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Interspecific relation of some Upper Devonian polygnathid conodonts

ABSTRACT: Specimens of *Polygnathus brevis* Miller & Youngquist varying in size were described under various specific names. The presented changes, which take place in the ontogenetic development of this species, allow to separate it from other species, in particular from *Polygnathus normalis* Miller & Youngquist. The new diagnosis of *P. brevis* comprises the characteristics of its adult forms, while that original one was based on a juvenile holotype. As shown by a review of the hitherto known specimens, the species *P. brevis* is short-ranged and restricted to the *Palma-tolepis gigas* Zone.

INTRODUCTION

The problems of the Middle and Upper Devonian conodonts of the genus *Polygnathus* Hinde, 1879, are in many aspects open to discussion both as to their biology and taxonomy. To a large extent it is a result of difficulties in separating of some closely allied species (cf. Ziegler 1965, Huddle 1970). The present contribution concerns the species *Polygnathus brevis* Miller & Youngquist — the ontogenetic development of which has not hitherto been recognized; as a result there existed a taxonomical misunderstanding and precluded a proper estimate its stratigraphic range. The species under study, *Polygnathus brevis* Miller & Youngquist, belongs to the polygnathids of the *Polygnathus normalis* group, very common in the Middle and Upper Devonian. The observations concerning this species have also essential bearings on the intraspecific variability of the common species *Polygnathus normalis* Miller & Youngquist, to which large specimens of *P. brevis* were assigned. A doubtness on the biological reality of *Polygnathus normalis* was previously expressed by Ziegler (1965) who regarded it as *Polygnathus normalis* s. l. The variability occurring in the ontogenetic development of *Polygnathus brevis* was traced in variously sized specimens coming from the limestones of the Manticoceras Stage from the Kadzielnia quarry at Kielce in the Holy

Cross Mts (Central Poland). Some specimens were also obtained from several additional localities in the same stage of the Holy Cross Mts.

Forms here recognized as *Polygnathus brevis* have hitherto been described under various specific names. The holotype of Miller & Youngquist (1947, Pl. 74, Fig. 9) is a small specimen, c. 0.7 mm in length. Later, much larger specimens were found by other authors who did not relate them with *P. brevis*, but considered them as gerontic forms of other species. Thus, some specimens, the smallest of which was 1.3 mm long, were recognized by Müller & Müller (1957, p. 1,088) as mature specimens of *Polygnathus granulosus* Branson & Mehl. Helms (1961, p. 683) correctly found, however, that they fall under the diagnosis of *P. brevis*. Actually, *P. granulosus* belong to the "nodocostatus"-group and occurs in the Famennian, while the holotype of *P. brevis* and the specimens of the species found by Müller & Müller (1957) came from the Manticoceras Stage. On the other hand, Anderson (1966, pp. 412—413), followed by Druce (1969, p. 102) and Szulczewski (1971, pp. 49—50), recognized the specimens, referred by Müller & Müller (1957) to *Polygnathus granulosus* and the specimens, designated by Miller & Youngquist (1947) as *Polygnathus? rugicosta*, as gerontic forms of *Polygnathus normalis* Miller & Youngquist. At the same time, Anderson (*op. cit.*) separated them from his specimens, designated as *P. brevis* which, unfortunately, had not been illustrated.

The material in hand allows to find *Polygnathus brevis* as a distinct species. The forms, described by Müller & Müller (1957) as *P. granulosus*, as well as by Anderson (1966) and the present writer (Szulczewski 1971, Pl. 19, Fig. 3) as gerontic individuals of *P. normalis*, are in fact large specimens of *P. brevis*. The available specimens correspond to an ontogenetic series, in which the smallest individuals are 0.8 mm and the largest more than 2.6 mm (nearly 3.0 mm) in size. In various growth stages, there, however, persist definite morphological characters, which are varying to such a degree as to allow one for a distinct separation of *P. brevis* from *P. normalis* in all their growth stages. The series under study links the holotype of *P. brevis*, which unfortunately is one of the smaller specimens of this species, with large forms, erroneously assigned to *P. granulosus* or *P. normalis*.

SYSTEMATIC DESCRIPTION

Polygnathus brevis Miller & Youngquist, 1947 (Pl. 1, Figs 1—7 and Pl. 2, Figs 1—4)

1947. *Polygnathus brevis* n. sp.; Miller & Youngquist, p. 514, Pl. 74, Fig. 9.
 1947. *Polygnathus? rugicosta* n. sp.; Miller & Youngquist, p. 515, Pl. 74, Fig. 15 [broken specimen].
 1957. *Polygnathus granulosa* Branson & Mehl; Müller & Müller, p. 1088, Pl. 135, Figs 2, 3; Pl. 141, Fig. 1.

