

ONTOGENY OF THE EODISCID TRILOBITE *SHIZHUDISCUS LONGQUANENSIS* FROM THE LOWER CAMBRIAN OF CHINA

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ABSTRACT. The eodiscid *Shizhudiscus longquanensis* occurs abundantly in the Lower Cambrian Shuijintuo Formation, Pengshui, Sichuan, China. Phosphatized specimens in excellent preservation have been isolated from a single limestone lens, and include a few protaspides and disarticulated examples of all subsequent growth stages. From this material the ontogeny of *S. longquanensis* is described and reconstructed. Of particular note are two large spines on the axis of the transitory pygidium which eventually become those of the second and third thoracic segments. The visual surface first appears in the earliest meraspid, with a single lens flanked by two half lenses. An immature specimen of *Shizhudiscus* sp. from Shaanxi Province shows that this trilobite genus was already capable of full enrollment in the degree 0 meraspid stage.

THE small isopygous eodiscids are a specialized group of trilobites, occurring as a common element in Cambrian faunas of world-wide distribution. Whereas their morphology is well understood, their ontogeny has been poorly known until recently, when Rushton (1966) and Jell (1970, 1975a) described growth series with degree 0 meraspides. A further study was made by Hu (1971), though only one specimen which he described as a paraprotaspis is correctly assigned to an eodiscid (Jell 1975a). Zhang (1989) and Shergold (1991) were able to elucidate largely complete growth series of two related eodiscid trilobites from the Lower Cambrian of China, and the Middle Cambrian of Australia respectively. Both of these descriptions included convincing protaspides.

Many eodiscid genera have been described from southwest China, and some of these, as Zhang Wen-Tang (1987) suggested, may be synonymous and should be merged. Amongst these, two genera that are probably synonymous are *Shizhudiscus* and *Hupeidiscus*, which were defined principally on the characters of their pygidia. The differences in pygidial morphology, in the opinion of Zhang Wen-Tang, however, are not such as to warrant generic status. If this view is accepted, *Shizhudiscus* would have to be regarded as a junior synonym of *Hupeidiscus*. The cranidia of the two genera are very similar, though there are some minor differences. Whether or not to synonymize these two genera depends upon how to evaluate similarities and differences, and here ontogenetic studies can provide additional sources of data. In general terms (Robison 1967; Ludvigsen and Chatterton 1980), ontogeny has proved very useful in providing reliable criteria for the assignment of some trilobite taxa and in determining relationships between groups.

In the present paper we show remarkable changes in the development of *Shizhudiscus longquanensis*, especially in the pygidium with its distinct pleural furrows, fine tubercles, and the strong axial spikes that appear first on the transitory pygidium, and are present in the holaspis on the second and third thoracic segments. Such pronounced morphological changes should provide many reliable indicators for assessing the relationship between *S. longquanensis* and other closely related eodiscid groups.

Unfortunately, scarcely anything is known about the ontogenetic development of *Hupeidiscus*, in which the adult pygidium does not have pleural furrows. We therefore retain the name *Shizhudiscus* in the present study, rather than synonymizing it with *Hupeidiscus*, in view of the relatively limited number of characters of taxonomic value common to both, as so far known. The proposal of Zhang

Wen-Tang seems reasonable, and further investigations of eodiscid ontogeny should help to resolve the problem.

The rich and specialized eodiscid fauna of southwest China is largely contemporaneous with the Lower Cambrian high phosphate concentration episode described by Cook and Shergold (1984), with which this local diversification is associated. Zhang & Clarkson (1990) gave a detailed description of the structure and meraspid to holaspid development of the eyes of the Chinese eodiscids *S. longquanensis* and *Neocobboldia chinlinica*, and their meraspid to holaspid development. We also discussed the phosphatic preservation of the material and presented an account of the locality and stratigraphy of the section from which the material came. All the *Shizhudiscus* specimens came from a single lens within the upper part of the Lower Cambrian Shuijintuo Formation at Longquanxi in Pengshui, Sichuan, and they were regarded as belonging to a single more-or-less contemporaneous population. No material other than that from this single lens was included, thus avoiding confusion with different morphs or shifts in modal size that may have developed within a time span (see Sheldon (1988)). The same approach has been taken here, and all the phosphatized specimens of *S. longquanensis* used in the present study were likewise retrieved from a single horizon. A few cranidia (Pl. 2, fig. 6) belonging to another eodiscid occur at this level, these are strikingly different and easily distinguished from *S. longquanensis*.

Here a virtually complete growth series of *S. longquanensis* is described. Though all the specimens are disarticulated, the strikingly well-preserved material provides a firm basis for assessing the relationship of this genus to other eodiscids, and indeed the affinities of the eodiscids with other trilobite groups. In addition we discuss moult stages and growth instars of *Shizhudiscus*, the enrollment mechanism of the adult exoskeleton, and the early development of its eyes (as complementary to our earlier paper, Zhang & Clarkson 1990), and its possible life-cycle pattern.

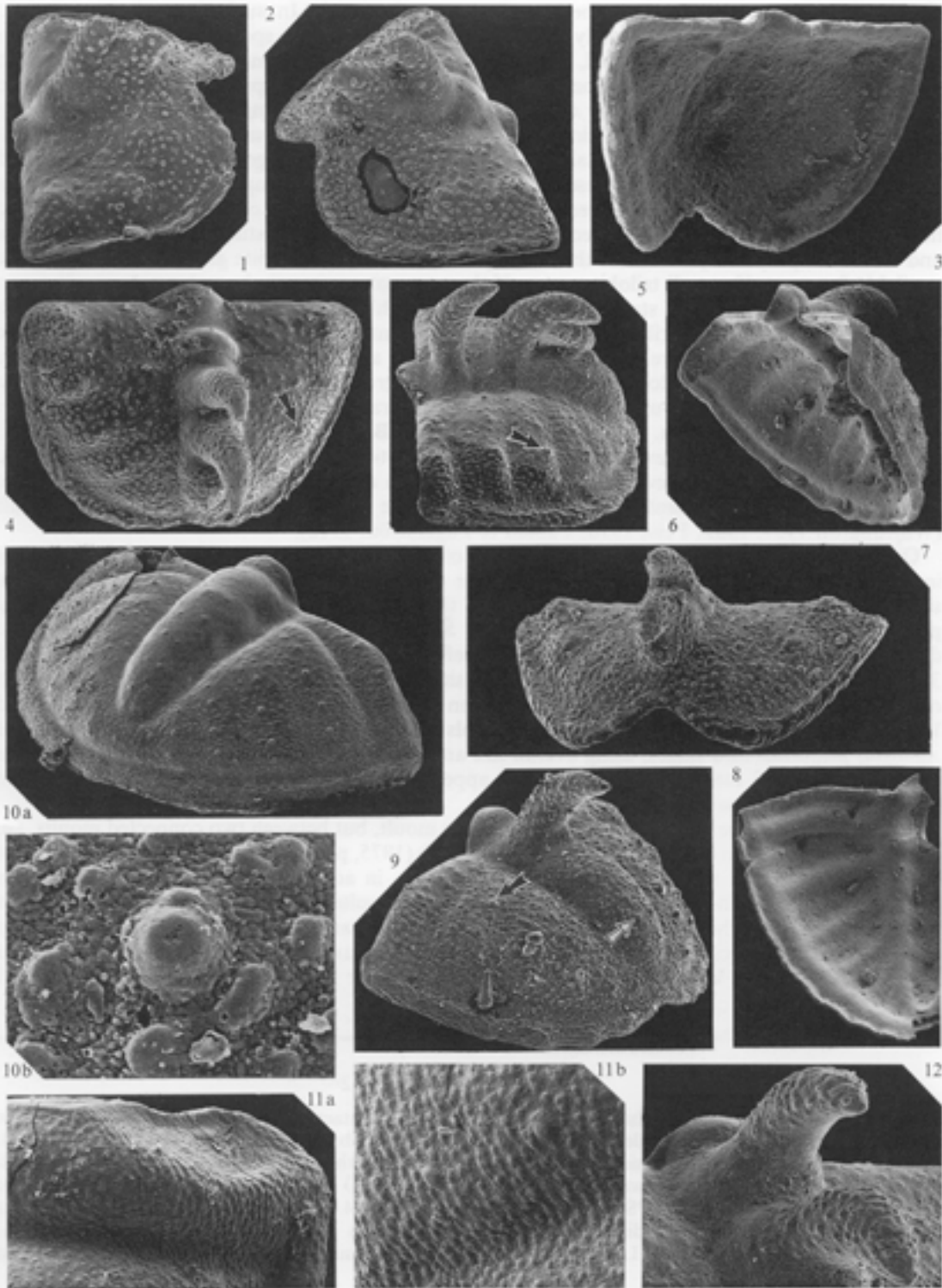
Material. All specimens figured or discussed in this paper are now housed in the Chengdu Institute of Geology and Mineral Resources, Chengdu, People's Republic of China.

