



MANSUYIA SUN, 1924 AND TSINANIA WALCOTT, 1914 FROM THE FURONGIAN OF NORTH CHINA AND THE EVOLUTION OF THE TRILOBITE FAMILY TSINANIIDAE

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Abstract: The Furongian trilobite family Tsinaniidae is characterized by a highly effaced surface and forms an important constituent of the Furongian trilobite faunas of east Gondwana. However, the origin of the characteristic morphology of this family has remained unclear. Only recently has the tsinaniid trilobite *Lonchopygella megaspina* been suggested to represent an intermediate stage in the evolutionary transition to other tsinaniids on the basis of the trunk segmentation. Here, we report successive occurrences of four species of the kaolishaniid genus *Mansuyia* and a tsinaniid trilobite *Tsinania canens* from the Furongian (late Cambrian) Chaomidian Formation in Shandong Province,

China. A cladistic analysis including these taxa reveals that the four species of *Mansuyia* constitute stem-group taxa to the family Tsinaniidae, rendering *Mansuyia* and the Kaolishaniidae paraphyletic. The youngest species of *Mansuyia*, *M. taianfuensis*, turns out to be the immediate sister taxon of the Tsinaniidae, displaying a closely similar morphology to the tsinaniid trilobite, *Shergoldia laevigata*. The generic and familial boundary therefore situated between *M. taianfuensis* and *S. laevigata*.

Key words: Tsinaniidae, North China, paraphyly, evolution, trilobite.

THE trilobite family Tsinaniidae Kobayashi, 1933 belongs to the Superfamily Leiestegioidea and includes the trilobites, which are isopygous and have a smooth dorsal surface and the supramarginal condition of the anterior branches of facial suture (for more detailed diagnosis of the family; Zhu *et al.* 2007). This family is an important constituent of the Furongian trilobite faunas of east Gondwana, mainly occurring in North China, South China and Australia. Despite its characteristic morphology, the evolutionary origin of the family Tsinaniidae has remained unclear for a long time. Kobayashi (1952) mentioned that the Tsinaniidae may have been derived from *Mansuyia* Sun, 1924 or other similar forms. In contrast, Zhu *et al.* (2007) considered the Tsinaniidae as closely related to the Asaphidae, on the basis of some shared morphological features with the tsinaniid trilobite, *Shergoldia laevigata* Zhu, Hughes and Peng, 2007, such as conterminant hypostomal condition, eight homonomous thoracic segments in the holaspide phase, isolated form of the S1 furrows, the presence of bacculae and eye socles and the absence of the circumocular suture. However, Park and Choi (2009) disagreed with the asaphid affinity

of the Tsinaniidae, based on the ontogenetic data of the tsinaniid trilobite, *Tsinania canens* (Walcott, 1905), and Zhu *et al.* (2010) also disproved the asaphid affinity using new material of *Guangxiaspis guangxiensis* Zhou, 1977, which appears to be phylogenetically closely related to *S. laevigata*. While documenting the ontogeny of *T. canens*, Park and Choi (2009) found that the immature *T. canens* retained genal spines and a pair of pygidial spines. Park and Choi (2009) stated that the presence of genal and pygidial spines in the morphologically immature *T. canens* supports its close affinity to leiestegioids and further emphasized that *Mansuyia* displays intermediate morphological features between *T. canens* and older leiestegioids such as *Kaolishania* Sun, 1924 and *Prochuangia* Kobayashi, 1935. *Kaolishania* and *Prochuangia* have well-incised furrows on the dorsal surface with broadly rounded anterior border, and *Mansuyia* has a somewhat effaced dorsal surface and a weakly angulated anterior border, whereas *T. canens* has a highly effaced dorsal surface and angulated anterior border. This implies that *T. canens* may have originated from *Mansuyia*-related trilobites. Recently, Zhu *et al.* (2013) suggested that

Lonchopygella megaspina may represent the intermediate step between the mansuyines/basal leiostrigioids and other tsinaniids, on the basis of the developmental mode of trunk segmentation.

This study documents the occurrences of two trilobite genera, *Mansuyia* Sun, 1924 and *Tsinania* Walcott, 1914, from the Chaomidian (Chaumitien) Formation, Shandong Province, China. *Mansuyia* belongs to the family Kaolishaniidae, while *Tsinania* to the Tsinaniidae. Fortey (1997) and Adrain (2011) treated the Kaolishaniidae as a family of the Suborder Leiostegiina and the Tsinaniidae as belonging to the Suborder Illaenina. Four species of *Mansuyia* occur successively in the studied section: that is, from old to young *Mansuyia orientalis* Sun, 1924, *M. chinensis* (Endo, 1939), *M. tani* Sun, 1935, and *M. taianfuensis* (Endo, 1939). Tracing the morphological changes in *Mansuyia* is expected to reveal the origination of the family Tsinaniidae from the Kaolishaniidae.

FOSSIL LOCALITY AND MATERIAL

The Cambrian sedimentary rocks of the North China Platform are considered to have formed in an extensive epeiric sea (Meng *et al.* 1997) and are well exposed in Shandong Province. The Cambrian succession in this province consists of six lithostratigraphic units: Liguan, Zhushadong, Mantou (Manto), Zhangxia (Changhia), Gushan (Kushan) and Chaomidian (Chaumitien) formations in ascending order (Zhang and Jell 1987; Chough *et al.* 2010).

Material for this study was recovered from the Chaomidian Formation in the Tangwangzhai section (116°51'42"E, 36°30'33"N) located close to Gushan, Shandong Province, China (Fig. 1). The Chaomidian Formation in Shandong Province comprises various carbonate facies such as limestone–shale couplets, microbialites, wackestones, packstones, grainstones and limestone conglomerates (Chough *et al.* 2010). The Tangwangzhai section has served as the type section of some middle Cambrian and Furongian strata of North China. The section exposes the upper part of the Zhangxia Formation, the Gushan Formation and the lower two-thirds of the Chaomidian Formation. The Chaomidian Formation exposed in this section is *c.* 128 m thick, of which the lower part is dominated by microbialite facies and the upper part is composed largely of wackestone to packstone facies (Chough *et al.* 2010).

The Chaomidian Formation contains six biozones: the *Chuangia*, *Changshania-Irvingella*, *Kaolishania*, 'Ptychaspid-Tsinania', *Quadraticephalus* and *Mictosaukia* zones in ascending order (Zhang and Jell 1987). The lower three biozones represent the Changshanian Stage, while the upper three biozones form the Fengshanian Stage. The

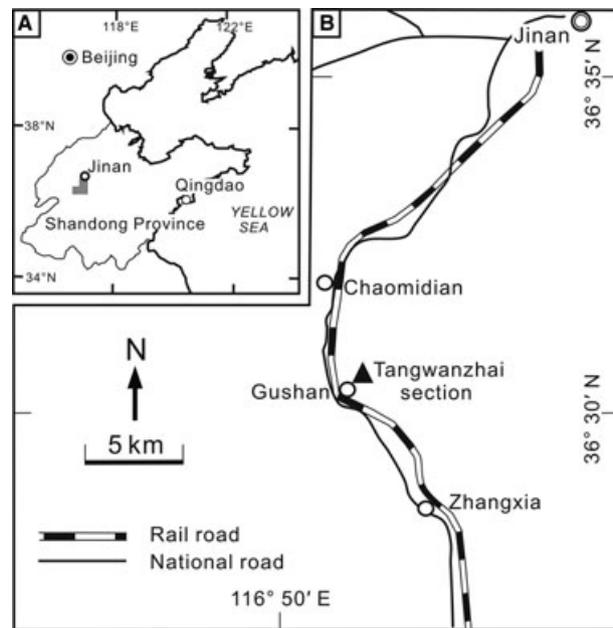


FIG. 1. Location maps. A, index map displaying the approximate location of the study area (shaded) in Shandong Province, China. B, the Tangwangzhai section (solid triangle), from which the material for study was collected, is located about 25 km south-west of Jinan, capital of the Shandong Province.

base of the *Chuangia* Zone is considered as the base of the Furongian Series in Shandong Province (Chen *et al.* 2011), whereas in Korea, the base of the *Fenghuangella laevis* Zone, which is succeeded by the *Prochuangia mansuyi* and *Chuangia* zones, represents the onset of the Furongian (Park and Choi 2011). The absence of the *Fenghuangella laevis* and *Prochuangia mansuyi* zones equivalent interval in Shandong Province is inferred a result of non-deposition due to subaerial exposure (Chen *et al.* 2011).

