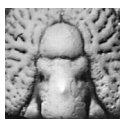


Intraspecific variation and taphonomic alteration in the Cambrian (Furongian) agnostoid *Lotagnostus americanus*: new information from China

SHANCHI PENG, LOREN E. BABCOCK, XUEJIAN ZHU, PER AHLBERG, FREDRIK TERFELT & TAO DAI



The concept of the agnostoid arthropod species *Lotagnostus americanus* (Billings, 1860), which has been reported from numerous localities in the upper Furongian Series (Cambrian) of Laurentia, Gondwana, Baltica, Avalonia, and Siberia, is reviewed with emphasis on morphologic and taphonomic information afforded by large collections from Hunan in South China, Xinjiang in Northwest China, and Zhejiang in Southeast China. Comparisons are made with type and topotype material from Quebec, Canada, as well as material from elsewhere in Canada, the USA, the United Kingdom, Sweden, Russia, and Kazakhstan. The new information clarifies the limits of morphologic variability in *L. americanus* owing to ontogenetic changes and variation within holaspides, including inferred microevolution. It also provides details on apparent variation of taphonomic origin. The Chinese collections demonstrate a moderately wide variation in *L. americanus*, indicating that arguments favoring restriction of *Lotagnostus* species to narrowly defined, geographically restricted forms are unwarranted. Species described as *L. trisectus* (Salter, 1864), *L. asiaticus* Troedsson, 1937, and *L. punctatus* Lu, 1964, for example, fall within the range of variation observed in *L. americanus*, and are regarded as junior synonyms. The effaced form *Lotagnostus obscurus* Palmer, 1955 is removed from synonymy with *L. americanus*. A review of the stratigraphic distribution of *L. americanus* as construed here shows that the earliest occurrences of the species in all regions of the world are nearly synchronous. • Key words: Cambrian, Furongian, agnostoid, *Lotagnostus americanus*, China, Quebec.

PENG, S.C., BABCOCK, L.E., ZHU, X.J., AHLBERG, P., TERFELT, F. & DAI, T. 2015. Intraspecific variation and taphonomic alteration in the Cambrian (Furongian) agnostoid *Lotagnostus americanus*: new information from China. *Bulletin of Geosciences* 90(2), 281–306 (11 figures, online appendix). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received January 31, 2014; accepted in revised form November 14, 2014; published online February 9, 2015; issued March 23, 2015.

Shanchi Peng, Xuejian Zhu & Tao Dai, State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing, China 210008; scpeng@nigpas.ac.cn, xjzhu@nigpas.ac.cn, daitao10@126.com • Loren E. Babcock, School of Earth Sciences, The Ohio State University, Columbus, OH 43210, USA, and Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden; babcockloren@gmail.com • Per Ahlberg, Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden; per.ahlberg@geol.lu.se • Fredrik Terfelt, Department of Physics, Division of Nuclear Physics, Lund University, Professorsgatan 1, SE-221 00 Lund, Sweden; fredrik.terfelt@nuclear.lu.se

Lotagnostus americanus (Billings, 1860) is an agnostoid arthropod having a distinctive morphology. The species has a relatively short stratigraphic range beginning about two-thirds of the stratigraphic distance above the base of the Furongian Series (Cambrian System). The species also has a near-global geographic distribution in open-shelf lithofacies, occurring both in limestone and fine siliciclastic beds. With these attributes, the first appearance datum (FAD) of the species stands out as an important international tie point in the upper part of the Furongian Series. For this reason, the FAD of *L. americanus* has been put forward as a possible horizon for defining the base of a global Cambrian stage. In a vote conducted in November

2004, Voting Members of the International Subcommittee on Cambrian Stratigraphy (ISCS), supported, by a strong majority, the establishment of a stage-level GSSP at a horizon coinciding with the FAD of *Lotagnostus trisectus* (a junior synonym of *L. americanus*) or another fossil in a comparable stratigraphic position. The stage so defined would replace provisional Stage 10 of the Cambrian System.

