

# Growth and Development of Agnostids *Pentagnostus proanabarensis* Fedoseev, 1999

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**Abstract**—Juvenile development of the Middle Cambrian agnostid trilobite *Pentagnostus proanabarensis* Fedoseev, 1999 is studied. A sequence of eight juvenile stages is defined based on changes in morphology and measurements. Three of them belong to meraspid degree 0, another three refer to meraspid degree 1, and two represent early holaspid stages. Neither the frequency distribution of the length of cephalons and pygidia nor the length-width scatter diagrams give clear clusters of molts; the number of juvenile molts can be estimated through the analysis of the posteroaxis length distribution. Thus, the measurements and morphology of some juvenile pygidia with vestiges of the pleural and postaxial furrows allow reconstruction of the number of segments during individual growth. At the initial stage of development, the pygidial axis of *P. proanabarensis* probably had four segments, the pygidial axis increased up to no less than six segments in adults.

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## INTRODUCTION

Agnostics, enigmatic Cambrian arthropods, are traditionally treated as trilobites, but their morphology differs from other groups of trilobites to such an extent that their origin and affinities are still unclear. The evolution of morphological characters, used for agnostid taxonomy above species level, is unknown. A description of the early development of these invertebrates may possibly provide a clue to this complicated issue.

Altogether, four species of agnostids are well illustrated in the literature as regards their juvenile development. These are *Peronopsis* sp. (Shergold, 1991), *Agnostus pisiformis* (Linnaeus, 1757) (Müller and Walossek, 1987), *Pseudagnostus benxiensis* (Qian, 1982), and *Trinodus elspethi* Raymond, 1925 (Hunt, 1967). The described and illustrated sequence of molts for *T. elspethi* and *A. pisiformis* is proved to represent a continuous ontogenetic series. Hereafter we term a continuous ontogenetic series as complete one, whereas separate larval stages are referred to as an incomplete series. The well-illustrated ontogeny for two other species is not proved to be a continuous series. Some publications illustrate early developmental stages of other agnostid species. The authors did not aim to study the ontogeny and only published photographs of available juvenile specimens. As a result images of juvenile specimens are not accompanied by descriptions and photographs are often of poor quality. Fragmentary information like this is known for the following species: *Tomagnostus fissus*, *T. corrugatus*, outlines or drawings of several juvenile specimens (Rushton, 1979); *Pseudagnostus communis*, three indistinct photographs

(Palmer, 1955); *Peronopsis scutalis*, two small photographs (Egorova and Savitskii, 1969); *Hypagnostus parvifrons*, *Ptyhagnostus richmondensis*, an incomplete juvenile series; *Baltagnostus eurypix*, *Cotalagnostus laevis*, *Utagnostus trispinulus*, small photographs of poor quality, and an incomplete series (Robison, 1964); *Ptychagnostus punctuosus*, two photographs (Opik, 1979); *Ptychagnostus occultatus*, small indistinct photographs, unproved complete ontogenetic series (Robison, 1984); *Geragnostus subobesus*, four larval stages illustrated with quality photographs (Chatterton and Speyer, 1997); *Condylopyge eli*, one image of a meraspid (Fletcher et al., 2005).

The available satisfactory descriptions illustrate Late Cambrian species. But the understanding of agnostid morphological evolution requires the knowledge of the developmental features of their earliest species. The abundant material, including juvenile forms, of *Pentagnostus proanabarensis* Fedoseev, 1999 (Fedoseev, 1999) at our disposal allowed the development of this species to be addressed and the variation of some morphological characters and the formation order of taxonomically important morphological characters to be studied.

## TERMINOLOGY

Agnostics grow in precisely the same manner as polymeric trilobites; i.e., by the insertion of new segments in the teloblastic growth zone, most likely, between the last and penultimate segments of the pygidium. The growth is accompanied by separation of

segments from the pygidium and integration into the thorax. Thus, the pygidium of a growing animal represents a dynamic area of growth with the addition of new segments in the posterior zone and the completely formed segments released anteriorly into the thorax. The pygidium of immature trilobites is thus referred to as transitory. The pattern of insertion and releasing of segments differs in different groups of trilobites.

The similarity of the growth mode in agnostids and polymerans enable the use of a common terminology for the description of this process (Harrington et al., 1959). It is proved that in the majority of polymeric trilobites and eodiscids (a group of miomerans), the development begins with a larval stage with undivided cephalon and pygidium. This is the protaspis stage. In agnostids, protaspides are not found, except for a questionable report for *P. benxiensis* (Qian, 1982). The separation of the cephalon and pygidium marks the onset of the meraspid period. The thoracic tagma or the thorax is formed during the meraspid period. An individual without thoracic segments is called meraspid degree 0 (M0); one with a single thoracic segment, meraspid degree 1 (M1), etc., up to the acquisition of the complete set of thoracic segments, which differs in different trilobite species. After that animals reach the holaspis stage (H). Agnostics have only two thoracic segments. Therefore, meraspides of agnostids can only have degree 0 or 1, and holaspides obviously have two thoracic segments. Full-sized individuals are considered adult or mature; here they are designated as A (referring to adult). The boundary between early holaspides and adult individuals is conditional. Individuals with a complete set of diagnostic characters of the genus and species are regarded here as adults.

But it is necessary to emphasize that agnostids differ from other trilobites, including eodiscids, in the extremely specialized morphology of the pygidium. Those researchers who paid attention to features of pygidial development of agnostids and had statistically valid material on the number of molts (Hunt, 1967; Müller and Walossek, 1987; Qian, 1982) distinguished groups or grades, corresponding to separate instars, within meraspid degrees. In these cases instars were numbered consequently by Roman letters or figures

without reference to meraspid degrees. Each instar, beside size features, has certain morphological distinctions. Up to three molts (a, b, c) are known within the degree 0, and four molts (a, b, c, d) are distinguished within the degree 1.

It seems logical to consider morphological changes in the sequence of consecutive molts; therefore, in this work molts are referred to as M0a–c and M1a–d, accordingly for meraspid degrees 0 and 1.

## MATERIALS

The studied collection of *P. proanabarensis* includes 2–3 thousand specimens of isolated cephalic and pygidial shields. Adult specimens in this material did not show the incomplete preglabellar and postaxial furrow making the diagnostic characters of the species *Pentagnostus proanabarensis*. At the same time, the variation of a close species *P. anabarensis* Lermontova, 1940 is very broad and includes similar variability of preglabellar and postaxial furrows. The studied species is also morphologically close to the American *Peronopsis brighamensis* (Resser, 1938). Therefore, the species determination of the available material is somewhat conventional. On the other hand, the goals of this research allow accuracy in species determination to be disregarded.

