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GENUS *POLONIPRODUCTUS* NOV. (BRACHIOPODA, DEVONIAN)

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A new devonoproductid genus *Poloniproductus* is described with the Eifelian *Productella varians* Biernat, 1966 as a type species. The Devonoproductinae Muir-Wood et Cooper are elevated to the familial rank. Taxonomic and evolutionary aspects of the genus and family are briefly discussed.

Key words: Brachiopoda, phylogeny, taxonomy, Middle Devonian, Eifelian, Poland.

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INTRODUCTION

Re-examination of the Middle Devonian (Eifelian) productaceans of Poland proved the presence of a new member of the devonoproductids, *Poloniproductus* gen. n., with *Productella varians* Biernat, 1966 as a type species. This species coming from the brachiopod shales (Skaly Beds of the Świętokrzyskie (Holy Cross) Mts: Biernat 1966) is described in details and figured. The new genus is one of the oldest known members of the devonoproductids. It shows, apparently, a few morphological features of productellids, mostly expressed in the structure of the pedicle valve and not included in the diagnosis of subfamily Devonoproductinae Muir-Wood et Cooper, 1960. This group differs sufficiently enough in the morphology and evolutionary characters from the other productaceans to be removed from the family Productellidae (Johnson 1976). As a result, this group is here treated as a separate family named Devonoproductidae Muir-Wood et Cooper, 1960, and a few other genera are attributed to it. As show the recent studies (Lazarev 1986, Biernat and Lazarev this paper) devonoproductids, although moderately differentiated, constitute a quite characteristic brachiopod group.

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OUTLINE OF THE DEVONIAN PRODUCTACEANS PHYLOGENY

The Australian *Chattertonia campbelli* ("*Spinulicosta*" *campbelli* Chatterton, 1973), was until now the earliest species known of the genus *Chattertonia* Johnson. This species is of late Early Devonian and possibly Middle Devonian (?Givetian) age and was a productoid genus assigned, at first, to the family Productellidae (Johnson 1973: 789). Recently, a new species of *Chattertonia*, *Ch. sinensis* Wang Yu et Rong Jia Yu has been found in the Yukian Formation (China) corresponding to *Nowakia zlichoviensis* Zone, Early Eifelian (Dr. Rong Jia Yu's oral communication).

Johnson followed Chatterton's discussion (Chatterton 1973: 79—80) on evolutionary problems of both the early productellids like "*Spinulicosta*" *campbelli* (?related to chonetoids in possessing, among others, characteristic anderidia) and of productellids as a whole (?evolved from some irregularly costate chonetoids). Furthermore, Johnson recognized also linkage of *Chattertonia* with chonetoids as being very probable.

Two years later, Johnson in his phylogenetic scheme suggested for the Middle Devonian productacean genera, interpreted the genus *Chattertonia* as the ancestor for two diverging branches (named families), namely Productellidae and Leioproductidae (Johnson: 1978: fig. 4). Moreover, he included *Chattertonia* in the family Leioproductidae together with *Devonoproductus* and an unidentified species from the Eifelian of Canada cited as "*Productella*" sp. (Perry *et al.* 1974). Note that this Canadian form appears to be a quite characteristic devonoproductid.

However, there appears some controversy when considering both the generic contents of the family Leioproductidae and the use of the familial name in the context of the genus *Devonoproductus* and its allies.

Firstly, an assignment of *Chattertonia* and *Devonoproductus* to the same family seems unjustified. *Chattertonia* in its shell outline and the general morphology (i.e. linear to sublinear area — ginglymus, spine ridges on the pedicle valve, no pseudodeltidium) has much more in common with the genus *Spinulicosta* (Johnson 1976: 790, compare Chatterton 1973: 79—80) or *Productella* Hall than with *Devonoproductus*.