The holotype of *L. americanus* (Billings, 1860) is from the Lévis Formation, Quebec, Canada. It was originally assigned to *Agnostus americanus* by Billings (1860). Rasetti (1944) also assigned topotype specimens to *Agnostus*. Ludvigsen & Westrop (1989) transferred the species to

Lotagnostus and synonymized two species, *Agnostus innocens* Clark, 1924 and *Lotagnostus obscurus* Palmer, 1955, with *L. americanus*. Ludvigsen & Westrop's (1989) synonymy was followed by Peng & Babcock (2005), who synonymized additional species based on morphologic variation observed in *Lotagnostus* material described from other regions. The synonymy of Peng & Babcock (2005) has been widely adopted (Terfelt & Ahlgren 2007; Terfelt *et al.* 2008; Lazarenko *et al.* 2008a, b, 2011; Rushton 2009; Ahlberg & Terfelt 2012). Rushton (2009, p. 276) added one more species, *Lotagnostus sanduensis* Lu & Chien (*in* Lu & Qian 1983), to the synonymy of *L. americanus*.

Recently, Landing *et al.* (2010, 2011) and Westrop *et al.* (2011) raised objections to the species concept of *L. americanus* and other agnostoid species, preferring concepts based on very narrow limits to morphologic variation. Westrop *et al.* (2011) refigured specimens previously assigned to or synonymized with *L. americanus* and split the taxon into several species, most of which were previously synonymized. In resurrecting the synonymized forms, Landing *et al.* (2010, 2011) and Westrop *et al.* (2011) emphasized narrow limits of morphologic variability and downplayed the possibility of intraspecific variation and variation introduced by taphonomic processes. They also employed definitions of species characterized by highly restricted geographic ranges, single localities in most cases.

This paper responds to the arguments raised by Westrop *et al.* (2011) on the concept of *Lotagnostus americanus* and by Landing *et al.* (2011) on the purported diachroneity of the first occurrences of *Lotagnostus*. The present study focuses on material from large collections made in three regions of China, but draws on comparative material from elsewhere in the world.

In our view, the morphologic and geographic limits placed on *L. americanus* and other agnostoids cited by Landing *et al.* (2010, 2011) and Westrop *et al.* (2011) are overly restrictive, and have resulted in an over-splitting of species. Intraspecific morphologic variation in agnostoids has been documented by numerous authors, as emphasized by Rowell *et al.* (1982), Pratt (1992), and Peng & Robison (2000). Taphonomically induced variation has also been described, and it is particularly striking when comparing specimens preserved in limestone with others preserved in shale (*e.g.* Babcock *et al.* 2012). As discussed below, key species used for the recognition of horizons containing the Drumian Stage, Guzhangian Stage, Paibian Stage, and Jiangshanian Stage GSSPs are variable in morphology, even within collections from a single locality or horizon (Robison 1984; Peng & Robison 2000; Peng *et al.* 2004, 2009, 2012c; Babcock *et al.* 2007). Rowell *et al.* (1982) provided a quantitative assessment of morphologic variation in agnostoids associated with the upper part of Stage 5

and the lower part of the Drumian Stage, and their work emphasizes a wide range of morphologic variation within certain agnostoid species.

Many agnostoids, and especially those used to identify marker horizons in the upper half of the Cambrian System, are widely distributed in open-shelf lithofacies around the margins of paleocontinents. Ecologically, most are inferred to have been nektic or pelagic, and less commonly nektobenthic (*e.g.* Robison 1972, 1994; Müller & Walossek 1988). Species filling such ecologic niches can be expected to show wide morphologic variation across broad geographic space, in contrast to, for example, nektobenthic polymerid trilobite species that inhabited more variable habitats of restricted inner-shelf environments. Inner-shelf-dwelling polymerids can be expected to show higher levels of endemism, although the species definitions of agnostoids advocated by Landing *et al.* (2010, 2011) and Westrop *et al.* (2011) are extremely narrow even compared to most definitions of endemic polymerids.

