DOI:10.19800/j.cnki.aps.1994.01.003
第33卷第1期 古生物学报 Vol. 33, No. 1
1994年1月 ACTA PALAEONTOLOGICA SINICA Jan., 1994

特马豆克期三叶虫 *Dichelepyge lata* Peng 的个体发育*

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内 容 提 要

记述了产于湘西泸溪特马豆克期锅塘组的刺尾虫类三叶虫 *Dichelepyge lata* 的个体发育过程。其最显著的变化有头鞍形状和比例的改变，头鞍沟、颈沟与背沟的分离，鞍前箍(parafrontal band)的出现与消失，胸部肋区和轴部比例宽度的改变，尾部的形状和比例的变更，尾边缘的出现和肋沟深度的增加，以及后侧刺的位置逐渐前移。组成成虫期个体的前8个体节(6个胸节和前2个尾节)极有可能在分节0期(measpid Degree 0)便已形成。从分节3期(meraspid Degree 3)起在带后侧刺的体节与轴后区(postaxial field)之间又发育出一个新的体节。过渡期尾部(transitory pygidium)在分节0期或分节1期发育出后侧刺，在分节4期又同时长出3对侧刺，其中最后一对侧刺与后侧刺一道形成成年期尾部的尾刺。

关键词 个体发育 刺尾虫类 宽双爪尾虫 特马豆克期 湖南

ONTOGENY OF *DICHELEPYGE LATA* PENG (TRILOBITA, TREMADOCIAN) FROM LUXI, WESTERN HUNAN

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Key words: ontogeny, ceratopygid, *Dichelepyge lata*, Tremadoc, Hunan

* 国家自然科学基金资助项目。

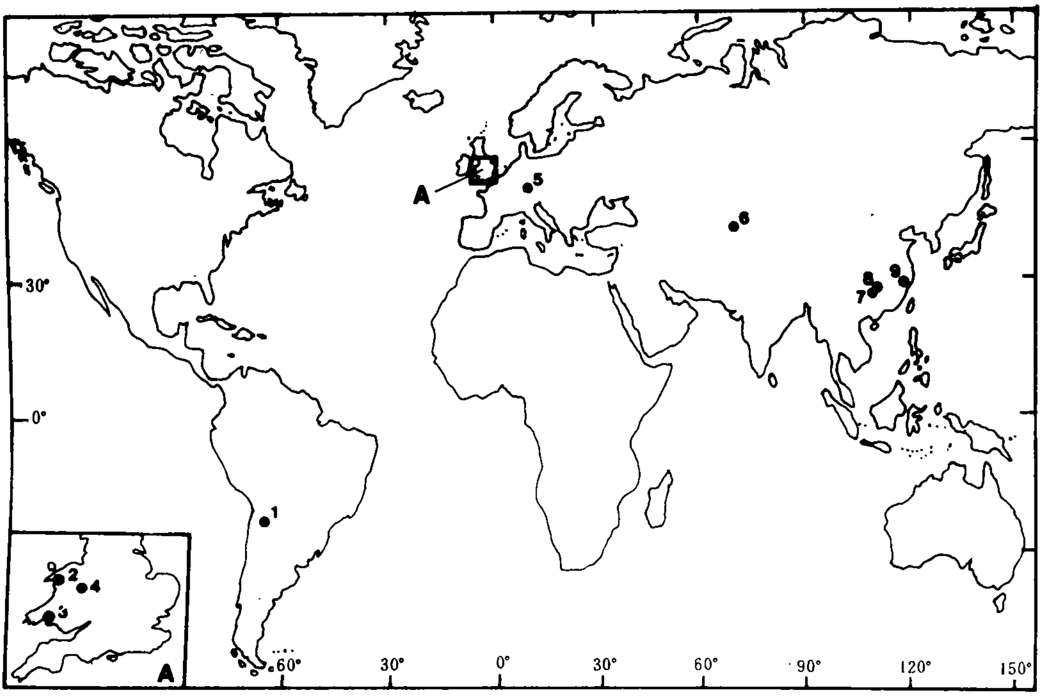
ABSTRACT

Here described in detail is ontogeny of the ceratopygid *Dichelepyge lata* from the Guotang Formation in Luxi, western Hunan. The most distinct changes during its growth are the shape and proportion of glabella, the isolation of the glabellar and occipital furrows from the axial furrow, the appearance and obliteration of the parafrontal band, the proportional width of adaxial portion of thorax, the shape and proportion of pygidium and pygidial axis, the appearance of the pygidial border, the depth of the pleural furrows, and the location of the posterolateral spines. The 8 segments comprising thorax, and the first two pygidial segments in holaspis are very probably formed at the meraspis Degree 0. One more pleural segment on pygidium is subsequently added between the segment with posterolateral spines and the postaxial field. Posterolateral spines are certainly present in Degree 1 and persist in later developing stages. Subsequently 3 pairs of short lateral spines appear in meraspis Degree 4 with the posterior pairs retained in holaspides.

INTRODUCTION

Although our knowledge on the ontogeny of trilobites has been largely improved in recent decades through the effort of many trilobite workers, e. g. Whittington (1957), Chatterton (1980), Hu (1986) and Fortey and Chatterton (1988), the development of ceratopygids so far is still relatively little known. Over the past years, Yang (1978, pp. 66—67, text-figs. 7, 8) has illustrated some meraspid cranidia and pygidia of *Proceratopyge*; Rushton (1983, p. 134, text-fig. 7) has shown ontogenetic changes in cranidia of the same genus; and Owens *et al.* (1982, pl. 4, fig. b) have figured a meraspid exoskeleton of *Dichelepyge phylax*. The present material from the early Tremadocian Guotang Formation in Luxi County, Hunan, China includes a gradational size series of cranidia and pygidia of *D. lata* in different ontogenetic stages, enabling the first description of these stages in a ceratopygid.

