some of them were partially filled with limestone, there being preserved uncrushed. Among more or less complete specimens there is clearly bimodal size distribution with three macroconchs somewhat more than 200 mm in diameter and two microconchs about 100 mm in diameter. The microconchs are more prominently ribbed. One of the two almost complete microconchs (EMAUG Cz V-5a) is ornamented mostly with trifid polygyrate ribs separated by singular intercalatory ribs; the pattern of ribbing is surprisingly variable. Among four more fragmentary microconch specimens there are some with distinct polygyrate ribbing (Pl. 3:2) and some with bifid ribs dominating (Pl. 5:2). The second complete microconch (EMAUG Cz V-7) has only bifid ribs. Similar variability characterizes the macroconchs. Some show their inner whorls rather densely ribbed with a high ratio between primary and secondary ribs (Pl. 3:1, 4) while others seem to have

only bifurcate robust ribbing throughout their early ontogeny (Pl. 5:1). It is difficult to evaluate the taxonomic importance of this variation with such poorly preserved specimens. Nevertheless, no apparent morphological gap has been identified between these extreme morphologies (Fig. 2, 3) and it remains possible that the whole sample represents a single species.

The two most complete microconch specimens do not have margins of their apertures preserved.

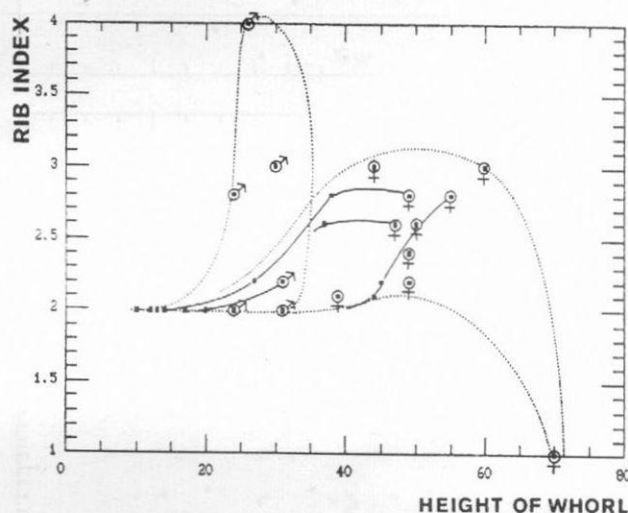


Fig. 2 - Ontogenetic changes in rib furcation pattern in the sample of *Zarajskites scythicus* (Vischniakoff 1882) from bed 52 of Czarnogłowy, Pomerania, NW Poland. Measurements of proposed macro- and microconchs indicated with sex symbols.

RELATIONSHIPS OF THE POMERANIAN AMMONITES

It is now quite clear that both the West Pomerania and the Pilica Valley outcrops of the latest Jurassic represent the same intracratonic sea basin (Kutek & Zeiss 1974) and most probably the ammonites from these two areas belonged to the same continuity of populations of the virgatitids. The area occupied by the Polish virgatitid lineages extended probably at least to the Skagerrak, judging from records of *Zarajskites scythicus* in erratic boulders in Denmark (Skeat & Madsen 1898).

It was suggested for the ammonites from Świetoszewo that they represent an intermediate stage in evolutionary development of the lineage, located between *Z. scythicus* (Vischniakoff) and *Z. zarajskensis* (Michalski), deserving recognition as a separate chronospecies (Dzik 1986: p. 81). Arkell (1935), while discussing relationships of Portlandian ammonites from Dorset, already introduced a name for the Świetoszewo species, namely *Provirgatites*