1966. *Polygnathus normalis* Miller & Youngquist; Anderson, pp. 412—413 [pars].
 1966. *Polygnathus brevis* Miller & Youngquist; Anderson, p. 411 [non-illustrated].
 1970. *Polygnathus* sp.; Seddon, pp. 744, 751, PL 13, Fig. 10.
 1971. *Polygnathus normalis* Miller & Youngquist; Szulczewski, pp. 49—50 [pars], PL 19, Fig. 3 [only].
 1971. *Polygnathus granulatus* Branson & Mehl; Schumacher, Table 13, Pl. 16, Fig. 22.

Diagnosis. — Unit strongly arched and gently incurved or slightly sigmoidal. Platform broad anteriorly and tapering posteriorly. Upper surface ornamented in anterior part, except adcardinal throughs, with strong transverse ridges. The posterior part of the platform covered by transverse ridges intersected but uninterrupted by low carina. Nodes, separated or fused into short hieroglyphic ridges, may additionally cover posterior part of the platform with a distinct tendency to be located near the margins. Free blade relatively short. Lower side marked by a sharp keel and a narrow, elongate basal pit which occur at the one-fourth of the platform.

Description. — An asymmetric unit having a short, free blade and a large, strongly arched and gently incurved to slightly sigmoidal platform. The stout free blade in mature specimens is composed of several denticles completely coalescent below their apices. An incurved or sigmoidal carina is high, denticulate in the anterior part of the platform and very low in the posterior part where it forms a narrow, incipient ridge. The anterior part of the platform is broad, flattened and covered with coarse, transverse ridges. They do not extend to the carina which is bordered by smooth, moderately deep adcardinal throughs formed at one-third of the platform and gradually deepened anteriorly. Flexures in the outer and inner margins distinctly set off the anterior part of the platform from the posterior one. The latter is relatively narrow, tapering posteriorly and sharply terminating. It may be incurved or gently sigmoidal. One to seven (depending on the specimen's size) widely spaced cross ridges, bent anteriorly near the margins of the platform, extend this part of the upper surface not interrupted by carina. Irregular nodes, which may also be fused into short hieroglyphic ridges, are most densely concentrated near the margins. The lower side displays a strongly developed raised keel and a narrow, elongate basal pit which occur in the first anterior quarter of the platform. The crimp is broad.

Remarks. — The above diagnosis and description concern mainly mature specimens. The holotype of Miller & Youngquist is, unfortunately, a juvenile specimen, devoid of many diagnostic characters. Almost all the specimens available have a basal filling obscuring the lower surface, which is, however, shown by Müller & Müller (1957, Pl. 135, Fig. 8b).

ONTOGENETIC DEVELOPMENT OF *POLYGNATHUS BREVIS*

Polygnathus brevis is among the species of *Polygnathus* which display relatively large changes in their ontogenetic development. These changes concern the following characters:

- 1) The differentiation of the platform into the anterior and posterior parts.
- 2) The differentiation of the sculpture on the upper surface of platform.
- 3) The upturning of platform margins in the anterior part.
- 4) The fusion of the denticles of the free blade and gradual disappearance of white matter.

The first two characters represent the most conspicuous symptom of the ontogenetic variability of *P. brevis* and they occur simultaneously.

The division of the platform into a wide anterior and a narrow posterior part, a characteristic feature of *P. brevis*, is not visible in young specimens, whose platform is wide, tapering and sharply terminating. The entire platform is ornamented by strong transverse ridges, which do not reach the carina. In some specimens, the posterior part may be covered with nodes. The carina is relatively high and markedly serrate posteriorly. The denticles of the free blade show white matter and their tips are discrete. The margins of platform are raised, its outer and inner parts inclined to carina and, consequently, the unit is V-shaped in transverse section.