Dichelepyge is one of the characteristic ceratopygids with two pairs of pygidial spines and, in most cases, swollen anterior bands of thoracic pleurae in holaspid period. Its cranidium resembles that of *Hysterolenus*, but with an even broader (sag.) preglabellar area. This genus is widely distributed and appears to be confined to the early Tremadocian. It was first recorded from the early Tremadocian *Kainella pascuali* Zone of Argentina (Harrington and Leanza, 1952, 1957), and later, discovered in succession from the Leimitz Shale of Hof, Bavaria (described as species of *Lichapyge*) (Sdzuy, 1955), the Kendyktas Formation of the Kendyktas Mountains, southern Kazakhstan (described under the name of *Biconipyge*) (Lisogor, 1961), the Shineton Shale of the Cardington District, Shropshire, England (Hutchison and Ingham, 1967), the Tremadocian *Clonograptus tenellus* Zone of the Carmarthen District, South Wales (Cope, *et al.*, 1978; Owens *et al.*, 1982), the top of the Dolgellau Member of the Cwmhesgen Formation in North Wales, which Rushton (1982) considered to be pre-Tremadocian in age, the *Dichelepyge sinensis* Zone of the Yinchupu Formation in western Zhejiang (Lu and Lin, 1984) and the *Onychopyge-Hysterolenus* Zone of the Panjianzui Formation in the Cili-Taoyuan border area, western Hunan (Peng, 1984) (text-fig. I).



TEXT-FIG. 1 Distribution of *Dichelepyge* in the world. 1. Argentina. 2. North Wales. 3. South Wales. 4. England. 5. Bavaria. 6. Kazakhstan. 7. Luxi, western Hunan. 8. Wa'ergang, northwestern Hunan. 9. Western Zhejiang.

Dichelepyge lata Peng, 1984 differs from other species of *Dichelepyge* mainly in having widely divergent preocular sutures, proportionally wide (tr.) adaxial portion of thorax and short but wide and less segmented pygidial axis. While proposing *D. lata* as a new species, the writer had only two pygidia in hand, which were collected from the lower part of the Panjiazui Formation at Wa'ergang, Taoyuan, Hunan. Subsequently, he recognized that an exoskeleton also obtained from Taoyuan and described as *Hysterolenus asiaticus* Lu by Liu (1982, p. 334, pl. 230, fig. 1) was conspecific with *D. lata*. In the winter of 1985, a large collection of the species was obtained from a section of the early Tremadocian Guotang Formation near Xiaozhang, Luxi County, Hunan. All these materials serve as the basis for this paper.

The terminology used here basically adopts those defined by Whittington (1957, 1959), with modifications suggested by Shergold (1972, 1975). The specimens illustrated were blackened with dilute ink and whitened with magnesium oxide powder before being photographed. They are prefixed NIGP and deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, 210008 Nanjing, PRC.

LOCALITY AND PRESERVATION

The new material of *D. late* comes from the section measuring some 2km south of Xiaozhang, Luxi, and some 140km southeast of the type locality of the species at Wa'ergang, Taoyuan, northwestern Hunan (Peng, 1984). All specimens were collected from a single bed of 3.5m thick greenish grey, fine shale, weathered from marlite, in association with species of *Micragnostus*, *Shumardia (Conophrys)* and *Macropyge* (for details see Peng 1991). Most specimens are preserved as disarticulated, more or less distorted moulds with original profile or slightly flattened.

DESCRIPTION OF ONTOGENY

Family Ceratopygidae Raymond, 1913

Genus *Dichelepyge* Harrington and Leanza, 1952

Synonym: *Biconipyge* Lisogor, 1961, p. 72.

Type species: *Dichelepyge pascuali* Harrington and Leanza, 1952, p. 203; from *Kainella merdionalis* Zone of Lower Tremadocian, Argentinae, by original designation.

Dichelepyge lata Peng, 1984

(Pl. I, figs. 1—14; Pl. II, figs. 1—10)

1982 *Hysterolenus asiaticus* Lu, Liu, p. 334, pl. 230, fig. 1.

non 1959 *Hysterolenus asiaticus* Lu, Lu. p. 19, pl. 4, fig. 1.

1984 *Dichelepyge lata* Peng, p. 374, pl. 4, figs. la, b; pl. 5, fig. 11.

1991 *Dichelepyge lata* Peng, p. 153, pl. 4, figs. 1—4.

Holotype: An external mould of pygidium (Peng, 1984, pl. 4, fig. 1a), NIGP 83055 from *Onychopyge-Hysterolenus* Assemblage Zone, Wa'ergang, Taoyuan, northwestern Hunan.

Additional material: More than sixty specimens of cranidia, pygidia, librigenae and exoskeletons in different growth stages from which the only protaspis, 13 cranidia, 9 pygidia and 2 exoskeletons (NIGP 112537—112557) were selected for illustration.

Diagnosis: Species of *Dichelephge* with broad (sag.) preglabellar area, smoothly rounded preocular sections of facial sutures, gently tapering and laterally constricted glabella with 4 pairs of lateral furrows isolated from axial furrows. Pleural region of thorax 2/3 as wide (tr.) as the axis; very gently swollen anterior pleural band of thoracic segment and transverse triangular pygidium with wide (tr.) axis (revised by Peng, 1991, p. 153/

164).

Protaspid period

The only one protaspid specimen (Pl. 1, fig. 1) in hand is 1.34 mm in length (sag.) and ovate in outline. The axis is strongly convex, tapering rearward, well-defined laterally by axial furrows, anteriorly rounded, with a maximum width at the midlength of the first ring, divided into 8 rings by furrows, with the anterior ring furrow being the shallowest and appearing interrupted sagittally by a median node (?). The second ring furrow is much deeper than the anterior one but shallower than following ones. The frontal lobe is the longest, about two times as long as wide. The second and the third (the occipital) rings are about equal in length (sag.), subelliptical in outline, and the following rings are progressively shorter (sag.) and narrower (tr.) rearward. The pleural region is flat, with very faint transverse furrows at the level of the third ring furrow. The protopygidium is semicircular, bearing obscurely 3 short, oblique pleural furrows.

This protaspis is characterized by its ovate outline and strongly convex, distinctly segmented axis, with an obscurely subdivided pleural region.