All specimens studied are located on a single limestone plate originating from the Amydai section on the Olenek River in the eastern Siberian Platform, the upper part of the *Kounamkites* Zone, Middle Cambrian (Pl. 13, figs. 1, 2). Remains of *Peronopsis* sp. occur on the same plate (four pygidial and two cephalic shields and some juvenile pygidia apparently belonging to another *Peronopsis* species). The assemblage also includes some remains of polymeric trilobites (Pl. 13, fig. 1).

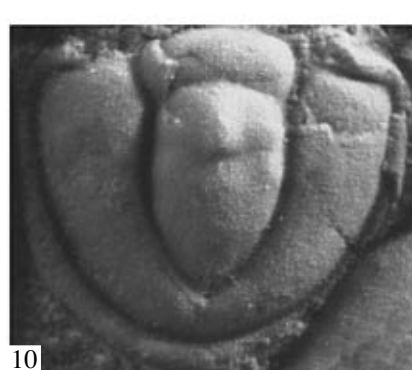
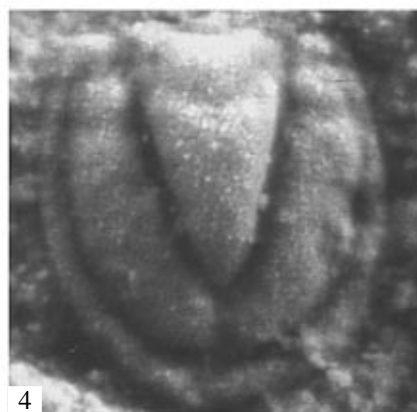
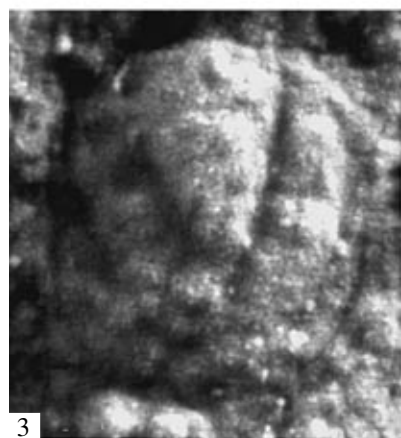
## METHODS

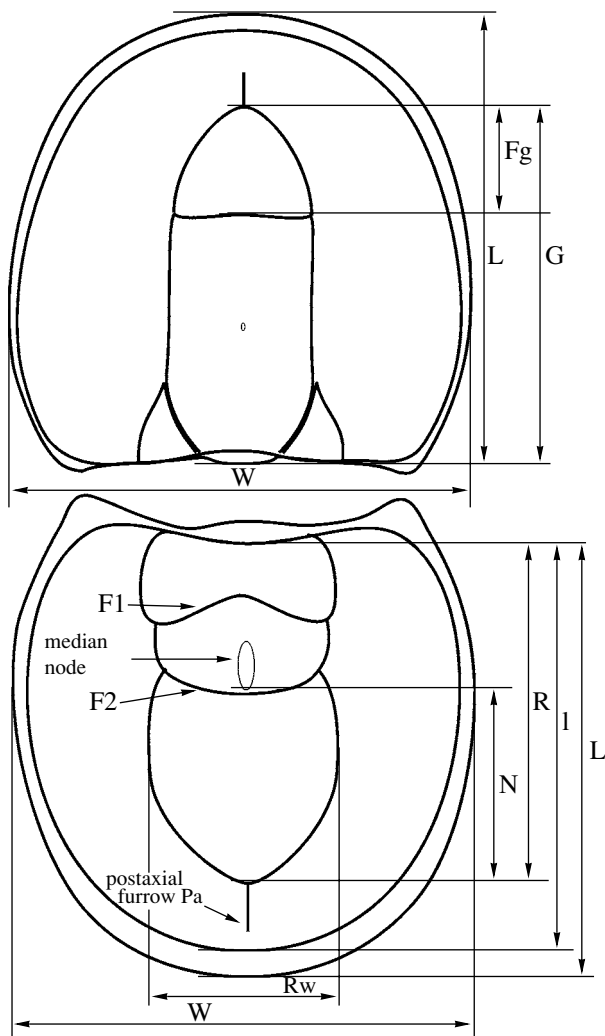
Measurements were made on about 300 cephalons and 300 pygidia of adult and juvenile individuals. In addition to general dimensions, length (L) and width (W) of cephalic and pygidial shield, some other pygid-

### Explanation of Plate 13

**Figs. 1–11.** Age stages of *Pentagnostus proanabarensis* Fedoseev, 1999, represented by pygidia; (1) specimen PIN, no. 5094/1 with the abundant species, below left is the pygidium of *Oryctocephalidae* ( $\times 1$ ); (2) the same specimen showing cephalons and pygidia of the dominant species, in the center is the pygidium of *Peronopsis* sp. ( $\times 7$ ); (3) specimen PIN, no. 5094/113, pygidium of early meraspid M0a, length is 0.484 mm, four segments are present on the pleurae and axis; (4) specimen PIN, no. 5094/122a, pygidium of early meraspid M0b, length is 0.578 mm, T1 is expressed on pleurae and on the axis. On the latter, only as superficial depression, frequently indiscernible on other specimens; (5) specimen PIN, no. 5094/17, pygidium of early meraspid M0c, length is 0.781 mm, T1 is distinct on pleurae and the axis, T2 is on pleurae, node looks like a sharp depression in the posterior end of the axis; (6) specimen PIN, no. 5094/22a, pygidium of late meraspid M1a, length is 0.80 mm, furrows of T2 are distinct; (7) specimen PIN, no. 5094/120, pygidium of late meraspid M1b, length is 0.828 mm, three segments are distinct on the posterior part of the axis; (8) specimen PIN, no. 5094/16b, pygidium of late meraspid M1c, length is of 0.922 mm, typically central position of the node and completely formed articulating half-ring; (9) specimen PIN, no. 5094/15, early holaspis, length is 0.937 mm, F1 and F2 are not formed; (10) specimen PIN, no. 5094/14, late holaspis, the length is 1.35 mm, F1 is distinct, F2 is small, weak, other specimens of this stage F2 is almost not expressed; (11) specimen PIN, no. 5094/231, pygidium of an adult *P. proanabarensis*, length is 2.94 mm, all characters are completely formed, the postaxial furrow is effaced.

Plate 13





**Fig. 1.** Scheme of measurements of pygidial characters of *Pentagnostus*.

ial measurements were taken: length measured to the border furrow (L), length (R) and width of the axis (Rw), and the posteroaxis length (N). The latter measurement was taken from the edge of the axial node because juvenile individuals do not have yet the transaxial furrow F2, which separates the anterior and posterior parts of the axis. The scheme of measurements is shown in Fig. 1. Some additional qualitative characters recorded include

the presence or absence of postaxial furrow (PA), the shape of the axis, the height of pleurae, and the presence or absence of transaxial furrows (F1 and F2).