Narrow definitions of agnostoid species essentially preclude the possibility of recognizing individual species as intercontinentally distributed. This view contrasts with evidence published by many specialists, who have long noted that many agnostoids have similar morphologies and similar ranges of morphology in collections made from widely separated areas of the world (*e.g.* Daily & Jago 1975; Rushton 1978; Ergaliev 1980, 1983; Lu & Lin 1980, 1984, 1989; Robison 1982, 1984, 1994; Shergold *et al.* 1990; Peng 1992; Pratt 1992; Shergold & Laurie 1997; Peng & Robison 2000; Ahlberg 2003; Choi *et al.* 2004; Peng *et al.* 2004, 2009, 2012c; Peng & Babcock 2005; Babcock *et al.* 2007; Jago & Cooper 2007; Lazarenko *et al.* 2008a, b, 2011; Terfelt & Ahlberg 2010; Terfelt *et al.* 2011; Ahlberg & Terfelt 2012). Evidence of species that were broadly distributed in open-shelf lithofacies accords well with the interpretation that many agnostoids, at least in their juvenile stages, were nektic or pelagic. It implies not only that they were dispersed around the margins of individual paleocontinents, but that they were also dispersed intercontinentally through the open ocean.

Morphologic variability in specimens we have assigned here to *L. americanus* was first shown clearly by the sclerites described by Troedsson (1937, pl. 1, figs 1–16; here Figs 5, 6) as *L. asiaticus* from the “Torsuq tagh Formation”, Quruq tagh, Xinjiang, China. The holotype exoskeleton of *L. asiaticus* is indistinguishable from the holotype pygidium and topotype cephalon of *L. americanus* in almost every respect (see comparison in Fig. 5). Troedsson's (1937) sclerites, which are from a single locality in the Charchaq Range, vary in having a weakly to strongly furrowed cephalon with normal sized basal lobes and a faint to distinct trisection of the posteroaxis of the pygidium. As such, these specimens exhibit nearly all the features used by Westrop *et al.* (2011) to split *L. amer-*

icanus into a variety of “species”. Troedsson (1937, p. 25) remarked on the morphologic variation of *L. asiaticus* (= *L. americanus*), stating “I have found it impossible to keep those forms [weakly and strongly furrowed sclerites] separate, and am convinced that they all belong to one and the same species”.

Morphologic variability similar to that noted by Troedsson (1937) is evident in the collections of *L. americanus* described previously from western Zhejiang and northwestern Hunan, China, and the Khos-Nelege River, Siberia, Russia (Lu & Lin 1984, 1989; Peng 1992; Lazarenko et al. 2008a, b, 2011). Variability is evident in the material from Canada, including the type and topotype specimens from Quebec, and in sclerites from Nova Scotia. Material from Sweden likewise shows similar variability (Westergård 1922, Ahlberg & Ahlgren 1996, Terfelt et al. 2008, Ahlberg & Terfelt 2012, Babcock et al. 2012). Recently, Babcock et al. (2012) and Peng et al. (2012a) reported evidence that populations referable to *L. americanus* have moderately wide morphologic variability, some of which is due to taphonomic alteration, and that the species has a broad palaeogeographic distribution.

In investigating a potential GSSP candidate section for provisional Stage 10, at Wa’ergang, Taoyuan, northwestern Hunan, China, we assembled a large collection of *L. americanus* that shows the range of morphologic variation for the species described previously from elsewhere in the world. The figured sclerites (Figs 1–3) are from a short stratigraphic interval (about 7 m) in the lower part of Stage 10 in the candidate section. For comparison, some material first described in earlier papers has been re-illustrated with new photographs, and it tends to confirm that some species such as *L. asiaticus*, *L. punctatus*, and *L. trisectus* are best included in the synonymy of *L. americanus*. The comparative specimens include:

1. All available types of *Lotagnostus asiaticus* Troedsson, 1937, plus two cephalae not previously illustrated; all from a single locality [locality 22 at Charchaq Ridge, Kuruktag (Quruq tagh), Xinjiang, NW China] and preserved in black limestone.
2. All sclerites assigned to *L. asiaticus* by Lu & Lin (1989); all preserved in black limestone from a single level in the Siyanshan section, Changshan, western Zhejiang.
3. The holotype exoskeleton of *Lotagnostus punctatus* Lu, 1964 and some of the sclerites assigned by Lu & Lin (1984, 1989) to the species, of which a cephalon was discussed by Westrop et al. (2011); the holotype and a topotype exoskeleton, figured here are preserved in shale, whereas the other specimens are preserved in black limestone.
4. Sclerites from black limestone at a single collecting level in the Shenjiawan section, northwestern Hunan, figured by Peng (1984, 1992) under the name of *L. punctatus* Lu, 1964.

5. Images of specimens assigned to *L. americanus* from the Khos-Nelege River, Russia, provided by T.V. Pegel, showing morphologic variation and upsection microevolution of *L. americanus* in Siberia.

After study of the specimens from China, and review of comparative material from elsewhere, we conclude that *Lotagnostus americanus* is a distinctive species of moderately variable morphology and that it has a worldwide distribution. The species concept was well diagnosed by Ludvigsen & Westrop (1989) and Peng & Babcock (2005) although *L. obscurus* Palmer, 1955, which falls outside the variability of *L. americanus*, is best excluded as a synonym.

Technical methods

Photographic technique

All specimens from China figured in this paper, except for two exoskeletons preserved in shale (Fig. 9B, C), were blackened with dilute ink and coated with magnesium oxide powder before being photographed. Specimens, except for those in Figs 8 and 10 were photographed with a Zeiss stereomicroscope (Model SteREO Discovery.v20) having a digital head and a circle light providing uniform lighting mounted around the objective lens (see appendix at www.geology.cz/bulletin). This technique minimizes exaggeration of the scrobiculation, furrows, and other characters between specimens. However, image contrast is normally low, so contrast of the images was increased slightly using Adobe Photoshop CS6 software. The photographic technique differs from the traditional method of using strong directional lighting from the upper left. The latter style of photographic method emphasizes the expression of scrobiculation, furrows, and other features between individual specimens. The traditional method appears to have been used to photograph many of the *Lotagnostus* specimens illustrated previously.

Measurements

Measurements of newly illustrated specimens were made from the images of sclerites using the ruler tool in Adobe Photoshop CS6. Measurements of British and Canadian sclerites were made from images published by Rushton (2009) and Westrop et al. (2011).

Morphologic variation of *Lotagnostus americanus* from northwestern Hunan

Sclerites illustrated in Figs 1–3 were recently collected from an outcrop exposing the lower part of provisional

Stage 10 in the Shenjiawan Formation, Wa'ergang section, northwestern Hunan, China. The interval, 7.22 m thick, extends from 2.60 m below to 4.62 m above the level of collection WT 28 of Peng (1992). At the time of Peng's (1992) publication, collection level WT 28, which is 37.5 m above the base of the Shenjiawan Formation (692.5 m above the base of the underlying Huaqiao Formation) was the lowest known occurrence of *L. punctatus* (= a junior synonym of *L. americanus*) in the section. Refined, bed-by-bed collecting has resulted in the discovery of *L. americanus* 7.85 m below the 1992 position. The lowest known occurrence of *L. americanus* in the Wa'ergang section is in collection W684.65, which is 29.65 m above the base of the Shenjiawan Formation (684.65 m above the base of the underlying Huaqiao Formation). The figured specimens of *L. americanus* (Figs 1–3) derive from the lower part of the stratigraphic range of the species. The total range of *L. americanus* in the Wa'ergang section is about 100 m (Peng 1984).