Meraspid period

Among the material of meraspides, only a complete but slightly disarticulated exoskeleton in the collection definitely belongs to Degree 3 (Pl. 1, fig. 13). In addition, the cranidium attached with a thoracic segment and the pygidium displaced may be of Degree 1 (Pl. 1, fig. 6). For other specimens, the development stages of the cranidia can only be recorded by their sizes, while those of the pygidia could be determined by the numbers of the pleural segments anterior to the segment which projects the posterolateral spine.

A) Degree 0—Degree 1. The smallest transitory pygidium in the present material (Pl. I, fig. 5) with a length (sag.) of 1.00 mm is probably of meraspis Degree 0. It is semielliptical, 0.8 as long as ide, with transverse anterior margin and acutely rounded anterolateral corners. The axis, occupying 0.62 of the total pygidial length (sag.), is very narrow, strongly convex, tapering gently rearward with a prominent articulating half-ring defined posteriorly by a deep, rearward-bent articulating furrow, 6 (?) poorly defined rings and a tiny terminal piece. The pleural region is very gently convex (tr.), divided into 7 pleurae. The pleura is transverse on the first segment and increases obliquity posteriorly. The pleural furrows are broad and distinct, and the interpleural furrow is weakly defined. The border and border furrow are obscurely present. It is uncertain whether or not the pygidium bears pygidial border spines.

Three cranidia, 1.52, 1.50 and 1.55 mm in length (sag.) respectively (Pl. I, figs. 2—4), may be of meraspis Degree 0 or Degree 1. They are evenly rounded anteriorly, and their length (sag.) is equal to the cranidial width (tr.) at posterior margin. The glabella is cylindrical, parallel-sided or slightly expanded forward, rounded anteriorly, about 0.60, 0.58 and 0.59 as long (sag.) as cranidium respectively. Three pairs of glabellar lateral furrows are visible in all three specimens, with the preoccipital pair (1p) longest and deepest, running strongly oblique rearward, and the median pair (2p) and the anterior pair (3p) notched on the glabellar sides. The prominent glabellar node is sited posteriorly between the preoccipital furrows, about one-third of the combined length of the glabella plus occipital ring from the rear of the cranidium. The occipital ring is convex (sag., tr.), slightly widened sagittally, and the occipital furrow is well-defined, deepened laterally. The preglabellar area, occupying 0.40—0.42 of the total cranidial length (sag.), is very wide (sag.), slightly upturned anteriorly and bears an incomplete median preglabellar ridge connecting posteriorly with the parafrontal band immediately in front of the glabella, which joins the ocular ridges abaxially. The ocular ridge running transversely is relatively longer and stronger than those in the following development stages. The crescentic palpebral lobe is placed anterior to the mid-length of the glabella (in between 3p and 2p). The palpebral area is half as wide as the glabella. The preocular sections of the facial suture diverge forward and curve smoothly inward to enclose a transversely elliptical preglabellar area, while the postocular sutures diverge outward rapidly, enclosing the rectangular posterior area. The posterior border is narrow (exsag.) and strongly convex, bearing an obscure fulcral socket at about 2/3 its length (tr.) from the axial furrow.

The next largest cranidium (PI. 1, fig. 6) is 1.83 mm long, attached with one thoracic segment. It is much smaller than that of meraspis Degree 3 and very probably of meraspis Degree 1. The associated pygidium (PI. 1, figs. 7a, 7b), 1.09 mm long and preserved as an external mould, may belong to the cranidium. The cranidium shares the same outline, the same location of palpebral lobe and the same courses of facial sutures with the cranidia described above. The parafrontal band, however, has been obliterated and the incomplete preglabellar ridge becomes ill-defined. In contrast, the fulcral socket on the posterior border becomes distinct. The glabella is more or less pestle-shaped.

The transitory pygidium shares the same outline and the same pattern of the pleurae with the smallest pygidium in the Luxi material, but has one pair of very delicate postero-lateral spines that seem to have derived from the seventh pleurae. The axis is slightly shorter proportionally (0.56 of the total pygidial length), and the borders are somewhat more defined than in the preceding stage.

The next largest cranidium, 1.86 mm in length (sag.) (P1. I, fig. 9), is probably also of meraspis Degree 1. It appears to be indistinguishable in morphology from the cranidium of P1. I, fig. 6 and only slightly larger in size.

In these degrees the cranidium is characterized by the presence of the rather defined parafrontal band in the earlier stage, the wide (sag.) preglabellar area, the cylindrical or pestle-shaped glabella and the obliteration of the parafrontal band in later stages. The most distinct features of the transitory pygidium are the semicircular outline, with long but narrow axis and poorly defined borders.

B) Meraspis Degree 2. Three transitory pygidia (Pl. I, figs. 8, 10 and 11), measuring 1.28 mm, 1.24 mm and 0.95 mm long and 2.28 mm, 2.00 mm and 2.28 mm wide respectively, are of meraspis Degree 2 as their pleural field contains 6 pleurae, with one more pleura than those in the succeeding Degree 3 transitory pygidium. The posterolateral spines have derived from the sixth segment, after which the postaxial field bears three faint ridges, the postaxial ridge and the paired anterior bands of an incomplete pleural segment. The first and the last pygidia appear to be transversely and longitudinally compressed respectively. All the three pygidia have a distinct, broad border that is flat in the first two (figs. 8 and 10) but concave in appearance in the last one (fig. 11) because of compression. As in preceding stages, the axis is narrow (tr.) and long (sag.) in the first one, but widened (tr.) and shortened (sag.) in the other two because of compression. The axis and pleural fields are poorly segmented in the first one but well divided in the other two, with the anterior and posterior bands appearing ridge-like and separated by the broad pleural furrows.

The cranidium in Pl. I, fig. 12, 1.90 mm in length (sag.), is larger in size than the Degree 1 cranidium. It has a glabella similar to those in the later ontogenetic stages, with 2p and 3p isolated from the axial furrows, and bears paradoublural lines on the preglabellar area, a character also seen in later ontogenetic stages. Moreover, it lacks the preglabellar ridge that is usually eliminated in the succeeding stages. Since it is much smaller in size than the Degree 3 cranidium which is sagittally 2.25 mm long, it is here considered to be possibly of a meraspis Degree 2. Otherwise, it may belong to a peramorphic individual.

