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PALEONTOLOGY

Peristomal Modifications of Upper Jurassic Perisphinctids (Ammonoidea)

by

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Summary. The length of lappets, lateral apertural extensions of ammonites, is found to depend on the ultimate shell diameter. In the case of *Otosphinctes-Dichotomosphinctes-Dichotomoceras* fauna the length of lappets increases along with the increase of the ultimate shell diameter up to some 65 mm, showing thereafter a distinct trend to reduction and finally to complete reduction at diameters over 200 mm. Moreover, it seems that their macroconchs less than 200 mm in diameter were lappetted. The dependence of the length of lappets on the shell diameter does not support the hypothesis of a sexual function of the lappets but rather implicates that they were a ballast device acting when the shell growth finally ceased.

Introduction

Lappets, lateral apertural extensions of Jurassic ammonites, are the subject of remarkable interest since the last decades of the 19th century. The discussions primarily concerned two questions: (1) whether or not the lappets are signs of maturity of ammonites, and (2) what was their function. The positive answer to the former question was given by studies of Makowski [10] and others, whereas the latter is still debatable. Various authors attributed different but mostly sexual functions to the lappets (see [10, 6] for discussions of previous views). In the theory of sexual dimorphism in ammonites ([10, 4, 5] and references cited therein) the lappetted ammonites were interpreted as males or microconchs of larger forms with a simple sinuous peristome, interpreted as females or macroconchs.

Differences in the length of lappets were found in *Kosmoceras* faunas by Brinkman [2] and Lange [9] and interpreted in terms of dependence on the phylogenetic age of a species [9, p. 64]. In turn, the analysis of evolutionary series of Upper Jurassic *Aulacostephanus* fauna [16] showed complete reduction of lappets along with an increase of the ultimate shell diameter. If this is the case, then either Ziegler is right stating that "im Verlauf der Stammesentwicklung entstehen dabei Macroconchs aus Microconchs" [16, p. 79], or the lappets are the feature of ammonites with the final shell diameter not exceeding a certain size interval. A few evolutionary series displaying a distinct tendency to shell size changes are known at present,

e.g. *Glochiceras* and *Creniceras* [15, 16] and *Otosphinctes-Dichotomosphinctes--Dichotomoceras* [7, 3, 18]. The latter series appeared suitable for the analysis of changes in size and length of lappets versus the ultimate shell diameter.

Changes in the size of lappets in Oxfordian microconchs

The analysis was carried out on over 20 representatives of a relatively well-known evolutionary series of Upper Jurassic (Oxfordian) perisphinctids, *Otosphinctes→ Dichotomosphinctes→Dichotomoceras*, collected in the Częstochowa area, Polish Jura Chain, as well as on some other forms of this series figured in the literature (mostly by Arkell [1] and Enay [7]). Perisphinctids of this series and their close allies show a distinct tendency to increase the ultimate shell size [7] from some 40 mm or less to over 240 mm, which is followed by a decrease to less than 50 mm [3, 18]. The material available is rather innumerous, as forms with peristome are very rare, and those with measurable undamaged lappets are still scarcer. However, when the length of lappets is plotted versus the shell diameter, a distinct relationship is found (Fig. 1). The length of lappets markedly increases along with an increase of the shell size from about 35 to 60—70 mm. The largest lappet attained by the perisphinctid available (Pl. I, Photo 1) equals about 43% of the shell diameter. A relatively larger lappet — equalling about 48% — is displayed by *Perisphinctes* (*Otosphinctes*) *laisinensis* Lor. figured by Enay [7]. It may be mentioned here that in some other groups of ammonites the lappets are larger and, as far as we know, the record is held by *Kosmoceras castor* figured by Lange [9], which displays a lappet equal to 77% of the shell diameter. A further increase of the shell size does not lead to any further increase of either the relative or absolute length of lappets. Quite conversely, the curve of changes of the lappet length versus the ultimate shell size shows a distinct peak at about 65 mm diameter and gently descends thereafter (Fig. 1). It follows that the lappet length is no longer proportional to the shell diameter but, after reaching a certain maximum, it shows a distinct tendency to decrease. Although the number of specimens sufficiently preserved for studying these changes is rather small (about 10 plus those figured by other authors), any further trend to increase the length of lappets is improbable and a trend to their reduction seems to be marked. Specimens over 100 mm in size do not display lappets but rather elongate apertural lips. The apertural "lips" become narrower and shorter along with a further increase of the shell size and the lappet length/shell diameter ratio decreases down to 5% or less in the case of forms attaining about 180 mm in size (Fig. 1). It seems that specimens attaining over 200 mm in diameter may be completely devoid of lappets, as a few forms exceeding 180 mm in size and bearing relict lappets, if any, are available. It should be noted that the maximum size attained by a representative of the series, *Perisphinctes* (*Dichotomosphinctes*) *wartae bedoensis* Collignon figured by Malinowska [11], equals over 240 mm; unfortunately, the peristomal part of this specimen is broken off.

Along with the shell size reduction (*Dichotomosphinctes wartae* Buk. and its descendants; see [3, 18]), large lappets appear once more.