Meraspid grades were diagnosed based on pygidial morphology and dimensions, mainly by the presence or absence of incipient thoracic segments in the transitory pygidium.

## RESULTS

### 1. Morphological Changes during Ontogeny

All pygidial shields in the available material could be subdivided into a number of clear morphological forms. These forms replace each other with the size increase, i.e., they characterize age variation. Morphological characters of these age groups are described below.

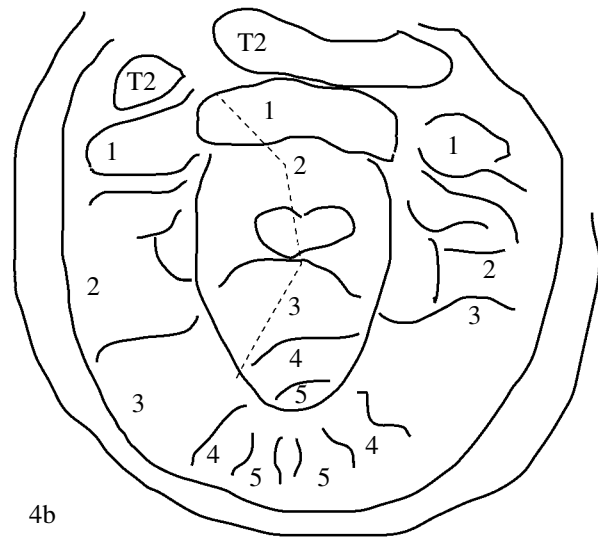
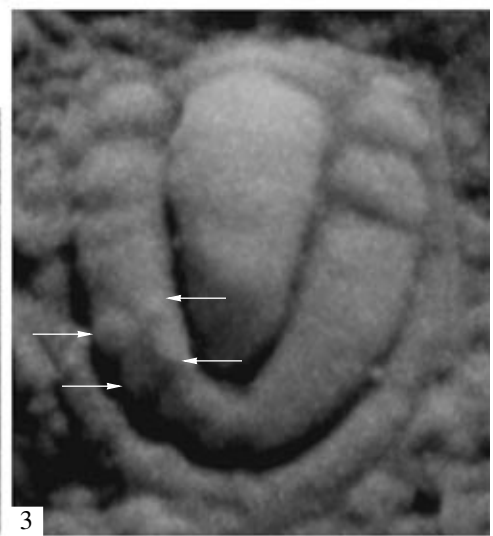
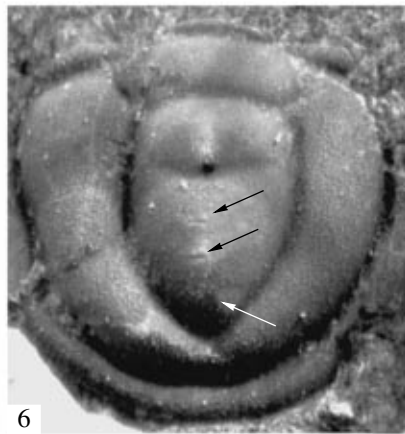
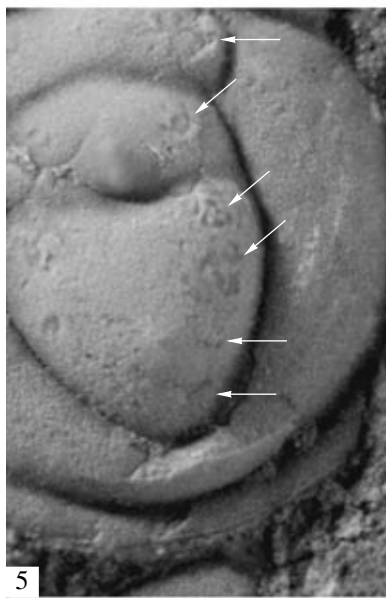
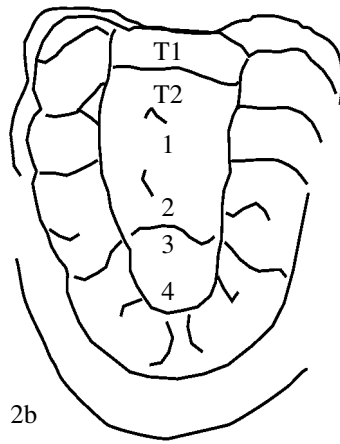
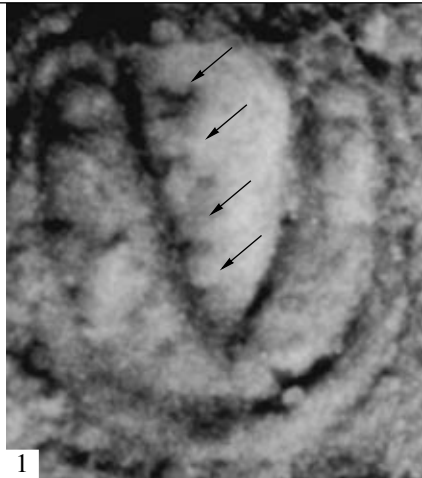
**Meraspis M0a.** The average length is 0.57 mm (Pl. 13, fig. 3). The pygidium is ovoid at the posterior edge, with parallel sides; the border is convex, expanded at the posterior margin, narrowed along the pygidial sides, without spines; the border furrow is nondeliquate and of medium width. The pleurae are rather low, of uniform height along the entire length; no pleural furrows are present; the postaxial furrow is wide and shallow. The axis has a triangular shape, without furrows or median node. The illustrated specimen shows three visible transverse constrictions on the pleurae and axis, thus implying the presence of four metameres.

**Meraspis M0b.** The average length is 0.62 mm (Pl. 13, fig. 4). The pygidium is oval shaped; the border is convex, it is expanded at the posterior margin, without spines; the border furrow is nondeliquate and narrow; pleurae are low, equally high along the entire length. The pleural furrow of the first thoracic segment (T1) and the postaxial furrow are present. The axis is triangular without furrows. The node is not present. The axis sometimes bears four pits (Pl. 14, fig. 1), their position possibly points to five axial metameres.