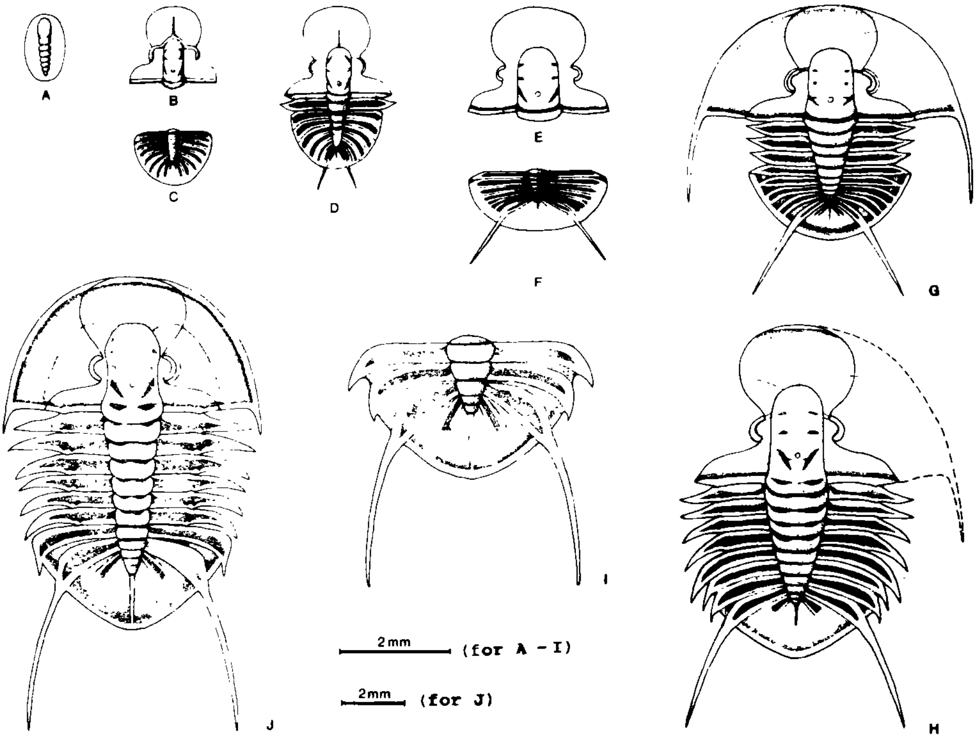
This stage is characterized by the occurrence of pygidial borders and by the deep pleural furrow defining the ridge-like pleural bands. The paradoublural lines might occur in this stage.

C) Meraspis Degree 3. The complete exoskeleton of meraspis Degree 3 (Pl. I, fig. 13) is ovate in outline, about 0.6 as wide as long. The largely distorted cephalon is approximately 2.25 mm long and the pygidium is 1.30 mm long. The third thoracic segment is partly preserved on the left side. The glabella in the cranidium of nearly the same size (Pl. II, fig. 1, 2.23 mm in length) is moderately convex, nearly parallel-sided, slightly expanded outward at its base and rounded anteriorly, with 3 pairs of lateral furrows. The preoccipital furrow is adaxially bifurcated into two short branches directed obliquely forward and rearward respectively. The 2p and 3p furrows are short, transverse, with their inner ends markedly deepened and distal ends isolated from the axial furrows. The occipital furrow is deep, transverse medially with distal ends slightly curved forward and connected with axial furrow. The glabellar node is placed between the preoccipital furrows. The anterior area is evidently shortened (sag.), occupying only 0.34—0.36 of the total cranidial (cephalic) length and bearing a pair of faint paradoublural lines extending as anteriorly-bent curvatures from the preglabellar furrow at the anterolateral corners of the glabella to the preocular sutures at the level of the posterior fourth of the sagittal length of the preglabellar area from the glabella. The preglabellar ridge is reduced into a very short and feeble bar. The palpebral lobe is semicircular, placed between 2p and 3p, well defined by the palpebral furrow. The ocular ridge is oblique rearward, with its inner end slightly anterior to 3p. The posterior sections of the facial suture enclose a transverse triangular posterolateral limb. The librigena is subtriangular, with broad and gently convex genal area, very slightly concave lateral border furrow and long and slender genal spine, and appears to be without paradoublural lines. The thorax consists of 3 segments. Each segment bears a strongly convex (tr.) ring defined by the incised ring furrow and a pleura with a broad and deep pleural furrow, a distinct fulcrum at 3/5 the pleural length (tr.) to the axial furrow, and a pointed tip. The transitory pygidium is twice as long as wide, with entire lateral margin. As in preceding growth stages, the pygidium bears only one pair of spines. The axis occupies 0.52 of the total pygidial length and bears 5 rings and a terminal piece. The postaxial ridge is clearly defined. The pleural field is divided into six segments, with posterolateral spines projecting from the fifth one. Behind the posterolateral spine, a new pleural segment seems to occur in front of the postaxial field. The pleural bands are still of simple ridges. The border furrows are wide and concave, defining the narrow and convex borders.

Degree 3 is characterized by the appearance of one more pleural segment in the postaxial field and the proportionally shorter axis than those in the preceding stages.

D) Meraspis Degree 4—Degree 5. The next two largest cranidia (Pl. Ⅰ, fig. 14 and Pl. Ⅱ, fig. 2) are 2.76 mm and 3.20 mm in length (sag.). They are smaller than the smallest holaspid cranidium (not figured, 3.50 mm in length) and are considered as in between meraspis Degree 4 and Degree 5. The former may be somewhat transversely compressed. The glabella slightly tapers forward, expands outward at the base, and is more or less acutely rounded anteriorly, with 3p and 2p isolated from the axial furrow and 1p strongly oblique rearward and obscurely bifurcated. The occipital furrow is notably deepened laterally, with distal ends disconnected from the axial furrows. The ocular ridge is almost eliminated. The palpebral lobe lies closer to the glabella than in earlier development stages, extending from the level of the middle of the median lateral lobe to 3p. The preglabellar area occupies 0.32—0.34 of total cranidial length.