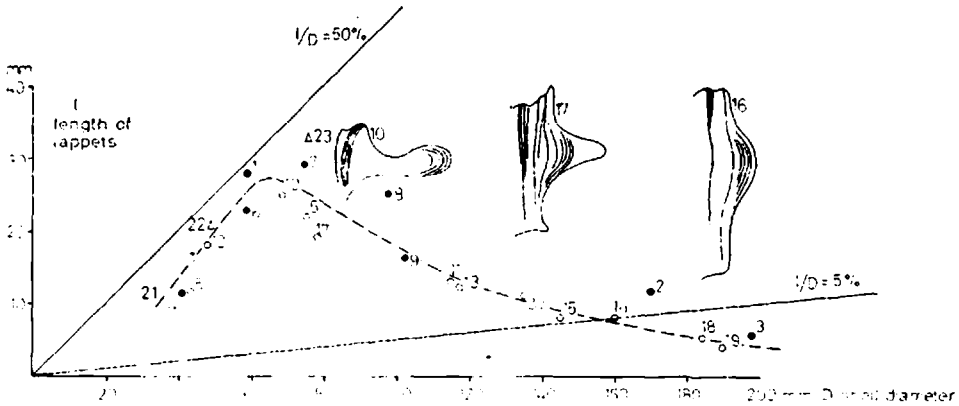

Figure 1. Length of lappets versus shell diameter of perisphinctids of *Otosphinctes→Dichotomosphinctes→Dichotomoceras* series

Forms figured by Enay [7]: 1 — *P. laisinensis* Lor. ([7], Pl. 32, Fig. 5), 2 — *P. elisabethae* Riaz ([7], Pl. 31, Fig. 4), 3 — *P. dobrogensis* Simion. ([7], Pl. 29, Fig. 4), 4 — *L. patturatensis* Lor. ([7] Text-fig. 123—6b), 5 — *P.* sp. n. aff. *P. trichoplocus* Gemm. ([7] Text-fig. 119—5). Forms figured by Arkell [1]: 6 — *P. ouatius* Buck. ([1] Pl. XVII, Fig. 5a), 7 — *P. rotoides* Ronch. ([1] Pl. XVI, Fig. 5; Diameter as read from Text-fig. 23), 8 — *P. rotoides* Ronch. ([1], Pl. XVI, Fig. 5), 9 — *P. auriculatus* Ark. ([1], Pl. B, Fig. 3).

Polish material from the Częstochowa area: 10 — *P.* (*Otosphinctes*) sp., Kl 8/×/52, Przybynów, Plicatilis Zone, Antecedens Subzone, 11 — *P.* (*Otosphinctes*) sp., Kl 16/20a, Jaworznik, Plicatilis Zone, Antecedens Subzone, 12 — *P.* (*Otosphinctes*) sp., Kl 25/61, Żarki, Plicatilis Zone, Antecedens Subzone, 13 — *P.* (*Otosphinctes*) sp., Kl 25/63, Żarki, Plicatilis Zone, Antecedens Subzone, 14 — *P.* (*Otosphinctes*) sp., Br 11/87, Prędziszów, Plicatilis Zone, Antecedens or uppermost Tenuicostatum Subzone, 15 — *P.* (*Dichotomosphinctes*) cf. *antecedens*. Salf., Br 11/036, Prędziszów, Plicatilis Zone, Antecedens Subzone, 16 — *P.* (*Dichotomosphinctes*) *wartae* Buk., Br 02/070, Zawodzie, Transversarium Zone, 17 — *P.* (*Dichotomosphinctes*) sp., Zawady, Transversarium or lower Bifurcatus Zone, coll. by A. Bittner; 18 — *P.* (*Dichotomosphinctes*) sp. ex gr. *wartae* Buk, Br 02/223, Zawodzie, Transversarium or uppermost Plicatilis Zone, 19 — *P.* (*Dichotomosphinctes*) sp., Zawodzie, Transversarium or uppermost Plicatilis Zone, 20 — *P.* (*Dichotomoceras*) sp., Biskupice, Bifurcatus Zone.

For comparison: 21 — *Mirosphinctes niedźwiedzkii* (Siem.) (Enay, [7], Text-fig. 160-3), 22 — *Nebrodites* (*Passendorferia*) *czenstochovensis* (Siem.), Kl. 25/52, Żarki, Plicatilis Zone, Antecedens or upper Tenuicostatum Zone, 23 — *N.* (*P.*) *birmensdorfensis* (Mo esch), Zawady, Transversarium Zone, coll. by A. Bittner

The review of literature on Oxfordian perisphinctids of this evolutionary series revealed several lappetted forms (figured by Arkell [1], Enay [7] and others), which generally match the above scheme (Fig. 1). In the case of other Oxfordian perisphinctids there are certain differences with respect to that scheme, particularly in the case of more involute forms such as *Subdiscosphinctes*,? *Rasenia* (Pl. I, Photo 6) displaying lappets shorter and more lip-like at the comparable diameters.

Quenstedt ([12], Pl. 94, Figs. 54—55) figured two peristomal fragments of Malma perisphinctids identified as *Ammonites* cf. *plicatilis* and *A. ernesti*, respectively. These perisphinctids, attaining presumably over 200 mm in diameter, display fairly large lappets. However, even if those forms belong to the *Otosphinctes-Dichotomosphinctes* series they would fit the above scheme of the relative reduction of the length of lappets, as in that case the lappet length/ultimate shell diameter ratio would be less than 10%.

Analyses of lappeted *Orthosphinctes* and *Ataxioceras* figured by Quenstedt [12] and Geyer [8] implicate that in those groups the peak of the curve of the lappet length versus the ultimate shell diameter appears somewhat later, at about 90 mm in diameter. It is possible that in some groups it may be marked earlier.

It follows that after reaching a certain diameter representatives of a given evolutionary series may have lost lappets. Therefore the passage from *Aulacostephanus volgensis* to the macroconch-like, lappet-less *A. autissiodorensis* [16] seems fairly probable and the find of transitional forms with reduced lappets would be its unequivocal evidence.