**Meraspis M0c.** The average length is 0.76 mm (Pl. 13, fig. 5). The pygidium is of regular oval form; the posterior marginal expansion is almost not expressed; the border is flattened, without spines; the border furrow is nondeliquate and narrow. The pleurae are of medium height, flattened in the posterior part of the pygidium. The two pleural furrows of the first and second thoracic segments (T1, T2), as well as the post-

### Explanation of Plate 14

**Figs. 1–6.** Specimens of *Pentagnostus proanabarensis* Fedoseev, 1999 showing segmentation of the pygidium; (1) specimen PIN, no. 5094/232, meraspis M0b, length of the pygidium is 0.625 mm; arrows specify boundaries of segments of the transitory pygidium; (2) specimen PIN, no. 5094/117, (2a) meraspis M0c, length is 0.734 mm and (2b) its traced sketch, T1 and T2 are thoracic segments, figures indicate axial segments; (3) specimen PIN, no. 5094/233, meraspis M0c, length is 0.75 mm, arrows indicate double globules of the second segment M2 of the pygidium; (4) specimen PIN, no. 5094/125, meraspis M1b, length is 0.89 mm, (4a) ventral side and (4b) its traced sketch, T2 and five more segments are visible on the axis, segments of pygidial pleurae apparently have a complex structure and it is, therefore, difficult to determine position of pleural and interpleural furrows; (5) specimen PIN, no. 5094/235, imprints in places of the attachment of appendages on the pygidium, length is 2.5 mm, arrows indicate attachment sites of appendages; (6) specimen PIN, no. 5094/236, length is 1.97 mm, arrows show incisions on the posterior part of the axis, marking four segments in this area.



axial furrow, are clearly seen on pleurae. The axis is of the triangular shape, its posteroaxis is rounded; the transaxial furrow delimits the narrow first thoracic segment. The posterior end of the axis is sharply lowered; the bent zone probably indicates a position of the future axial node, although it is seen only in a few specimens. The pleurae of each segment consist of four globules, well expressed in one specimen of this age (Pl. 14, fig. 3). It is worth noting that pleurae of both small and large specimens frequently bear (especially in the posterior part of pleurae) thin V-shaped furrows pointing up or down. The presence and shape of these furrows are most likely connected with the complex four-globule structure of the pleural segment.

*Meraspis* M1a. The average length is 0.815 mm (Pl. 13, fig. 6). The pygidium is oval; the margin is of uniform width, flattened, without spines; the border furrow is narrow and small. The pleurae are of medium height, lowered towards the posterior third of the pygidium. Only pleural furrows of the second thoracic segment (T2) are exposed on pleurae. The postaxial furrow is present in almost all specimens. The posteroaxis is rounded posteriorly and slightly expanded; the transaxial furrow separates an incipient second thoracic segment: the central lobe is not separated from the lateral one; the articulating half-ring is not formed. The posterior end of the axis sharply lowers at the level of one-third of the axis length; the bend place bears an axial node as a small swelling.

*Meraspis* M1b. The average length is 0.94 mm (Pl. 13, fig. 7). The pygidium is oval in shape; the margin is of uniform width, flattened, without spines; the border furrow is nondeliquate and narrow. The pleurae are of medium height, uniform along the entire length. The postaxial furrow is present. The posteroaxis has parallel sides. In the anteroaxis, the transaxial furrow separates the second thoracic segment. T2 is present as a ring of uniform width; the articulating half-ring is formed. The axis is of uniform height; the node is shaped like a wide bulge approximately in the middle of the axis.

*Meraspis* M1c. The average length is 1.02 mm (Pl. 13, fig. 8). The pygidium is semicircular; the margin is of uniform width, flattened, without spines; the border furrow is nondeliquate and narrow. The pleurae are of medium height, uniform along the entire length. The postaxial furrow is present. In the anteroaxis, the transaxial furrow separates the second thoracic segment. The V-shaped interpleural furrow is sometimes visible on the pleural part of T2; the articulating half-ring is formed. The posterior part of the axis is expanded. The axis is of uniform height; a node shaped like a wide amorphous bulge is approximately in the middle of the axis.

Early holaspis H1. The average length is 1.05 mm (Pl. 13, fig. 9). The pygidium is of semicircular shape, the border is flattened, uniformly wide, without spines; the border furrow is nondeliquate and narrow; the pleu-

rae are of medium height, uniform along the entire length of the pygidium. The node is of triangular form and has a central position. The postaxial furrow is shallow, in some specimens it is visible only in its anterior part. The axis is of suboval form; it is narrowed at the end of the first axial segment. Transaxial furrows are not present, only in some specimens a thin shallow first transaxial furrow is faintly expressed. The first axial segment is notably wider than the second one. The expansion of the posteroaxis is insignificant.

Late holaspis H2. The average length is 1.24 mm (Pl. 13, fig. 10). It differs from the previous stage in the expansion of the posterior part of the axis, more anteriorly placed node, and the presence of the first transaxial furrow. Some specimens bear a thin shallow second transaxial furrow.

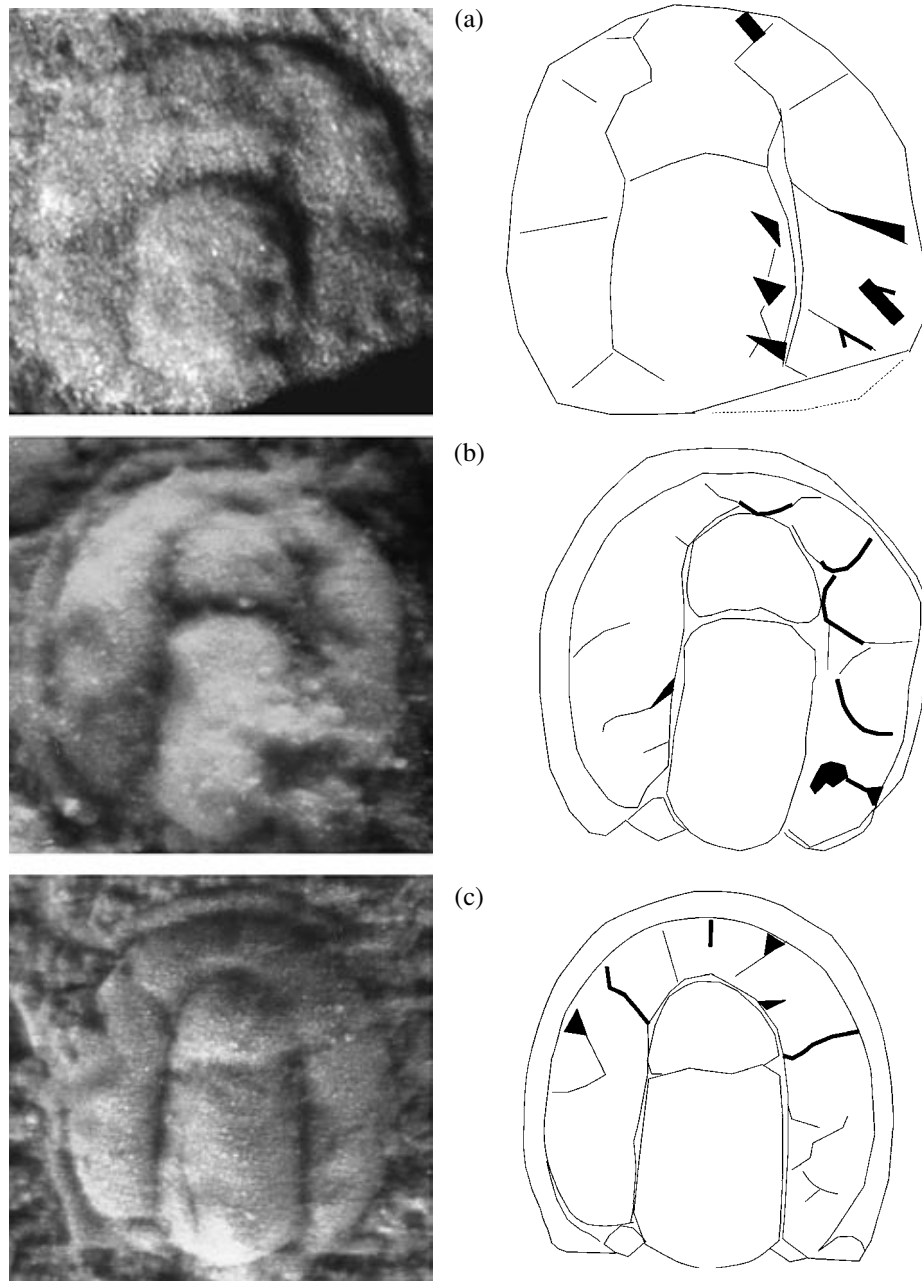
Adult stages. The maximum length is 3.6 mm (Pl. 13, fig. 11). Contrary to the previous stage, two transaxial furrows are present, the postaxial furrow disappears; the posteroaxis is expanded. The pygidium has all morphological characters of the species. Adult instars differ from each other only in size.