The meraspis Degree 4 transitory pygidium has 4 attached thoracic segments (Pl. Ⅱ, fig. 3). The axis of thorax is as wide as the adaxial portion of the pleural region, tapering rearward very gently, with ring furrows well defined and laterally deepened. The adaxial portion of the first pleura is convex, separated into a swollen, crescentic anterior band and a very narrow (exsag.) posterior band by a rearward-curved pleural furrow. The following pleural furrows are progressively straightened. The abaxial portion of the pleura is flat, pointed distally, with doublure bearing a panderian protuberance mesially (looking like a pit on the internal mould). The transitory pygidium is subtriangular, with incomplete later-



Text fig. 2. Ontogeny of *Dichelepyge lata* Peng. A. Protaspis, based on NIGP 112537; B and C. Meraspid cranidium and transitory pygidium, possibly Degree 0, based on NIGP 112539 and 112541; D. Meraspis, Degree 1, based on NIGP 112542 and 112543; E. Meraspid cranidium, possibly Degree 2, based on NIGP 112548; F. Transitory pygidium, meraspid Degree 2, based on NIGP 112547; G. Meraspis Degree 3, based on NIGP 112549 and 112551; H. Meraspis Degree 4, based on NIGP 112552 and 112553; I. Transitory pygidium, meraspid Degree 5, based on NIGP 112554; J. Holaspis, based on NIGP 112532.

al margin carrying 3 short lateral spines and a long posterolateral spine, which have derived from the first four segments respectively. The fifth pleura is very short (tr.), not across the border furrow. The axis comprises 4 rings and a tiny terminal piece, occupying some 1/2 the total pygidial length.

The Degree 5 transitory pygidium (Pl. Ⅱ, fig. 4) seems to have been transversely compressed, bearing two pairs of lateral spines in front of the posterolateral spines. The pleural field is narrow (tr., exsag.), divided into four pleurae and separated from the ridge-like borders by broad border furrows. The posterolateral spine is located at the midway of the border.

These stages are different from the preceding stages in the glabella which becomes tapering forward. The thorax is characterized by the appearances of the swollen anterior band and the wire-like posterior band on the first, and probably the second pleura, and the transitory pygidium by having lateral spines.

Holaspid period

The specimens of Pl. Ⅱ, figs. 5—10 except for the librigena (fig. 9), which may be of meraspis according to its size, are of holaspis. The exoskeleton (Pl. Ⅱ, figs. 7a, b) is ovate in outline, 2 times as long as wide, also transversely compressed, with cephalon ca. 4.7 mm and pygidium ca. 3.4 mm in length. The cranidia are 5.30 mm (Pl. Ⅱ, fig. 5) and 5.35 mm (Pl. Ⅱ, fig. 6), and the pygidia 3.00 mm (Pl. Ⅱ, fig. 8) and 2.90 mm (Pl. Ⅱ, fig. 10) in length (sag.). The glabella tapers forward, expanded gently outward at the base and constricted at 1p, rounded anteriorly, with truncated apex, bearing four pairs of glabellar furrows isolated from axial furrows. The 1p is deepest, obscurely bifurcated and strongly oblique rearward; the 2p and 3p are short, lying close to the axial furrow, while the 4p is shortest and faintly impressed. The occipital furrow is well defined, markedly deepened laterally, disconnected from axial furrows. The palpebral lobe is semicircular, situated close to glabella and immediately in advance of the mid-point of glabella. The ocular ridge is faint and short. The preocular sections of facial sutures diverge forward and gradually turn inward to form smoothly rounded curvatures, enclosing the preglabellar area that occupies some 0.3 of the total cranidial length and bears very short and obscure paradoublural lines. The postocular sutures are sinuous, diverging outward rapidly, enclosing blade-like posterior limbs. The posterior border bears a fulcral socket at 2/3 of its length (tr.) from axial furrow. The cephalic doublure is wide, with anterior end expanded in width adaxially and is divided sagittally by the median suture.

The hypostoma is ovate in outline, with strongly convex median body and wide and flat borders narrowing anteriorly.

The librigena is subtriangular in outline, with ridge-like eye socle, short genal spine, broad and concave border furrows and wide and flat doublure. The genal field bears paradoublural line which continues into the cranidium.

The thorax is composed of six segments, with axis tapering very gently rearward, flat adaxial portions being 2/3 as wide (tr.) as the axis, and flat, down-sloping abaxial portions tapering outward into pointed tips. The ring furrows are deepened laterally. The pleural furrow on the first two pleurae is curved, defining the wide (exsag.), swollen anterior and narrow (exsag.) posterior bands, while that on the succeeding pleurae is broad and transverse, defining the bar-like anterior and posterior bands. The doublure bears panderian protuberances.

The pygidium is subtriangular, with rounded anterolateral corners and narrow posterolateral borders, bearing one pair of short lateral spines directed rearward and another pair of long and strong posterolateral spines that are widely spaced at about 3/5 the way of the border from rear to anterolateral corner and directed rearward and slightly outward. The axis occupies some 1/2 of the total pygidial length (sag.), bearing 4 rings, 1 articulating half-ring and 1 tiny semicircular terminal piece; it is broad (tr.) and short (sag.), with straight sides converging strongly rearward and merging into a weak postaxial ridge which reaches to the border posteriorly. The pleural field contains 3 pairs of pleurae. The border furrow is broad and concave, and the borders are ridge-like in appearance.

This period is characterized by the glabella which tapers forward, truncated at its apex and bearing four pairs of lateral furrows, the pygidium with wide (tr.) and short (sag.) axis and two pairs of spines, with the anterior pair widely spaced.