The problem of the shape of peristome of small-size macroconchs

An opposite question arises — whether or not a decrease in size of macroconchs leads to the appearance of lappets in macroconch series. Here the data are still scarcer, as macroconchs from periods of far-going size reduction during the Oxfordian [3] are still little known. The corresponding strata yield some small Mediterranean *Kranaosphinctes* about 200 mm in diameter and characterized by variocostate ribbing (typical of macroconchs — [4], p. 28, [17], p. 156) and with the rostrum-type peristome, regarded as characteristic of microconchs (see [4], p. 28, [14], p. 9). Representatives of this group, which measure about 180 mm in size, display ornamentation transitional between iso-and variocostate ones (Pl. V, Photos 1, 2), but, unfortunately, their peristomes are damaged. There is also a single form (Pl. VI, Photo 2) about 100 mm in size, lappetted and displaying sculpture closer to that of the macroconches allocated in *Kranaosphinctes* than to that of their microconchs, some *Otosphinctes* [7].

Moreover, there are some variocostate forms assignable to the subfamily Idoceratinae (see Pl. VI, Photo 1 and Text-fig. 2) with the peristome of the microconch lappetted type.

Little is known about small-sized macroconchs, the sexual counterparts of the *Otosphinctes* (proper)→*Dichotomosphinctes*→*Dichotomoceras* series. Dwarfish macroconches of *Dichotomoceras* recently identified (Brochwicz-Lewiński, in preparation; see [3], Pl. VI, Photo 1), attaining about 200 mm in size, have the peristome broken off. There are some early *Arisphinctes* or *Perisphinctes* s. stricto, measuring about 200 mm in size. The forms do not achieve ridge-like ribs on the final body chamber, which are typical of this group, but may hardly be considered as immature (approximated suture, the final body chamber almost a whorl long). The peristomes displayed by them are similar to those found in small-sized *Kranaosphinctes*, i.e. closer to those of giant microconchs than to the ones typical of full-size macroconchs (see Pl. III).

Conclusions

1) The lappet size appears somewhat dependent on the shell size. In an evolutionary series or population of closely related ammonites differing in size it is possible to find a size interval at which the lappets attain the maximum length and size. Shells exceeding that size interval bear progressively smaller lappets, if any. The process of lappet reduction may be reversible in a given series.

2) The length and size of lappets may also depend on the mode of shell coiling. In perisphinctids, more involute forms such as *Subdiscosphinctes* and ? *Rasenia* bear generally smaller and shorter lappets than *Otosphinctes*→*Dichotomosphinctes*→

Dichotomoceras fauna at the comparable diameters. Generally, the more involute a perisphinctid, the smaller its lappets.

3) It is possible that large-size ammonites (macroconchs) devoid of lappets obtain them along with the shell size reduction (or had them before attaining the large ultimate sheel size); in such a case "macroconchs" would give rise to "microconchs" (or vice versa). Therefore it is also possible that both macro- and microconchs bore lappets in the times of size reduction or dwarfism and not in the times of gigantism.

4) The above phenomena of lappet length reduction along with the increase of the ultimate shell size or shell involuteness make it necessary to reevaluate the criteria for the identification of micro- and macroconchs. But it should be noted that it is not in contradiction with the phenomenon of sexual dimorphism in ammonites, as it was admitted by Makowski ([10], p. 56) that "in my ammoncids the apertures of large and small forms show no differences at all".

5) It is also desirable to reevaluate the association of the lateral lappets with the sexual function, suggested by several authors (see [10, 13, 6] and others). The fact that the lappets may disappear in certain shell-size intervals speaks against the above assumption. It should be taken into account that lappets "may have added weight anteriorly to alter the orientation of the conch" ([6], p. 64). Such a function of the lappets seems to be confirmed by the occurrence of certain forms such as *Cleistosphinctes* Arkell, 1953, and similar ones with lappets projected downwards and embracing the sides of preceding whorls or even umbilicus and thus hardly applicable to any sexual function. The latter point of view is also supported by a high variability in shape of lappets, observed even in the case of a single species of *Kosmoceras* [9] and of the series discussed here. If it is the case, then along with the increase of the shell size and weight the ballast device of the lappet type would be less and less effective. Therefore, it seems that the above-described phenomenon can be explained much more easily if lappets are assumed to have an asexual function.

If the ballast function of the lappets is the case, then their appearance at the end of the shell growth may be explained in two ways: (1) they were formed in order to compensate for the effect of the rapidly growing sexual organ on the shell buoyancy or, which is less probable, (2) to reestablish the shell buoyancy in a new environment —but here it is also necessary to assume that the ammonites grow and mate in different environments).

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REFERENCES

[1] W. J. Arkell, *A monograph on the ammonites of the English Corallian Beds*, I—XIV, Palaeont. Soc. Mon., London, 1935—1948.

[2] R. Brinkmann, Abh. Ges. Wiss. Göttlingen, math. phys. Kl., N. F., **13** (1929), 1—123.

[3] W. Brochwicz-Lewiński, Z. Różak, *Time-changes in Oxfordian ammonite fauna of the Polish Jura Chain; some reflections*, Bull. Acad. Polon. Sci., Sér. Sci. de la Terre, **22** (1974), 113—125.

[4] J. H. Callomon, Trans. Leicester lit. phil. Soc., **27** (1963), 21—56.

[5] — , *Dimorphism in Jurassic ammonites; some reflections*, in: G.E.G. Westermann (ed.), *Sexual dimorphism in fossil metazoa and taxonomic implications*, IUGS Series A, No. 1, E. Schweizerbart'sche Verlagsbuchhandlung, pp. 111—121, Stuttgart, 1969.

[6] R. A. Davis, Bull. Am. Paleont., **62** (1972), 27—130.

[7] R. Enay, Nouv. Arch. Mus. Hist. Natur. Lyon, **8** (1966), 1—624.

[8] O. F. Geyer, Palaeontographica, Abt. A, **117** (1961), 1—157.

[9] W. D. Lange, Munster Forsch. Geol.-Paläont., **27** (1973), 1—209.