Secondly, the inclusion of *Devonoproductus* in the family Leioproductidae (compare Muir-Wood and Cooper 1960, Johnson 1976) may be questioned, for this could suggest that *Leioproductus* and the related genera

are phylogenetically very close to *Devonoproductus* and its allied forms. Altogether, it can be said that *Leioproductus*, in contrast to *Devonoproductus*, is more clearly allied to the productellid group (compare also Lazarev 1986). This may be inferred mostly from the general shell morphology (i.e. shell spinous and rugose) and phylogeny (probably derived out of productellids). The early Middle Devonian *Productella* is the likely ancestor of *Leioproductus* and its allies.

Based on the modern data, *Leioproductus* is known to occur in the Late Devonian (*Clymenia* Zone) and leioproductids as a group appear in the Early Famennian (? via *Ardiviscus* Lazarev; fig. 1). This group is recognized to be the first within productids to develop a comparatively high visceral cavity. Apparently, this cavity is associated with the ptychoporous lophophor (characteristic of Productidina) of the Falafer type (Grant 1972). Such a cavity, together with "trails", may be used as highly significant characters which separate members of leioproductids from *Productella*.

Devonoproductus, the type genus of subfamily Devonoproductinae Muir-Wood et Cooper, 1960 appears already in the Middle Eifelian ?via *Poloniproductus*. The genus *Devonoproductus* seems phylogenetically related especially with a group of genera assigned to a separate subfamily Eoproductellinae Rzonnsnitskaya (*sensu* Lazarev 1986; herein fig. 1) which reveals the surface radial striation inherited from chonetids. It is worth mentioning that within members of this subfamily some tendency occurs of weakening to a varying degree of radial striation or, even, of its loss in part. For instance, *Striatoproductella* shows delicate radial striation on the brachial valve only and *Poloniproductus* is devoid of striae altogether but this may be a secondary character.

Eoproductellines appear in the Early Devonian and the ?Early Siegenian *Eoproductella* is the probable ancestor. Note that it is not unlikely, after all, that devonoproductids could arise also amongst the early productellids, similarly as linoproductids, by developing, among other features, lamellose and non-spinous brachial valve. But even if so, there is no doubt that *Devonoproductus* differs sufficiently enough from *Leioproductus* in its phylogeny and morphological aspects (i.e. low visceral cavity, divided cardinal process, the developed series of dorsal trails, marginal ridges and dental cavities). Therefore, no reason remains to include the genera discussed in the same family, and there is enough evidence to consider them as members of two separate families: Leioproductidae and Devonoproductidae.

Finally, one can argue that devonoproductids could be derived from some eoproductellids (or productellids). Subsequently from devonoproductids could derive such genera as *Productina* Sutton and *Poloniproductus* gen. n.

the Middle Devonian (Givetian) *Devonoproductus* sp. from the Świętokrzyskie Mountains, Poland (pl. 18: 3; pl. 20: 16). Some or all of these ornamental structures in the adult stage could play a role of "trails" at the time of their growth at the valve margin" (Brunton 1985). However, they remain comparatively rather short in all known devonoproductids — and this seems to be a general character also of all of the non-geniculate species (Brunton 1985).

In our material only one specimen of *Devonoproductus* aff. *sericeus* (Buch) from the Frasnian of Timan, USSR, preserves a series of lamellae which are longer on the anterior half of the brachial valve and much shorter posteriorly (fig. 3). It seems possible that in the living condition these concentric elements on the posterior part of the brachial valve were originally short and do not result of a later fragmentation.

As viewed in longitudinal and cross sections, *Poloniproductus varians* in fully grown shells (up to about 26 mm in length) shows in the most posterior part of the brachial valve, just beneath the beak, very few rugae irregular, slightly wavy in appearance and spacing (pl. 19: 1, 2; pl. 20: 16; fig. 2).