All the specimens were collected from *c.* 8-m-thick interval of wackestone and grainstone, which lies 60 m above the base of the formation in the section (Fig. 2). This interval represents the upper part of the *Kaolishania* Zone and the lowermost part of the 'Ptychaspid-Tsinania' Zone. The base of the 'Ptychaspid-Tsinania' Zone has been thought to have coincided with the FADs of *Ptychaspid* and *Tsinania* (Zhang and Jell 1987). However, recent detailed taxonomic research on the trilobites from the Chaomidian Formation has revealed that all the ptychaspid trilobites from this interval should be assigned to *Asioptychaspid* Kobayashi, 1933, not to *Ptychaspid* Hall, 1863 (Kim 2012). Accordingly, this study hereafter uses the *Asioptychaspid-Tsinania* Zone rather than the traditional 'Ptychaspid-Tsinania' Zone for the biozone between the *Kaolishania* and *Quadraticephalus* zones. Fossils for this study were collected from ten horizons, marked from bottom to top as CLT08 to CLT17 (Fig. 2). A total of 196 specimens were prepared and examined for this

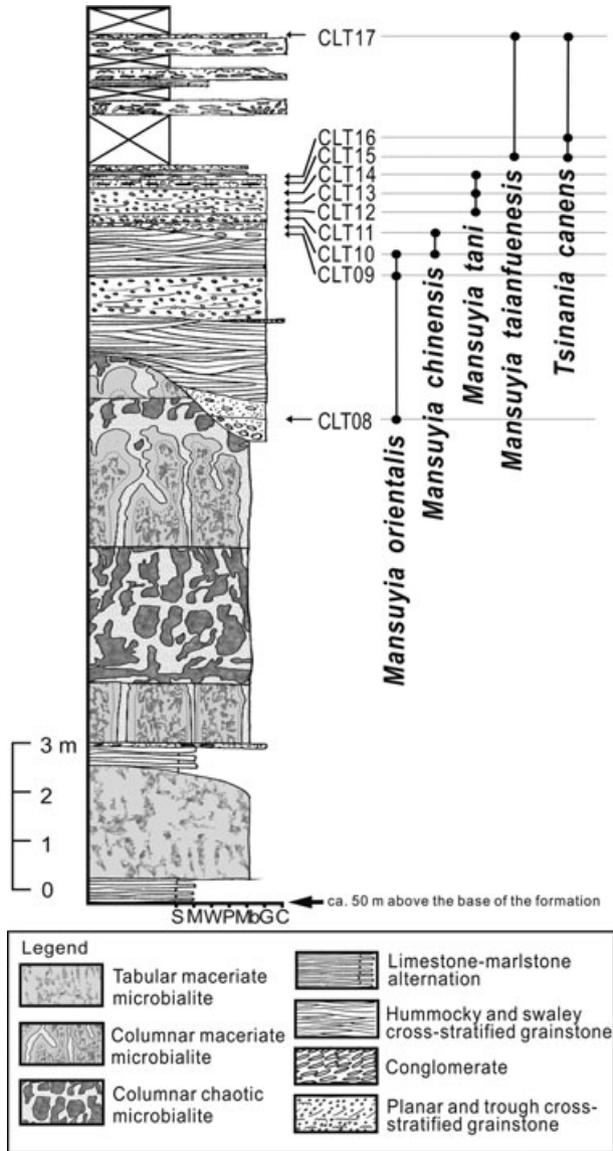


FIG. 2. Stratigraphic column of the middle part of the Chamidian Formation showing the lithology, sampling horizons and the occurrences of *Mansuyia* and *Tsinania*. S, Shale; M, mudstone; W, wackestone; P, packstone; Mb, microbialite; G, grainstone; and C, conglomerate.

study. Specimens employed in this study are deposited in the Palaeontological Laboratory of Seoul National University, prefixed with SNUP.

SYSTEMATIC PALAEOLOGY

The terminology for description in this study generally follows that of Whittington and Kelly (1997), but the glabella as used herein excludes the occipital ring. Terms for orientation are always indicated in reference to standard

plane: that is, length means sagittal or exsagittal distance, while width refers to transverse distance. Descriptive terms for facial sutures, such as ‘divergent convex’ and ‘parallel straight’, are used as in Henningsmoen (1957).

Family KAOLISHANIIDAE, Kobayashi, 1935

Genus MANSUYIA Sun, 1924

Type species. *Mansuyia orientalis* (Grabau) Sun, 1924 from Fengshan Stage in Yehli Limestone, Liaoning, China.

Other species. *Mansuyia tani* Sun, 1935; *Paramansuyella puteata* Endo, 1937 in Endo and Resser 1937; *Paramansuyia chinensis* Endo, 1939; *M. manchurica* Kobayashi, 1952; *M. hopeiensis* Kobayashi, 1960; *M. trigonalis* Kobayashi, 1960; *M. laevigata* Zhou in Zhou et al. 1977; *M. pulchra* Zhou, 1977 in Zhou et al. 1977; *M. zhuitunensis* Liu, 1982; *M. granosa* Zhang in Qiu et al. 1983; and *M. angustilimbatus* Qian, 1994. All of the species are reported from the *Kaolishania* Zone of North China.

Emended diagnosis. Cranium weakly to moderately convex; frontal margin broadly rounded to bluntly pointed medially; glabella slightly convex, gently tapering forward; anterior border furrow wide and shallow; anterior border gently upturned; anterior border furrows curved rearward abaxially; palpebral ridges faint; palpebral areas c. 50 per cent of glabellar width; palpebral lobes located posteriorly to glabellar midpoint. Pygidium semicircular in outline; axis with 6–8 axial rings and a terminal piece; a pair of pygidial spines developed from posterior band of first pleurae and anterior band of second pleurae; and border indicated by slope break or very shallow border furrow. Surface moderately to strongly effaced.

Remarks. Sun (1924) established the type species of *Mansuyia*, *M. orientalis*, based on four cranidia and five pygidia from the upper Cambrian of North China. Later, Sun (1935) placed the four cranidia in a new genus *Taishania*. The five pygidia remaining in *Mansuyia* include two morphological groups, causing taxonomic debate on the generic concept of *Mansuyia* (Resser, 1942; Kobayashi, 1952; Shergold, 1972): two pygidia (Sun 1924, pl. 2, fig. 7i, j) were originally collected by Grabau from the Fengshan Limestone of Hebei Province, while the other three (Sun, 1924, pl. 2, fig. 7f–h) were obtained from the Kaolishan Formation of Shandong Province by Sun (1924). Resser (1942) and Shergold (1972) acknowledged that *M. orientalis* was based on the concept of Grabau’s *Ceratopyge orientalis*, so that they designated the former two specimens (fig. 7i, j) as the type material. To the contrary, Kobayashi (1952) argued that Sun (1924) described *M. orientalis* with the other pygidia in mind (fig. 7f–h). In fact, as mentioned in Sun’s explanations of figures, Grabau’s pygidia are too

poorly preserved to characterize the species (Sun, 1924, p. 101), and the new specimens of *M. orientalis* illustrated by Sun (1935) are similar to the latter three pygidia. Subsequent workers have apparently referred to Sun's figure 7f–h (Lu *et al.* 1965, p. 416; Zhang and Jell 1987, p. 225; Qian 1994, p. 125). Zhang and Jell (1987) designated one of the pygidia illustrated by Sun (1924, pl. 3, fig. 7f) as the lectotype of the type species, *M. orientalis*.