INSTARS AND MOULTING

Trilobites grew during successive moults, and it is probably the case that the majority of trilobite specimens found are exuviae. In some instances, and particularly in fine sediment, individuals of a

EXPLANATION OF PLATE I

Shizhudiscus longquanensis S. G. Zhang and Zhu. Lower Cambrian; Pengshui, Sichuan. Figs 1–12; pygidia. 1, PSO 5610; (M0a) with three axial segments, posterior two bearing spines, $\times 167$. 2, PSO 5616; lateral view of (M0b), showing a further ring added behind the two spinose rings, $\times 135$. 3, PSO 5621; oblique ventral view of (M0a), showing W-shaped outline of the posterior margin, where the doublure is virtually absent, $\times 167$. 4, PSO 5580; oblique dorsal view of (M0c), with two further rings behind the spinose rings; the first thoracic segment appears to be nearly ready to separate from the transitory pygidium. 5, PSO 5561; lateral view of (M2); the axis behind the two spinose rings bears about four segments and the pleurae have five ribs with tubercles (arrowed) behind the interpleural furrow; a tubercle (arrowed) has appeared on the pleural rib, $\times 98$. 6, PSO 5615; oblique ventral view of (M3), $\times 68$. 7, PSO 5605; posterodorsal view of (M0b), showing the W-shaped posterior border with fine ridges and an additional ring behind the spinose rings, $\times 133$. 8, PSO 5620; ventral view of (H0), with the third thoracic segment attached, $\times 65$. 9, PSO 5617; oblique-lateral view of (M2), with the first ring bearing a single spine, and about 5 rings behind it on the axis; the paired tubercles on the axis are indicated by a white arrow, and the tubercles on the pleural ribs by a black arrow, $\times 103$. 10a–b, PSO 5614; 10a, oblique posterolateral view of (H2); seven axial rings can be recognised by means of the paired tubercles, $\times 70$; 10b, detail of the tubercle on the pleural rib; an aperture may be present in the centre of the tubercle, which is surrounded by fine granules, $\times 1170$. 11a–b, PSO 5613; 11a, right articulating facet of a holaspid, $\times 146$; 11b, details of tubercles and granules on the pleural rib and furrow, $\times 228$. 12, PSO 5619; detail of the two spines on the axis of (M1), $\times 188$.



ZHANG and CLARKSON, *Shizhudiscus*

single species may be found together in all stages of growth. In such cases the ontogenetic development of the species can usually be worked out by studying the specimens in gradational size series. The terms protaspid, meraspid, and holaspid (Raw 1925) are commonly used to describe the main stages of growth in trilobites. The terms anaprotaspid, metaprotaspid, and paraprotaspid have also been used, and as the ontogeny of trilobites has become increasingly well known many new descriptions, often with new terminology, have become available. The use of two sets of terms has seemed to some authors a potential source of confusion and Edgecombe *et al.* (1988) and Chatterton *et al.* (1990) felt that these terms have little value for comparing trilobite ontogenies across the whole group. They preferred to describe ontogenies in terms of protaspid, meraspid, and holaspid stages alone. This, it is agreed, would bring uniformity to the study of trilobite ontogenies and would simplify comparisons of the development of different trilobite groups. These terms are available for most, if not all trilobites, even if they are not necessarily homologous.

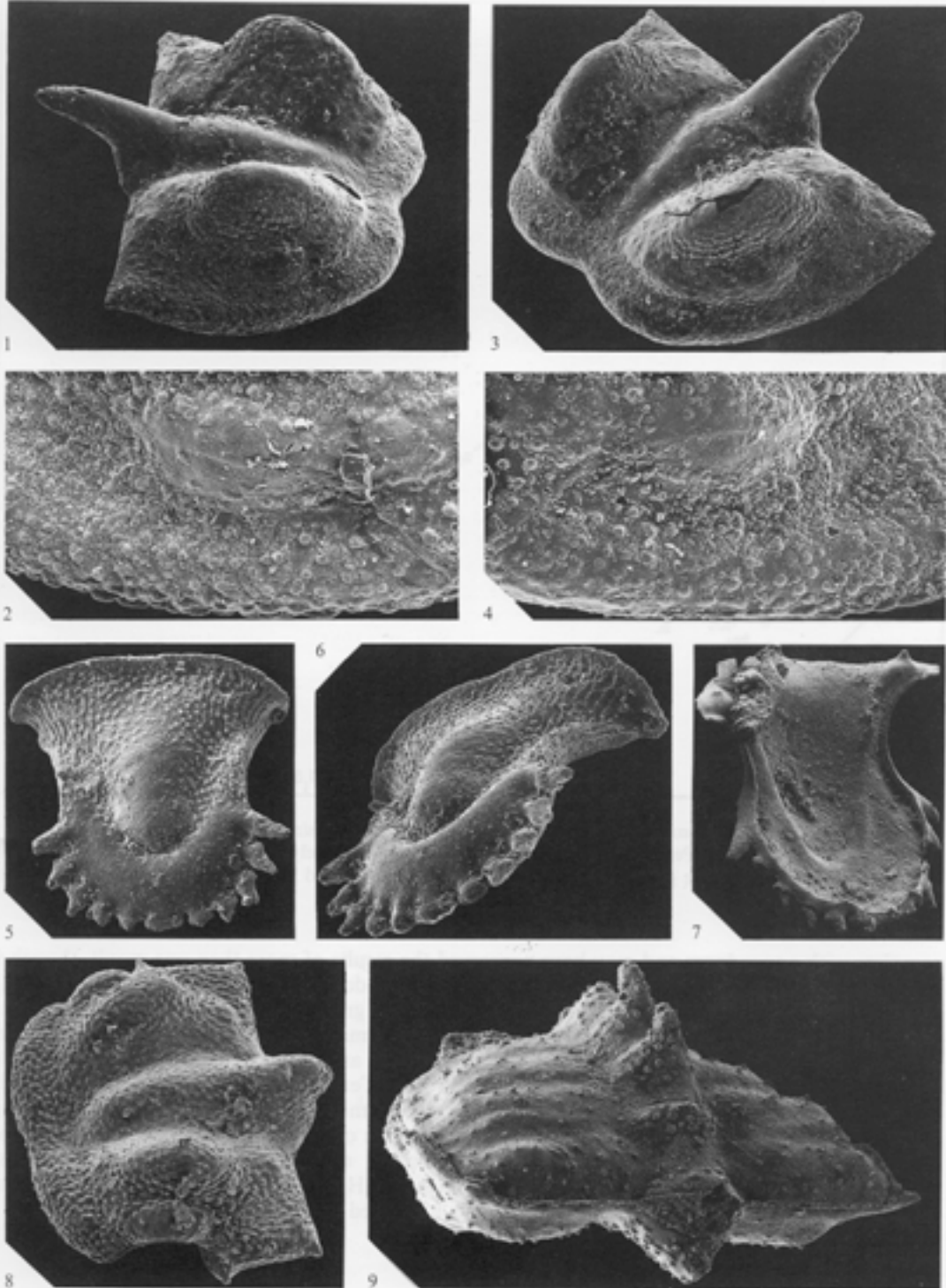
Whereas the use of such a standard terminology is highly desirable, it is not always possible to put it into practice. In some trilobites, disarticulated elements cannot always be assigned to a specific growth stage, especially where only parts of the ontogeny are known; likewise problems may arise where the ontogeny of the trilobite is unusual. Where the growth stages are represented by complete individuals it is possible to use the number of free thoracic segments present as a standard in determining meraspid instars, as originally suggested by Barrande (1852). Thus Degrees 0, 1, 2, 3 etc. define the meraspid's developmental stage by denoting the number of articulated thoracic segments. Each degree, however, may include more than a single moulting episode, and in some cases more than one segment may be released from the transitory pygidium at a single moult (Whittington 1957, 1959; Feist 1970; Pabian & Fagerström 1972).

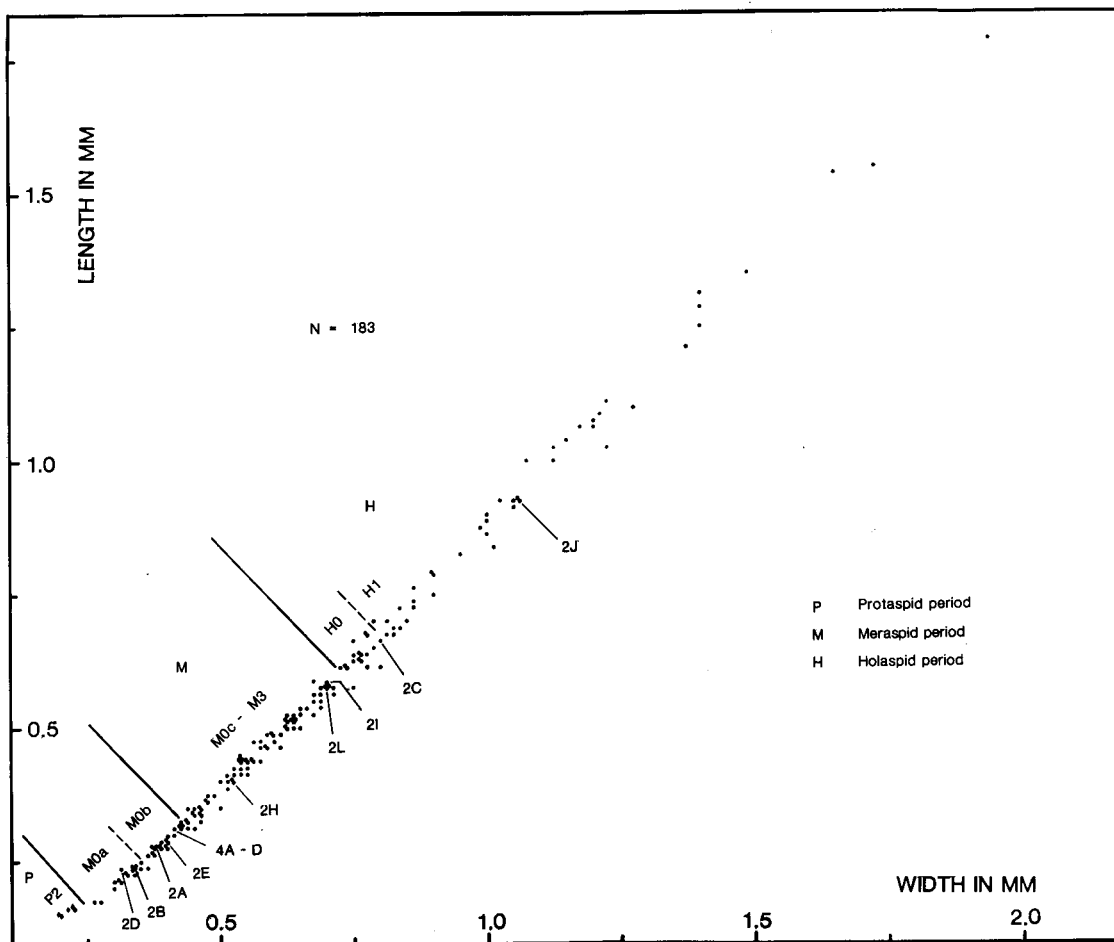
On the other hand, the increase in the number of axial rings appears to relate closely to growth instars. It thus seems reasonable to subdivide the protaspid and meraspid periods into stages or substages according to the number of rings in the rachis of the protopygidium or transitory pygidium. This same idea has been used by Šnajdr (1981) in elucidating the ontogenetic development of *Scharyia*. Tripp and Evitt (1983) defined substages within the protaspid stages 2 and 3 of *Dimeropyge virginensis*, and used clear and simple symbols to describe the changes in shield outline and the increase in number of tubercles on the outer surfaces of the cranidia. Müller and Walossek (1987) likewise adopted concise symbols for subdividing meraspides and holaspides of *Agnostus pisiformis* into stages, using overall size and configuration of the tagmata, and the degree of development of the excellently preserved appendages. This was particularly useful because agnostids have only two thoracic segments.