All subsequent concentric lamellae are usually present on the anterior half of valve, corresponding to the adult stage or almost so; some even splitting, being, however, generally of limited range (pl. 20: 1a). Some of the lamellae, at an appropriate period of growth, could be interpreted also as trails. Lamellae, as a rule, are delicate and rather densely arranged, much as in, for example, the Carboniferous *Productina pectinoides* (Phillips) from Spain (Prinz 1969: fig. 15) in which, however, such structures are comparatively longer.

In the Carboniferous productids a series of dorsal trails is confined to the marginal rim (= margin of visceral disc) as, for example, in the Marginiferinae (*sensu* Lazarev 1984), or the diaphragma in Productininae

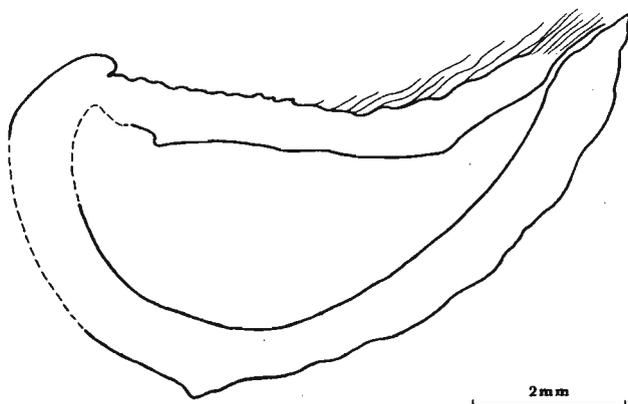


Fig. 2. *Poloniproductus varians* (Biernat) from the Eifellian of the Świętokrzyskie Mountains, ZPAL Bp. XV/5: longitudinal section of the shell with short dorsal lamellae.

(*sensu* Lazarev 1984). Hence, it seems quite evident that these structures started to develop after the visceral regions attained their complete growth as in, among others, *Levitusia* Muir-Wood et Cooper (Brunton 1981). In other words, this could mean that the trails appeared generally late in ontogeny, for example, in adult (shell relatively large) but not yet old individuals. This is why Lazarev (1981, 1984) suggested the time of the trails appearance in *Productus* sp. as corresponding with maturity of an animal and thus he correlated their succeeding appearance with breeding cycles (compare Brunton 1985).

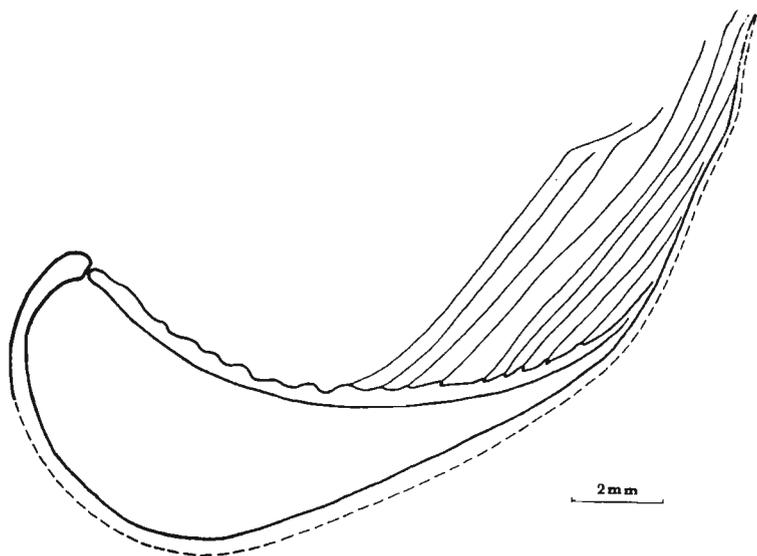


Fig. 3. *Devonoproductus* aff. *sericeus* (Buch) from the Upper Devonian (D₃fr₂), vetlo-sljanskaya svita, Timan, Ukhta river, USSR: longitudinal section of the shell showing long dorsal lamellae.