The reviewed morphological changes in the growth series of *P. proanabarensis* may be summed up as follows: (1) In the course of growth, transaxial furrows T1, T2, F1, and F2 are sequentially formed anteriorly; (2) The postaxial furrow is present in juvenile individuals up to the late holaspis stage and disappears in adults as pleurae merge behind the axis; (3) The axial node becomes discernible at the stage M0c; (4) The axis shape changes from initially triangular to typical semicircular with the expanded posteroaxis at M1c or at early holaspis stage. Pleurae become relatively high only at the M1 stage.

#### *Age Changes of Cephalons*

The sample of cephalons could not be subdivided by morphological characters into uniform age stages. Nevertheless, the morphology of the smallest cephalons of the studied agnostid species is notable. Judging by size, they belong to the M0 stage (Figs. 2a–2c).

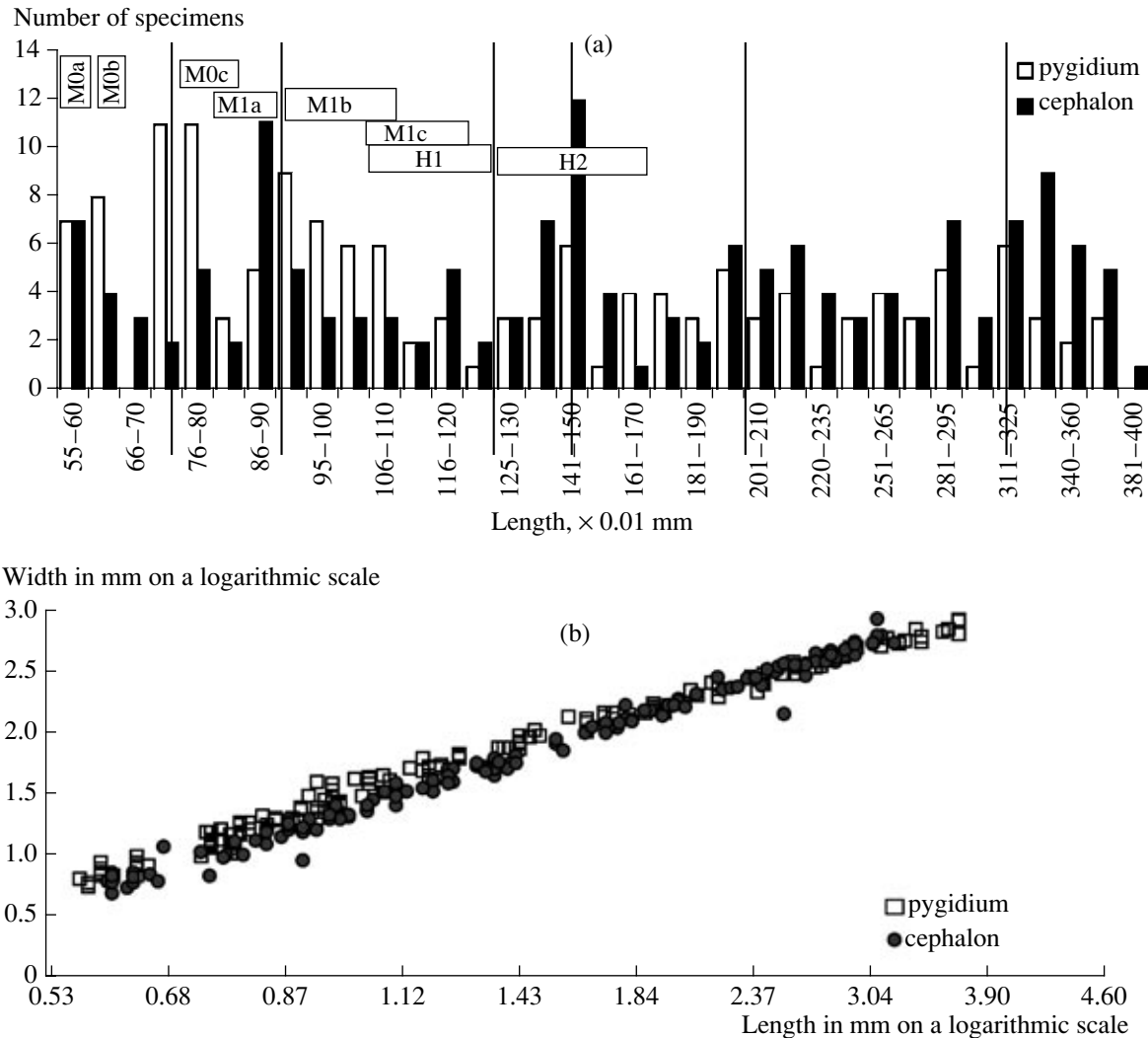
The smallest forms, presumably M0 and M1a, have no basal lobes. The anteroglabella in small specimens, referred by size to the M0 stage, is two-thirds of that in mature forms. The pleurae of specimens without basal lobes sometimes bear symmetrical furrows, probably indicating an earlier segmentation. These vestigial furrows are traced in Fig. 2. There are not less than four pairs of these furrows, although there may even be five pairs. The first pair is situated anterior to the glabella with the posterior ends of the furrows joining (Figs. 2b, 2c). In the smallest individuals, these furrows are not yet separated from the anterior part of the glabella, being integral with it (Fig. 2a). At this initial ontogenetic stage, the upper part of the glabellar furrow is not yet formed. It can be assumed that the formation of the glabella with the effaced glabellar furrow of the *Hypagnostus* type is