Within a single stage there may be more than one moult, but between two connected moults, i.e. from one ecdysis (E) to the next (as in Henningsmoen's (1975, p. 180) intermoult cycle) only a single stage need be defined morphologically. There could be, in addition, some bias in interpretation depending upon whether the specimens examined were moulted exuviae or dead carcasses, and it would be desirable, where possible, to be sure of this before assigning them to stages. Thus Tripp and Evitt's (1983) specimens were probably mainly exuviae, and were assigned to moults within a stage. In Müller and Walossek's (1987) study, on the other hand, the carcasses were preserved

EXPLANATION OF PLATE 2

Shizhudiscus longquanensis S. G. Zhang and Zhu; 1-4, PSO 5718; intact (M0b) cephalon. 1, laterodorsal view of right-hand side, $\times 117$. 2, detail of 1 showing the right librigena with three small lenses, $\times 364$. 3, laterodorsal view of left hand side, $\times 117$. 4, detail of 3 showing the right librigena and small lenses, $\times 364$. 5-7, Hypostomata of an unknown ?polymerid trilobite; 5-6; PSO 5991; 5, ventral view, $\times 135$; 6, oblique posteroventral view, $\times 165$. 7, PSO 5990; laterodorsal view, $\times 94$. 8, PSO 5194; oblique lateral view of a cranidium of an unknown eodiscid trilobite, $\times 122$. All from Lower Cambrian, Pengshui, Sichuan; 9, ZB9Ca001; *Shizhudiscus* sp. Lower Cambrian, Zhenba, Shaanxi. Lateroposterior view of an enrolled (M0) exoskeleton, $\times 140$.

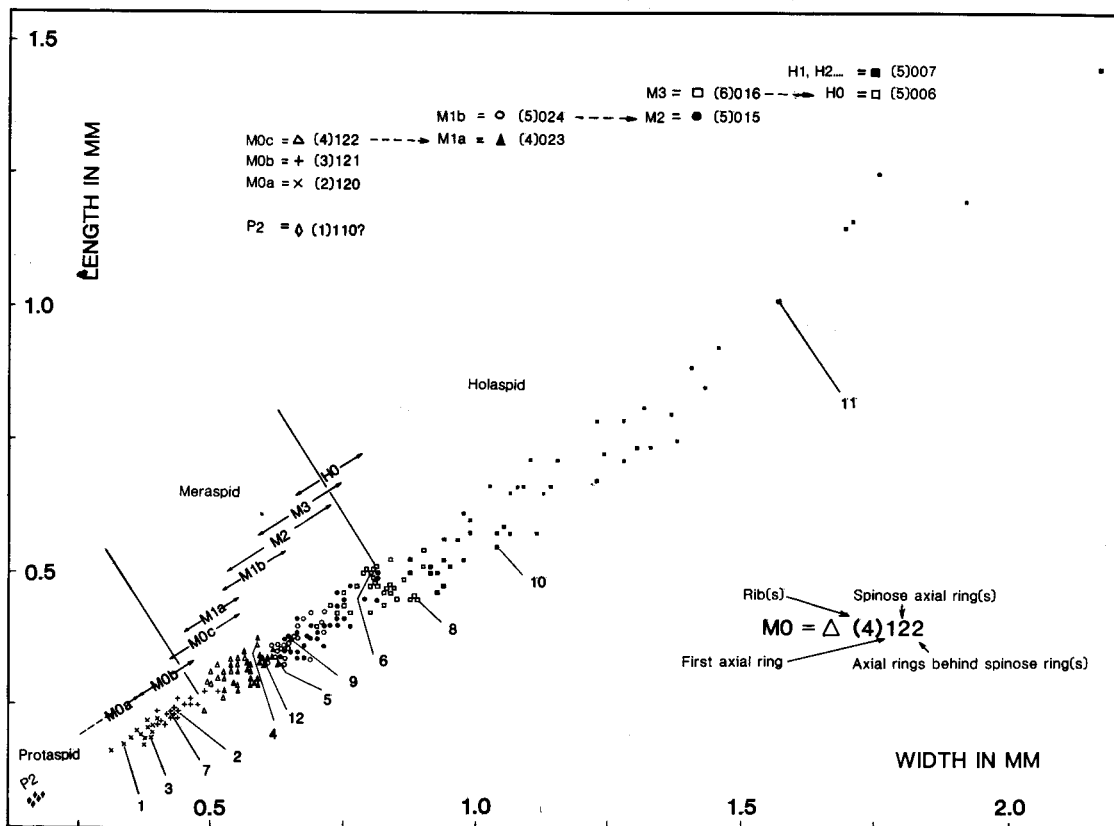




TEXT-FIG. 1. Plots of measurements for 6 cephalae and 177 cranidia of *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui, Sichuan; showing an approximately isometric growth pattern. Possible instars occur within the three growth periods. The Arabic numerals and letters correspond to the specimens illustrated in Text-figures 4 and 6.

complete with appendages and may have conserved the results of more than one moult, though it is also likely that the differences between adjacent stages, as defined by Müller and Walossek merely reflects the variation in morphology of an individual with growth, from one ecdysis to the next.

It is likely, as Henningsmoen (1975) suggested, that the majority of remains found are exuviae. Most of the specimens used in the present study, occurring as they do in a disarticulated state and in densely packed associations (Zhang and Clarkson 1990, Text-fig. 3A), are probably exuviae. Only a few, possibly the five nearly complete protaspides, and more certainly specimens illustrated in Pl. 1, fig. 8 and Pl. 2, figs 1–4, may have been the remains of dead animals (though they became disarticulated after death). The much more common exuviae record the ‘instantaneous’ morphologies proper to each moulting event, i.e. stage E in Henningsmoen’s (1975, p. 180) division of the intermoult cycle for trilobites. Our analysis has relied very largely on these.



TEXT-FIG. 2. Plots of measurements for 203 pygidia of *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui, Sichuan; showing nine possible instars (overlapping to some extent), within the three growth periods. The Arabic numerals correspond to the specimens illustrated in Plate 1.

Quantitative definition of instars

In many previous studies of trilobite ontogeny the instars have been defined quantitatively (Palmer 1957, 1958, 1962; Hunt 1967; Robison 1967; Jell 1975a; Romano 1976; Busch and Swartz 1985; Brezinski 1986).

In order to analyse statistically how *Shizhudiscus longquanensis* increases in linear dimensions during ontogeny we measured two parameters. These were the length (sag.) from the anterior to the posterior margin, and the width (trans.) between the palpebral lobes; this was effected in five almost complete protaspides (Text-fig. 3A-H), one cephalon (Pl. 2, figs 1-4), and 178 cranidia (Text-fig. 4A-L). Because these two dimensions could be measured with great accuracy in the isolated specimens, even some incomplete or damaged specimens could be included. In the scatter diagram (Text-fig. 1), the 183 points representing all cephala and cranidia suggest an approximately isometric increase, but there is no more than a hint of clusters corresponding to possible moult stages. It is not possible therefore to define the growth stages in this way. The relatively even spread of points denotes that changes in the morphology of the cranidium or cephalon were fairly gradual, so these likewise give no help in defining instars.

Whereas ontogenetic changes in the 203 pygidia of *S. longquanensis* which we have measured are gradual, there are particular characters that can be traced all the way from their earliest stages to their final form. Of these the most striking are the two axial spines which form on the protopygidium and move progressively forward, and are eventually released anteriorly to form the dorsal 'thorns'

of the last two thoracic segments. These can be used as developmental markers in the same way that Stubblefield (1926), and Fortey and Owens (1991) traced successive stages of the ontogeny of *Shumardia pusilla* by means of the long macropleural spines. We have been able to recognize ten kinds of pygidium (Pl. 1, figs 1–12), excluding the protopygidium, and have assigned these to ten corresponding growth stages (eleven with the protopygidium) (Text-fig. 2). There may in fact have been more growth stages; individuals corresponding to younger instars seem not to have been preserved. The scatter diagrams (Text-figs 1–2) show a fairly even spread of points. Thus the size range for any one developmental stage (of the cranidium or pygidium) must have been quite variable, for there is no clear pattern of instar peaks. It has not proved possible to identify distinctive growth stages or instars, either using morphological features of the exoskeleton or statistical analysis. This accords with Zhang's (1989) equivalent investigation of the ontogeny of *Neocobboldia chinlinica*, which likewise lacks instar peaks, especially in the adults. In both these eodiscid trilobites therefore, the size ranges of each instar overlap, and this may be a feature common to eodiscids generally. This lends support to Sheldon's (1988) argument that it is not possible to define instars on the basis of size alone, and we agree also with his view that in some previous studies too few specimens have been used for meaningful statistical analysis of size-frequency distribution during ontogeny.