It would appear that trails are rather highly specialized morphological structures evolved in specialized, short living (throughout the Middle-Late Devonian — Permian time) groups of productaceans. Within Eifelian devonoproductids the lamellae (trail elements) have irregular spacing (fig. 2). Those achieved by the Givetian-?Famennian devonoproductids are distinct and comparatively long elements regularly arranged on the anterior half of the brachial valve (fig. 3). Within other Carboniferous and Permian productaceans these structures are, as a rule, quite long, extending much further beyond the edges of the dorsal valve. A common feature for all is the comparative thinness of the lamellae and some tendency towards splitting.

Functional interpretation. — Generally speaking, the dorsal lamellae — trails — are striking structures of probable adaptational character and may

have developed in response to particular environmental conditions. Their proper function still remains difficult to explain. Several authors have already discussed this problem, among others Schiells (1968), Lazarev (1981, 1984), Brunton (1985). When reviewing all the available suggestions it seems quite possible that they served not one but several functions (compare, among others, Schiells 1968). It is also likely that their function could be differentiated in relation to a particular growth stage of an animal.

In this paper only a few suggestions are considered in relation to the function of trails. One function might be protection. It seems that these dorsal concentric structures, either separately or in a set, could protect an animal from the entry into its shell interior of large particles of sediments. Perhaps they could also serve to protect the animals from potential predators. This function, however, seems rather debatable. Predation seems to appear rather accidentally and perhaps did not affect significantly brachiopod shells. In fact, no serious signs of predation are noted on the fossils, although this may depend on sampling. As shown in studies of recent brachiopods (Richardson 1985), disturbance of those animals, particularly when their shell is closed, by predators is minimal, so much so that brachiopods are not sought as food by other animals.

Another function recently discussed by Brunton (1985) is their significance for compensation or enlargement of the visceral cavity with growth and also in maintaining the commissural fit of the geniculate forms. This explanation seems very convincing also for devonoproductids. The compensation problem has been regarded previously by Miloradovitsch (1945) but in the context of the marginal structures.

It should be mentioned that within the productids there is not always a definite relation between the development of geniculation and the occurrence of a series of trails. As a rule, the majority of geniculated groups are devoid of dorsal trails and conversely, non-geniculate groups, such as devonoproductids possess them. For example, in early Marginiferinae, non geniculate to very weakly geniculate (as *Eomarginifera* Muir-Wood et Cooper), the anterior edge of the brachial valve shows short trails (Lazarev 1984; fig. 4) somewhat as in *Poloniproductus* (herein fig. 2). This could indicate the development of dorsal trails in, among others, *Marginifera*, prior to the geniculation.

That the trails might serve as possible temporary repositories for the larvae has been suggested by Lazarev (1981, 1984). Supposedly, each separate trail when it appeared could have formed a potential temporary pouch in which larvae could safely survive the earliest growth stages up to the time when settlement would be possible. This controversial interpretation needs, however, much more and careful evidence. In fact, our knowledge of the details of the brachiopod development is very limited.

DESCRIPTION

Family Devonopproductidae Muir-Wood et Cooper, 1960
(*ex Devonopproductinae Muir-Wood et Cooper, 1960*)

Emended diagnosis.—Small productaceans with spinose ventral and non-spinose but lamellose dorsal valves; radial striation sometimes lacking; cicatrix present or absent; area (ginglymus) low and linear; in the dorsal interior alveola present of traceable in the early growth stages; characteristic low and papillose ridge encircling and well delimiting the antero lateral sides of the visceral disc from a short anterior part of valve corresponding to the trail of the late growth stage; lateral ridges in the ventral interior well defining the auricular chambers.

Genera assigned.—*Devonopproductus* Stainbrook, 1943 (= *Striatopproductus* Nalivkin, 1947), *Chonopectoides* Crickmay, 1963, ?*Orbinaria* Muir-Wood et Cooper, 1960, ?*Productellina* Reed, 1943, *Polonipproductus* gen. n.

Stratigraphical and geographical ranges.—?Early Middle Devonian to Late Devonian, distributed throughout the world.