**Fig. 2.** Cephalons of early meraspides of *Pentagnostus proanabarensis* Fedoseev, 1999 and their outline drawings: (a) specimen PIN, no. 5094/237, cephalon length is 0.48 mm, the furrow around the anterior part of the glabella is not formed; (b) specimen PIN, no. 5094/115, the cephalon length is 0.594 mm, the furrow around the glabella is fully formed; (c) specimen PIN, no. 5094/126, cephalon length is 0.719 mm.

a heritage of this juvenile stage. Rather than becoming obliterated at later ontogenetic stages, the furrow around the anteroglabella does not develop at all. The preglabellar furrow does not develop in this species and its traces are not found in any of the specimens. If, as it is believed, the preglabellar furrow marks the fusion suture of genae ahead of the glabella, then the anterior portion of the pleurae described above should degrade. Alternatively, the preglabellar furrow is formed as a result of the division of the anterior pleural segment.

The second pair of vestigial furrows on the genae of the cephalon runs from the middle of the anterior part of the glabella, the third is at the level of the transglabellar furrow. The vestiges of the fourth and fifth furrows are visible in the middle and lower part of the glabella. The fifth pair of furrows is not visible clearly in any specimens. The number of furrows on the genae allows the existence of six segments in the cephalon of agnostids to be inferred.



**Fig. 3.** Length measurements of cephalons and pygidia of *Pentagnostus proanabarensis* Fedoseev, 1999: (a) frequency distribution of length; rectangles stands for meraspid stages with pygidia of the corresponding length; (b) pygidial length/width scatter diagram.

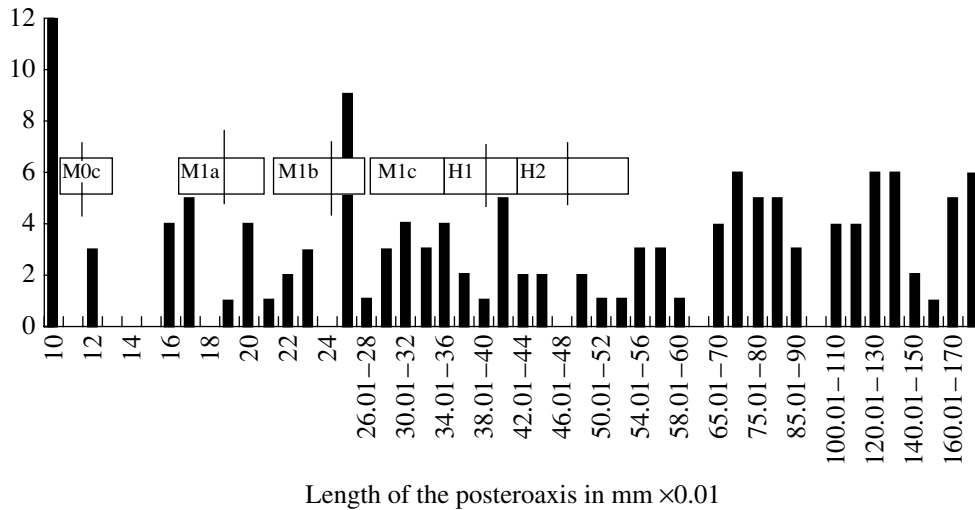
Four pits are visible (Fig. 2a) on the posteroglabella of the smallest specimens. The origin of these structures is not clear. But their presence suggests the presence of four segments in the posteroglabella, including the basal lobe segment. The formation of the basal lobes was not observed in the material studied.

## 2. Length Frequency Distribution of Pygidia and Cranidia in *P. proanabarensis*

The length frequency distribution of cephalons and pygidia gives an integral picture of the linear growth, molts, size variability within each molt and death rate (also including taphonomic factors). The combination of these three processes results in a very complex picture of size frequency distribution. Results of total measurements (including all cephalons and pygidia on the selected square) of cephalic and pygidial length are

shown in Fig. 3. It is generally obvious that the length frequency distributions of cephalons and pygidia coincide. It means that the illustrated size distribution is objective and the material is quite representative.

The growth of trilobites occurs in steps separated by molts; therefore, it would be logical to expect a relatively regular gaps in length distribution. However, neither the instar points nor the number of molts can be inferred from the frequency distribution of the lengths of cephalons and pygidia. The number and position of molts also is usually determined from length-width scatter diagrams of cephalons or pygidia (Jell, 1975; Hunt, 1967). But this representation of the size distribution is also of no use (Fig. 3b). However, the length/width ratio shows coordinated changes for cephalons and pygidia, reaching similar maximum values. It means that data point groupings are not incidental and do not merely reflect errors of measurements of the



**Fig. 4.** Length frequency distribution of the posteroaxis part of *Pentagnostus proanabarensis* Fedoseev, 1999; rectangles stand for meraspid stages with transitory pygidia having posteroaxial parts of the corresponding length.

sample. In order to determine the number of molts, the length distribution is considered below with regard to defined ontogenetic forms as well as other size parameters of agnostids.

Figure 3a illustrates the size limits of ontogenetic stages M0a–H2. This graph shows that in the species studied, minimal values in the frequency distribution do not always correspond to limits between age stages. One of the frequency minima is just in the middle of the H2 stage. Minimal values in size distribution coincide with the boundaries between grades M0b and M0c, M1a and M1b, and H1 and H2. Stages M0c and M1a, as well as M1c and H1, nearly completely overlap in linear dimensions. This overlap is easily explained. The thoracic segments are released from the pygidium during these stages, thus compensating for the increase in the length of pygidium during the molt. To put it differently, the increase of the pygidium during a molt does not much exceed the length of the released thoracic segment. The described size distribution of ontogenetic stages shows why some size groups can include representatives of different consecutive larval stages.

The growth of trilobites, including agnostids, occurs by the addition of segments at the posterior part of the axis. In this connection, the growth of agnostids is more clearly reflected in the increased length of the posteroaxis. Measurements of this part are only possible starting from the M0c stage since the median node, which marks this segment, becomes visible only at this stage. The posteroaxial length frequency distribution and corresponding ontogenetic stages are shown in Fig. 4. As expected, posteroaxis lengths in consecutive ontogenetic stages do not overlap and plot strictly one after another. A slight overlap is present only between H1 and H2. Thus, it is obvious that defined ontogenetic

stages result from consecutive molts and the addition of segments in the posterior part of the axis.