[10] H. Makowski, Palaeontologia Pol., **12** (1962), 1—92.

[11] L. Malinowska, Acta Palaeont. Pol., **17** (1972), 167—1242.

[12] F. A. Quenstedt, *Die Ammonites des schwabischen Jura. III. Der Weiss Jura*, E. Schweizerbart, pp. 816—1140, Stuttgart, 1888.

[13] P. C. Sylvester-Bradley, *Comparative and functional sex in Ostracods and Cephalopods*, in: G.E.G. Westermann (ed.), *Sexual dimorphism in fossil metazoa and taxonomic implications*, IUGS Series A, No. 1, E. Schweizerbart'sche Verlagsbuchhandlung, pp. 243—258, Stuttgart, 1969.

[14] G. E. G. Westermann, *Form, structure and function of shell and siphunucle in coiled mesozoic ammonoids*, Life Sci. Contr., **78**, Royal Ontario Mus. (1971), 1—39.

[15] B. Ziegler, Evolution, **13** (1959), 229—235.

[16] — , Jh. Ges. Naturkunde Wurttemberg, Jh. **127** (1972), 75—79.

[17] A. Zeiss, *Dimorphismus bei Ammoniten des Unter-Tithon*, in: G. E. G. Westermann (ed.), *Sexual dimorphism in fossil metazoa and taxonomic implications*, IUGS Series A, No. 1, E. Schweizerbart'sche Verlansbuchhandlung, pp. 155—164, Stuttgart, 1969.

[18] Dara-Moni Duong, *L'Oxfordien moyen et supérieur à facies grumeleux de la cluse de Chabrières (Basses-Alpes): milieu de sedimentation, biostratigraphie, paléontologie*, D. Sc. thesis, Universite Claude Bernard—Lyon, No. d'ordre: 138, Lyon, 1974,

В. Брохвич-Левиньски, З. Ружак, **Модификации апертуры верхнеюрских перисфинктов**

Содержание. Длина апертуральных ушков перисфинктов оказывается быть зависимой от диаметра раковины. В случае аммонитов из эволюционной серии *Otosphinctes→Dichtomosphinctes→Dichotomoceras* длина ушков увеличивается вместе с ростом диаметра раковины до диаметра 65 мм. Для больших диаметров свойственна редукция абсолютной и относительной длины ушков. Образцы достигающие размеры свыше 200 мм диаметра могут вообще быть избавлены ушков. Не исключено, что макроконхи самок достигающие в диаметре менее 200 мм обладали ушками. Зависимость длины ушков от конечной величины раковины является противоречащим доказательством гипотезы усматривающей в ушках их полоыую функцию. Найболее вероятным кажется, что ушки исполняли роль баласта [6].