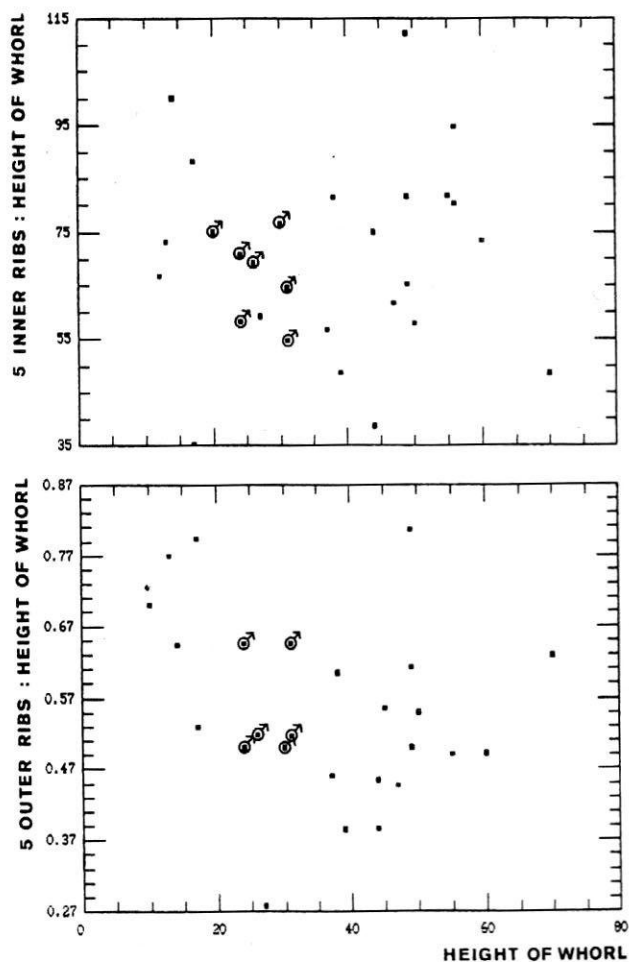


Fig. 3 - Distribution of relative inner and outer ribs density (distance between every fifth rib : height of whorl) in ontogeny (expressed by height of whorl) in the sample of *Zarajskites scythicus* (Vischniakoff 1882) from bed 52 of Czarnogl'owy, Pomerania, NW Poland. Measurements of proposed microconchs indicated with male sex symbols.

pomerania. From the stratigraphically preceding populations in the Pilica Valley (Fig. 4, 5), attributed to *Z. scythicus*, it differs in much more restricted stage of dense ribbing and a slight tendency to separate bunches of virgatotome ribs in microconchs by depressions wider than these in between regular secondary ribs. This typically virgatitid feature is strongly developed in its successor, *Z. zarajskensis*.

Provirgatites compressodorsatus (Fiebelkorn), with which Richter (1931) identified the Czarnogowy species, was based on a macroconch found as a loose block of white limestone in unspecified place in Pomerania (Fiebelkorn 1893). It seems more likely that it is conspecific with the S'wie, toszewo species although available evidence does not allow this to be determined with certainty. The preservation of the specimens collected by Konrad Richter does not allow study of the ornamentation of the juvenile stages, but available data fit, more or less, the Brzostowka population of *Z. scythicus*, suggesting a transitional

position between samples a3 and b1 of Kutek & Zeiss (1974), thus between defined populations of *Z. quenstedti* and *Z. scythicus* (see Fig. 4, 5).

RELATIONSHIPS OF THE VIRGATITIDAE

With new data on the sexual dimorphism in the Virgatitidae it is now clear that the most characteristic feature of family is the morphology of the microconchs. They show a complex ontogeny of ornamentation, with dense bifurcate ribbing at early stages and polygyrate (or virgatotome) ribbing at later stages, and the straight terminal aperture without lappets. This is a combination of three independent features that seems to be unique among the late Jurassic ammonites. Polygyrate ribbing and a simple microconch aperture also characterizes the Valanginian polyptychitids, while the lack of lappets associated with morphologically distinctive densely ribbed early stages, makes the virgatitids similar to the British lineage of the pectinatitids. The pattern of ribbing is quite commonly a subject of homeomorphy among the Mesozoic ammonites. The most fundamental question for resolving the evolutionary relationships of the virgatitids is thus whether the disappearance of lappets in the perisphinctacean ammonites took part only once or was repeated several times.

The best record of the transformations of the terminal microconch aperture is that presented by Cope (1967, 1968, 1978) for the pectinatitid lineage in the Kimmeridge Clays of Dorset (Fig. 6). The oldest member of the lineage, cooccurring with *Aulacostephanus*, still possessed small lappets in its microconchs (Cope 1968), that disappeared almost completely when *Gravesia* was associated with the lineage (Cope 1967). In effect of subsequent evolution a long ventral horn developed (Cope 1967), typical for *Pectinatites*, but later the horn gradually disappeared marking transition from *Pectinatites* to *Pavlovina* (Cope 1978: p. 490). It is of much interest to note that together with disappearance of the lappets and development of the horn an early stage of dense ribbing developed and expanded in the conch ontogeny while the last whorl developed polygyrate furcations in some ribs.