The division of platform into the anterior and posterior parts, which develops with growth, takes place, at first not very distinctly, by a flexure of the inner margin of the platform. At the same time, the sculpture of the platform becomes markedly variable. The anterior part preserves its pattern of ornamentation characteristic of the juvenile stage of growth, while the posterior part is ornamented by fine transverse ridges and nodes. In the posterior part of the platform, the carina is, in this stage, already low and intersected by transverse ribs. Specimens of this size from Iowa (Müller & Müller 1957, Pl. 135, Fig. 2; Pl. 141, Fig. 1) display the anterior part of the platform covered to a considerable extent with nodes, while the specimens from the Holy Cross Mts corresponding in size have very few nodes, the ornamentation of this part of their platform being composed almost exclusively of ridges. The free blade has as yet distinctly separated denticle tips and its anterior margin happens to be also serrate (Pl. 1, Fig. 4b). The teeth do not bear white matter.

The largest specimens have the anterior and posterior parts of the platform, distinctly separated from each other by the flexures of the inner and outer margin of the platform.

PL. 1

Figs 1—7: *Polygnathus brevis* Miller & Youngquist

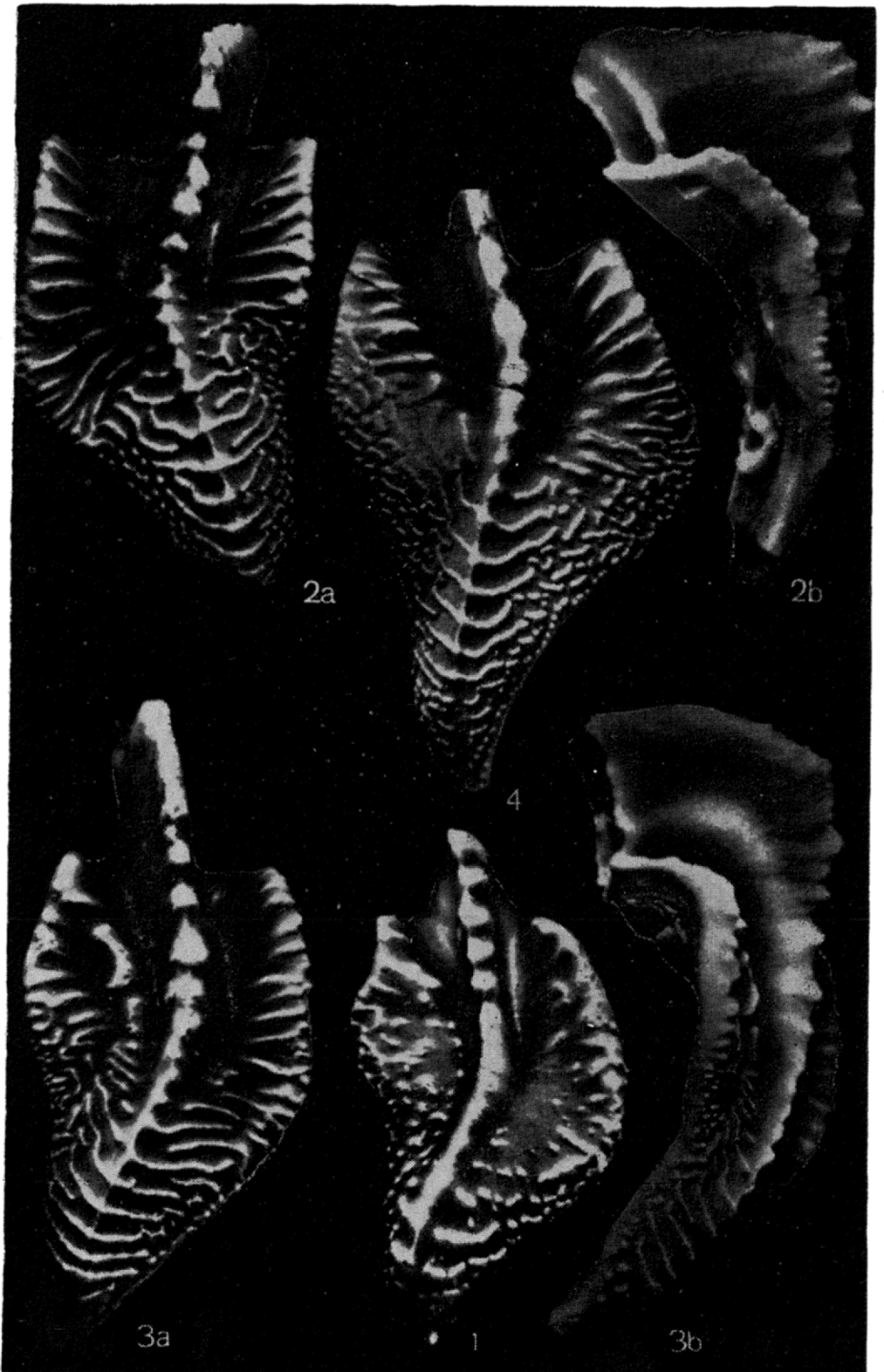
1 upper view of small hypotype (IGP/S. 170) from Kadzielnia (X. 166); 2 upper view of the hypotype (IGP/S. 171) from Kostomłoty (KT. 19); 3 upper view of the hypotype (IGP/S. 172) from Kadzielnia (X. 166); 4a upper, 4b lateral views of the hypotype (IGP/S. 173) from Kadzielnia (X. 166); 5 upper view of the hypotype (IGP/S. 174) from Kadzielnia (X. 166); 6 upper view of the hypotype (IGP/S. 175) from Kadzielnia (X. 166); 7a upper, 7b lateral views of the hypotype (IGP/S. 176) from Kadzielnia (X. 166)