Sclerites of *Lotagnostus* from the sample interval, 34.9 to 42.12 m above the base of the Shenjiawan Formation, include a number of holaspisid exoskeletons of varying lengths and many isolated cephalon and pygidia. They are construed as representing a single species, *L. americanus*, and the morphologic differences they show in cephalic and pygidial features are interpreted as intraspecific variation, some probably related to ontogeny. Some specimens are indistinguishable from the holotype and topotype specimens from Quebec, Canada, but the full range of variation extends through the morphological expression exemplified in most forms synonymized under *L. americanus* by Ludvigsen & Westrop (1989), Peng & Babcock (2005) and Rushton (2009), except for the highly effaced *L. obscurus* Palmer, 1955.

Cephalic scrobiculation. – Early holaspisids in the new collection from the lower Shenjiawan Formation either lack scrobiculation or have obscure scrobiculation on the genal fields (Figs 1A–C, 2A, B, H, I). Late holaspisids generally have moderate to strong scrobiculation (Figs 1E–G, 2C–F). One dorsal exoskeleton (Figs 1D, 2G with cephalon 3.9 mm long) and one late holaspisid cephalon (5.35 mm long) show weak scrobiculation (Fig. 2K–N). The 5.35-mm-long cephalon is almost identical with a topotype cephalon from the Lévis Formation (Westrop *et al.* 2011, fig. 5D–G). Cephalic scrobiculation in large exoskeletons (Figs 1E–G, 2C–F) is closely comparable in expression to that in a topotype cephalon from the Lévis Formation (Westrop *et al.* 2011, fig. 6E–G). The largest cephalon in

the new collection (Fig. 2J; 8.2 mm in length) shows strong genal scrobiculation.

Position of axial node on the glabella. – The glabellar node in early holaspisids lies subcentrally on M1 plus M2 lobes (Figs 1B, C, 2H, I) but moves forward in later holaspisids to a level close to the F2 furrow (Figs 1G–I, 2K). We have not observed any difference in this feature between the sclerites from Hunan and Quebec.