Mansuyia is characterized in its cranidium by the anterior border furrow adaxially curving rearward to meet the preglabellar furrow, preglabellar field variable in length and occasionally preserving longitudinal genal caeca, and a relatively long anterior cranial border that is gently upsloping. In regard to these morphological features, *Mansuyia* is comparable to *Mansuyites* Shergold, 1972, but differs in having smaller palpebral lobes and more effaced furrows and absent bacculae.

Mansuyia orientalis Sun, 1924

Figure 3

- 1924 *Mansuyia orientalis* Sun, p. 50 (*pars*), pl. 3, fig. 7f–h. non i, j.
 1924 *Chuangia batia* (Walcott, 1905); Sun, p. 58, pl. 4, fig. 4a–d.
 1935 *Mansuyia orientalis* Sun; Sun, p. 58, pl. 2, figs 20–24.
 1965 *Mansuyia orientalis* Sun; Xiang in Lu *et al.*, p.416, pl. 79, figs 5–11.

- 1983 *Mansuyia orientalis* Sun; Qiu *et al.*, p. 189, pl. 63, figs 13–14.
 1987 *Mansuyia orientalis* Sun; Zhang and Jell, p. 225, pl. 110, figs 5–11.
 1991 *Mansuyia orientalis* Sun; Shergold, p. 32, pl. 2, figs 1–10.
 1994 *Mansuyia orientalis* Sun; Qian, p. 125, pl. 32, figs 5–12; pl. 33, figs 1–5.

Lectotype. Pygidium figured by Sun (1924, pl. 3, fig. 7f) and subsequently designated by Zhang and Jell (1987, p. 225).

Diagnosis. A species of *Mansuyia* having clearly incised axial and occipital furrows, a broadly rounded anterior cranial margin and long anterior border. Pygidium having well-defined pleural and inter-ring furrows and a relatively broad pygidial axis with six axial rings and a terminal piece.

Description. Cranidium convex, subrectangular in outline; surface smooth; anterior cranial margin weakly pointed medially. Glabella convex, moderately tapering forward, slightly constricted anteriorly, 1.2 times longer than wide, c. 60 per cent of cranial length; axial furrows deep, slightly curved inward at anterior end of palpebral lobes. Glabellar furrows obsolete or faint. SO simple, moderately deep, abaxially curved forward. Occipital ring c. 13 per cent of cranial length. Anterior cranial border slightly upturned; anterior border furrow very shallow medially, as deep as axial furrow abaxially. Preglabellar area weakly convex, fan-shaped, downsloping forward with radiating

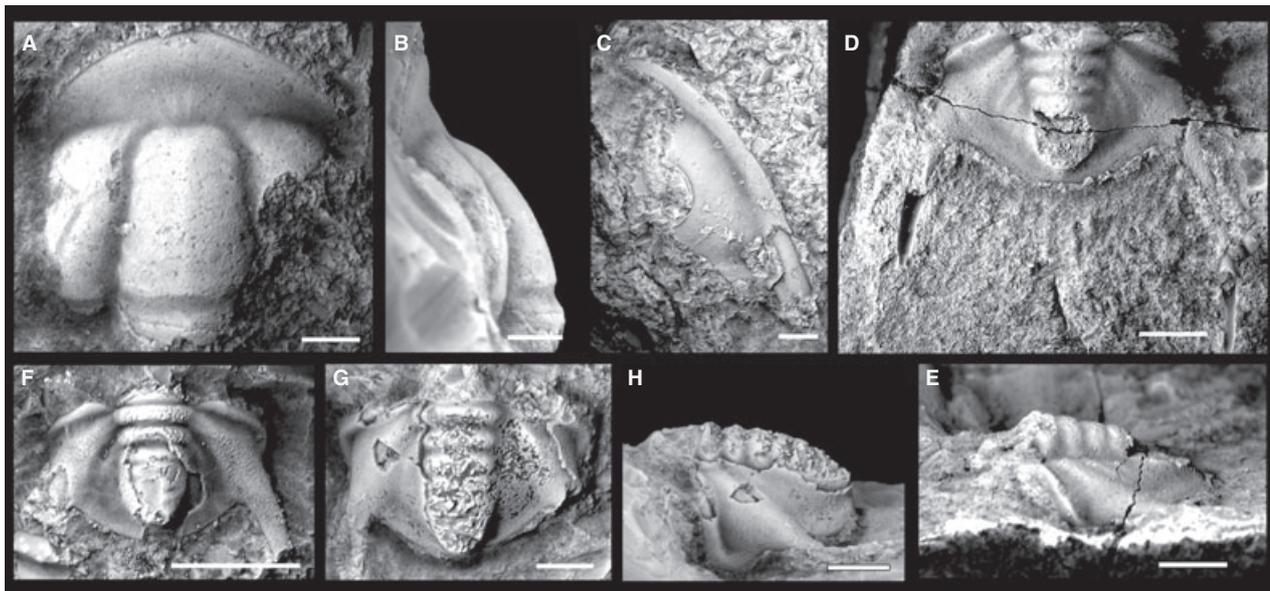


FIG. 3. *Mansuyia orientalis* (Sun, 1924) from the Tangwangzhai section, Shandong Province, North China. A–B, internal mould of cranidium, SNUP 5186: A, dorsal view and B, lateral view. C, librigena, SNUP 5187. D–H, pygidia. D–E, pygidium, SNUP 5188: D, dorsal view and E, lateral view. F, partly exfoliated pygidium, SNUP 5206. G–H, partly exfoliated pygidium, SNUP 5207: G, dorsal view and H, lateral view. All scale bars represent 2 mm.

caeca. Preocular area as wide as glabellar frontal lobe; palpebral area *c.* 40 per cent of glabellar width; posterior area of fixigena short, triangular in outline, abaxially downslowing. Palpebral lobes located slightly posterior to glabellar midlength; palpebral ridges moderately convergent forward. Anterior branch of facial suture strongly divergent convex.

Librigena convex, longer than wide. Genal field convex. Eye socle furrow clearly incised, narrow and shallow. Lateral border furrow moderately deep, wide, but shallow in posterior part; lateral border narrow, extending rearward into genal spine. Surface smooth except anterior end of lateral border ornamented with parallel lirae.

Pygidium strongly convex, semicircular in outline excluding pleural spines, 1.5 times wider than long. Pygidial axis with six axial rings and a terminal piece, strongly convex, gently tapering rearward, *c.* 37 per cent of pygidial width; terminal piece reaching to posterior border; axial furrow very shallow around terminal piece. Pleural field moderately downslowing; pleural furrows shallow except anterior two, sharply directing rearward posteriorly to pleural spine; interpleural furrows obsolete; pygidial spine base convex, formed by fusion of posterior band of first pleurae and anterior band of second pleurae. Pygidial border moderately wide and flat, interrupted by pleural spine; border furrow shallow but distinct. Surface densely tuberculated in small specimens, but smooth in larger ones.

Material examined. One cranidium and a pygidium from CLT08, a librigena from CLT09 and two pygidia from CLT10.

Occurrence. Kaolishania Zone of the Chaomidian Formation in the Tangwangzhai section, Shandong Province, China.

Remarks. *Mansuyia orientalis* is one of the least effaced species of *Mansuyia*. It is characterized by a very wide anterior border and deep axial furrows on both cranidium and pygidium. Its pygidium has the widest axis among the species of *Mansuyia*, about 37 per cent of the pygidial width, and distinct pleural furrows and border. This species is the oldest species of *Mansuyia* recovered in this study. The single cranidium (Fig. 3A) is an internal mould and has a rather broad anterior border, compared with the previously reported cranidia of *M. orientalis*. The length of anterior border is variable in *M. orientalis* and may have been enhanced because the specimen is preserved as an internal mould.

Mansuyia chinensis (Endo, 1939)

Figure 4

- ?1924 *Chuangia batia* Walcott, 1905; Sun, p. 58, pl. 4, fig. 4a–c.
 1939 *Paramansuyia chinensis* Endo, p. 9, pl. 2, figs 3–10, non 35.
 1965 *Mansuyia chinensis* (Endo); Xiang in Lu *et al.* 1965, p. 417, pl. 79, figs 12, 13.

non1994 *Mansuyia chinensis* (Endo); Qian, p. 125, pl. 33, figs 12, 13.