It appears thus that all the basic features of some ancestral form of the virgatitids can be identified in the pectinatitid lineage. If spatial (and evidently also temporal) proximity of these lineages are taken into account, a parallel evolution is highly unlikely to occur there. Instead, it seems reasonable to seek the roots of the virgatitid lineage among the pectinatitids. The alternative, lithacoceratid affinities would require independent development of complex ontogeny (in South German lithacoceratids the microconch is

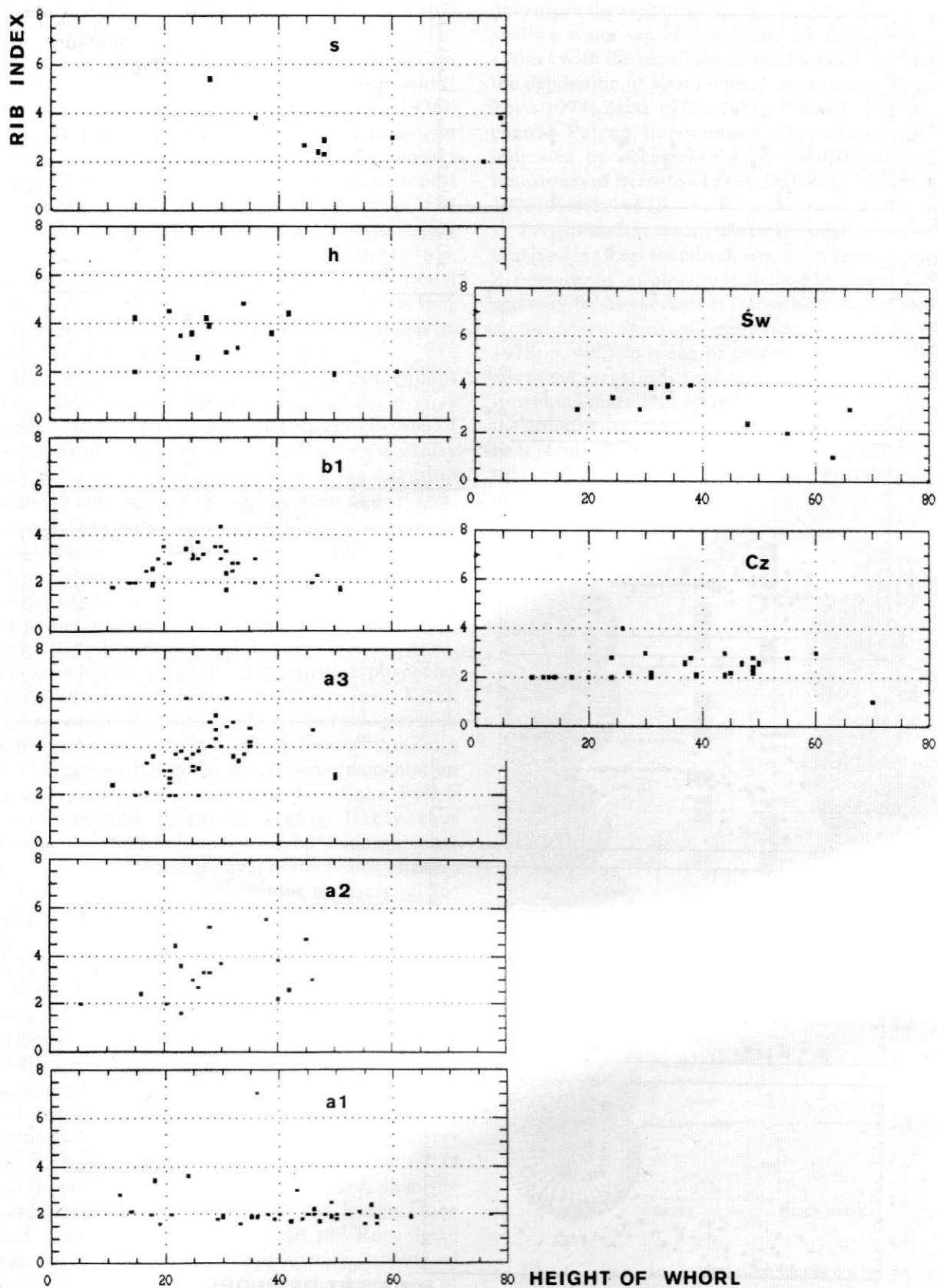


Fig. 4 - Proposed position of the Czarnogłowy and Świetoszewo populations of Zarajskites in relation to the reference standard of Brzostówka. Scattergrams of rib index (ratio between external and internal ribs) against height of whorl (as a measure of ontogeny) given for each sample.