The length distribution of the posterior part of the axis within each ontogenetic stage is noteworthy. There are two local maxima within each stage, i.e., bimodal length distribution. It can be interpreted as the presence of ontogenetically fast and slow growing individuals. It is important that clearly seen troughs in the frequency distribution of posteroaxial lengths correspond to the unevenness in length distributions within each stage rather than to transitions between ontogenetic stages. It turns out that peaks in this distribution correspond to a sum of fast-growing individuals of the previous ontogenetic and slow-growing animals of the following ontogenetic stage, while lows indicate boundaries of slow and fast growing stages. This hypothesis, if accepted, easily explains why the last group of data points (the largest specimens) has such a small range of variability. It is approximately half as high as that in other groups of data points separated by troughs in the graph. The largest individuals represent only a fast-growing part of the last ontogenetic stage, whereas slow-growing part of the last stage falls in the previous size group. Thus, there are altogether six molts of meraspid stages, two molts of holaspid stage, and three molts of full-size adult individuals.

Unfortunately, we fail to find an unequivocal morphological or numeric criterion for an easy discrimination between slow-growing and fast-growing groups. As a first approximation, it is notable that fast-growing individuals do not have the postaxial furrow up to degree M1, and at early holaspid stage it is almost reduced showing a vestigial form typical of *P. anabarensis*. Even early M0 have no postaxial furrows. In slowly growing individuals, the postaxial furrow appears already at the earliest stage. This situation can

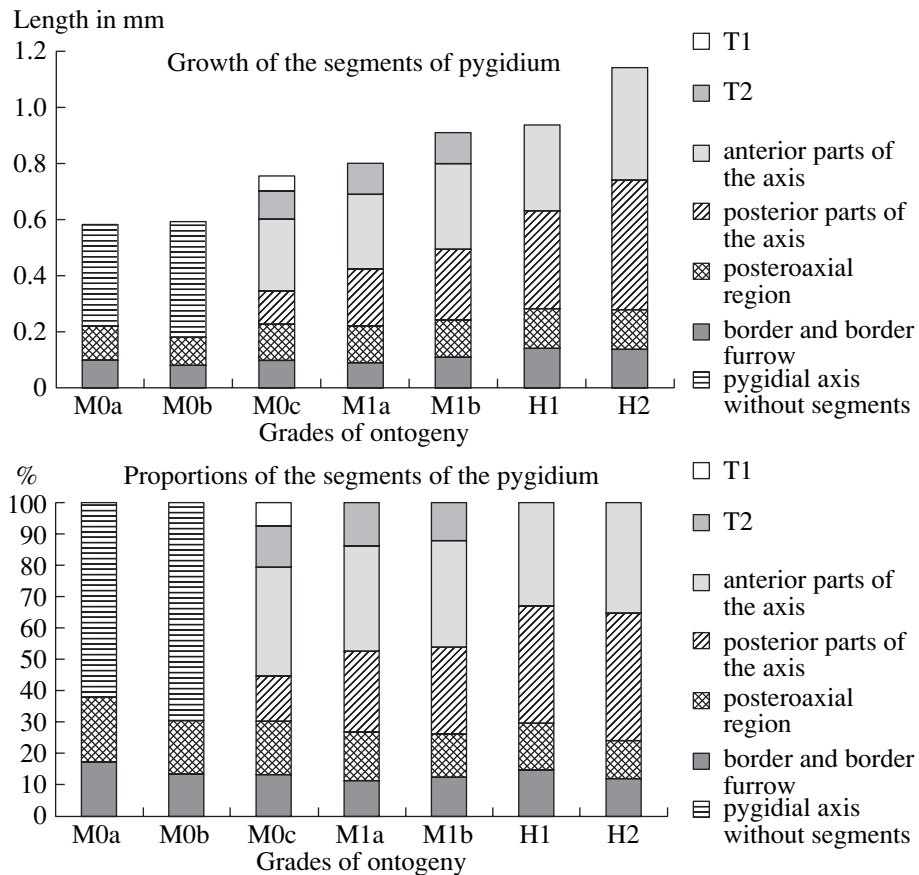
**Table 1.** Measurements of *P. proanabarensis*, mean values in mm

Stages Features	M0a	M0b	M0c	M1a	M1b	M1c	H1	H2	A3
L	0.575	0.625	0.76	0.815	0.94	1.02	1.05	1.24	3.6
I	0.47	0.565	0.66	0.71	0.81	0.89	0.91	1.05	3.4
R	0.385	0.46	0.53	0.575	0.61	0.745	0.8	0.9	3.1
N			0.11	0.18	0.245	0.3	0.38	0.48	1.75
T1			0.05						
T2				0.10	0.11	0.12			
PA	±	±	±	+	+	+	+	±	
F1	-	-	-	-	-	-	-, ±	±	
F2	-	-	-	-	-	-	-	±	

indicate the presence in the material of a mixture of two sibling species, relatively equal in numbers, or sexual dimorphism within the species studied. In the first case it is assumable that the slowly growing specimens of the sample represent *P. anabarensis*. This form shows a broad variability and in a number of Siberian sites lacks vestigial preglabellar and postaxial furrows typical of this species.

### 3. Growth and Number of Segments in *P. proanabarensis*

As it was shown above, size values show a quite complex distribution within each ontogenetic stage. This is why only meraspid degrees, which allow the use of morphological distinguishing features, have been studied with respect to size variation.



**Fig. 5.** Growth dependant changes of transitory pygidium in *Pentagnostus proanabarensis* Fedoseev, 1999.

Mean values of size measurements disregarding differences between slow and fast-growing dimorphs were used in the analysis of growth. These average values are tabulated in Table 1 and also shown in Fig. 5.

Figure 5 shows absolute and relative size change at the transition between ontogenetic stages. The growth of trilobites of the studied species occurs basically by the increase of the posteroaxial lobe. The length of the posteroaxis increases from 14 to 36%, i.e., by a factor of 2.5, while other parts, such as border, pleurae behind the axis, and the anteroaxis, increase only by a factor of 1.5. Further growth does not affect the lateral margin, slower growth of the anterior axial segments compared to those of the posteroaxis continues. For example, the latest size group, compared to stage H2, shows changing proportion of the pygidium, with the two anterior segments increasing by a factor of 3.2; the posterior part, by a factor of 3.6; and the pleurae behind of the axis, by a factor of 2.

At least for meraspid stages it is possible to assume that faster posteroaxial growth indicates, among other factors, the addition of segments. At the M0a stage, some specimens display four segments (Pl. 13, fig. 3). At the M0b stage, there are five segments (Pl. 14, fig. 1), and at M0c stage, six segments (Pl. 14, figs. 2a, 2b). It is thus becomes clear why at the M0a and M0b stages no median node is present on the axis. This segment is simply absent at the M0a stage, with a teloblastic segment occupying its position, fourth from the beginning of the transitory pygidium. At the M0b stage, the segment bearing the future node is already present but, apparently, the node is not yet formed. However, it is possible that it may be already expressed in on some M0b specimens. The node forms at the stage of six segments, when one segment already separates it from the last growth zone segment. But it is quite possible that the penultimate segment, not the last one, represents the teloblastic zone. Then it is logical to expect the occurrence of the node at the M0c stage rather than at M0b.