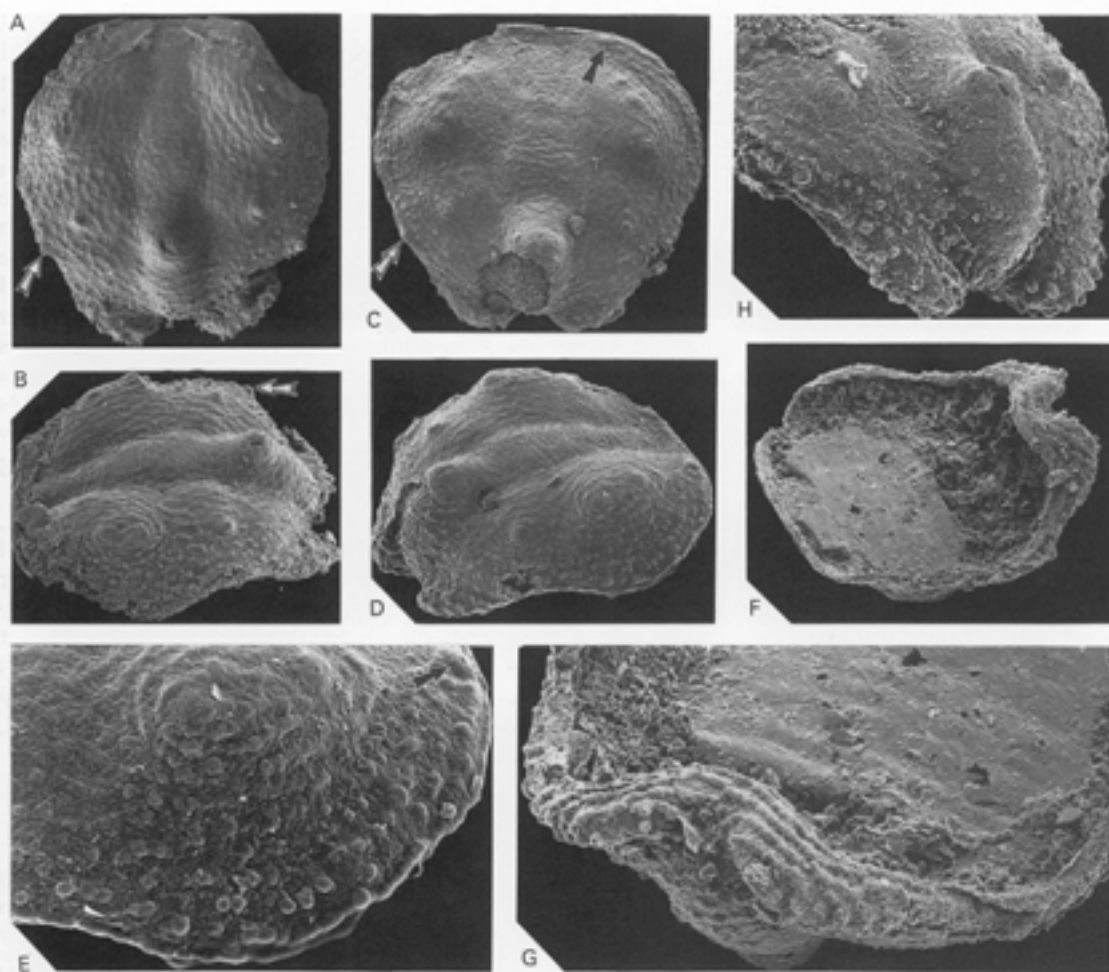
As ontogeny progressed, the limited evidence of instar groupings seen in the early larvae is lost, as clearly shown by the meraspid specimens in Text-fig. 2. The main reason for this is the shape and size at any one time, of the transitory pygidium. The three thoracic segments were formed one after the other during the meraspid period, being generated and then released forward from the transitory pygidium. The transitory pygidium thus varied markedly in dimensions, showing in the scatter diagram as a broad range of individuals for a single instar, and individual groups of different instars would overlap. This accords with the explanation for overlap of trilobite instars in size-frequency distributions previously given by Palmer (1958), Robison (1967), Sheldon (1988) and Zhang (1989), all of which have proved equally suitable for eodiscid trilobites.

ONTOGENY OF *SHIZHUDISCUS LONGQUANENSIS*

Whereas it is possible to define at least nine instars for the pygidium of *S. longquanensis* on the basis of axial rings and thoracic segments, no such discrimination is possible for the corresponding instars of the cranidia. We have no complete meraspid or holaspid exoskeletons which might show directly which developmental stage for the cranidium relates to a known transitory pygidium. Moreover, morphological changes in the cranidia with ontogeny are very gradual, and size-overlapping makes it impossible to distinguish potential instar peaks for the cranidium by quantitative measurement alone. The succession changes from one ontogenetic stage to the next. Despite this limitation, the enrollment mechanism of this eodiscid trilobite that we have been able to demonstrate may allow, to some extent, the correspondence between some of these isolated cranidia and pygidia to be traced. The disappearance of the bacculae and the genal spines may also be used in the subdivision of growth series. Most disarticulated exoskeletons therefore can be referred, with reasonable confidence, to meraspid and holaspid periods, and even to particular growth stages. The ontogenetic series of *S. longquanensis* is summarized below.

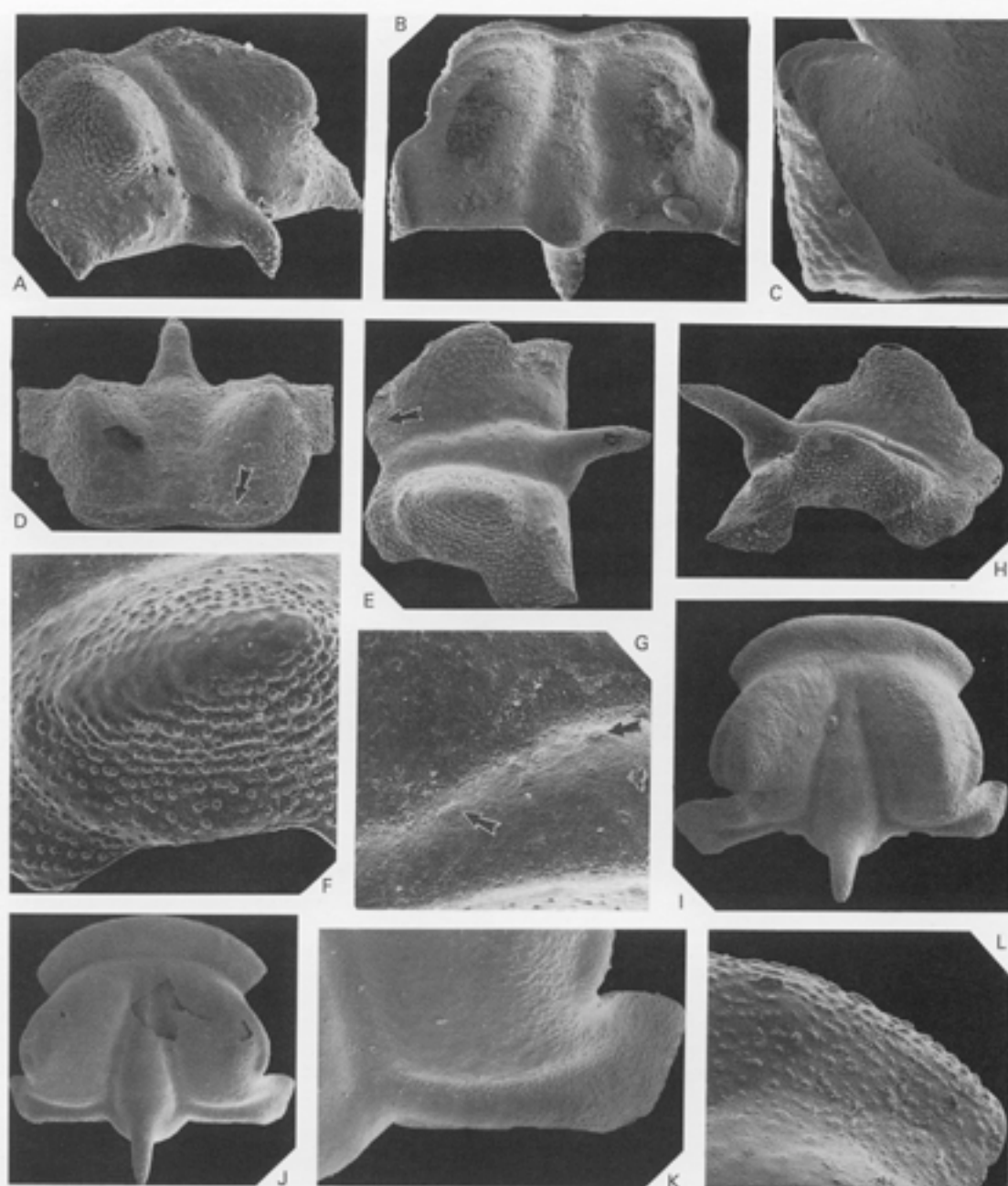
Protaspid period

Stage 2 (P2). This stage is represented by five subovate, entire exoskeletons (Text-figs 3A–H, 7A–C); these are all late protaspides. They are moderately convex transversely, but much more strongly convex sagittally, since the protopygidium is strongly bent downwards. They range in length from 0.22 to 0.25 mm, and in width from 0.20 to 0.23 mm. The axis, which may consist of five(?) or six segments is defined laterally by deep but relatively wide axial furrows. The glabella, tapering forwards, has three glabellar lobes, weakly convex and separated by faint transverse furrows. The fourth lobe on the glabella is the occipital ring, which forms a high, rounded node, often indented



TEXT-FIG. 3. *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui, Sichuan. A-H, protaspides (P2). A-B, PSO 5982; dorsal and lateral views of an almost complete exoskeleton with the genal tubercles (arrowed) preserved, $\times 175$. C-G, PSO 5981; c, dorsal view; the tubercle is indicated by the white arrow, and the anterior border tubercle by the black arrow, $\times 175$. D, oblique lateral view, $\times 175$. E, detail of D, showing fine granules arranged in rows on the outer surface of the right side of the cephalon, where as yet the facial suture and librigena have not differentiated, $\times 482$. F, lateral ventral view, $\times 175$. G, postero-ventral view, showing details of granules and fine ridges, $\times 350$. H, PSO 5983; oblique lateral view of posterior part of the exoskeleton, ornamented with fine granules, $\times 295$.