Remarks.—This group is quite characteristic and distinguished from other groups of the Devonian productaceans mostly in having distinct lateral ridges, usually well defining the low auricular chambers of the pedicle valve and marginal ridges bearing large papillae. Another feature are the differently developed concentric lamellae on the brachial valve.

On the basis of these features subfamily Devonopproductinae Muir-Wood et Cooper is here excluded from the family Leiopproductidae Muir-Wood et Cooper (or Productellidae Schuchert et Le Vene: Johnson 1976). The rank of this group is elevated to the family Devonopproductidae within the suborder Productidina, especially when taking into account phylogenies of the relevant groups (compare pages 60—62).

To the family Devonopproductidae is here included the genus *Orbinaria* Muir-Wood et Cooper. However, considering some of its morphological features such as development of auricular chambers and dorsal trails which still remain poorly known, this assignment is tentative. With regard to the genus *Productellina* Reed it remains, up to now, a provisional member of the devonopproductids because of its insufficiently known shell morphology, the available type material of Reed being in a very imperfect state of preservation (Muir-Wood and Cooper 1960: 180).

Among the other Devonian productaceans a mention should be made to the genus *Striatopproductella* Krylova, 1962 (= *Hanaeproductus* Ficher et Havlíček, 1978). In members of this genus a series of trails on the brachial valve may also appear. However, this feature, rather highly characteristic of devonopproductids, usually appears very late in ontogeny within this genus, namely, in the latest growth stage only and is not always present, perhaps not developed, on the large shells of probably adult individuals. In addition, a series of trails may also be developed on the pedicle valve. Development of trails in *Striatopproductella* is correlated with thickenings of the anterolateral margins of both valves of the shell and with their separation. The radially striated brachial valve of *Striatopproductella* is another feature shared in common with some members of Devonopproductidae such as *Devonopproductus*. However, the characters of shell shape and some details of the internal structure readily define *Striatopproductella* and separate it from the known members of the family Devonopproductidae.

Genus *Polonipproductus* gen. n.

Type species: *Productella varians* Biernat, 1966.

Derivation of the name: *Polonipproductus*—coming from Poland.

Diagnosis. — Small productoids usually with distinct cicatrix; pedicle valve spinose, brachial valve with concentric lamellae (?traces of trails) of variable appearance and irregular distribution; alveola traceable in immature specimens.

Remarks. — The genus is very close to *Devonoproductus* and is doubtless related to it, differing somewhat in lacking radial ornament on both valves of the shell and in the generally irregular spacing of the concentric lamellae on the brachial valve. With regards to *Devonoproductus* it is a much more progressed form developing both the fine but distinct radial striation and the concentric lamellae which start from the most posterior part of the brachial valve and are regularly spaced all over the whole valve surface.

Species assigned. — *Poloniproductus varians* (Biernat, 1966); "*Spinulicosta spinulicosta*" (Hall) described and figured by Racheboeuf (Racheboeuf 1983: 154); "*?Productella*" sp. in Perry *et al.* 1974.

Stratigraphical and geographical ranges. — Middle Devonian-Eifelian; cited, up to the present from Europe and Canada.

Poloniproductus varians (Biernat, 1966)

(pl. 17—20; fig. 2)

1966. *Productella varians* Biernat: 1966, pl. 11: 1—23.; pl. 12: 1—16; pl. 13: 1—10; figs. 19—21.

Description. — Small, thick-shelled; area-ginglymus low, linear; pseudodeltidium absent, ears small but distinctly marked providing some posterior support for the dorsal valve; pedicle valve more convex posteriorly, brachial valve gently to rather strongly concave, non geniculate.

Ornamentation. Radial ornament, in general, lacking and present only in some shells, but if developed it is vestigial only. Concentric rugae low, rounded of irregular spacing across the whole valve length. Concentric growth lines sometimes of lamellar appearance. Spines confined to the pedicle valve arranged in a row close to the hinge line and scattered over the whole surface with rough quincuncial arrangement on rugae much like "*Spinulicosta spinulicosta*" (Hall) from the Eifelian of France (Racheboeuf 1983: pl. 3).