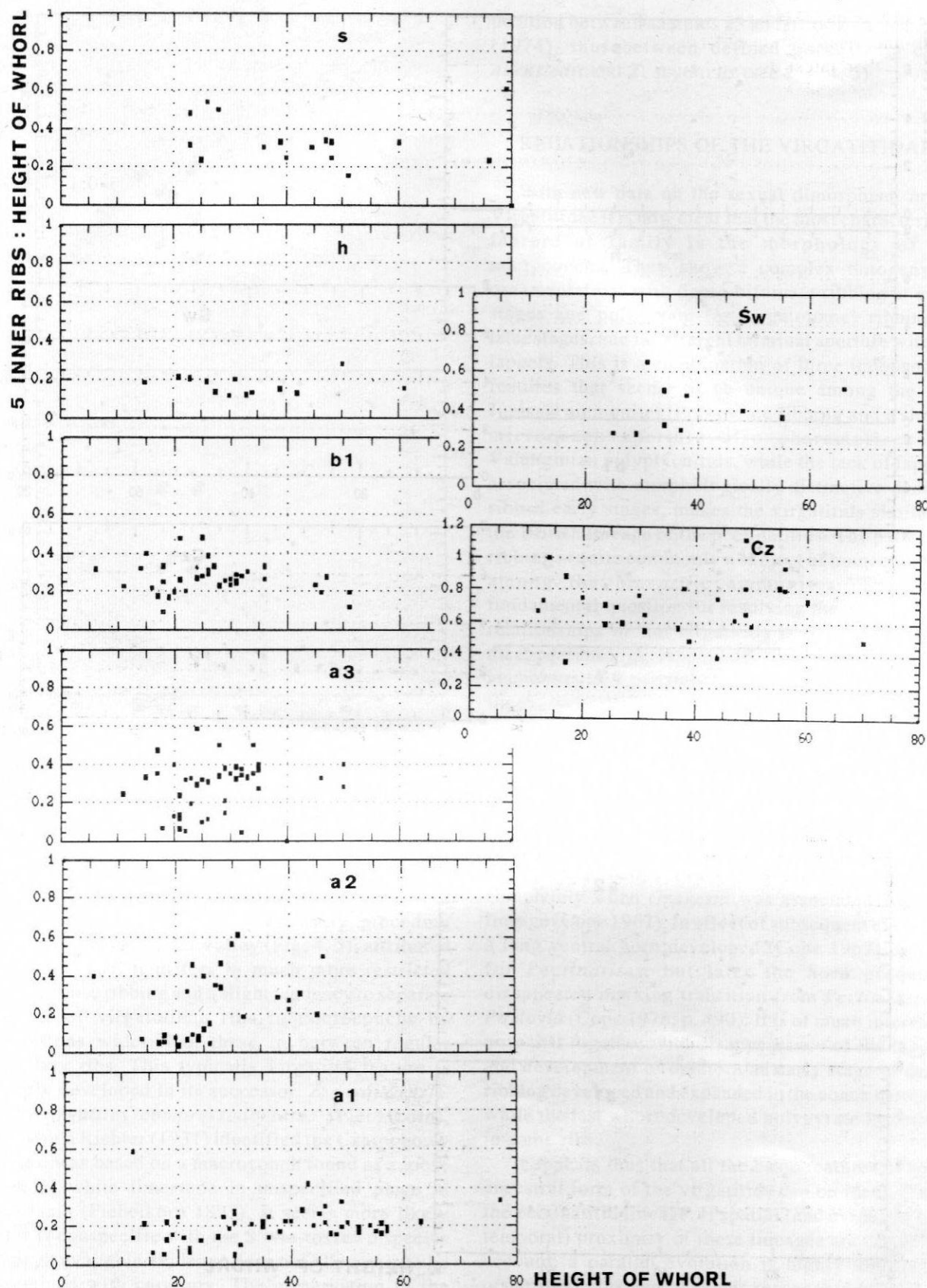


Fig. 5 - Proposed position of the Czarnogłowy and Świetoszęwo populations of Zarajskites in relation to the reference standard of Brzostowka. Scattergrams of relative inner ribs density against height of whorl given for each sample.

uniformly, even if densely, ribbed: see Zeiss 1968: Pl. 10) and disappearance of lappets.

Two other latest Jurassic groups of ammonites lacking lappets in microconchs, the dorsoplanitids (see Spath 1936: Pl. 29) and pavloviids (Cope 1978), appear at approximately the same level in Dorset being probably also derivatives of the *Pectinatites* lineage (Cope 1978: p. 522). Both show a more robust and seemingly more primitive ribbing pattern than *Pectinatites* but the early ontogeny of *Pavlovia* clearly reveals its proximity to *Pectinatites*. Spath (1936 p. 68) indicated presence of some forms transitional between *Dorsoplanites* and *Pavlovia*. There is thus no need to assume repeated reduction of lappets in independent perisphinctacean lineages.