Syntype. Five cranidia designated by Endo (1939, pl. 2, figs 3–6, 10), registered under two numbers, USNM 96103 and 96101.

Diagnosis. A species of *Mansuyia* with weakly incised axial furrow and obsolete occipital furrow. Pygidium having faint pleural and inter-ring furrows and axis with seven axial rings and a terminal piece.

Description. Cranidium subrectangular in outline; anterior cranidial margin bluntly pointed medially; surface smooth. Glabella tapering forward, moderately convex; axial furrows faint glabellar width *c.* one half of cranidial width; glabellar frontal lobe weakly impressed in the middle; glabellar furrows very faint; S1, S2 and S3 wide and very shallow. Anterior cranidial border wide (sag.), slightly upturned with rounded anterior margin. Occipital furrow obsolete; posterior margin of occipital ring moderately rounded posteriorly. Palpebral lobe one-third of glabellar length, located posterior to glabella midlength. Palpebral ridge faint. Fixigenal field as wide as one half of glabellar width. Anterior branch of facial suture weakly divergent convex. Posterior branch of facial suture divergent straight. Posterior border narrow. Posterior border furrow wide and shallow, but deep distally. Posterolateral projection downslowing abaxially.

A single fragmentary librigena having broad and flat base of genal spine; lateral border furrow moderately deep and wide; lateral border relatively wide. Librigenal field surface granulose.

Pygidium semicircular in outline, slightly wider than long, moderately convex. Axial furrow shallow; axis tapering rearward with seven axial rings and a terminal piece; inter-ring furrows faint. Anteriormost axial ring *c.* 35 per cent of pygidial width. Terminal piece nearly reaching posterior border. Pleural field weakly convex. First pleural furrow deeper than other pleural furrows; other pleural furrows faint, running obliquely backward. Posterior band of first pleura and anterior band of second pleura forming the base of pleural spines. Pleural spines as long as pygidial width, directed obliquely backwards. Posterior border furrow wide and extremely shallow.

Material examined. Thirty-two cranidia, 15 pygidia and a librigena from CLT 10 and CLT 11.

Occurrence. Kaolishania Zone of the Chaomidian Formation in the Tangwangzhai section, Shandong Province, China.

Remarks. This species is more effaced than *M. orientalis*, but the anterior border furrows and axial furrows are still visible. It displays a range of variation in the preglabellar area: some have the glabella abutting the anterior border (Fig. 4A, C and H), while others have a glabella slightly retracted backward, displaying a wide plectrum connecting to the anterior border (Fig. 4B, D, E and I). Some specimens possess ornamentations on the cranidial surface, such as fine granules or pits. The furrows on the

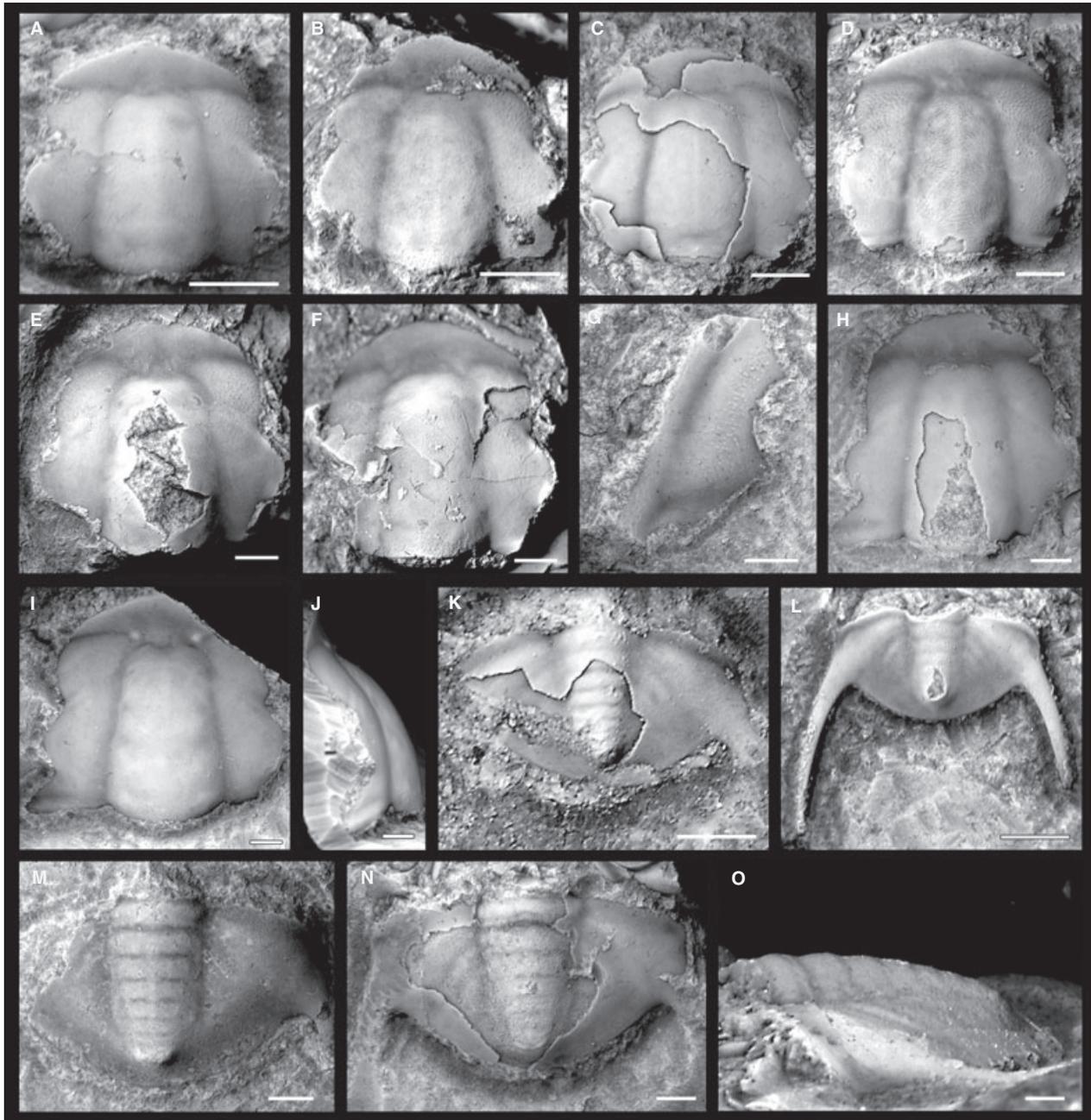


FIG. 4. *Mansuyia chinensis* (Endo, 1939) from the Tangwangzhai section, Shandong Province, North China. A–F, cranidia: A, SNUP 5208; B, SNUP 5209; C, partly exfoliated cranidium, SNUP 5210; D, SNUP 5211; E, SNUP 5212; and F, SNUP 5213. G, fragmentary librigena, SNUP 5214. H, cranidium, SNUP 5215. I–J, cranidium, SNUP 5189: I, dorsal view and J, lateral view. K–M, pygidia: K, SNUP 5216; L, SNUP 5190; and M, internal mould pygidium, SNUP 5217. N–O, partly exfoliated pygidium, SNUP 5218: N, dorsal view and O, lateral view. All scale bars represent 2 mm.

pygidium are either obsolete or faintly recognizable. This species has one more axial ring than *M. orientalis*. The number of axial rings in the pygidium is indeterminate in a testaceous pygidium (Fig. 4L), but the interring furrows are clearly seen in exfoliated specimens (Fig. 4M–O).

Mansuyia tani Sun, 1935

Figure 5

- 1913 *Hysterolenus?* sp. Walcott, p. 219, pl. 22, fig. 9.
 1935 *Mansuyia tani* Sun, 1935, p. 59, pl. 5, figs 12–15.
 1937 *Hysterolenus* sp.; Resser and Endo, p. 342, pl. 71, fig. 3.