by a short longitudinal furrow. Behind the occipital ring is a rather convex axial part, which curves sharply downward to meet the posterior border. The rachis is more strongly curved than the adjacent regions of the protopygidium (borders and pleural areas), and tucks into the posterior sinus so that the rear border of the protopygidium is W-shaped. There are no transverse furrows visible on the protopygidial axis, but its length would suggest that two rings were present. The anterior margin is nearly straight, and the anterior border, defined by a rather shallow anterior border furrow, is very narrow, bearing two anterior tubercles. The doublure is likewise very narrow. The two elliptical fixigenal lobes are prominent, located on the anterior part of the pleural region. Behind these lobes are a pair of rounded bacculae, positioned in the posteropleural areas. The exoskeleton curves ventrally to form the doublure along the free border on the ventral side, so that



TEXT-FIG. 4. *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui. A-L; cranidia. A, PSO 5210; oblique posterodorsal view of (M0b), $\times 122$. B, PSO 5202; ventral view of (M0b), $\times 122$. C, PSO 5209; ventral view of (H0), showing the genal doublure, $\times 235$. D, PSO 5198; antero-dorsal view of (M0a), showing the anterior tubercle (arrowed), $\times 118$. E, PSO 5204; lateral dorsal view of (M0b); arrow indicates the anterior border tubercle, $\times 102$. F, detail of E, showing granules arranged in a concentric ellipse surrounding the fixigenal lobe, $\times 300$. G, detail of E, showing the tubercles (arrowed) on the glabella, $\times 300$. H, PSO 5165; oblique-lateral view of (M1)?, $\times 78$. I, PSO 5211; dorsal view of (M3), $\times 56$. J, PSO 5185; dorsal view of mature cranium, $\times 34$. K, detail of J, showing right genal angle and fine granulation on the posterior fixigenal area, $\times 95$. L, PSO 5167; fine granules on the anterior border of (M3), $\times 245$.

the doublure along the posterior margin also has a W-shaped outline. In ventral view the doublure is quite inflated and widest at the posterior margin, but tapers rapidly anteriorly to become very narrow along the anterior margin. On the external surface of the cuticle is a fine reticulate sculpture composed of fine ridges and granules. The fine ridges are found on the axis, the inner parts of the fixigenal areas of the cephalic region and the doublure. The granules, however, are concentrated chiefly on the outer parts of the fixigenal areas and on the protopygidium. A pair of small tubercles is located on the posterolateral borders (Text-fig. 3A-C), which develop during subsequent growth stages into short genal spines. The articulation between the cephalic region and the protopygidium is not yet developed at this stage, but its position can be inferred from the location of the bacculae, genal tubercles, and occipital ring.

Meraspid period

In all trilobites, meraspid degree 0 (M0) is defined upon the first appearance of articulation. In the case of *S. longquanensis* the smallest isolated transitory pygidium has only three axial rings. More axial rings are gained with growth but none is released as a thoracic segment until the axis consists of five rings. This situation is the same as in the transitory pygidia of *Neocobboldia chinlinica*. This emphasizes the fact that the M0 transitory pygidia of eodiscids gain axial rings step by step before the first thoracic tergite forms; the meraspid degree 0 is here divided into substages corresponding to the number of axial rings. Thus the three metaprotaspid stages (Mp0-2) of *N. chinlinica* should be revised as three meraspid substages (M0a-c). By the same reckoning, the meraspid period of *S. longquanensis* is divided into seven stages or substages (M0a, M0b, M0c, M1a, M1b, M2, M3), defined on the basis of rings added to the pygidial axis and the release of thoracic segments anteriorly. Since the exoskeletons are incomplete, however, the corresponding meraspid cranidia cannot be referred to particular growth stages. These range in size from 0.18 to 0.52 mm in length and from 0.30 to 0.87 mm in width. There are some evident, though gradual changes in morphology in progressively larger meraspid cranidia (Text-fig. 4H-I). Thus the anterior margin loses its indentation and becomes outwardly curved; this is accompanied by the broadening of the anterior border. As the fixigenal areas continue to elevate, each of the fixigenal lobes and the adjacent bacculae merge into a single high lateral lobe. The glabellar lobe becomes somewhat inflated yet remains of relatively low convexity and lies well below the level of the fixigenal lobes. The axial furrows become increasingly deep and narrow and the posterior furrow appears. On both sides of the cranidium the sinus representing the last librigena has become relatively long and wide, suggesting the addition of more lenses to the visual surface. The short genal spike underwent a contraction and all that remains of it finally is a rounded genal angle (Text-fig. 4C).

Substage (M0a). It is at this growth stage that the first articulating hinge develops, so that the transitory pygidium becomes free; all material is thus represented by disarticulated cranidia and transitory pygidia. The cranidia (Text-figs 4B-D, 7D) are subtrapezoidal in outline, with lengths ranging from 0.18 to 0.25 mm, and widths from 0.30 to 0.38 mm. The axis tapers forwards and is defined by deep and narrow axial furrows. Both the paired, elliptical, fixigenal lobes and the surrounding fixigenal areas are strongly elevated and peaked. Although the glabellar and occipital furrows are very weak, the four glabellar lobes that they define can be faintly distinguished. Of these the front glabellar lobe is elliptical in outline and moderately convex, the next two are progressively wider and more convex, and the most posterior lobe forms the widest part of the axis. The occipital ring is remarkably convex and bears a strong spine. The anterior border is somewhat curved backwards centrally, and bears two distinct anterior tubercles (Text-fig 4D) in front of the large fixigenal lobes.

These lobes by this stage are highly convex, and the rounded bacculae posterior to them have become prominent. There is an ocular ridge extending laterally from each side of the frontal glabellar lobe, fused with the palpebral lobe to form a forwardly curved broad ridge between the anterior border and the fixigenal lobe. By this stage the facial suture has moved from the ventro-

lateral side to the anterolateral surface of the cephalon, so that there is an evident sinus where the librigena is lost. The lateral border has broadened and is defined by a shallow lateral border furrow, but the posterior border furrow is not as yet present. The genal spine is short and posterolaterally directed. In ventral view the anterior part of the doublure is very narrow, as is the librigenal doublure (Text-fig. 4B). The posterolateral corner of the doublure, however, carries a broad, triangular doublure with tuberculate ornamentation (Text-fig. 4C). There is by now a substantial change in surface sculpture; the fine reticulation of the outer surface has been replaced by a granulose texture, concentrated particularly on the anterior and lateral borders, the fixigenal areas, as concentric ellipses on the fixigenal lobes, and clustered towards the tip of the occipital spine. On the axis and the posterior fixigenal areas some other, rather large granules are scattered.

The transitory pygidia (Pl. 1, figs 1, 3) are, like the cranidia, subtrapezoidal in outline with a pronounced 'larval notch'. For this stage they range from 0.16 to 0.23 mm in length and 0.30 to 0.39 mm in width. The axis, consisting of three segments, is very strongly elevated, with the axial furrows hardly defined. The axial rings likewise are so tightly fused that they can only be distinguished by the two strong spines borne by the rear two rings and by the rather weak transverse axial furrow separating the first ring from the second. The two axial spines rise abruptly and are nearly straight, with only their apices pointing backwards. The lateral and posterior borders are moderately convex, and separated from the pleural areas by shallow border furrows. At the anterolateral corners of the pygidium is a pair of swellings. These develop into lateral pleural lobes when the segment bearing them is released to form the first thoracic segments. Two further pairs of swellings, more posteriorly located, define the positions of other pleural ribs. The outer surface of the exoskeleton is covered with fine granules, most of which are concentrated upon the posterior pleural regions, but fine ridges are only to be found upon the borders. At this stage in development, the doublure beneath the posterior border is hardly in evidence (Pl. 1, fig. 3).

Substage (M0b). The cranidia (Text-fig. 4A, E-G) are morphologically similar to those of the preceding substage, and are mainly distinguished by their size and their correspondence with pygidia of equivalent dimensions on the scatter diagram (Text-fig. 1). Their lengths range from 0.25 to 0.34 mm, and widths from 0.38 to 0.47 mm. The only appreciable changes are that the fixigenal lobes have become still higher, and the occipital spine is more elongated. The ventral morphology is like that of preceding substage. Likewise the granulation on the surface of the exoskeleton is now more clearly defined, and the concentric ellipses round the fixigenal lobes more pronounced and regular (Text-fig. 4F).

The M0b substage is much more clearly determined by the morphology of the pygidia (Pl. 1, figs 2, 7). These range from 0.23 to 0.27 mm in length and 0.39 to 0.40 mm in width. Whereas they retain many morphological characteristics from earlier stages they differ in that an additional axial ring has appeared at the rear of the axis, a pair of pleural ribs has been added posteriorly, and the transverse axial furrow between the first and second rings has now become distinct.

Substage (M0c). During this substage the fifth axial ring appears posteriorly and increases markedly in size, while the first transverse axial furrow and the first pair of interpleural furrows join to form a continuous faintly incised furrow, defining the rear edge of the first thoracic segment (which will soon separate from the transitory pygidium). This first thoracic segment includes the first axial ring, which lacks a spine (Pl. 1, fig. 4; Text-fig. 7F). It may well have still been connected to the articulating half-ring of the second segment (still part of the transitory pygidium) (by an arthroial membrane).

Stage (M1). As the first thoracic segment is released, the sixth axial ring and the fifth pair of pleural ribs develop at the rear of the transitory pygidium. This now has five axial rings and four pleural ribs, and such morphology defines substage (M1a; Pl. 1, fig. 12). During subsequent growth the pygidium gains a new axial ring (the seventh), and a new pair of pleural ribs but at this stage no further thoracic segment is released. There is still only one free thoracic tergite. We may therefore

assign pygidia which have reached this stage of development (Pl. 1, fig. 5, Text-fig. 7G) to substage (M1b).

Stage (M2). As development proceeds the second transverse axial furrow, together with its associated interpleural furrows, form a new articulation separating off a second thoracic segment from the transitory pygidium. The release of this second segment accompanies the appearance of the eighth axial ring, defining stage (M2). The transitory pygidium now bears only a single spine (Pl. 1, fig. 9, Text-fig. 7H).