PLATE I

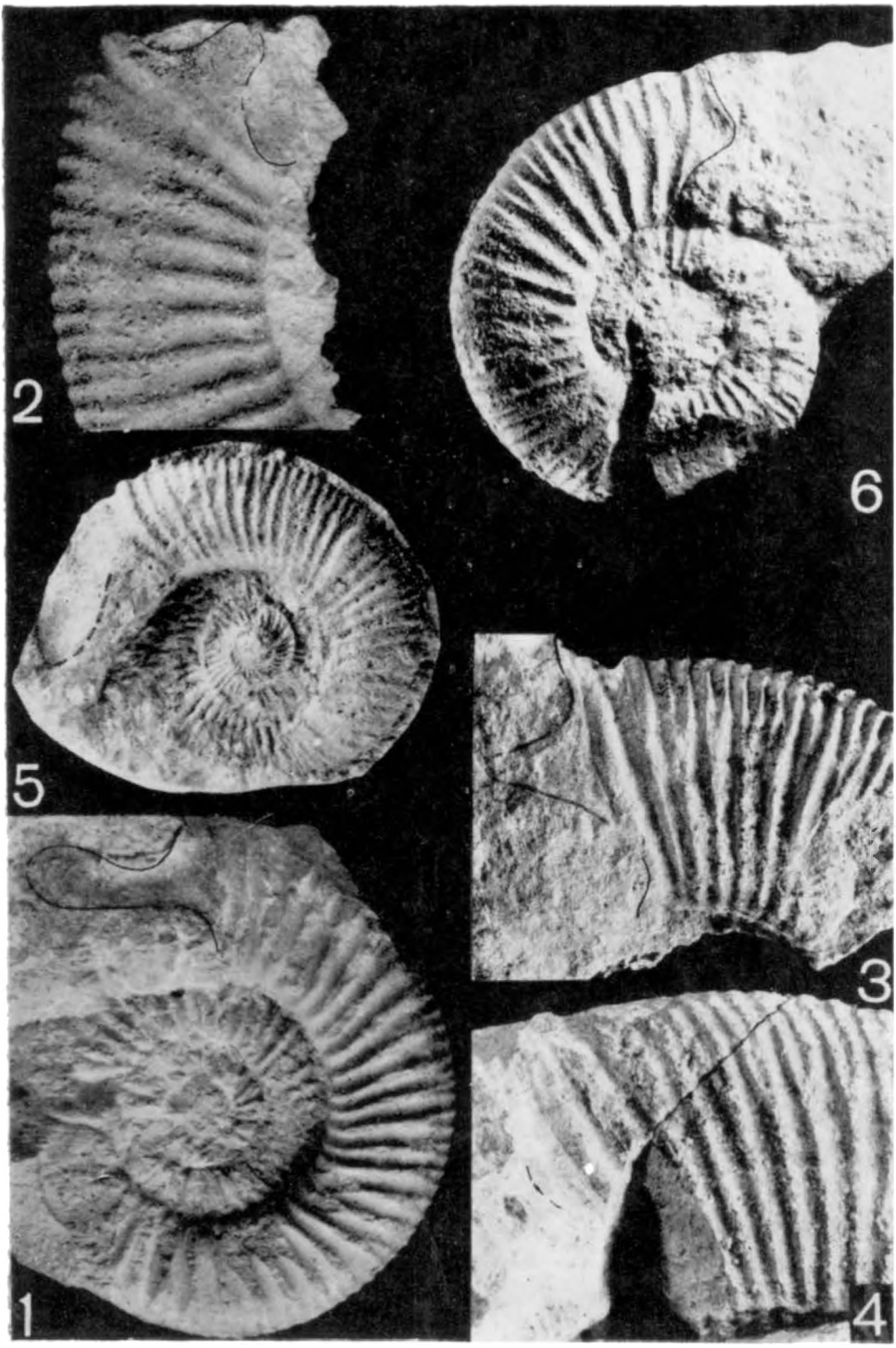

Photo 1. *Perisphinctes* (*Otosphinctes*) sp., Kl 8/×/52, *D* (diameter) — 69 mm, Przybynów
Photo 2. *P.*(*O.*)sp., Kl 25/71, *D* — 117 mm, Żarki
Photo 3. *P.*(*Dichotomoceras*) sp., Br 36/A/011, *D* — 125 mm, Biskupice
Photo 4. *P.* (*Dichotomosphinctes*) *wartae* Buk., Br 02/070, *D* — 160 mm, Zawodzie
Photo 5. *Nebrodites* (*Passendorferia*) *czenstochovensis* (Siem.), Kl 25/52, *D* — 49 mm, Żarki
Photo 6. ? *Rasenia* sp., R — 171a, *D* — 62 mm, Niegowonice

PLATE II

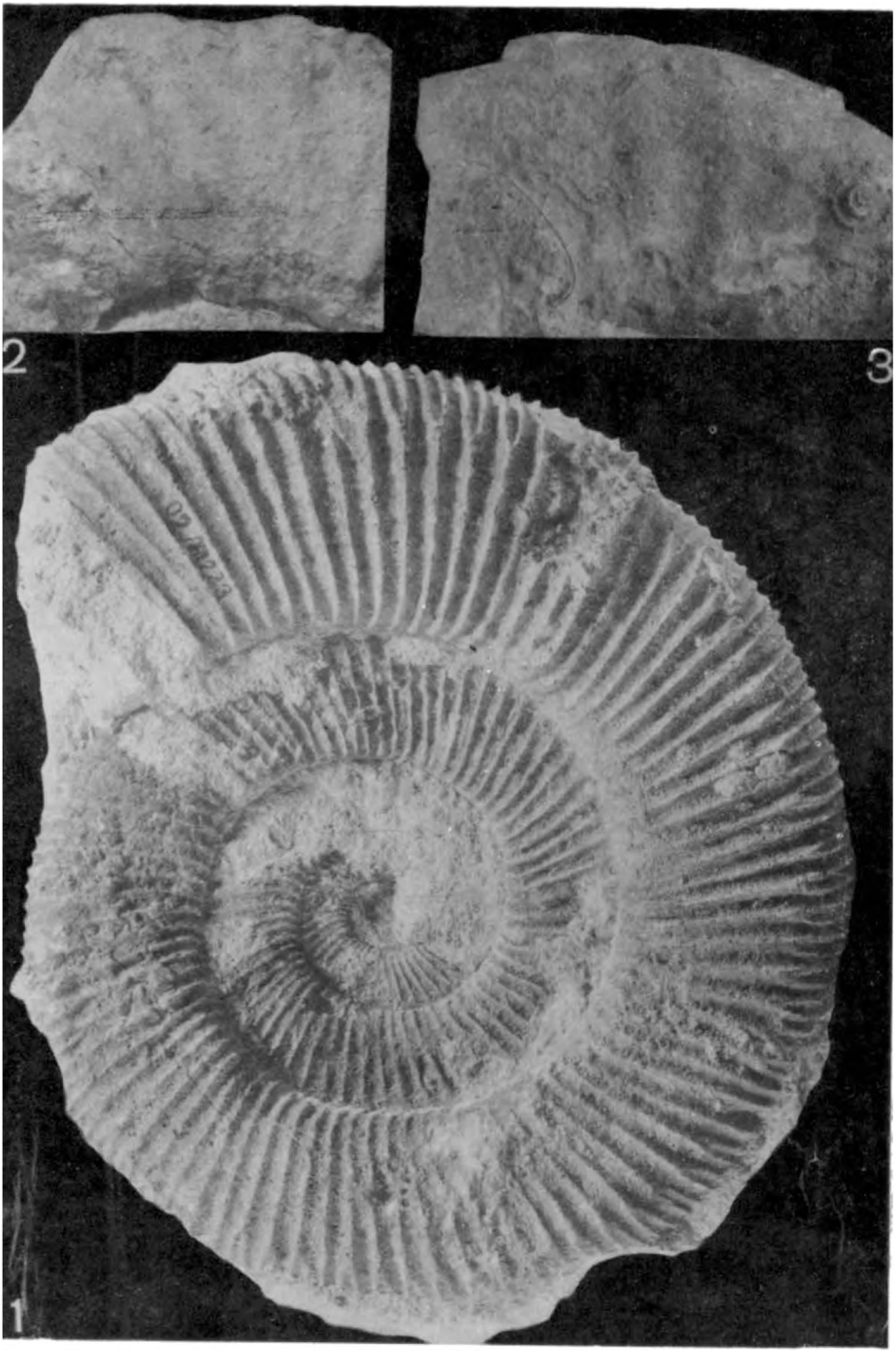

Photo 1. *Perisphinctes* (*Dichotomosphinctes*) sp. ex gr. *wartae* Buk., Br 02/223, *D* — 184 mm, Zawodzie
Photo 2. Peristome of macroconch *Perisphinctes* (*Perisphinctes*) cf. *cautisnigrae* Ark., Br 05/202, *D* — 340 mm, Zawodzie
Photo 3. Peristome of macroconch *Subdiscosphinctes* (*Aureimontanites*) sp., Br 36/F/002, *D* — 281, Choroń