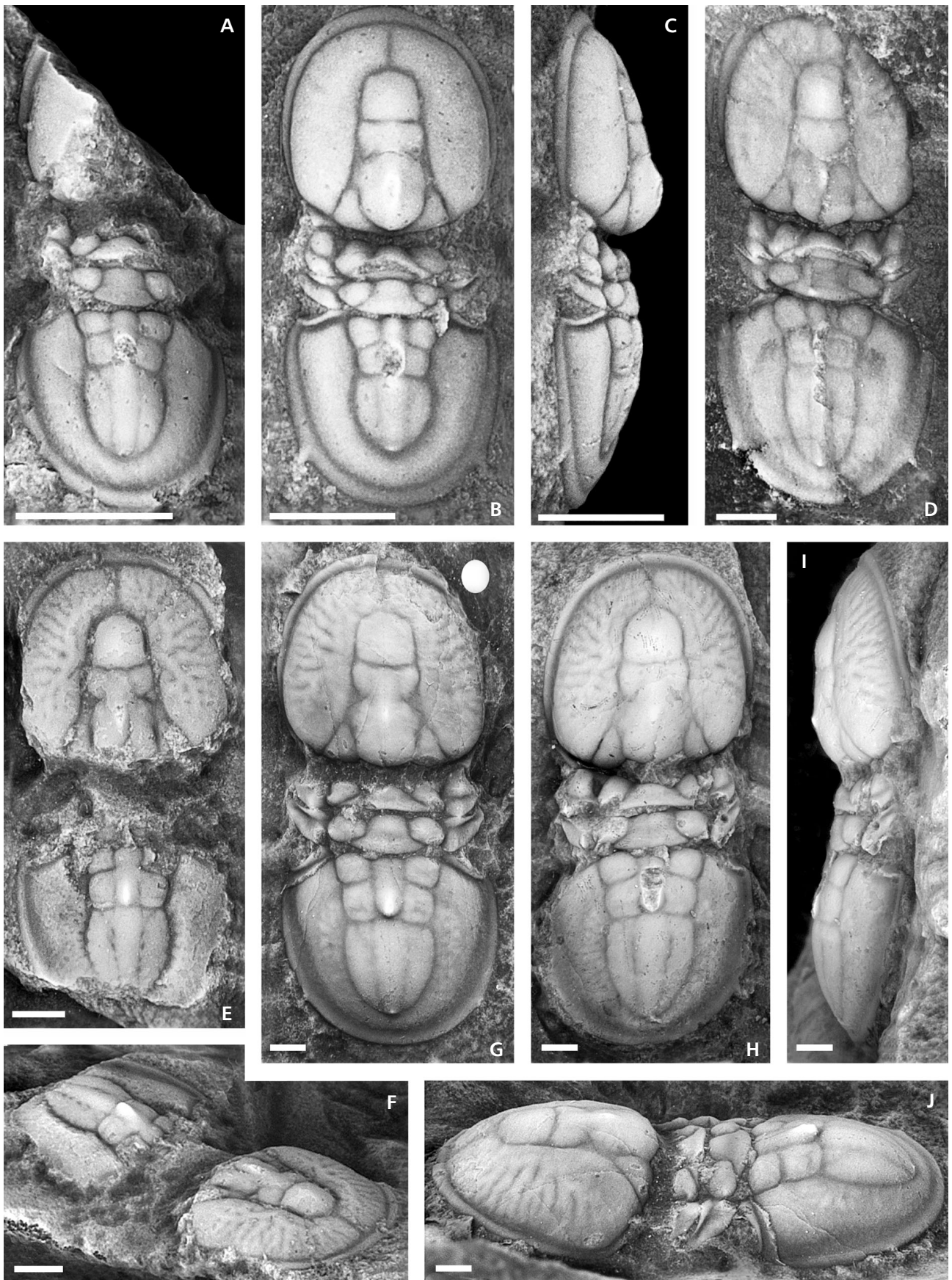
F3 lateral glabellar furrow. – The F3 furrow in early holaspisids is transverse (Fig. 1B) or gently curved backward (Fig. 1D, 2G–I). In late holaspisids, the F3 furrow is gently curved backward. There appears to be no difference in this feature between late holaspisids from Hunan and Quebec.

Basal lobes of the glabella. – Basal lobes on most specimens from northwestern Hunan are simple, subtriangular, and distinct. On a few sclerites (Figs 1E, 2H) the basal lobes look to be conterminous with the lateral portions of the M2 glabellar lobe, making it appear as if the basal lobes are elongated (see discussion below under the sections on *Lotagnostus punctatus* or *L. trisectus* as a junior synonym of *L. americanus*).

Measured lengths of the basal lobes of figured seven cephalon are 34.2% to 37.5% of the length of the posteroglabella. The ratios for the basal lobes of these seven sclerites are 0.342 (Fig. 1B), ~0.351 (Fig. 1E), 0.359 (Fig. 1G), 0.353 (Fig. 1H), 0.358 (Fig. 2G), 0.370 (Fig. 2H), and 0.375 (Fig. 2K). For one cephalon (Fig. 1E) the ratio is questionable; for another cephalon (Fig. 2J), no basal lobe is available to measure. The ratios, calculated from published illustrations of topotype cephalon from Quebec (Westrop *et al.* 2011, figs 5D, 6C, F, H), are 0.363 (fig. 5D), ~0.328 (fig. 6C), ?0.346 (fig. 6F), and ~0.349 (fig. 6H). Ratios derived from the topotypes fall within the range shown in the figured sclerites from western Hunan. However, the basal lobes are not as well preserved or exposed in the Canadian specimens, and we consider the ratio derived from only one cephalon (Westrop *et al.* 2011, fig. 5D) to be precise and reliable.