Stage (M3). Following upon this, the pygidium gains the ninth axial ring and a new pair of pleural ribs, and with further development the final articulation forms, separating the third thoracic segment from the pygidium (Pl. 1, fig. 6). This stage (M3) is represented by spineless pygidia with six axial rings and five pairs of pleural ribs. These indicate clearly that after the third thoracic segment was released at the M3 stage, no further axial rings or pleural ribs appeared.

Besides changes in the axial rings, pleural ribs, and thoracic segments, to which we have referred, there are other minor changes. The W-shaped posterior margin of the transitory pygidium becomes semicircular, but with numerous small serrations along a free margin. The granules on the cuticle do not seem to increase in size but a few somewhat larger granules (tubercles) appear in the early meraspid (Pl. 1, fig. 4) arranged in pairs on each axial ring and in rows on each pleural rib, just behind the interpleural furrow (Pl. 1, figs 5–9). As development proceeded the whole exoskeleton became progressively more convex.

Holaspid (H0) period

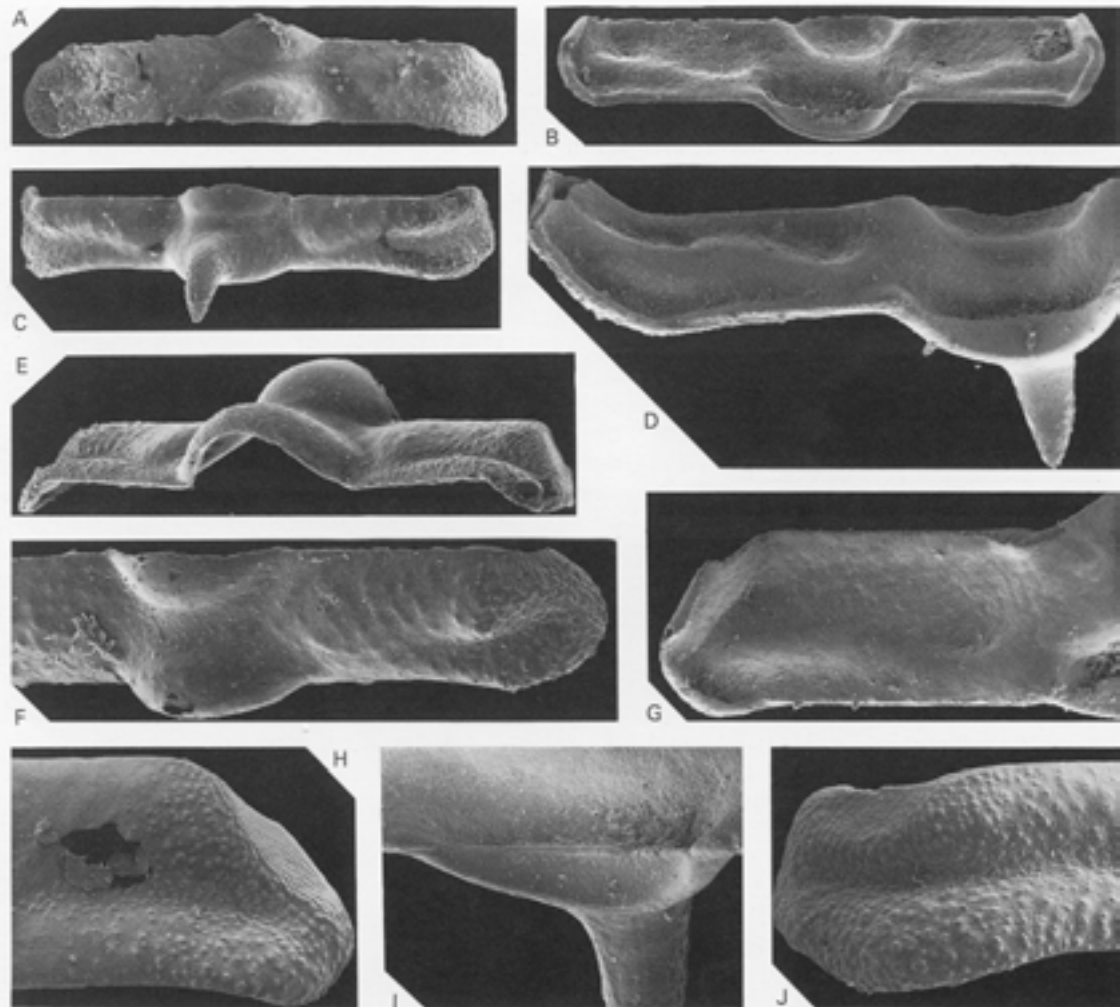
This begins when the third thoracic segment is liberated from a pygidium bearing six axial rings and five pairs of pleural ribs. Most holaspid cranidia and pygidia show comparatively few reliable criteria which would enable them to be assigned to particular instars, and only the axial rings and paired pleural ribs can be used to distinguish early holaspid pygidia (H0) from those of later holaspides (H1, H2...).

The cranidia (Text-figs 4J–K, 7I) of the early holaspid period share many morphological features with those of later meraspides. As the cranidia become progressively larger and more fully inflated the anterior border becomes wide and moderately convex, while the anterior border furrow becomes wide and deep. The fixigenal areas attained a considerable elevation, and while the palpebral lobe became distinct, the ocular ridge all but disappeared. The glabella is by this stage very much tapered (and less elevated) forwards, but the occipital ring and the rear part of the glabella are much swollen. The three glabellar lobes are now only faintly defined by scarcely visible furrows. While the occipital spine remains prominent, its growth rate seems to have reduced and it is relatively shorter than in the earlier stages.

The pygidium of the early holaspis bears six axial rings and four pleural ribs. With further growth it gains a tenth and final axial ring, and a further pair of pleural ribs. Thereafter, there are no rings or ribs added. There are some supplementary changes in the holaspid pygidia though these cannot be used to distinguish growth instars. Thus, as the rachis expanded the axial furrows became quite faint, but the seven axial rings can still be distinguished by their paired axial tubercles, which become very prominent. Likewise, the tubercles arranged in rows on the pleural ribs just behind the interpleural furrows are distinct. With inflation of the pleural area the pleural furrows became shallow, but still visible, while the axial furrows and the border furrows became more deeply incised. The border, by the later holaspid stage is relatively narrow, and its free margin weakly serrate. The fine granules on the outer surface of the pygidium seem to have remained much the same size and are mainly concentrated on the border and on the posterolateral and rear parts of the pygidium.

Thoracic segments

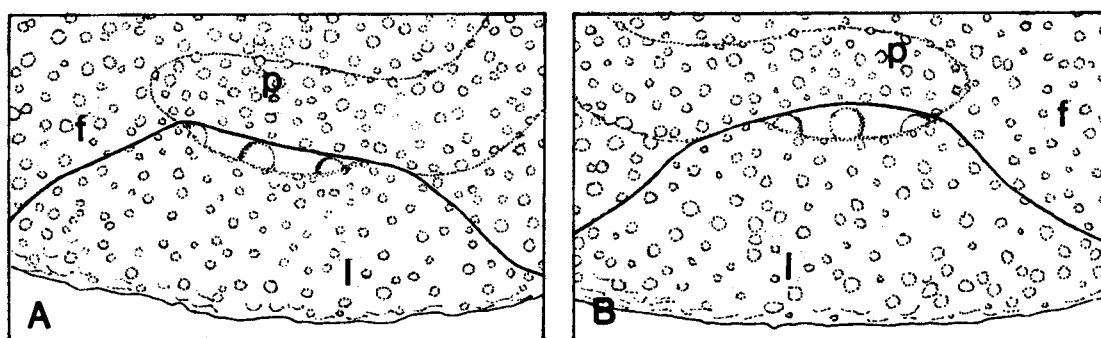
The thoracic tergites were probably released one by one from the anterior part of the transitory



TEXT-FIG. 5. *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui, Sichuan. A-J thoracic segments. A, PSO 5962; dorsal view of the first thoracic segment of M1, $\times 91$. B, PSO 5960; ventral view of the first thoracic segment of M3, $\times 81$. C, PSO 5952; oblique dorsal view of a second (or third) thoracic segment of M2, $\times 80$. D, PSO 5959; ventral view of a second (or third) thoracic segment of a holaspid, $\times 117$. E, PSO 5954; lateral anterior view of the first thoracic segment of H0, $\times 81$. F, PSO 5955; dorsal view of the first thoracic segment of M2, $\times 157$. G, PSO 5957; ventral view of the left side of the first thoracic segment of H, $\times 91$. H, PSO 5958; dorsal view of a first thoracic segment of holaspid, showing the articulating facet, $\times 142$. I, PSO 5938; ventral view of a second (or third) thoracic segment of holaspid, showing the doublure under the axial ring, $\times 190$. J, PSO 5969; dorsal view of a second (or third) thoracic segment of holaspid, showing the left articulating facet, $\times 160$.

pygidium, as we have described (though it is possible that more than one was liberated at one time). These are mostly found isolated, and only a few segments were still attached to the transitory pygidium (Pl. 1, fig. 8), or ready to separate from it. (Pl. 1, figs 4, 6). It is difficult, therefore, confidently to assign any one segment to a particular growth stage, though simple comparisons of the width of any thoracic segment with a pygidium of approximately the same width allows an approximation.