Brachial valve spine-free but distinctly dimpled; concentric rugae developed across the visceral disc, thickened to a varying degree and more prominent in the anterior three-third of valve. The rugae seem to be devoid of lamellae. The latter, if developed should be remarkably short and delicate, hence, unlikely to be preserved in the fossil state. The first observable rugae preserving traces of concentric lamellae occur at a distance of about 2.5 mm—3.5 mm from the dorsal beak. They are extremely thin, about 0.3 mm—0.5 mm long, and narrow anteriorly (pl. 19: 1, 2; pl. 20: 1ab) and remain short as mentioned for *Devonoproductus* aff. *sericeus*.

In the anterodorsally growing shell of *P. varians* (the brachial valve grows from almost flat to rather deeply concave) the concentric lamellae become, from the anterior half of valve, successively longer and perhaps more densely arranged and sometimes splitting (pl. 20: 1a). They may attain a length of about 3.5 mm or more. Additionally these lamellae are undulated, along their length (fig. 4: 16), for they closely adhere an uneven brachial valve surface in fossil state.

It seems that the above situation is a stage corresponding to the maturity and the concentric lamellae, at the time of their forming at the valve margins, could be interpreted as trails (comp. Brunton, 1985).

With progressive growth, concentric lamellae on the *Poloniproductus varians* shell become shorter and more densely packed (growth being slower) and this is probably evidence of the beginning of the gerontic stage (pl. 19: 2).

The concentric rugae are developed on both valves of shell but to a lesser degree on the spinose pedicle valve than on the brachial valve which remains only lamellose.

It should be noted that, supposedly in the living devonoproductids all the developed concentric lamellae stood almost perpendicularly to the brachial valve surface or were, to a varying degree, anchylosed to it, in a similar to that in the atrypids for example (compare Cooper 1976).

The picture presented of the concentric lamellae in *Poloniproductus varians* is, probably, characteristic of all other early Middle Devonian devonoproductids. Future studies based on the more adequate material will confirm this.

Interior. Pedicle valve (pl. 17: 5) apical ridge, teeth and lateral ridges well developed; surface on both sides from the lateral ridges papillate, the papillae continuing anteriorly to surround the anterolateral parts of valve; muscle field occupying almost the whole umbonal part of valve and delimited by lateral ridges. Adductors sometimes raised, oval in outline; diductors weakly marked on both sides of adductors.

Brachial valve (pl. 17: 1—4). Cardinal process of somewhat varying appearance, dental cavities wide; alveola weakly marked and only in early growth stage. Median septum usually extending to a half or more of the valve length. Muscle field distinct with the median adductors weakly delimited from the lateral ones. Brachial ridges well developed, the lateral ones separating the ears and anteriorly passing into the densely papillate marginal rim. This ridge forms a distinct step separating the visceral disc from a short trail.

Remarks. — *Poloniproductus varians* is very comparable with the Canadian "*Productella*" sp. (Perry *et al.* 1979) but the latter possesses much shorter area-ginglymus — comprising a half of the maximum shell width, less marked internal characters in the brachial valve, i.e. muscle scars lacking (not preserved?), the brachial ridges undeveloped — but this may be a question of the adolescent age of the illustrated form. "*Spinulicosta spinulicosta*" (= *Poloniproductus* sp.) is very much of *Poloniproductus varians* appearance having lateral ridges in the ventral interior and papillose marginal rim in the dorsal interior and also spacing of the concentric lamellae similarly irregular all over the brachial valve surface (see Racheboeuf 1983: pl. 3: 8, 10, 14; here herein pl. 17: 1—4).