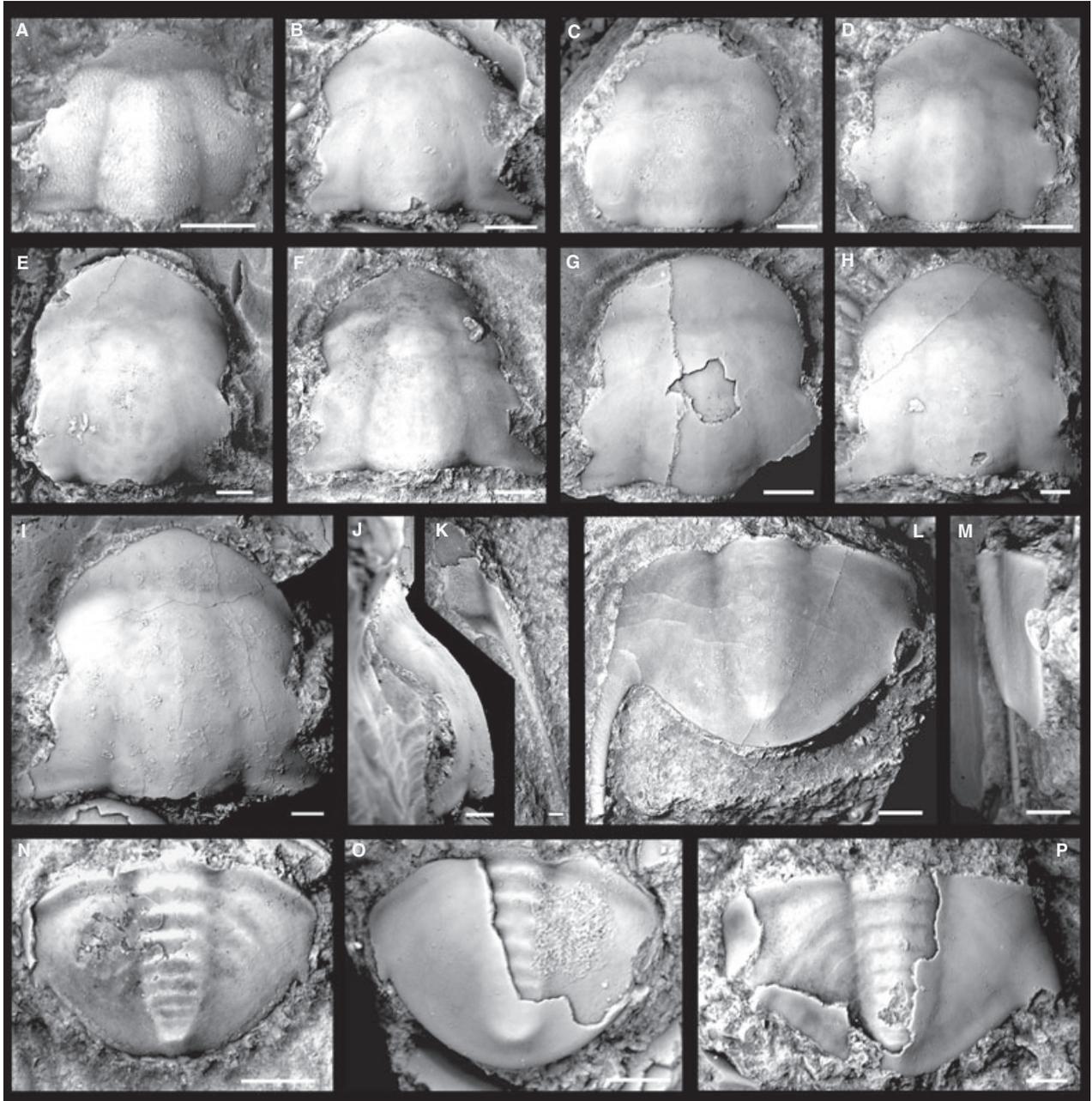


FIG. 5. *Mansuyia tani* Sun, 1935 from the Tangwangzhai section, Shandong Province, North China. A–H, cranidia: A, SNUP 5219; B, SNUP 5220; C, SNUP 5140; D, SNUP 5221; E, SNUP 5222; F, SNUP 5223; G, SNUP 5224; and H, SNUP 5225. I–J, cranidium, SNUP 5191: I, dorsal view and J, lateral view. K, librigena, SNUP 5192. L–M, pygidia, SNUP 5193: L, dorsal view and M, lateral view. N, internal mould of pygidium, SNUP 5226. O–P, partly exfoliated pygidium, SNUP 5227, and P, SNUP 5194. All scale bars represent 2 mm.

1939 *Paramansuyia chinensis* Endo, p. 9, pl. 2, fig. 35.

1952 *Mansuyia manchurica*, Kobayashi, p. 148.

non1975 *Mansuyia* cf. *tani* Sun; Shergold, p. 182, pl. 39, figs 3–7, text-fig. 59.

?1994 *Mansuyia chinensis* (Endo); Qian, p. 125, pl. 33, figs 12, 13.

Lectotype. Cranidium figured by Sun (1935, pl. 5, fig. 12), designated herein.

Diagnosis. A species of *Mansuyia* with highly effaced surface and broad anterior border. Pygidium with eight axial rings and a terminal piece.

Description. Cranidium subcircular in outline, moderately convex, surface highly effaced. Glabella tapering forward, 60–70 per cent of cranidial length and c. 40 per cent of cranidial width; glabellar furrows obsolete; axial furrow effaced but recognizable; preglabellar furrow very shallow and wide; occipital ring short,

less than one-fifth of glabella length; occipital furrow obsolete. Anterior border broad, 21–29 per cent of cranial length; anterior border furrow shallow and wide. Fixigenal field moderately wide, as convex as glabella. Palpebral lobe one-fourth of cranial length, located slightly posterior to glabellar midlength; palpebral furrow faint; palpebral ridge hardly recognizable. Anterior branch of facial suture moderately divergent convex. Posterior branch of facial suture divergent straight. Posterior border furrow shallow and broad; posterior border weakly convex. Posterolateral projection downsloping abaxially.

A fragmentary librigena with a long genal spine; genal field sculptured with fine granules around the eye socle. Eye socle furrow weakly incised. Lateral border narrow, continuing rearward into genal spine; lateral border furrow moderately deep.

Pygidium semicircular in outline, *c.* 1.3 times wider than long; slightly convex; surface highly effaced. Axial furrow very shallow; axis tapering rearward with eight axial rings and a terminal piece; inter-ring furrows obsolete; anteriormost axial ring *c.* 32 per cent of pygidial width. Terminal piece nearly reaching to posterior border. Pleural field weakly convex. Posterior border not recognized due to obsolete border furrow. Furrows only visible in exfoliated specimens.

Material examined. Twenty-eight cranidia, 33 pygidia and a librigena from CLT 12, CLT13 and CLT 14.

Occurrence. *Kaolishania* Zone of the Chaomidian Formation in the Tangwangzhai section, Shandong Province, China.

Remarks. This species is similar to *M. chinensis* in having a subcircular cranidium, slightly arched cranial border, wide anterior border and convex glabella. Sun

(1935) erected this species on the basis of one poorly preserved cranidium, two pygidia that are internal moulds and one testaceous pygidium (Sun 1924, pl. 5, figs 12–15). The poorly preserved cranidium illustrated by Sun (1924, pl. 5, fig. 12) has more clearly defined axial furrows and palpebral ridges than the specimens of *M. tani* in this study, which may be ascribed to possible exfoliation. The internal moulds of pygidia illustrated by Sun (1935, pl. 5, figs 13, 14) display more than eight axial rings, and the testaceous pygidium (Sun 1935, pl. 5, fig. 15) is almost identical to the testaceous one of this study (Fig. 5L).