The hypothesis of the ancestor-descendant relationship between *Pectinatites* and *Zarajskites* requires clarification of the evolutionary position of the Tethyan genus *Pseudovirgatites*, generally accepted to be close to the ancestry of the virgatitid lineage (Kutek & Zeiss 1974). The wide, even if rare, occurrences of early virgatitids in the middle European Tethys was the main reason to propose lithacoceratid roots for them. The crucial point of the discussion is evidently the morphology of the microconch aperture in *Pseudovirgatites*. In the Klenčnice beds, known from the Bohemian-Austrian border area, macroconchs of *P. scruposus* (Oppel), the type species of the genus, co-occur with *Isterites austriacus* Kutek & Zeiss, which is a prominently ornamented possible microconch with polygyrate or virgatitome ribs (Zeiss 1977). It closely resembles in size and ornamentation the above proposed microconchs of the Polish virgatitids and it seems highly likely that *Pseudovirgatites* had the same kind of dimorphism as *Zarajskites*. The oldest member of the Polish lineage, *P. puschi* Kutek & Zeiss may thus be ancestral for both the other, supposedly slightly younger, Tethyan species of *Pseudovirgatites* and the Polish-Russian lineage of *Zarajskites*.

If the virgatitids are really descendants of the pectinatitids the earliest stage of the evolutionary development must thus have taken place later than the disappearance of lappets and development of the dense juvenile ribbing recorded in the Dorset section. This would require reconsideration of currently accepted correlations between the British and Russian zonations (Zeiss 1977; Cope 1978). The bed a-1 in Brzostowka would then be much younger than the Dorset assemblage above the Yellow Ledge Stone Band, perhaps even younger than the Rope Lake Head Stone Band where dense juvenile ribbing of *Pectinatites* appears. At the time of the deposition of these strata some derivatives of the British lineage would invade the Polish-Danish Through sea and, being geographically isolated from the west,

developed the virgatitid lineage (Fig. 6). In relatively shallow water sea of Pomerania the lineage became extinct with the incursion of the Purbeck facies after the deposition of strata with *Z. pomerania* (Kutek & Zeiss 1974; Zeiss 1977). In the Pilica Valley area of central Poland it continued somewhat longer as indicated by occurrence of *Z. zarajskensis* in the limestones of Brzostowka (Michalski 1890; Lewinski 1923; Kutek 1967).

Progalbanites albanii (Arkell) from the base of the Portland in Great Britain shows much resemblance to *Z. pomerania*, as already indicated by Arkell (1935) and may be its successor. Dense bifurcate ribbing is almost absent in its ontogeny (see Spath 1936; Cope 1978: p. 490) so it can be compared only with more advanced virgatitids (not older *Z. pomerania*) while its ribbing resembles relatively primitive members of the group (not younger than *Z. pomerania*). This may be a result of migration in the opposite direction to that marking the origin of the Polish-Russian virgatitids.

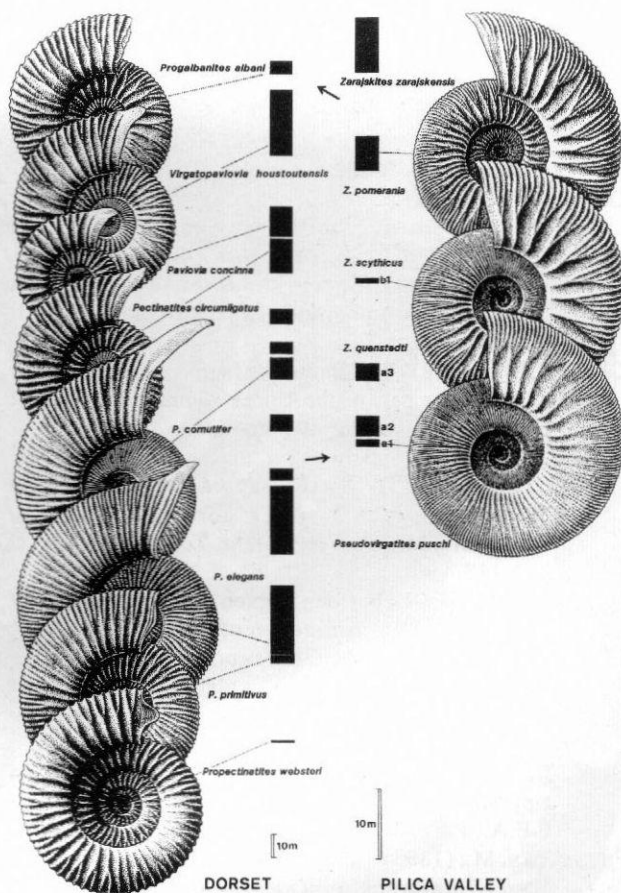


Fig. 6 - Proposed correlation between the series of samples from the Kimmeridge Clay of Dorset and the Brzostowka section. Illustrated mature microconch apertures in successive samples (based on Cope 1967, 1968, 1978 and Dzik 1990).