The transitory pygidium loses one segment between molts M0c and M1a. One available specimen of the ventral side of grade M1b shows six segments (Pl. 14, figs. 4a, 4b), i.e., as many segments as are visible on the dorsal side of some other specimens of the same age stage. Most likely it means that previous grade M1a has five segments, grade M1c has accordingly seven segments, and H1, six segments. The available material does not show if more segments are added with further growth. But the presence of at least four segments in the posterior part of the axis is beyond question. The posteroaxial region in one of specimens displays three or even four pairs of intricately shaped imprints marking attachment places of appendages (Pl. 14, fig. 5). Another specimen shows three incisions on the median part of the posteroaxis, probably indicating the position of four segments (Pl. 14, fig. 6).

## CONCLUSIONS

(1) The ontogeny of *P. proanabarensis* is shown to include stages of meraspides, holaspides, and mature forms. The meraspid period has two degrees: degree 0 and degree 1, according to the number of free thoracic segments. Meraspid degrees are subdivided into three grades. Each grade is characterized by a set of specific morphological features. M0a has a triangular axis, shows no segmentation, its median node is not expressed; the postaxial furrow is present as a broad flat depression, or is absent. M0b has a triangular axis and the T1 segment on pleurae; median node is not visible. M0c has a triangular axis, the T1 segment is on pleurae and on the axis, the T2 segment is on pleurae, the median node is expressed as an abrupt elevation of the axis, and the postaxial furrow is present. M1a has the triangular axis, the pleurae and axis bear the second thoracic segment without the articulating half-ring, the median node is in the form of a large bulge, the postaxial furrow is present. M1b has a slightly expanded posteroaxis, the second thoracic segment is present on pleurae and the axis, the articulating half-ring is underdeveloped, the median node is in the form of a large bulge, the postaxial furrow is present. M1c has a slightly expanded posteroaxis, the second thoracic segment is present on pleurae and the axis, this segment frequently bears a thin interpleural furrow, the articulating half-ring is developed, the median node is formed with a central position on the axis, the postaxial furrow is present. H1 has the expanded posterior part of the axis, no transaxial furrows on the axis, the median node is developed and decreases in size, the postaxial furrow is present. H2 has the expanded posteroaxis, the axis has the first transaxial furrow, the second one is underdeveloped, the median node has characteristic definitive outlines and shape, the postaxial furrow is somewhat effaced.

Basal lobes are formed at M1 stage synchronously, with the relative length of the anterior part of the glabella increasing by a factor of 1.5 and thus reaching the size of adult forms.

(2) Dimensions of the posterior part of the axis, i.e., the part directly responsible for the growth of trilobites, regularly increases in the sequence of juvenile forms. Their ranges do not overlap in contrast to the other characters. It allows the interpretation of the recognized forms as separate molts during ontogeny.

(3) Length frequency distribution of pygidial and cranial shields and also some other measurements do not show a clear division into separate molts. In the case of the species studied, it can be accounted for by the presence of fast and slow growing forms within each molt stage. In general, the size increase during molts is compensated for by the length reduction due to the release of thoracic segments and thus disguises gaps in the distribution of linear dimensions at early ontogenetic stages.

(4) At the earliest M0a grade, the transitory pygidium of *P. proanabarensis* probably includes four segments. With each molt of the sequence, the posterior part of the axis forms a new segment. The transitory pygidium loses two segments: one between the two meraspid degrees and one between meraspid degree 1 and the holaspid stage. Thus, the pygidium of the adult trilobite *P. proanabarensis* includes at least six segments.

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#### REFERENCES

1. B. D. E. Chatterton and S. E. Speyer, "Ontogeny," in *Treatise on Invertebrate Paleontology: Part O. Arthropoda 1: Trilobita, Revised* (Univ. Kansas Press, Lawrence, 1997), pp. 173–247.
2. L. I. Egorova and V. E. Savitskii, "Stratigraphy and Biofacies of the Cambrian of the Siberian Platform," Tr. SNIIGGiMS, No. 43, 293.
3. A. V. Fedoseev, "Distributional Patterns of Ptychagnostidae (Trilobita) in the Amydaiskii Section of the Amgian Age," *Geol. Geofiz.* **40** (10), 1411–1424 (1999).
4. T. P. Fletcher, G. Theokritoff, Lord G. Stinson, and G. Zeoli, "The Early Paradoxidid Harlani Trilobite Fauna of Massachusetts and Its Correlatives in Newfoundland, Morocco, and Spain," *J. Paleontol.* **79** (2), 312–336 (2005).
5. H. J. Harrington, R. C. Moore, and C. J. Stubblefield, "Morphological Terms Applied to Trilobita," in *Treatise on Invertebrate Paleontology: Part O. Arthropoda 1* (Univ. Kansas Press, Lawrence, 1959), pp. 117–126.
6. A. S. Hunt, "Growth, Variation, and Instar Development of an Agnostid Trilobite," *J. Paleontol.*, No. 1, 203–208 (1967).
7. P. A. Jell, "Australian Middle Cambrian Eodiscoids with a Review of the Superfamily," *Palaeontogr. Abt A* **150** 1–97 (1975).
8. K. Müller and D. Walossek, "Morphology, Ontogeny, and Life Habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden," *Fossils and Strata*, No. 19, 1–123 (1987).
9. A. A. Opik, *Middle Cambrian Agnostics: Systematics and Biostratigraphy* (*BMR Bull.* 172), Ed. by W. H. Oldham (Canberra, 1979), Vol. 2, p. 78.
10. A. R. Palmer, "Upper Cambrian Agnostidae of the Eureka District, Nevada," *J. Paleontol.* **29**, 86–101 (1955).
11. Qian Yi-yuan, "Ontogeny of *Pseudagnostus benxiensis* sp. nov. (Trilobita)," *Acta Palaeontol. Sin.* **21** (6), 632–643 (1982).
12. R. A. Robison, "Late Cambrian Faunas from Western Utah," *J. Paleontol.* **38** (3), 510–566 (1964).
13. R. A. Robison, "Cambrian Agnostida of North America and Greenland: Pt I. Ptychagnostidae," *Univ. Kansas Paleontol. Contrib.*, No. 109, 28–33 (1984).
14. A. W. A. Rushton, "A Review of the Middle Cambrian Agnostida from the Abbey Shales England," *Alcheringa*, No. 3, 43–61 (1979).
15. J. Shergold, "Protaspid and Early Meraspid Growth Stages of the Eodiscid Trilobite *Pagetia ocellata* Jell, and Their Implications for Classification," *Alcheringa*, No. 15, 65–86 (1991).