Like in *M. chinensis*, this species also displays a range of variation in the preglabellar field so that some specimens have a wide plectrum (Fig. 5B–D, F and G), which is, however, difficult to see in the effaced specimens. This species has a flatter glabella, a more effaced surface and one more axial ring than *M. chinensis*. The inter-ring furrows are not visible in the testaceous specimen (Fig. 5L, M), but are clearly seen in the exfoliated specimens (Fig. 5N–P). It is noteworthy that the smallest cranidium (Fig. 5A) has a granulose and less effaced surface compared with the larger cranidia, implying that the surface became effaced with growth.

Mansuyia taianfuensis (Endo, 1939)

Figure 6

1939 *Dictya taianfuensis* Endo, p. 11, pl. 2, figs 21–23.

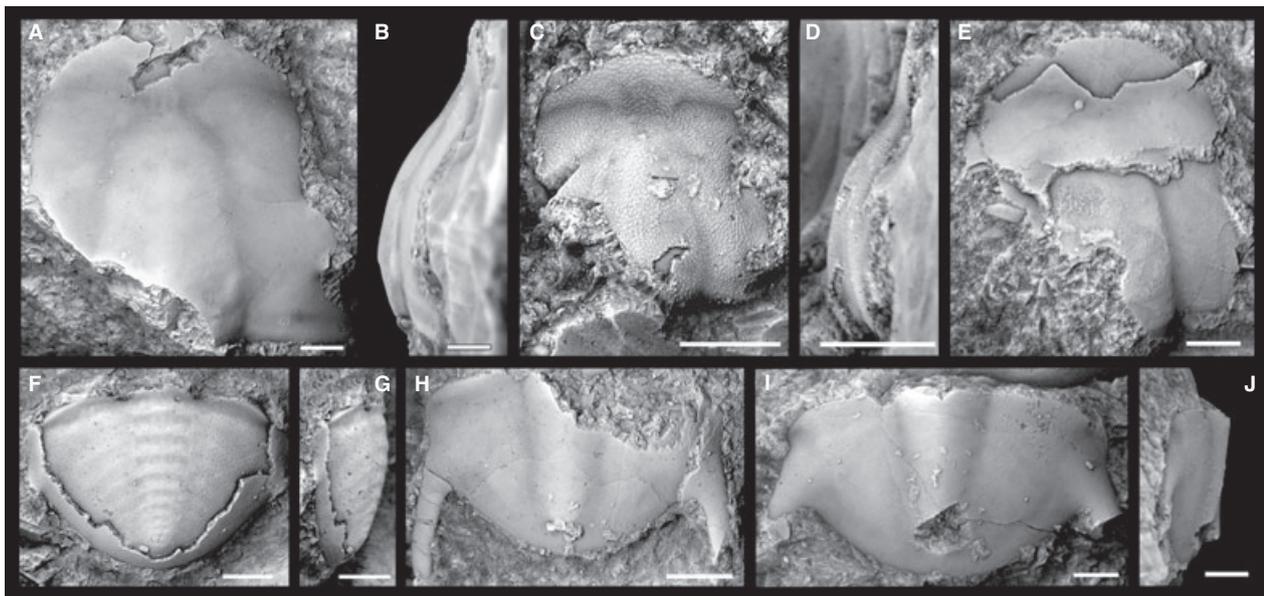


FIG. 6. *Mansuyia taianfuensis* (Endo, 1939) from the Tangwangzhai section, Shandong Province, North China. A–B, fragmentary cranidium, SNUP 5195: A, dorsal view and B, lateral view. C–D, fragmentary cranidium, SNUP 5228: C, dorsal view and D, lateral view. E, partly exfoliated fragmentary cranidium, SNUP 5229. F–G, partly exfoliated pygidium, SNUP 5230: F, dorsal view and G, lateral view. H, fragmentary pygidium, SNUP 5196. I–J, pygidium, SNUP 5231: I, dorsal view and J, lateral view. All scale bars represent 2 mm.

- 1987 *Shergoldia taianfuensis* (Endo); Zhang and Jell, p. 198, pl. 89, figs 1–3.
 1987 Tsinaniidae gen. and sp. indet.; Zhang and Jell, p. 198, pl. 89, figs 6, 7.

Lectotype. Cranidium (USNM 96108) figured by Endo (1939, pl. 2, fig. 21), subsequently designated by Zhang and Jell (1987).

Diagnosis. A species of *Mansuyia* with a highly effaced surface with low convexity and conical glabellar front. Pygidium with more than nine axial rings including a terminal piece.

Description. Cranidium subcircular in outline, weakly convex, surface highly effaced. Glabella tapering forward, more or less conical in frontal part; *c.* 65 per cent of cranidial length and *c.* 45 per cent of cranidial width; glabellar furrows obsolete; axial furrow weakly incised, but effaced; preglabellar furrow very shallow and wide; occipital furrow obsolete. Anterior border moderately wide, *c.* 25 per cent of cranidial length; anterior border furrow shallow and wide, broadly V-shaped, forming a plectrum. Fixigenal field as flat as glabella. Palpebral lobe one-quarter of cranidial length, located slightly posterior to glabellar midlength; palpebral furrow obsolete; palpebral ridge faint. Anterior branch of facial suture parallel straight to slightly divergent straight. Posterior branch of facial suture divergent straight. Posterior border furrow very shallow and moderately wide; posterior border flat. Posterolateral projection slightly downslipping abaxially.

Pygidium semicircular in outline, *c.* 1.5 times wider than long; weakly convex; surface highly effaced. Axis slightly elevated above pleural field; axial furrow very shallow; axis tapering rearward with more than nine axial rings; inter-ring furrows obsolete; anteriormost axial ring *c.* 28 per cent of pygidial width. Posterior border and posterior border furrow not recognizable due to effacement. Shallow furrows only observed in exfoliated specimens.

Material examined. Six fragmentary cranidia and seven fragmentary pygidia from CLT 15 and a cranidia from CLT 17.

Occurrence. *Asioptychaspis-Tsinania* Zone in the Chaomidian Formation, Tangwangzhai section, Shandong Province, China.

Remarks. This species is the most strongly effaced species of *Mansuyia* with lowest convexity. The highly effaced surface has caused confusions in taxonomic assignment of the cranidia and pygidia. Endo (1939) erected this species as a new species of *Dictya* Kobayashi, 1933, which is a genus of the Tsinaniidae. However, on the basis of the presence of paired pygidial spines, this species is transferred to *Mansuyia*. This study recognizes for the first time the pygidia of *M. taianfuensis*, and the pygidia of *M. taianfuensis* were previously identified as tsinaniid pygidia under the open nomenclature by Zhang and Jell (1987, p. 198). The pygid-

ium of this species is so effaced that it is similar to the pygidia of tsinaniid trilobites, apart from the presence of paired pygidial spines. As in *M. chinensis*, the smallest cranidium (Fig. 6C) displays a more deeply incised anterior border furrow and a granulose surface.

Family TSINANIIDAE Kobayashi, 1933

Genus TSINANIA Walcott, 1914

Type species. *Illaeonurus canens* Walcott, 1905 from the Chaomidian Formation, Jinan, Shandong Province, China.

Other species. *Tsinania longa* Kobayashi, 1933; *Tsinania? humilis* Kobayashi, 1933; *T. acuta* Sun, 1935; *T. peipingense* Sun, 1935; and *T. tingtaohengi* Sun, 1935.

Remarks. The generic concept of *Tsinania* is well summarized by Zhang and Jell (1987), which is followed herein.