CONCLUSIONS

Early virgatids are characterized by the presence of dense bifurcate ribbing at early stages, followed by polygyrate or virgatotome ribbing. Microconchs developed a straight terminal aperture at the end of this stage reaching diameter of approximately 100 mm. Macroconchs continued their growth producing an evolute shell, twice as large in diameter, ornamented with weak polygyrate ribs that tend to change into bifurcate or even simple closer to the aperture. The only other group of latest Jurassic

ammonites that shows similar morphology of the sexual dimorphs is the British lineage of *Pectinatites*. It seems thus reasonable to propose ancestry for the Polish-Russian and Tethyan Virgatitidae in this lineage at the stage when dense juvenile ribbing was well developed but the apertural horn has not yet reached its specialized appearance.

This interpretation implies that the strata with *Pseudovirgatites* in central Poland are younger than the beds in Dorset with early *Pectinatites* (Fig. 6).

ACKNOWLEDGEMENTS

Significant part of the paper was prepared at the Geological Institute of the Greifswald University in 1988 during my scholarship granted by the Polish Academy of Sciences. The final version has been written while at the Institute of Geology and

Paleontology of the Tübingen University, where I have stayed as an Alexander von Humboldt fellow.

Dr. John C.W. Cope (University of Cardiff) has kindly commented the manuscript and improved its language.

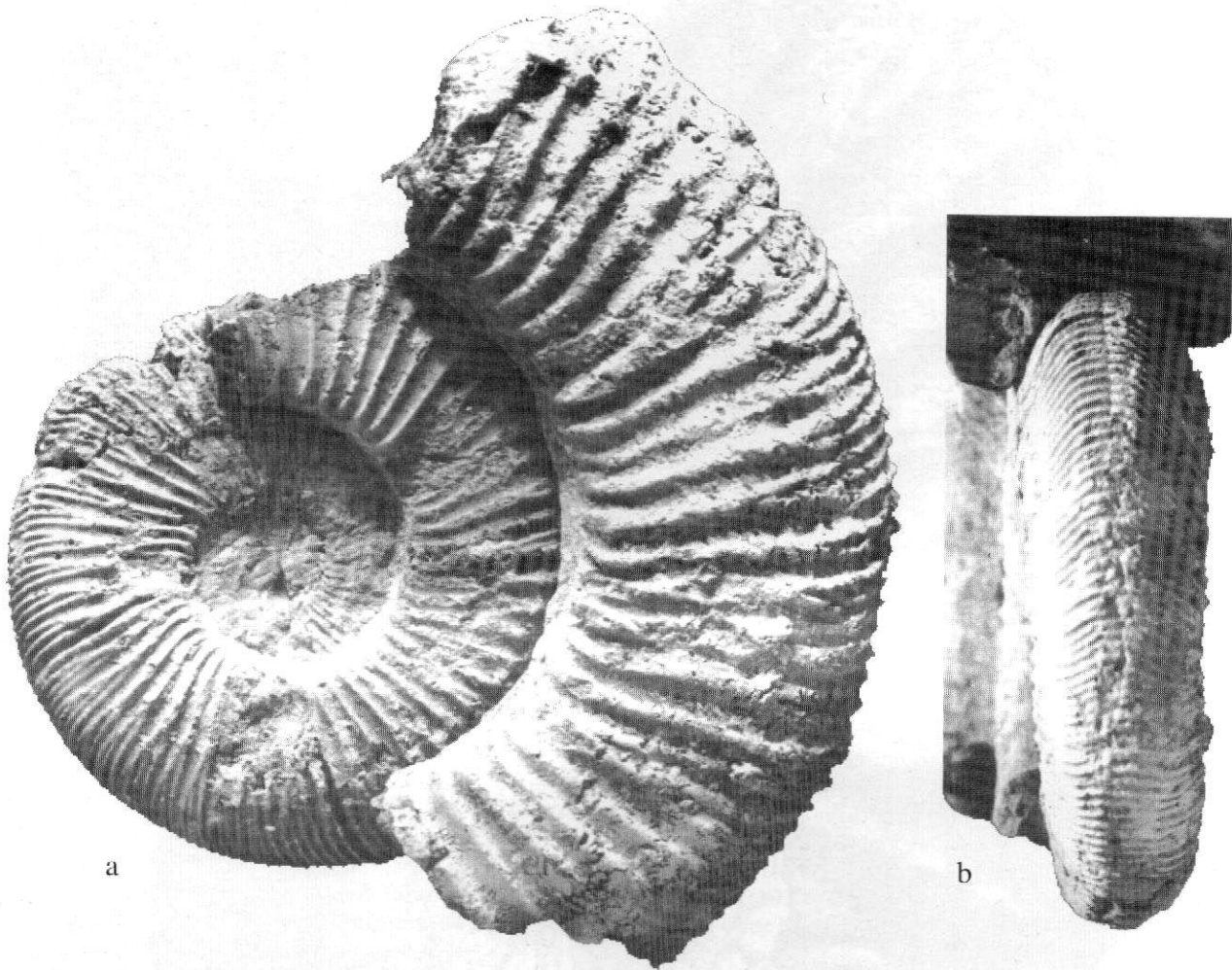
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Zarajskites pomerania (Arkell 1935), from Świętoszewo, Pomerania, NW Poland.