Discussion: Through his studies on the development of *Shumardia (Conophrys) pusilla*, Stubblefield (1926) has well demonstrated the formation of the trilobite thorax, which shows that the thoracic segments are released one by one from the anterior segments of the transitory pygidium and migrate forward during growth. Both Stubblefield (1926, p. 369) and Whittington (1957, pp. 435, 463; 1959, p. 136) approved of the hypothesis of Beecher (1896), that new somites are added by growth to the anterior border of the hindermost somite. The development of *Dichelepyge lata* provides new evidences supporting these viewpoints. The posterolateral spines of *D. lata* are present in a certain pygidial segment throughout the meraspid period (or from Degree 1 onward) as well as in the adult. No segment is added to the pleural field in front of the spinose segment and the pleural segments are progressively decreased in number during growth, indicating that all the segments subsequently developed into thorax have already formed as early as in Degree 0 as the anterior part of the transitory pygidium and are freed forward one after another with the increasing size. Such a process of release can be clearly observed in the later stages of the meraspid period (i. e. Degree 4 and Degree 5) when the lateral spines have been formed on the distal portion of the anterior pleurae. The lateral spines disappear one by one with the last pair retained in the holaspid period. Hu (1971) has shown that in *Crepicephalus deadwoodiensis* the lateral spines are also produced subsequently in the later meraspid stages by partly releasing the anterior segments of the transitory pygidium (Hu, 1971, p. 69, P1. 14, figs. 22, 23; text-fig. 42, k, m).

In *D. lata*, one of notable changes takes place in Degree 3 when an additional pleural segment has occurred in the postaxial field, immediately behind the macropleura with posterolateral spines and persists onward in succeeding stages, suggesting that it has been produced from the hindermost somite.

In the development of glabella, the present species may be slightly different from the British species *Dichelepyge phylax*. The present material indicates that the parafrontal band only occurs in Degree 0 and the pestle-shaped glabella in meraspis Degree 0 and Degree 1, but the material of *D. phylax* figured by Fortey and Owens (in Owens *et. al.*, 1982) has shown that the parafrontal band and the pestle-shaped glabella retain at least as late as in Degree 2 and the glabella may keep a pestle-shape in even still later stages (Owens *et al.*, 1982, P1. 4, a, b). As noted by Fortey and Owens (in Owens *et al.*, 1982, p. 13), the pygidium of the British species bears a postaxial ridge, without concentric lines on dorsal surface. The postaxial ridge observed from Degree 1 and later in *D. late* is certainly developed in other species of *Dichelepyge*, such as *D. biconis* (Lisogor, 1961, P1. 2, figs. 14, 15; P1. 3, figs. 1—4), *D. sinensis* (Lu and Lin, 1984, P1. 18, figs. 3, 4) and perhaps *D. pascuali*, the type species (see Harrington and Leanza, 1957, fig. 98, 1a). The concentric lines are also absent on the dorsal surface of the present species, but they appear to have been developed in *D. biconis* (Lisogor, 1961, *non* Rushton, 1982, P1. 4, fig. 4). In the holaspid period, the swollen pleural band is only seen in the first one or two thoracic segments of the present material, but it is developed in all the thoracic segments in other species, such as *D. pascuali*, *D. phylax* and *D. sinensis*, with a tendency to becoming progressively weaker posteriorly. This suggests either that the present exoskeleton, which is relatively smaller in size, is not fully mature, or that this character is of specific significance. The writer is in favour of the latter view, because the exoskeleton of *D. lata* figured as *Hysterolenus asiaticus* by Liu (1982, P1. 230, fig. 1) is of the same size as, or even larger than, some of the specimens from Argentina, British and western Zhejiang.

During the growth of the species the main changes may be summarized as follows:

1) Shape and convexity of glabella. The glabella is pestle-shaped in protaspis and pestle-or cylinder-shaped in earlier meraspides, and becomes tapering forward from Degree 3 and onward, with truncated apex in holaspides. The expansion at base takes place in Degree 3. The glabella is strongly convex in protaspis and gradually decreases in convexity during growth.

2) Glabellar furrow. Only one pair of glabellar furrows is faintly developed as a disconnected ring furrow in protaspis, and 3 pairs can be seen throughout the meraspid period, with the preoccipital furrows well defined and strongly oblique rearward. In later meraspides the preoccipital furrow becomes bifurcated and the median and anterior furrows are isolated from the axial furrows.

3) Occipital furrow. The occipital furrow is markedly defined in the protaspid period and earlier meraspid stages. From Degree 3 and onward, it becomes shallower medially and deeper laterally, with distal ends isolated from the axial furrows.

4) Preglabellar area. The preglabellar area is narrow (sag.) in the protaspid period, and becomes very broad (sag.) in meraspid and holaspid periods. It is relatively shortened (sag.) in proportion from Degree 0 and onward along with a progressive increase in width (tr.) (with length to width ratio ranging from 1 : 1.4 in Degree 0 to 1 : 2.6 in holaspis).

5) Paradoublural lines, preglabellar ridge and parafrontal band. The paradoublural lines occur from Degree 2 (or Degree 3) and onward. Both the parafrontal band and the incomplete preglabellar ridge are well present in Degree 0 or slightly later, and disappear respectively in Degree 1 and the holaspid period.

6) Palpebral lobe and ocular ridge. During growth, the palpebral lobe gradually moves rearward and inward with its outline almost unchanged. The ocular ridge is transverse and

distinct in meraspides of Degree 0 and Degree 1, slightly oblique in those of Degree 2 and Degree 3, and becomes very faint and short in later meraspid and holaspid stages.

7) Facial suture. The facial sutures are not known in protaspis. Both preocular and postocular sutures increase in divergence, even though very slightly, during growth.

8) Thorax. The adaxial portion of thorax is wider (tr.) than the axis in earlier meraspid stages, nearly as wide as the axis in meraspis Degree 4, but becomes narrower in holaspides.

9) Pygidium. From meraspis Degree 0 to holaspis, the pygidium changes from semicircular, semielliptical to subtriangular in outline with decreasing proportion. The axis is gradually shortened sagittally but widened transversely. The transitory pygidium loses one segment in each degree but gains one segment behind the spinose segment from meraspis Degree 3 and onward. The pleural furrows are considerably deepened from later stages of meraspis Degree 2 and onward, while the interpleural furrows become strikingly distinct; 3 pairs of lateral spines occur in Degree 4, with the posterior pair and the posterolateral spines retained in the holaspid period. The posterolateral spines gradually move abaxially during growth.