Tsinania canens (Walcott, 1905)

Figure 7

- 1905 *Illaeonurus canens* Walcott, p. 96.
 1905 *Illaeonurus* sp. Walcott, p. 222, pl. 23, fig. 6.
 1913 *Illaeonurus canens* Walcott, p. 222, pl. 23, fig. 3a–c.
 1913 *Illaeonurus ceres* Walcott; Walcott 1913, p. 223, pl. 23, fig. 4a.
 1913 *Illaeonurus dictys* Walcott, p. 224, pl. 23, fig. 5a.
 1913 Gen. and sp. indeterminate. Walcott, p. 224, pl. 23, fig. 8.
 1924 *Illaeonurus pagoda* Sun, p. 82, pl. 5, fig. 10a–c.
 1931 *Tsinania canens* (Walcott); Kobayashi, p. 186, pl. 20, figs 7–9.
 1931 *Tsinania canens* var. *pagoda* (Sun). Kobayashi, 1931, p. 186, pl. 20, fig. 10.
 1935 *Tsinania canens* (Walcott); Kobayashi, p. 306, pl. 5, fig. 20; pl. 6, figs 13, 14.
 ?1935 *Tsinania canens* var. *shansiensis* Sun, 1935, p. 53, pl. 5, figs 20, 21.
 ?1937 *Tsinania vulgaris* Resser and Endo, p. 295, pl. 56, figs 13–18.
 ?1937 *Tsinania convexa* Resser and Endo, p. 296, pl. 56, figs 19, 20.
 ?1937 *Tsinania longicephala* Resser and Endo, p. 296, pl. 55, figs 22–27.
 1944 *Tsinania canens* (Walcott); Endo, p. 95.
 1952 *Tsinania canens* (Walcott); Kobayashi, 1952, p. 150, pl. 13, figs 1–8, text-fig. 2.
 1957 *Tsinania canens* (Walcott); Lu, p. 269, pl. 147, figs 9, 10.
 1965 *Tsinania canens* (Walcott); Lu *et al.*, p. 341, pl. 63, figs 18–25.

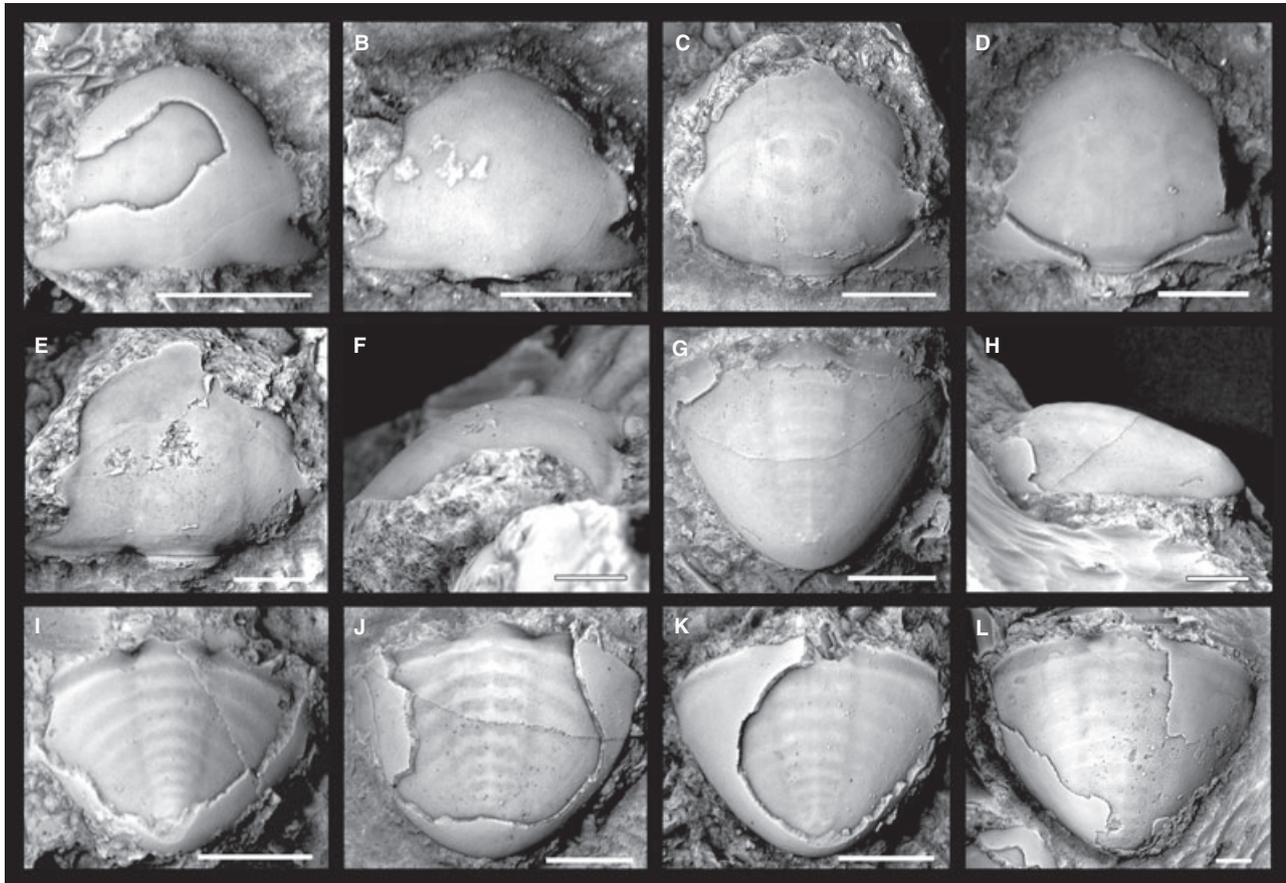


FIG. 7. *Tsinania canens* (Walcott, 1905) from the Tangwangzhai section, Shandong Province, North China. A–D, cranidia: A, SNUP 5232; B, internal mould of cranidium, SNUP 5233; C, internal mould of cranidium, SNUP 5234; and D, partly exfoliated cranidium, SNUP 5235. E–F, cranidium, SNUP 5162: E, dorsal view and F, lateral view. G–L, pygidia. G–H, internal mould of pygidium, SNUP 5236: G, dorsal view and H, lateral view. I–L, partly exfoliated pygidia: I, SNUP 5237; J, SNUP 5238; K, SNUP 5239; and L, SNUP 5163. All scale bars represent 2 mm.

1987 *Tsinania canens* (Walcott); Zhang and Jell, p. 195, pl. 86, figs 12–16, pl. 87, figs 1–14, pl. 88, figs 1–13; pl. 89, fig. 5.

Description. Cranidium subtriangular in outline; moderately convex; surface highly effaced. Axial furrow and glabellar furrow obsolete in testaceous cranidia; glabella, *c.* 75 per cent of cranial length. Occipital ring very short with transverse posterior margin; occipital furrow obsolete. Anterior cranial margin weakly pointed medially. Palpebral lobe semicircular, *c.* 25 per cent cranial length, located at glabellar midlength; palpebral furrow obsolete. Anterior branch of facial suture weakly convergent convex to parallel. Posterior branch of facial suture divergent sinuous. Posterior border furrow nearly obsolete; posterior border flat.

Pygidium subtriangular in outline, *c.* 1.2 times wider than long; moderately convex; surface highly effaced. No furrows recognized in testaceous pygidium, but very shallow furrows indicated in internal moulds. Axis *c.* 28 per cent of pygidial width, slightly tapering backwards with more than nine axial rings.

Material examined. Thirty cranidia and 47 pygidia from CLT15, CLT16 and CLT17.

Occurrence. *Asioptychaspis-Tsinania* Zone of the Chaomidian Formation in the Tangwangzhai section, Shandong Province, China.

Remarks. Detailed discussions on this species were given by Shergold (1975) and Zhang and Jell (1987). Zhang and Jell (1987) suggested a broad range of intraspecific morphological variations for this species. Park and Choi (2009) provided a detailed documentation on the ontogeny of this species and also described librigenae and thoracic segments of *T. canens*, which were recovered from the Hwajeol Formation of Korea.