1. Macroconch, Dohm's (1925: p. 36, Pl. 2:3) original in lateral view, EMAUG collection; x 1.
2. Microconch in lateral (a) and ventral (b) views, EMAUG collection; x 1.

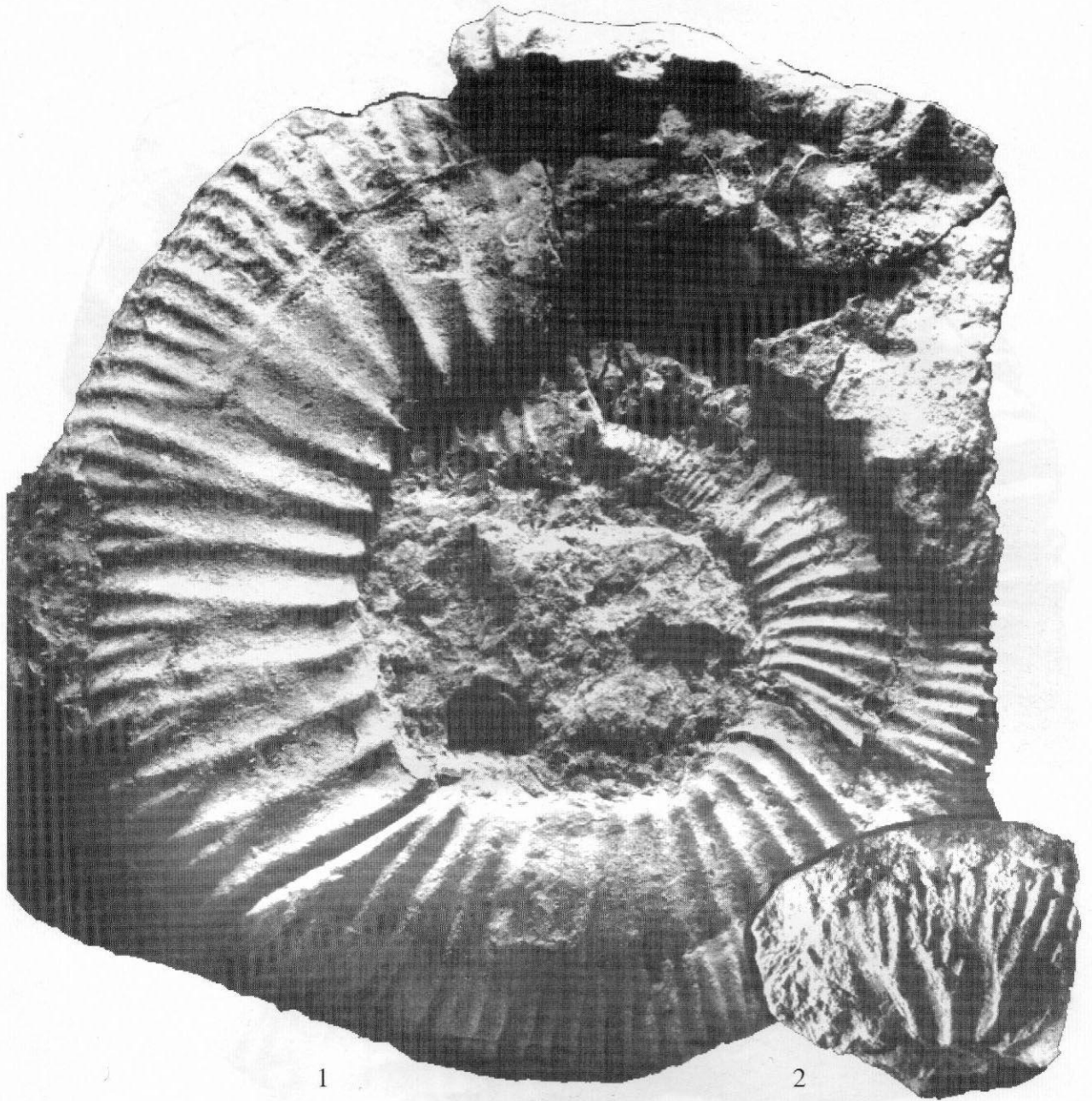


a

b

Zarajskites pomerania (Arkell 1935), from Świętoszewo, Pomerania, NW Poland.

1. Incomplete macroconch in lateral view (a) and ventral view of inner whorls (b), EMAUG collection; x 1.



Zarajskites scythicus (Vischniakoff 1882) from bed 52 of Czarnogłowy, Pomerania, NW Poland.