PLATE III

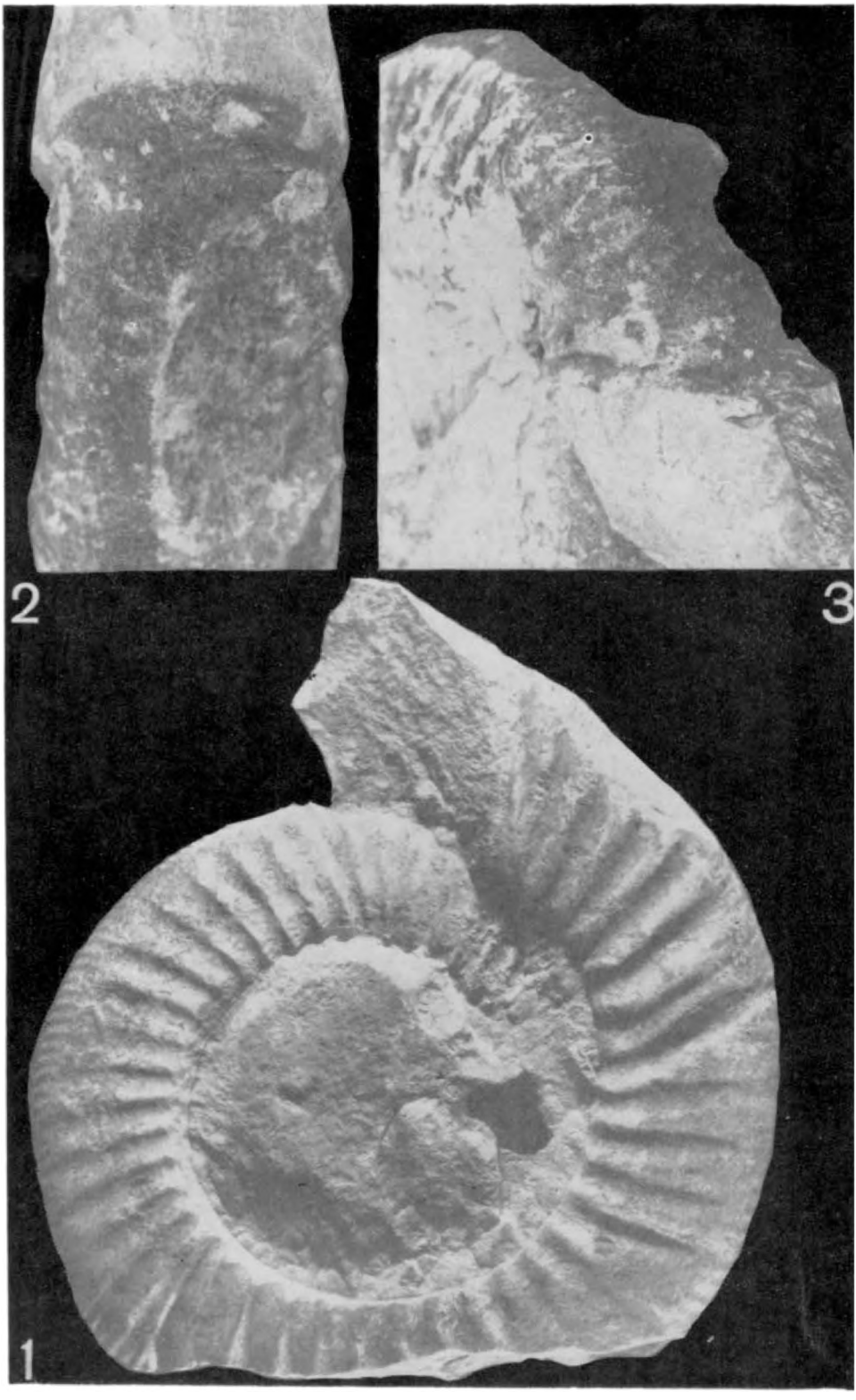

Photo 1. *Perisphinctes* (*Arisphinctes*) sp., Kl 25/91, *D* — 240 mm, Żarki
Photo 2. Ventral view of the peristome of the above specimen
Photo 3. Latero-ventral view of the peristome of the above specimen