PHYLOGENETIC ANALYSIS

Thirteen characters were coded for seven ingroup taxa. *Kaolishania granulosa* Kobayashi, 1933 was selected as the

outgroup. Park and Choi (2009) mentioned that *Mansuyia* displays an intermediate morphology between the older leiostrigoids, such as *Kaolishania* Sun, 1924 and *Prochuangia* Kobayashi, 1935, and the highly effaced *T. canens*, implying that *Kaolishania* and *Prochuangia* had a plesiomorphic morphology, compared with *Mansuyia* and *Tsinania*. Of the two older leiostrigoid genera, *Kaolishania* seems more proper outgroup for the present analysis because its stratigraphic occurrence is closer to that of *Mansuyia*: that is, all the *Mansuyia*-occurring interval in this study is considered as the upper part of the *Kaolishania* Zone, while the *Prochuangia*-occurring interval is usually far below, near the base of the Furongian Series (Qian, 1994; Park and Choi, 2011). A detailed morphology of *K. granulosa* Kobayashi, 1933 has been recently described on the basis of silicified material (Park et al. 2012), which makes character coding easy, hence selected as the outgroup. Only three tsinaniid trilobites, *T. canens*, *S. laevigata* and *Lonchopygella* sp., were included in the analysis, because other tsinaniid trilobites are poorly described and/or taxonomically unstable (Zhu et al. 2007). Moreover, the inclusion of other taxa would necessitate taxonomic revision, which is beyond the scope of this paper. The characters for *S. laevigata* were coded on the basis of the illustrations of Zhu et al. (2007), while those for *Lonchopygella* sp. from the photographs of newly collected specimens from Yunnan Province, China, which were provided by Xuejian Zhu (Nanjing Institute of Geology and Palaeontology). All characters were equally weighted and unordered.

The phylogenetic analysis was performed using PAUP 4.0 b 10 (Swofford 2003). Unavailable and inapplicable character states are coded as '?' and '-', respectively. Polymorphic characters are coded as '0/1'. The matrix was calculated using the heuristic search. A single maximum parsimonious tree (MPT) was obtained with the tree length of 24; consistency index is 0.833, retention index is 0.833 and rescaled consistency index is 0.694.

A single most parsimonious tree was obtained (Fig. 8). This tree demonstrates the paraphyly of the Kaolishaniidae by the exclusion of the Tsinaniidae. The kaolishaniid genus *Mansuyia* is rendered paraphyletic with the youngest species *M. taianfuensis* forming an immediate sister group to the Tsinaniidae. The synapomorphy of the family Tsinaniidae is the absence of the paired pygidial spines in the morphologically mature holaspid pygidia, which is a characteristic of the kaolishaniid trilobites. Although other tsinaniid species were not included in this analysis for the reason mentioned above, tsinaniid trilobites invariably lack the paired pygidial spines in the morphologically mature holaspid pygidia, and thus, other tsinaniids, if included, would have been fitted within the monophyly of the Tsinaniidae. It should be noted that the ingroup relationship of the Tsinaniidae is not

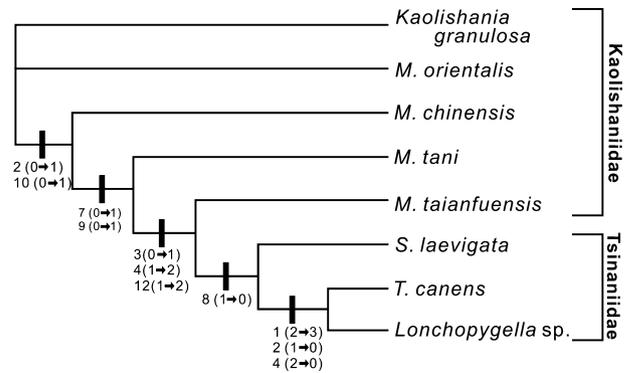


FIG. 8. Cladogram showing the relationship between the Kaolishaniidae and the Tsinaniidae. Only unambiguous characters are shown at each node with the state change indicated. See text for explanation.

consistent with the evolutionary scenario given by Zhu et al. (2013) in which the segmentation pattern was taken into account as well. This study focuses more on the cranidial and pygidial morphology, documenting a morphological transition in cranium and pygidium from *Mansuyia* to tsinaniids, while Zhu et al. (2013) provided an interesting scenario on the transition of the trunk segmentation from mansuyines/basal leiostrigoids through the *Lonchopygella*-like trunk morphology to other tsinaniids.

DISCUSSION

Because evolution always occurs at species or subspecies level, origination of a supraspecific taxon necessarily involves problems of putting a supraspecific taxonomic boundary at a certain speciation process, creating a paraphyly for the supraspecific taxon containing the ancestral species. This issue may become more evident in palaeontology because fossil data enable us to see the temporal aspect of evolution. Dealing with the phylogenetic relationship of the kaolishaniid genus *Mansuyia* and the family Tsinaniidae also provides a good opportunity to discuss this matter at the familial level. As demonstrated in the cladogram (Fig. 8), the species of the genus *Mansuyia* constitute stem-group taxa to the Tsinaniidae, with *Mansuyia orientalis*, *M. chinensis*, *M. tani* and *M. taianfuensis* progressively closer in phylogeny to the Tsinaniidae. Overall, being phylogenetically closer to the Tsinaniidae, there is a trend of being more effaced and more tsinaniid-like, and hence, the morphology of *Mansuyia taianfuensis* and *S. laevigata*, each of which belongs to different family, is closely comparable to each other: the main difference is the absence of the paired pygidial spines in the morphologically mature holaspid *S. laevigata*. The absence of paired pygidial spines in *S. laevigata* in a later developmental phase is a small difference that can be attained by a simple

evolutionary process. The close morphological similarity of *M. taianfuensis* and *S. laevigata* has led to incorrect assignment of cranidia of *M. taianfuensis* to *Shergoldia* by Zhang and Jell (1987). Moreover, because the pygidial morphology of *M. taianfuensis* is nearly identical to that of *S. laevigata* aside from the presence of paired pygidial spines in the morphologically mature holaspide pygidia, there has been confusion in assigning the pygidia of this species. Zhang and Jell (1987) suggested a possibility that the two pygidia (Zhang and Jell 1987, pl. 89, figs 6, 7) may represent immature forms of *Tsinania*. On the other hand, Kobayashi (1952) assigned a pygidium of this species to *Mansuyia tani* Sun, 1935. Such confusion in identification might be surprising given the fact that *Shergoldia* and *Mansuyia* are currently assigned to different families. Nevertheless, all the subsequent researchers have maintained the two familial concepts of the Kaolishaniidae and Tsinaniidae; the synonymy of the two families has never been attempted. This is because the morphology of the type species of Kaolishaniidae, *Kaolishania pustulosa* Sun (1924), is markedly different from that of the Tsinaniidae, *T. canens* (Walcott, 1905), so that the two species could hardly be regarded as belonging to the same family. We also maintain these as two separate families, recognizing the paraphyletic family Kaolishaniidae and the paraphyletic genus *Mansuyia* in this study. The recognition of paraphyly is in line with the growing number of recent studies that have pointed out the problem of recognizing only monophyletic taxa in classification (Brummitt 2002, 2003, 2006, 2008; Mayr and Bock, 2002; Nordal and Stedje 2005; Hörandl 2006, 2007, 2010; Van Wyk 2007; Podani 2009, 2010), although there has been opposition to the recognition of paraphyly in classifications (Nelson *et al.* 2003; Williams *et al.* 2005; Ebach *et al.* 2006; Schmidt-Lebuhn 2012).

CONCLUSIONS

Four species of the kaolishaniid genus *Mansuyia* and a tsinaniid trilobite *T. canens* occur successively in the Furongian Chaomidian Formation of the Tangwangzhai section, Shandong Province, China. A cladistic analysis demonstrates that the four species of the genus *Mansuyia* form stem-group taxa to the Tsinaniidae: *Mansuyia orientalis*, *M. chinensis*, *M. tani* and *M. taianfuensis* progressively closer to the Tsinaniidae, rendering the genus *Mansuyia* and the family Kaolishaniidae paraphyletic. In particular, *Mansuyia taianfuensis* comprises the most immediate sister taxon of the Tsinaniidae and has a closely comparable morphology with the tsinaniid *S. laevigata*. The generic and familial boundary should be drawn between the two species if the two families are to be distinguished from each other, rendering the genus *Mansuyia* and the family Kaolishaniidae paraphyletic.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Character list and matrix for cladistic analysis

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