The first of the three thoracic segments does not bear an axial spine (Text-fig. 5A-B, E-H). Such segments, though representing a broad, gradational size series in our material, are readily distinguished. The second and third thoracic segments have a prominent axial spine (Text-fig. 5C-D, I-J; Text-fig. 7I); it is not easy to distinguish the second from the third, for they are morphologically very similar. Before articulating, the axial spine on the presumptive third segment was the stronger and more highly curved, and it might be expected that this difference would be retained after release. Yet there is no convincing indication in the isolated spinose segments that this is so, and whether any one of these is a second or third segment remains unknown. In the



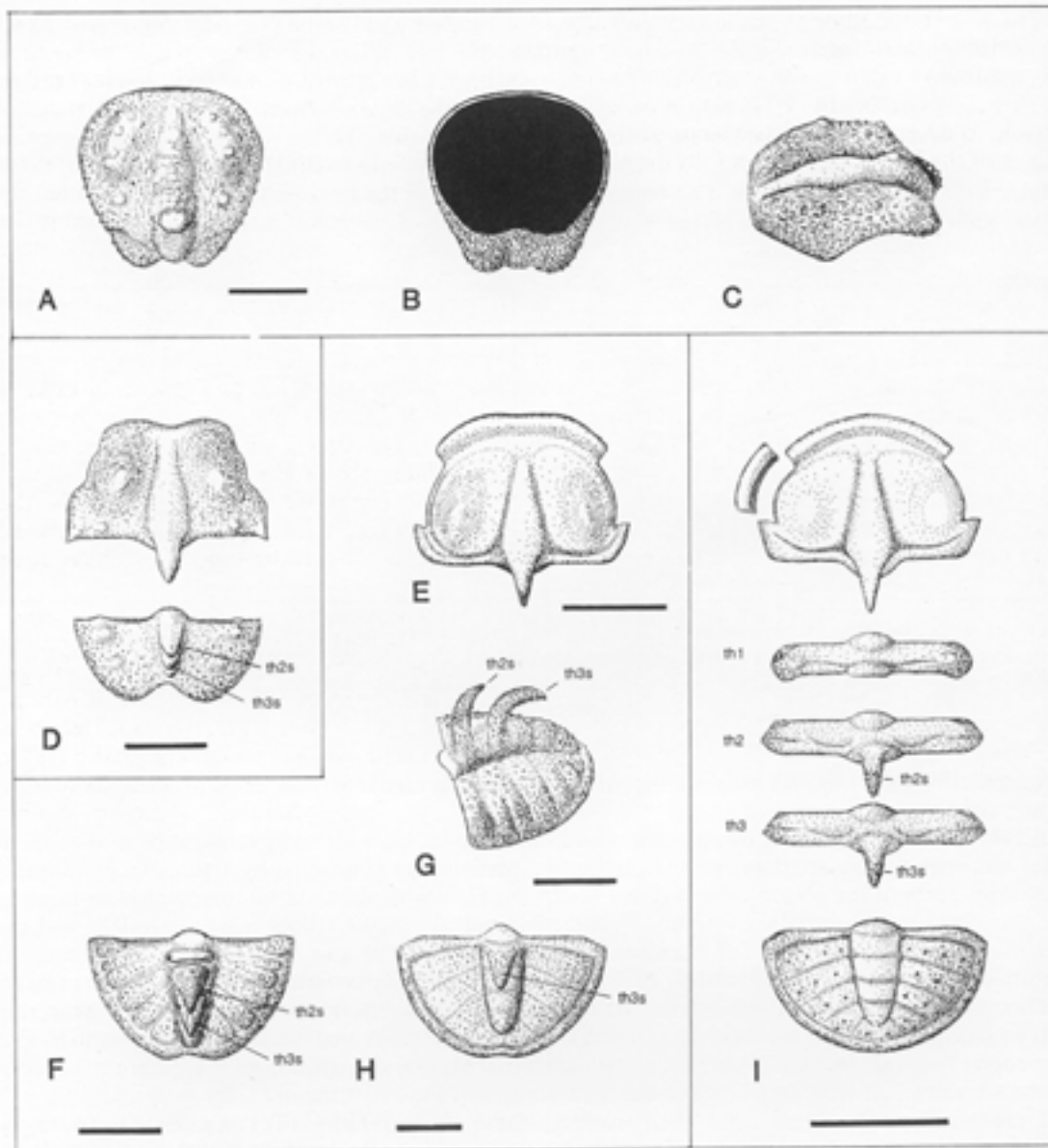
TEXT-FIG. 6. *Shizhudiscus longquanensis* S. G. Zhang and Zhu. Explanatory drawings of the cephalon illustrated in Pl. 2, figs 1-4. A, right librigena with visual surface present, showing one almost circular lens and two half-lenses. B, similar initial small lenses on the left librigena. f, fixigena; l, librigena; p, palpebral lobe thick line indicates suture line.

reconstruction (Text-fig. 7I), they are shown as identical, though it is recognized that they may differ in minor ways.

All the thoracic segments, whether meraspid or holaspid, have virtually straight pleural edges at front and rear, which acted as articulating hinges, presumably connected by arthrodial membrane. The outer parts of the pleura curved down ventrally. Here arthrodial membrane would be lacking, but the free parts formed a continuous protective wall when the trilobite was enrolled, and the articulating facets permitted full enrollment. The orientation of any isolated thoracic segment is readily determined by the articulating facets and the backwardly pointed axial spine where present. Each segment has an arched articulating half-ring, which would fit neatly under the larger axial ring of the preceding segment (or the occipital ring). The axial ring has a narrow doubleure with a straight free edge (Text-fig. 5B, D, I). It is likely that arthrodial membrane connected this edge to the front of the adjacent half ring. In our small thoracic segments, the articulating facets are present though not especially pronounced, and their surfaces bear fine granules (Text-fig. 5A, F). In larger specimens, however, the articulating facet has become more clearly developed, and the fine granules have extended into a series of fine parallel ridges (Text-fig. 5H, J). These may have been adapted for tight gripping of adjacent parts when the exoskeleton was enrolled.

Eyes

In our previous study (Zhang & Clarkson 1990, pl. 1, fig. 1a-b), the smallest librigena of *Shizhudiscus longquanensis* that we found bore nineteen lenses (including half-lenses). We estimated that this came from a late meraspid or early holaspid, and now that the ontogeny of this species is known in detail, we are able confidently to refer this librigena to the later meraspid (M3) stage, on account of its dimensions.



TEXT-FIG. 7. *Shizhudiscus longquanensis* S. G. Zhang and Zhu. Reconstruction of successive stages in ontogeny. A-C, protaspis in dorsal, ventral, and oblique-lateral views (cf. Text-fig. 3A, F, B). D, cranidium and pygidium of (M0a) stage (cf. Text-fig. 4A-B, Pl. 1, figs 1-2). E, cranidium of (M3) stage (cf. Text-fig. 4i). F-H, meraspis pygidia in dorsal view: F, (M0c) stage (cf. Pl. 1, fig. 4), G, (M1) stage (cf. Pl. 1, fig. 5), H (M2) stage (cf. Pl. 1, fig. 9). I, attempted reconstruction of adult exoskeleton (cf. Pl. 1, fig. 10a, Text-figs 4j, 5A, C). This is tentative, since exact matching of the developmental stages for the various tagmata is uncertain, as is the comparative morphology of the second and third thoracic segments. Scale bars: A-C = 1 mm; D-H = 2 mm; I = 5 mm.

In the course of this present work we found a single specimen of *S. longquanensis* with both eyes intact, representing a much earlier stage than any described hitherto. This adds valuable detail to what is already known about eodiscid eyes. Such preservation is very rare, for even in some enrolled

individuals (from other phosphatized material of *Shizhudiscus* sp. collected at Zhenba, Shaanxi) the librigenae are absent (Pl. 2, fig. 8). Our single specimen (Pl. 2, figs 1–4; Text-fig. 6A–B) is recognizable as a degree 0 meraspis (M0b) and is probably the remains of a dead individual rather than an exuvium (6A–D). Whereas we lack the intermediate stages between M0b and M3, it is still possible to determine the basic steps of the development of the eye.

Each of the librigenae bears a fully developed single lens with two half lenses on either side; these become the central lenses of the uppermost horizontal row in later growth stages. These lenses are widely separated from each other, and the lenses of the second horizontal rows are added below the spaces between them. Thus from the earliest stage of development, the pattern of hexagonal close packing, fundamental to trilobites (Clarkson 1975) is already in evidence. While the M0b eye has one complete and two half lenses, the M3 eye has nineteen (including six half-lenses, arranged in two horizontal rows of complete lenses with a further row of half-lenses below (Zhang & Clarkson 1990, p. 222). These are arranged in two horizontal rows of complete lenses with a further row of half-lenses below. In all trilobites new rows are always added below existing ones and expand laterally. In the eodiscids the newly formed rows consist of half-lenses which only become complete lenses at the next moult. It is evident that the eyes must have expanded very rapidly at front and rear after the M0b stage, to form the elongated visual surface seen in M3.

Assuming only one moulting in an instar; at least four moults were passed through in the transition from M0b to M3, so the increase of a single horizontal row required at least two ecdyses. If the rate of increase was approximately constant, the first lens would be expected to have been emplaced in the M0a stage, and possibly earlier.

The early emplacement of the lenses in eodiscids may be compared instructively with that in other trilobites. For example, even in the schizochroal-eyed Phacopina the early stages of eye development (Alberti 1972) are broadly the same. In both eodiscids and phacopids, in the earliest stages, a single small lens appears which retains its position thereafter on the upper horizontal row, and a pattern of hexagonal close packing develops as more lenses are emplaced. Furthermore, the initial lenses in *Shizhudiscus* are widely spaced, as they are in the Carboniferous *Paladin* (Clarkson & Zhang 1991); it is only later in development that the lenses become contiguous and the eye achieves a fully holochroal condition. The initial stages of development of trilobite eyes generally, therefore, exhibit patterns common to all.

Doublure and hypostomata

The doublure, as in *Pagetia* (Jell 1975; Whittington 1988) remains very narrow, but there may have been, in addition a flat crescent-shaped rostral plate (possibly uncalcified), extending as far as the anterior border furrow. This condition would be similar to that in olenelloids, and equivalent to the construction postulated by Whittington for *Pagetia*. Both Whittington (1988) and Fortey (1990) regard the eodiscid hypostome as natant, lying freely below the cephalon.

A few hypostomata (Pl. 2, figs 5–7) are present in our material. They bear fine granules and ridges and each has eleven radiating spines. These are figured here for completeness, but their morphology is quite different from that of other eodiscid trilobites, such as those of *Pagetia* (Öpik 1952; Jell 1975a), and *Neocobboldia* (Zhang 1989). The hypostomata figured here may therefore belong to an unknown polymerid.