Acknowledgments: The writer is grateful to Prof. Whittington (Sedgwick Museum, Cambridge University) for critically reading the manuscript with helpful comments, to Mr. Cheng Yong-an (No. 405 Geological Team, Hunan Bureau of Geology and Mineral Resources) for assistance in field work. The earlier work in this study was carried out in the Institute of Palaeontology, University of Wuezburg, West Germany during the writer's tenure of an Alexander von Humboldt Research Fellowship. Here the writer expresses his gratitude to Mr. H. Shirm of the Institute for taking photographs, and to Drs. W. Hammann and G. Geyer for their helpful discussion.

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[1993 年 5 月 3 日收到]

EXPLANATIONS OF PLATES

All figured specimens are from the Guotang Formation near Xiaozhang, Luxi, western Hunan, Horizon HLX 3, early Tremadocian in age. They were blackened with dilute ink and whitened with magnesium oxide powder before being photographed. Specimens are prefixed NIGP and deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, 210008 Nanjing, China

Plate Ⅰ

1—15. *Dichelepyge lata* Peng

1. Protaspis. exoskeleton. dorsal view. latex cast of external mould. ×27. NIGP 112537.
2. Meraspis Degree 0?. cranidium. dorsal view. latex cast of external mould. ×21. NIGP 112538.
3. Meraspis Degree 0?. cranidium. dorsal view. ×21. NIGP 112539.
4. Meraspis Degree 0?. cranidium. dorsal view. ×21. NIGP 112540.
5. Meraspis Degree 0. transitory pygidium. dorsal view. ×27. NIGP 112541.
6. Meraspis Degree 1. cranidium. dorsal view. latex cast of external mould. with attached thoracic and displaced pygidium (fig. 7a). ×21. NIGP 112542.

7a, b. Meraspis Degree 1. transitory pygidium. dorsal view. latex cast of internal mould (a) and external mould (b). dorsal view. ×21. NIGP 112543.

8. Meraspis Degree 1. transitory pygidium. dorsal view. ×21. NIGP 112544.
9. Meraspis Degree 1?. crandium. dorsal view. ×21. NIGP 112545.
10. Meraspis Degree 1. transitory pygidium. dorsal view. ×21. NIGP 112546.
11. Meraspis Degree 1. transitory pygidium. dorsal view. ×21. NIGP 112547.
12. Meraspis Degree 2?. cranidium. dorsal view. ×21. NIGP 112548.
13. Meraspis Degree 3. distorted exoskeleton. dorsal view. latex cast of external mould. ×13. NIGP 112549.
14. Meraspis Degree 4—5. cranidium. dorsal view. latex cast of external mould ×21. NIGP 112550.
15. Hypostoma of holaspis. part of the latex cast from the internal mould of exoskeleton shown in P1. Ⅱ. fig. 7. ventral view. ×14.