PLATE IV

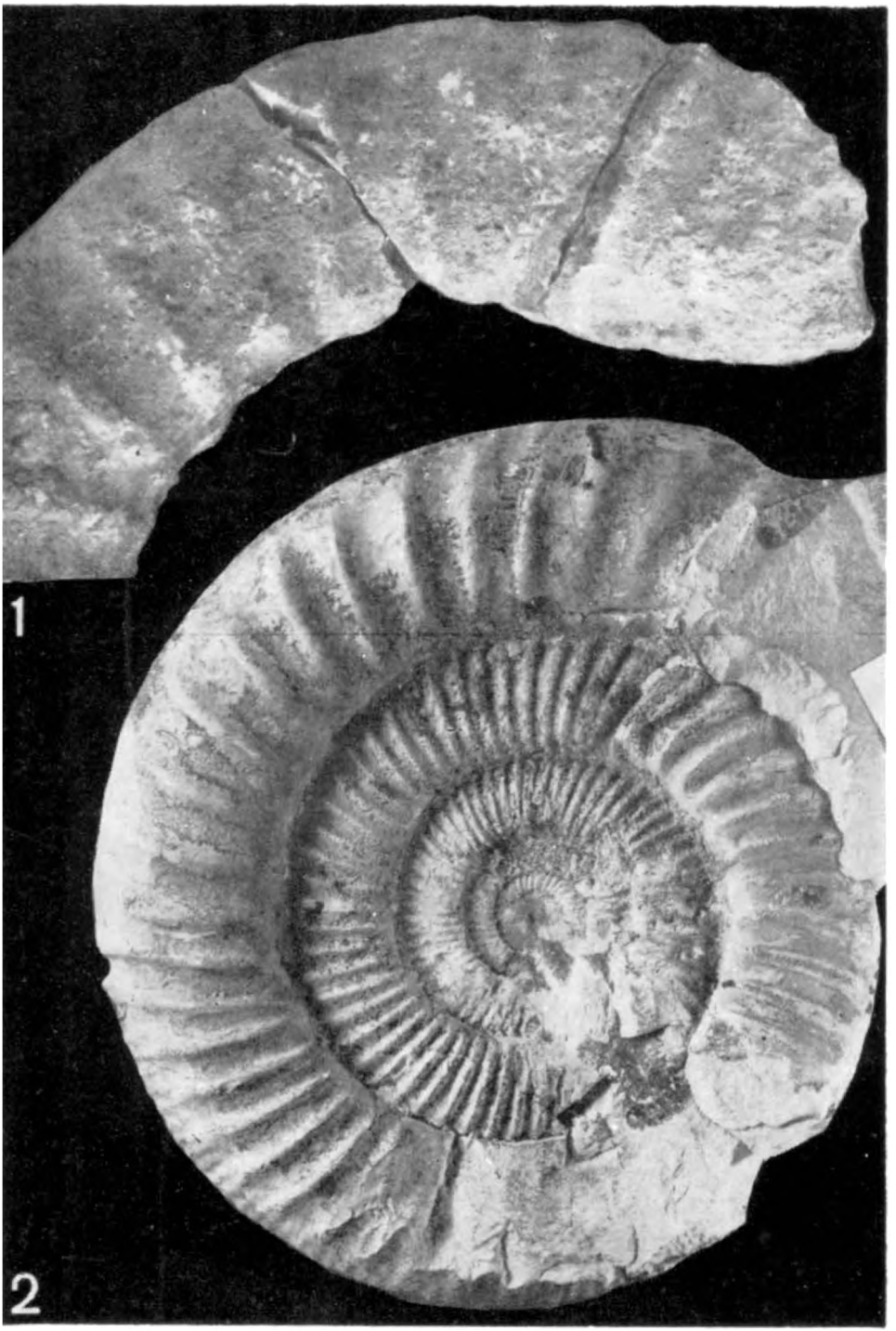

Photo 1. Peristomal part of *Kranaosphinctes* cf. *decurrens* Buck., Kl 25/41, *D*—230 mm, Żarki
Photo 2. *Kranaosphinctes* of the *K. promiscuus* group (Kl 16/2/51, *D* — 231 mm, Jaworznik) displaying peristome of the rostrum type