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GERTRUDA BIERNAT i STANISLAS S. LAZAREV

DEWOŃSKI RODZAJ POLONIPRODUCTUS NOV. (BRACHIOPODA)

Streszczenie

Rewizja eifelskiego brachiopoda z Gór Świętokrzyskich, *Productella varians* Biernat, 1966 wykazała, że brachiopod ten powinien być wyłączony z rodzaju *Pro-*

ductella Hall, 1867. Gatunek ten został wyznaczony jako typowy dla nowego rodzaju, *Poloniproductus*. Pokryta rzadkimi kolcami skorupka nóżkowa, skorupka ramieniowa z koncentrycznymi blaszkami, które w poszczególnych fazach wzrostowych mogły pełnić rolę welonu (trail), obecność uszek kardynalnych oraz występująca tylko w stadium młodocianym śladowa alveola wskazują na pokrewieństwo z rodzajami zaliczanymi dotychczas do podrodziny Devonoproductinae Muir-Wood et Cooper, umieszczanej w rodzinach Leioproductidae Muir-Wood et Cooper lub Productellidae Schuchert et Le Vene. Wymienione cechy mają wysoką wartość taksonomiczną co pozwoliło na podniesienie Devonoproductinae do rangi rodziny. Devonoproductidae charakteryzują dodatkowo następujące cechy: delikatne radialne prążkowanie obu skorupki, niska area (ginglymus) i wyraźnie zaznaczone jamy uszkowe wyodrębnione przez boczne grzbieciki na skorupce nóżkowej.

Praca została wykonana w ramach problemu CPBP 04.03.

EXPLANATION OF PLATES 17—20

Plate 17

Poloniproductus varians (Biernat), Middle Devonian, Eifelian, Świętokrzyskie Mountains

- 1—4. Brachial valves, ZPAL Bp. XV/1, 2, 3, 4: *a* concentric rugae of much irregular appearance and *b* internal features: cardinal process, median septum and muscle scars, $\times 3$.
5. Partly preserved pedicle valve, ZPAL Bp. XV/8: *a* external view with scattered spine bases, *b* internal view showing short and low median septal ridge and well outlined muscle scars, $\times 3$.

Plate 18

- 1, 2. Two adult specimens of *Devonoproductus* sp., ZPAL Bp. XV/305, 306, Middle Devonian, Givetian, Świętokrzyskie Mts.: *a* brachial valve, *b* pedicle valve, *c* posterior views; rather regular and distinct concentric rugae (*a*) on the brachial valves and rare spine bases (*b*) are shown, $\times 3$.
- 3, 4. *Devonoproductus karasikae* (Ljaschenko) on the rock surfaces, specimen $\frac{218}{426}$, Upper Devonian (D₃fr₁), verkhnetimanskij horizon, Timan, Ukhta river, USSR: 3 internal and external views of brachial valves; 4 fragmentary brachial valve with concentric, regular rugae and partly exfoliated pedicle valve, $\times 2$.

Plate 19

Poloniproductus varians (Biernat), Middle Devonian, Eifelian, Świętokrzyskie Mountains

- 1, 2. Adult shell in longitudinal section, ZPAL Bp. XV/5, SEM micrographs: 1 a fragment of a lamellose brachial valve, 60; 2 general view of a spinose pedicle and lamellose brachial valves, $\times 9$. See also pl. 20: 1, 3.

3. External view of an adult shell, ZPAL Bp. XV/6: *a* brachial and *b* pedicle valves, $\times 3$.

Plate 20

1. *Poloniproductus varians* (Biernat), ZPAL Bp. XV/5, Middle Devonian, Eifelian, Świętokrzyskie Mountains, SEM micrographs, longitudinal section: *a* splitted lamella, $\times 300$, *b* lamellae in the anterior part of brachial valve, $\times 70$. See also pl. 19: 2.
2. *Devonoproductus* sp., Middle Devonian, Givetian, Górnó, Holy Cross Mountains: fragment of brachial valve with distinct concentric rugae, $\times 10$.