Figs 8—12: *Polygnathus normalis* Miller & Youngquist

8 upper view of the hypotype (IGP/S. 181) from Kostomłoty (KT. 25); 9 upper view of the hypotype (IGP/S. 182) from Kostomłoty (KT. 25); 10a upper, 10b lateral views of the hypotype (IGP/S. 183) from Kostomłoty (Y. 5); 11 upper view of the hypotype (IGP/S. 183) from Górnó (G. 7) [the same specimen as in Szulczewski 1971, Pl. 18, Fig. 5]; 12 upper view of the hypotype (IGP/S. 184) from Kadzielnia (X. 166)

All figures X 36; taken by L. Łuszczewska, M. Sc.





Since the marginal ornamented parts of the anterior platform are flat, the platform loses its V-shaped outline in transverse section. Smooth adcarinal grooves starting at one-third of the length of the platform and deepening anteriorly detach ornamented platform from the carina. Anterior part of the platform is strongly extended. They may be bounded by incipient diagonal ridges. In addition to ridges, many nodes, mostly situated near the margins of the platform, appear in the posterior part, whereas the spaces between transverse ridges are smooth or ornamented by short intercalary ridges which do not reach carina. The ridges usually do not reach the margins of the platform but frequently bend anteriorly close by. The denticles of the free blade completely fuse together and are marked only by the serrate upper margin of the blade.

A COMPARISON OF *POLYGNATHUS BREVIS*
WITH *P. NORMALIS* AND THEIR ONTOGENY

As shown by the observation of the two species' variability in their ontogenetic development, the specimens of *P. normalis* (cf. Pl. 1, Figs 8—12) and *P. brevis* may be distinguished from each other in all the growth stages observed, that is, from 0.5 mm in length for the former and 0.7 mm for the latter species. In addition, these species differ from each other in the process of the developmental ontogenetic differentiation. In *P. normalis*, this process is relatively simple and involves few characters only, while in *P. brevis* it concerns a larger number of features and is of the nature of a more thorough morphological remodelling. A complex character of ontogenetic changes in *P. brevis* was a fundamental cause of taxonomic misunderstandings concerning specimens of this species.

As is a well-known thing, the dimensions of mature specimens may be among characters of some species of the platform conodonts, e.g. in the genus *Palmatolepis*. Specimens of *P. normalis* do not equal in size the largest individuals of *P. brevis*. The largest specimens of *P. normalis* illustrated (Mound 1968, Pl. 69, Figs 30—31; Szulczewski 1971, Pl. 19,

PL. 2

Figs 1—4: Large specimens of *Polygnathus brevis* Miller & Youngquist

1 upper view of the untypical hypotype with broken blade (IGP/S. 177) from Kadzielnia (X. 166); 2a upper, 2b lateral views of the hypotype (IGP/S. 178) from Kadzielnia (X. 166); 3a upper, 3b lateral views of the hypotype (IGP/S. 179) from Kadzielnia (X. 166); 4 upper view of the hypotype with broken blade (IGP/S. 180) from Kadzielnia (X. 166)

All figures X 36; taken by L. Łuszczewska, M. Sc.

Fig. 5 = Pl. 1, Fig. 11 in the present paper) reach 1.8 to 1.9 mm and a specimen shown in Pl. 1, Fig. 12 is 2.0 mm long, while specimens of *P. brevis* exceed at least 2.6 mm and probably even reach 3.0 mm. Large specimens of *P. brevis* could be, therefore, the more easily confused with gerontic stages of *P. normalis*.