PLATE V

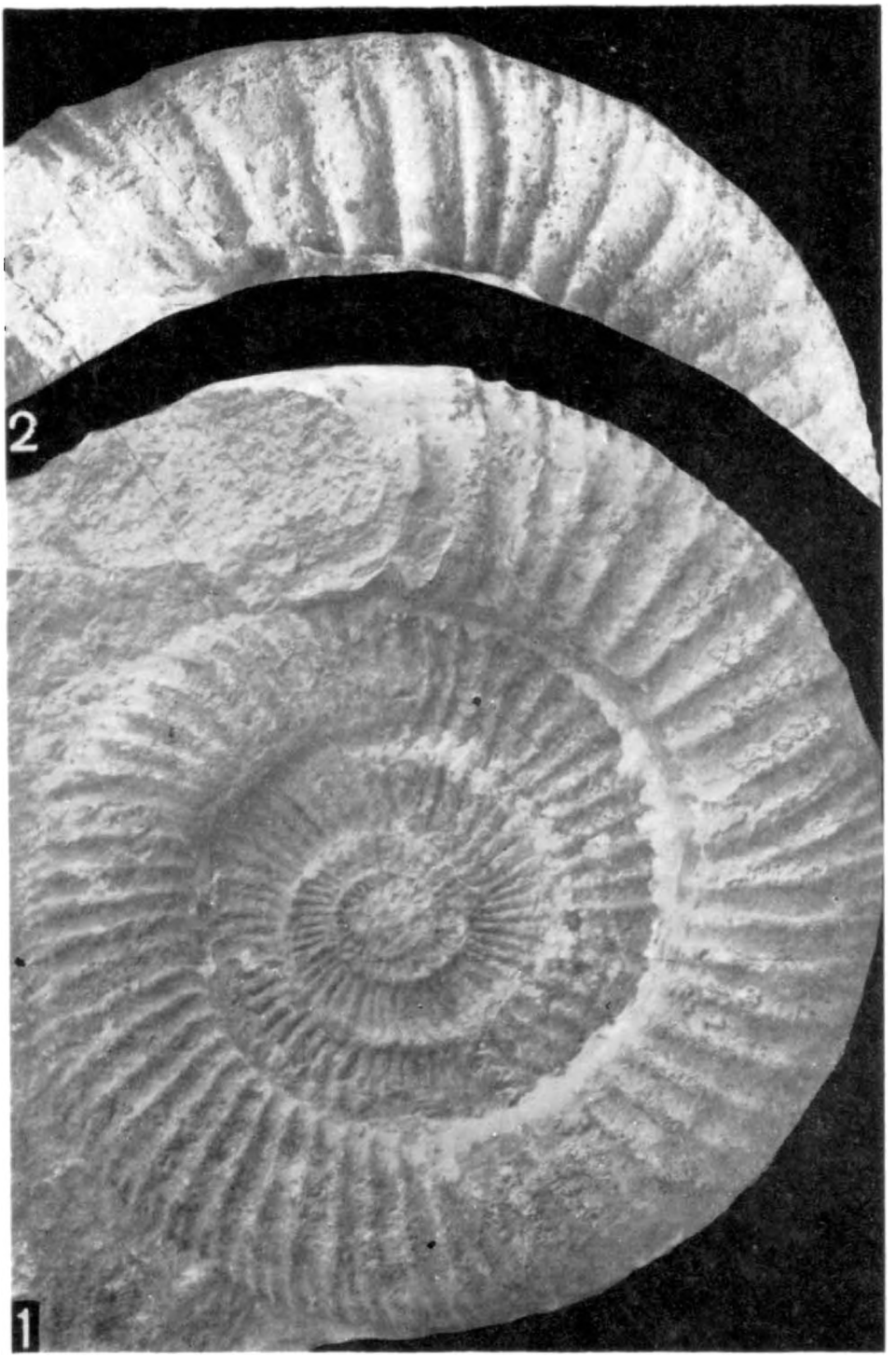

Photo 1. *Kranaosphinctes* of the *K. promiscuus* group (Kl 25/81, *D* — c. 180 mm, Żarki)
Photo 2. End part of the final body chamber of the above specimen displaying ornamentation of the macroconch type

PLATE VI

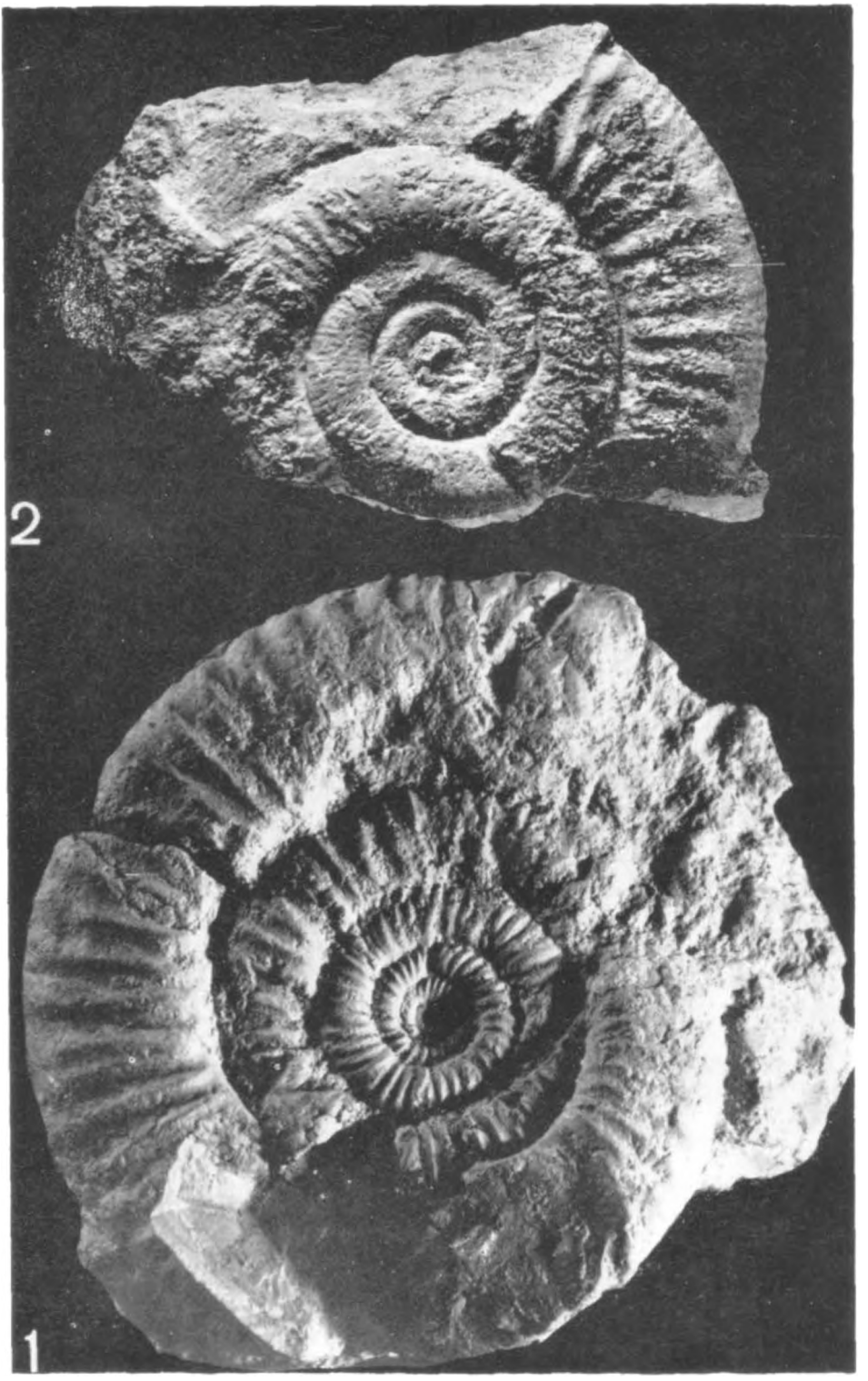

Photo 1.? *Kranaosphinctes* sp. (*D* — 103 mm, Bleszno): a form with fragmentarily preserved prominent lappets. Ornamentation of the final body chamber closer to that of the *Kranaosphinctes promiscuus* group than to that of their microconchs — *Otosphinctes*

Photo 2. Lappetted ammonite, presumably a macroconch from the family Idoceratinae; Br 25/006, *D* - c. 90 mm, Skrajnica