Cuticular sculpture

In many trilobites cuticular sculpture may change throughout ontogeny. Where preservation is exceptionally good, a network of fine ridges may be seen covering the larval exoskeleton; each of these cuticular polygons retains the shape of the epidermal cell below which secreted it. The cell polygons may still be visible in the adult, as in the very thin cuticle of *Homagnostus obesus* described

by Wilmot (1990). More commonly the cell polygons fade and are replaced by tubercles or other structures as in *Paladin* (Clarkson & Zhang 1990). This is also the case in the eodiscids *Neocobboldia* and *Shizhudiscus* where reticulation is only present on the external surface of late (P2) protaspides. The fine granules that appear later do not seem to bear any direct relationship to the epidermal cells.

Enrollment

Eodiscid trilobites undoubtedly possessed the ability to enroll, as shown by Jell's (1975a, 1975b) illustrations of phosphatized Middle Cambrian *Pagetia silicunda* and *Opsidiscus brevicaudatus*. The specimens were all tightly enrolled, with the cephalon and pygidium fitting snugly, and in some the visual surface was still attached.

A single phosphatized specimen of *Shizhudiscus* sp., from the Lower Cambrian of Zhenba, Shaanxi (Pl. 2, fig. 9), reveals some details of the enrollment mechanism in this genus.

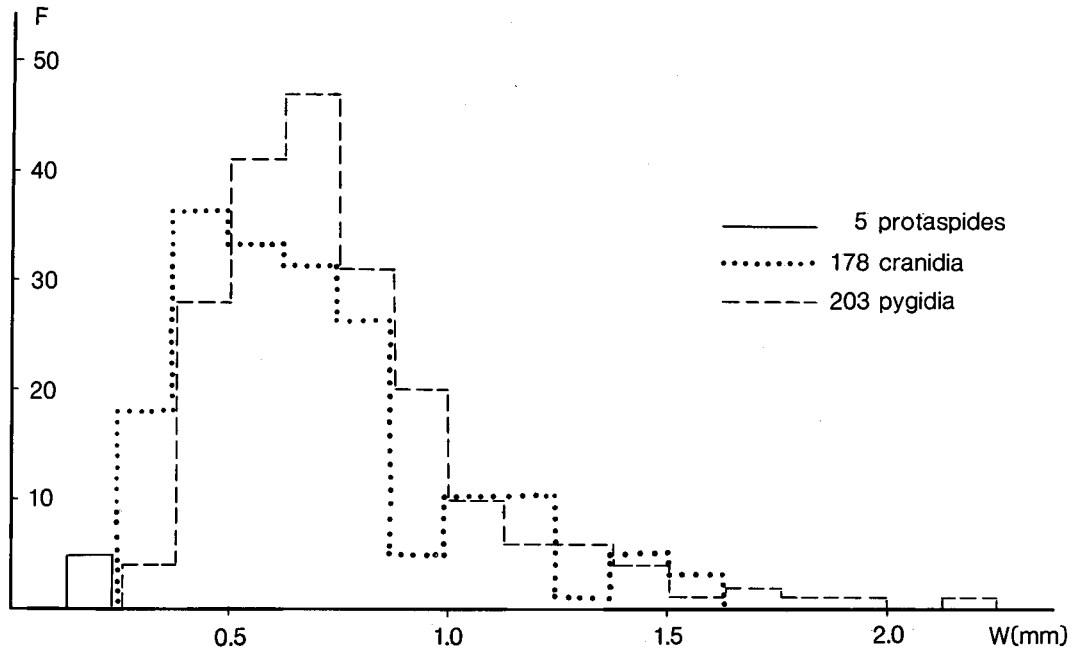
(a) The anterior border of the specimen, otherwise moderately rounded, is slightly indented centrally, thus matching the W-shaped margin of the pygidium. The future first thoracic segment is still welded to the transitory pygidium. Thus this enrolled individual can confidently be referred to the late meraspid period (M0c), by direct comparison with *S. longquanensis*. More importantly this specimen shows that full enrollment was possible even at this relatively early stage in ontogeny; the anterior margin of the transitory pygidium acted as a hinge which would permit the two exoskeletal parts to close up together. Agnostids (Jaekel 1909) likewise can enrol at meraspid degree 0 stage, as can trinucleids and raphiophorids, though must polymerids rely upon concerted movements of many segments and transverse joints for enrollment.

(b) Although no suggestion of a future articulatory joint is yet evident in the five smallest protaspides (P2) of *S. longquanensis*, its eventual position may readily be determined from the location of the paired bacculae and the prominent occipital ring. At the P2 stage, the small protopygidium is strongly curved downwards relative to the cephalon, but even if the protaspid were flexible the protopygidium and the ventral side of the cephalon could never make contact, and in any case would not match. The earliest stage at which true enrollment was possible is M0.

(c) Robison (1972) deduced a pelagic mode of life for the agnostids, on the basis of their global distribution, and considered the unique articulatory system and mode of enrollment as an adaptation to this life style. Müller and Walossek (1987) illustrated the enrollment mechanism of *Agnostus pisiformis* from the first meraspid to holaspid stage, and clearly the style of enrollment of the eodiscid *S. longquanensis*, in functional terms, has some characters in common with this. Thus in both eodiscids and agnostids the first meraspides could fold up and close tightly by means of a single articulation. As the thoracic segments were liberated from the transitory pygidium, so there would be more space within the enrolled exoskeleton for soft parts and appendages, especially in the three-segmented *Shizhudiscus*. In the opinion of Müller and Walossek (1987) *Agnostus* lived in a semi-enrolled state when active, and the body could not be stretched out fully without damage. The articulating facets in *Agnostus* are very narrow. In *S. longquanensis*, however, they are prominently developed on the thoracic segments (Text-fig. 5F, H, J) and the pygidia (Pl. 1, figs 10a, 11a), as they are in polymerid trilobites. This resemblance suggests that in contrast with the agnostids, the eodiscids were able to stretch out in a fully extended attitude, as well as having the facility for enrollment.

MODE OF LIFE

The morphology of eodiscid exoskeletons changes remarkably between protaspid and meraspid periods, as seen particularly in the pygidia of *Neocobboldia chinlinica* (Zhang 1989) and *Pagetia ocellata* (Shergold 1991). The two scatter diagrams (Text-figs 1–2) relate to size distribution of cranidia and pygidia respectively. There is a distinct gap between the pygidia of protaspid degrees



TEXT-FIG. 8. Histograms for 5 protaspides, 1 cephalon, 178 cranidia, and 203 pygidia of *Shizhudiscus longquanensis* S. G. Zhang and Zhu; Lower Cambrian, Pengshui, Sichuan. F, frequency; W, width between the palpebral lobes of the cranidium (or the cephalon), or width of the pygidium.

2 and 3, though no such gap is evident for equivalent cranidia. It is possible that the observed break in pygidial size results from collection or preservational bias for protaspides of the size represented by the gap and there is an evident contrast here with the pygidial size distribution of *Neocobboldia chinlinica* (Zhang 1989, fig 2), where the scatter of points is continuous. While this might support the idea of preservation failure for this stage in *S. longquanensis*, it could equally indicate a substantial morphological saltation relating to an abrupt change in mode of life. Evitt (1961) noted a striking difference in gross morphology between protaspides and meraspides of *Isotelus*, and Chatterton (1980) emphasized how significant metamorphosis occurred during the protaspid period or between protaspid and meraspid. A recent series of papers has highlighted this phenomenon (Fortey and Chatterton 1988; Chatterton and Speyer 1989; Speyer and Chatterton 1989; Chatterton *et al.* 1990). Besides the changes in overall morphology in *S. longquanensis* across this gap, two other striking modifications take place around the protaspid-meraspid transition; the achievement of enrollment ability and the appearance of visual surface, with its first small lens. It is likely that both these transformations were associated with a change in mode of life, or at least represent a radical increase in functional capacity to adapt to the environment.

The protaspides lacked eyes, the exoskeleton was strongly curved, and the pygidium was sharply bent down. Such morphology recalls that of the non-adult-like ovoid or inflated forms described by Speyer and Chatterton (1989) as typical of planktonic larvae, and in our view the protaspides of *S. longquanensis* were likewise planktonic.

Agnostid and eodiscid trilobites are regarded by many authors as sister-groups within the Trilobita (Fortey 1990). Other workers, whose views are summarized by Shergold (1991), classify eodiscids alongside the ptychopariids. Whereas the affinities of the eodiscids are still debated, one possibility is that the agnostids derived from eodiscids by a neotenus retention of planktonic larval habits. Such heterochrony would explain why agnostids are eyeless and have only two thoracic segments. Perhaps even the absence of a calcified protaspis in agnostids may be part of the same

paedomorphic complex. If so, a close relationship between agnostids and eodiscids would be favoured.

TAPHONOMY

No hypostomata in our material can be referred confidently to *S. longquanensis*. This may reflect a poorly mineralized ventral exoskeleton, but more probably results from transportation and sorting. Within the lens containing the trilobites, small-scale cross-lamination is apparent and the densely packed exoskeletons must have been a consequence of current concentration. The bell-shaped size–frequency diagram (Text-fig. 8) again suggests selective transportation and preservation. It is not very likely, however, that the individuals lived very far away from where they were buried, since delicate structures such as the eyes, fine granules on the cuticular surface and the long spines are well-preserved. It is considered probable that the protaspides (P2), though few have been preserved, likewise lived near their place of burial. Such rapid burial of many individuals tends to confirm that most of the individuals used in this study belong to a single species.

Speyer and Brett (1986), working with Devonian trilobites, proposed a number of trilobite taphofacies on the basis of preservation alone. Despite differences in age and hydrodynamic properties, the life environment of *S. longquanensis* may roughly be assigned to their Taphofacies 1. Changes in life habit during ontogeny, such as we have proposed here, involve adaptation to new ecological niches within the same taphofacies.

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