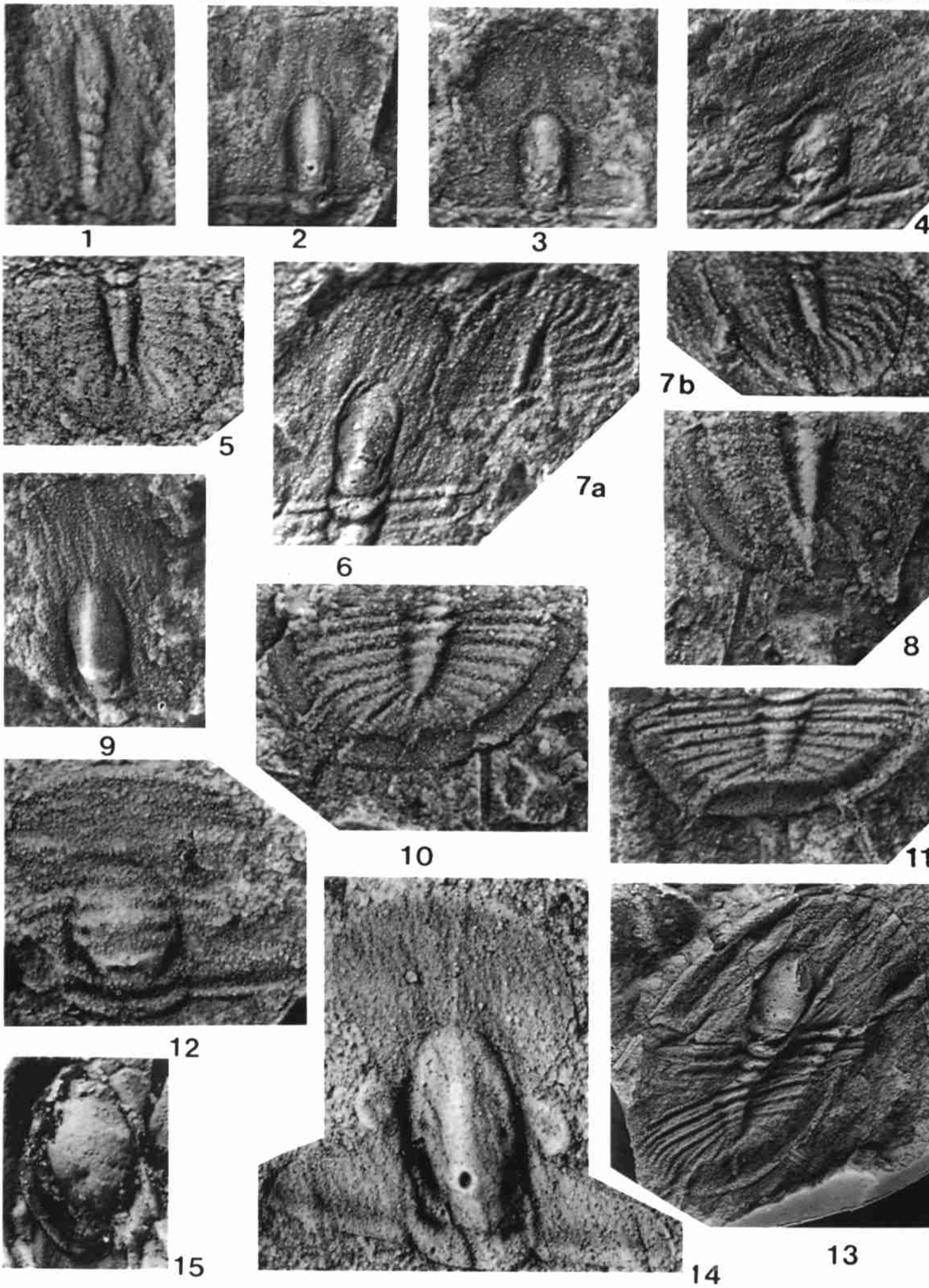
Plate Ⅱ

1—10. *Dichelepyge lata* Peng

1. Meraspis Degree 3. cranidium. dorsal view. ×13. NIGP 112551.
2. Meraspis Degree 3—5. crandium. dorsal view. ×13. NIGP 112552.
3. Meraspis Degree 4. transitory pygidium attached with 3 pairs of lateral spines and 4 thoracic segments. dorsal view. ×12. NIGP 112553.
4. Meraspis Degree 5. transitory pygidium with 2 pairs of lateral spines. latex cast of external mould. dorsal view. ×12. NIGP 112554.
5. Cranidium of holaspis. dorsal view. ×9. NIGP 112555.
6. Cranidium of holaspis. dorsal view. ×7. NIGP 112533.

7a, b. Exoskeleton of holaspis. internal mould (a) and latex cast of external mould (b). all ×7. NIGP 112532.

8. Pygidium of holaspis. dorsal view. latex cast of external mould. ×10. NIGP 112534.
9. Incomplete librigena of meraspis. dorsal view. ×16. NIGP 112556.
10. Pygidium of holaspis. dorsal view. latex cast of external mould. ×10. NIGP 112557.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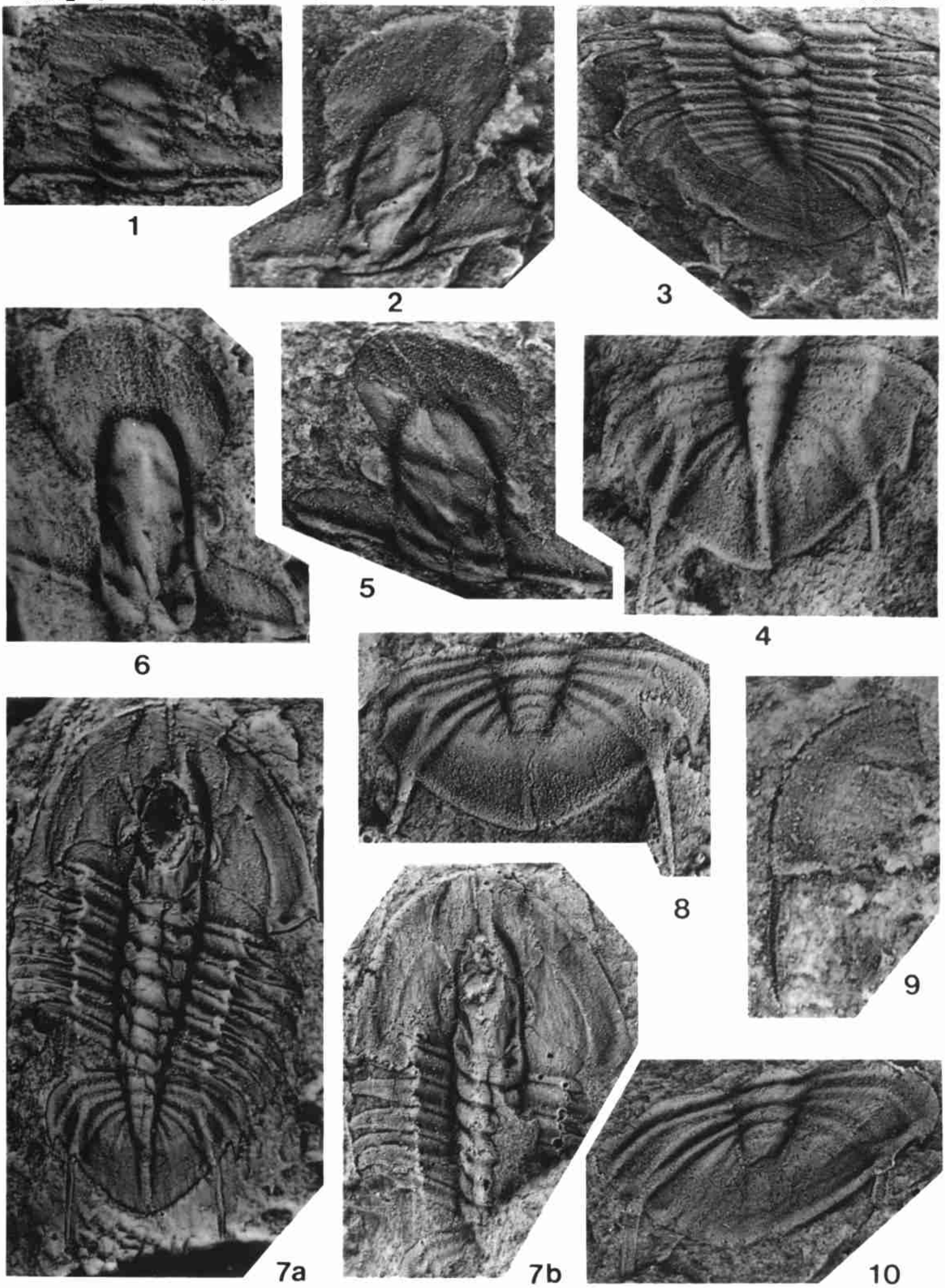
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