In *Polygnathus normalis*, the ontogenetic variability in the process of growth is relatively not very extensive. It primarily consists in replacing ridges with nodes from the posterior and anteriorly. Short part of the upper surface of the platform in large specimens is covered with nodes (cf. Mound 1968, Szulczewski 1971). The replacement of ridges with nodes is usually more rapid on the inner than on the outer side of the platform. Some of the large specimens have a considerably extended anterior part of the platform (Pl. 1, Fig. 11), but a constriction of its anterior end is observed as a result of the upturning of platform margins. In some of the large forms, the outline of the platform remains, however, the same as in small ones (Pl. 1, Fig. 12). In all growth stages, the free blade in *P. normalis* is longer than that in correspondingly large specimens of *P. brevis*. In contrast to *P. brevis*, even in large specimens of *P. normalis*, the denticles are discrete at a considerable height.

Thus, small specimens of *P. brevis* differ from *P. normalis* in the presence of a constriction, which is unornamented or ornamented by weak ridges in the anterior part of the platform and in a shorter free blade. Since they differ in several main characters listed in Table 1, it is relatively easy to distinguish large specimens.

Table 1

	<i>Polygnathus normalis</i>	<i>Polygnathus brevis</i>
Platform outline	lanceolate constricted anteriorly with upturning margins sharply terminating or spatulated	broad lanceolate broad anteriorly with adcarinal throughs tapering posteriorly, sharply terminating
Free blade	relatively long denticles distinct	relatively short denticles coalescent except their tips
Ornamentation of the upper sur- face	anterior part: weak ridges, or unorna- mented posterior part: nodes and/or ridges un- intersecting the ca- rina	anterior part: strong ridges posterior part: ridges intersecting the ca- rina, nodes at the peripheries

STRATIGRAPHIC CONSEQUENCES

Almost all specimens of *Polygnathus brevis*, both hitherto described and shown in the present paper, come from two Upper Devonian areas: Iowa, U.S.A. (Miller & Youngquist 1947, Klapper & Furnish 1963, Müller & Müller 1957, Anderson 1966) and Holy Cross Mts (Szulczewski 1971 and the present paper).

The following assemblage of conodonts has been contained, in addition to *P. brevis*, in the sample No. X. 166 from Kadzielnia from which most of the specimens illustrated come:

Ancyrodella gigas Youngquist
Ancyrodella lobata Branson & Mehl
Ancyrodella nodosa Ulrich & Bassler
Ancyrognathus asymmetrica (Ulrich & Bassler)
Icriodus symmetricus Branson & Mehl
Nothognathella sp.
Palmatolepis hassi Müller & Müller
Palmatolepis subrecta Miller & Youngquist
Polygnathus decorosus Stauffer
Polygnathus normalis Miller & Youngquist

This assemblage represents the Upper *Palmatolepis gigas* Zone (to Iδ).

The presence of *P. brevis* was also found in two more samples from Kadzielnia. The sample X. 158 contains species of *Ancyrodella*, *Icriodus* and *Polygnathus*, the same as those in the sample X. 166, as well as *Palmatolepis gigas* Miller & Youngquist and *P. subrecta* Miller & Youngquist. Thus, much the same as the sample X. 167, which contains:

Ancyrodella nodosa Ulrich & Bassler
Ancyrognathus triangularis Youngquist
Palmatolepis gigas Miller & Youngquist
Palmatolepis hassi Müller & Müller
Palmatolepis subrecta Miller & Youngquist
Polygnathus normalis Miller & Youngquist,

the sample X. 158 represents the Lower or Upper *Palmatolepis gigas* Zone (to Iγ — to Iδ).

Of the specimens from the Holy Cross Mts previously described by writer (Szulczewski 1971) as *Polygnathus normalis*, the presence of *P. brevis* has been found in the following samples:

Wietrznia II, sample V. 34 (Szulczewski 1971, Table 7), in the Lower *Palmatolepis gigas* Zone.

Kostomłoty, sample KT. 19 (Szulczewski 1971, Table 2), in the Upper *Palmatolepis gigas* Zone.

The specimen illustrated (Szulczewski 1971, Pl. 19, Fig. 3) comes from Kowala (*op. cit.*, sample 28, Table 9), from the Lower or Upper *Palmatolepis gigas* Zone.