Median indentation of acrolobe at anterior tip of preglabellar median furrow. – The indentation is variably developed on cephalon from northwestern Hunan. It is more or less distinct on some cephalon (Figs 1B, E, F, 2E–G, J), but seems to be absent or at least obscure on other cephalon (Figs 1G, 2H, K). This feature is also variable on specimens from

Figure 1. *Lotagnostus americanus* (Billings, 1860) from the Shenjiawan Formation, Wa'ergang section, Taoyuan, northwestern Hunan, South China, showing morphologic variation related in part to ontogeny. All holaspisid exoskeletons; collecting levels in meters (m) above the base of the Huaqiao Formation are indicated. • A, B, D, E, G, H – dorsal views, from 695.53 m, 699.5 m, 696.63 m, 693.5 m, 697.12 m, 697.12 m, NIGP 159589–159594; D – latex cast of external mold of specimen in Fig. 2G; G – retrodeformation, showing inferred strain ellipse. • C, I, J – lateral views. • F – anterolateral view. All scale bars = 1 mm.



Quebec. It is distinct on three-topotype cephalon figured by Westrop *et al.* (2011, figs 5D, 6F, H), but seems to be absent on two other cephalon (Rushton 2009, fig. 1L; Westrop *et al.* 2011, fig. 6C).

Posteroaxial trisection of pygidium. – Each of the pygidia in the new collection from Hunan shows a tripartite posteroaxis. The medial portion of the posteroaxis (intranotular axis), however, shows wide variation in morphology. Normally in specimens from northwestern Hunan the trisection is typically faint on early holaspides (Figs 1A–C, 3B, 9I; Peng 1992, fig. 6L) and more distinct on late holaspides (Fig. 1E, H; Peng 1992, fig. 6B). However, some late holaspide pygidia in the new collection also show weak trisection (Figs 1G, H, 2D). The intranotular axis on the pygidia from the Shenjiawan Formation is convex and moderately elevated above the lateral portions of the trisection (the extranotulars). In some specimens the intranotular axis is effaced and the positions of the notular furrows are indicated only by slope changes. Notulae are variably developed within the notular furrows. They are absent (Figs 1A–D, 2B, G), obscure (Figs 1H–J, 3B–F), or relatively distinct (Figs 1E, F, 3A).

A convex intranotular axis is present in the holotype and in a topotype of *L. americanus* from Quebec, Canada (Westrop *et al.* 2011, figs 5A–C, 6A–D). The intranotular axis is more strongly convex on pygidia of *L. trisectus* from Nova Scotia, Canada (Hutchison 1952), which were reassigned as *L. cf. L. trisectus* by Westrop *et al.* (2011, figs 2, 3). As discussed below, *L. trisectus* should be regarded as a junior synonym of *L. americanus*. Notulae are also variably developed on the material from Quebec. They are obscure in the holotype pygidium (Westrop *et al.* 2011, fig. 5A–C) and absent in other specimens (Westrop *et al.* 2011, fig. 6A).

Scrobiculation of the pygidium. – Among specimens in the new collection from Hunan, scrobiculation in the pleural field of the pygidium varies from absent to distinct. Commonly, the scrobiculation (if present) is weakly defined (Figs 1G–J, 3D–F), but some pygidia show clear, distinct scrobiculation. The scrobicular arrangement normally consists of short, bar-like furrows arrayed radially around the posteroaxial furrow plus densely scattered pits on the pleural field (Fig. 1E, F; Peng 1992, fig. 6E, G). Scrobiculae, if present, are observed to have the same pattern and variability in the pygidia from Quebec, which Westrop *et al.* (2011, p. 580) described as “smooth to weakly scrobicu-