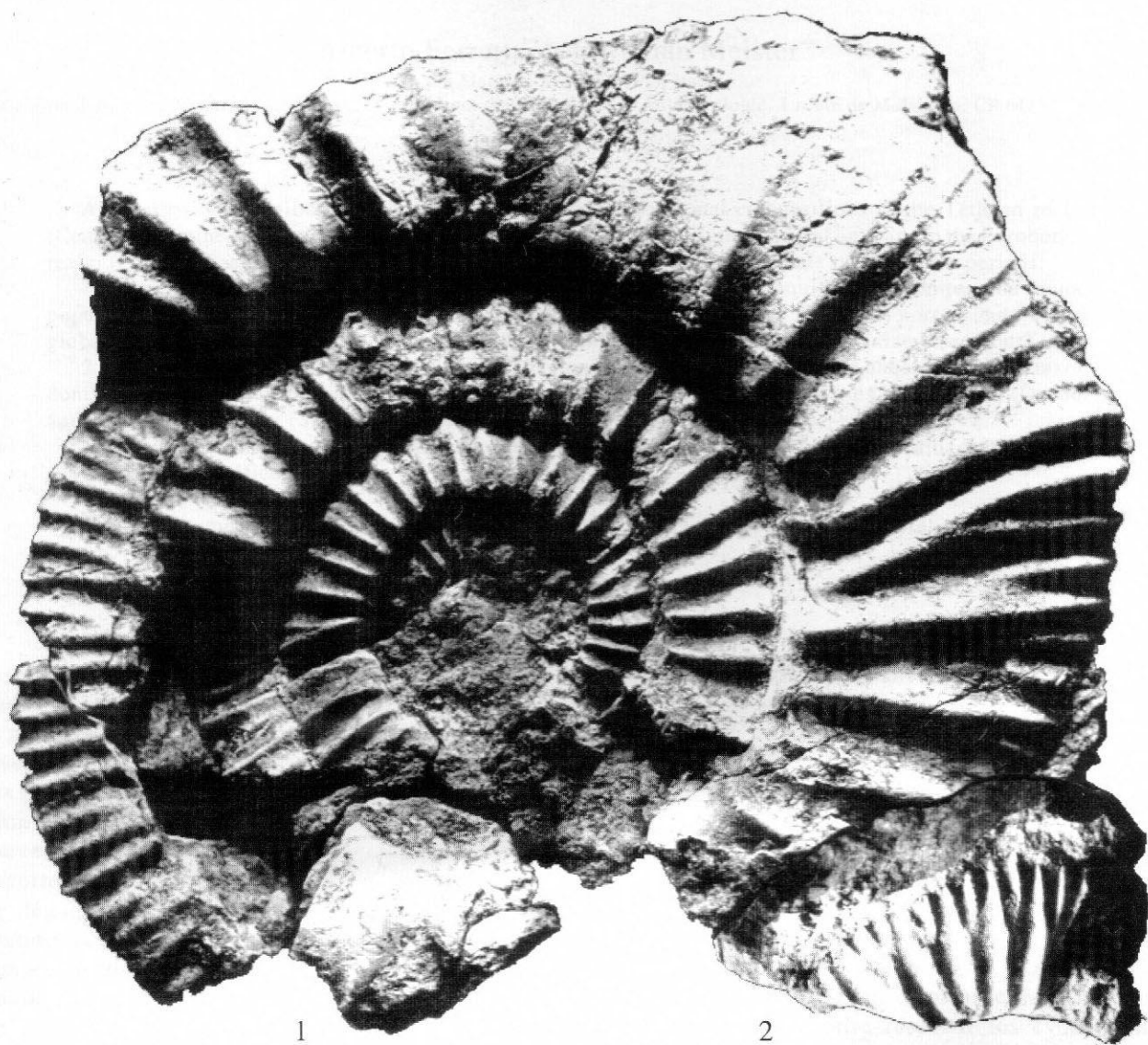
1. Crushed almost complete macroconch EMAUG Cz V-2, x1.

2. Fragment of microconch with virgatotome ribbing EMAUG Cz V-1, x1.



Zarajskites scythicus (Vischniakoff 1882) from bed 52 of Czarnogłowy, Pomerania, NW Poland.

1. Reverse side of the macroconch EMAUG Cz V-2 (see also Pl. 3:1) showing dense juvenile ribbing, x1.



Zarajskites scythicus (Vischniakoff 1882) from bed 52 of Czarnogłowy, Pomerania, NW Poland, coarsely ribbed morphs.
 1. Crushed almost complete macroconch EMAUG Cz V-3, x1.
 2. Fragment of microconch with bifurcate ribbing EMAUG Cz V-5a, x1.