The holotype of *P. brevis* comes from the part of the Sweetland Creek Shale, Iowa, U.S.A., which, according to Klapper & Furnish (1963, p. 402, Text-fig. 2), corresponds to the Upper *Palmatolepis gigas* Zone. Specimens illustrated by Müller & Müller (1957) come from the Amana Beds and from Independency Shale, Iowa, from layers containing an assemblage indicative of the Lower *Palmatolepis gigas* Zone. *Polygnathus brevis* (? *sensu* Anderson 1966) occurs in Iowa, in the Juniper Creek and Cerro Gordo Members of the Limy Creek Formation, also in the Lower *Palmatolepis gigas* Zone.

All specimens of *Polygnathus brevis*, found so far both in Iowa and in the Holy Cross Mts come, therefore, from the Lower and Upper *Palmatolepis gigas* Zone. The specimens (see synonymy) collected by Schumacher (1971, Table 13, p. 70—71) from the „Kenwood” Shale (Wisconsin) came from the mixed conodont faunas containing elements of the *Palmatolepis gigas* and some overlying zones.

Thus, it seems that *Polygnathus brevis*, as a short-living species may be restricted to the Lower and Upper *Palmatolepis gigas* Zone (*to I γ* — *to I δ*) and may be useful for an intercontinental correlation. This is also confirmed by the fact that Seddon's (1970) specimen, here considered as a juvenile form of *P. brevis*, comes from the Virgin Hills Formation, Canning Basin, Western Australia, from the *Ancyrognathus triangularis* or Lower *Palmatolepis gigas* Zone (*op. cit.*, p. 744).

A correct separation of *P. brevis* from *P. normalis* is very important for stratigraphy, since the latter species is very long-living and persists from the Middle Devonian to the Upper *Palmatolepis gigas* Zone (Ziegler 1962, p. 91). It was even recorded by Glenister & Klapper (1966, Table 5) from the Lower *Palmatolepis quadrantinodosa* Zone (*to II β*) and by Wolska (1967, p. 415) from the *Scaphignathus velifera* Zone (*to III α* —IV).

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**PROBLEMY TAKSONOMICZNE KILKU GÓRNODEWOŃSKICH KONODONTÓW
Z RODZAJU POLYGNATHUS HINDE**

(Streszczenie)

Problematyka środkowo- i górnodewońskich konodontów z rodzaju *Polygnathus* Hinde, 1879, obfituje w otwarte zagadnienia natury biologicznej i taksonomicznej. Wynikają one w znacznym stopniu z trudności rozgraniczenia przechodzących w siebie gatunków (por. Ziegler 1965, Huddle 1970). Szkic niniejszy ma na celu określenie zakresu zmienności gatunku *Polygnathus brevis* Miller & Youngquist, 1947, oraz wyświeślenie jego stosunku do gatunków pokrewnych. Okazy, które należy odnieść do tego gatunku, rzadko kiedy bywały opisywane pod właściwą nazwą, czego powodem było ustanowienie przez autorów gatunku jako holotypu okazu juvenilnego. Opisywane i ilustrowane później okazy były znacznych rozmiarów i zarówno zarysem jak i bogatą ornamentacją znacznie różniły się od holotypu; uznawano je zatem za okazy gerontyczne innych gatunków. Ostatnio przeważała opinia (Anderson 1966, Druce 1969, Szulczewski 1971), że są one gerontycznymi formami pospolitego gatunku *Polygnathus normalis* Miller & Youngquist, 1947. Odpowiednia kolekcja uzyskana

z frańskich wapieni z Kadzielnii, wzbogacona okazami pochodzącymi z kilku innych stanowisk franu w Górach Świętokrzyskich, pozwoliła na prześledzenie ontogenetycznej zmienności gatunku *Polygnathus brevis* od form małych (o długości ok. 0,8 mm) do okazów osiągających ok. 3 mm. Ustalono jednocześnie nową diagnozę tego gatunku, uwzględniającą charakter form dużych. W konsekwencji badany gatunek okazał się pospolitszy, niż można było do tej pory sądzić. Wyłączenie należących do niego form dużych z synonimiki innych gatunków zmieniło także wyobrażenie o zmienności wewnątrzgatunkowej *Polygnathus normalis*. Rozpatrzenie występowania *Polygnathus brevis* w górnym dewonie Gór Świętokrzyskich oraz w Ameryce Północnej i Australii wykazało, że gatunek ten był krótkotrwały i jego zasięg jest ograniczony do obydwóch podpoziomów poziomu *Palmatolepis gigas* (to Iy—δ). Posiada on zatem istotne znaczenie stratygraficzne na skalę międzykontynentalną.

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