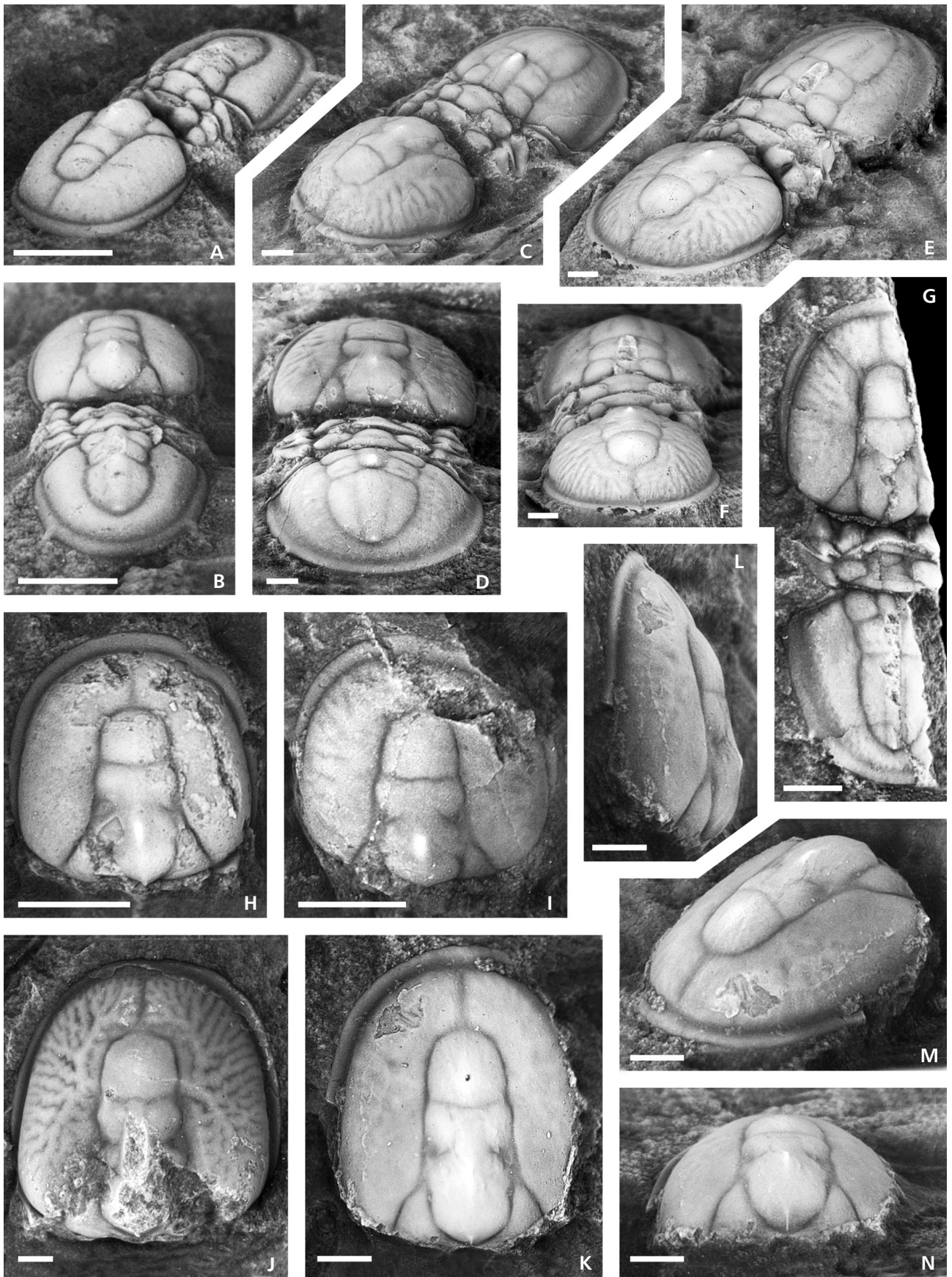
late”. The radial bar-like furrows and densely scattered pits are present on the holotype pygidium of *L. americanus* (Westrop *et al.* 2011, fig. 5A–C).

Other characters expressed in the illustrated specimens from Quebec and the new specimens from Hunan were compared. Overall, there appear to be no consistent differences in the proportional length of the axis in either the glabella or the pygidium. The proportional lengths of the anteroglabella, the posteroglabella, the anteroaxis, and the posteroaxis (with M1 and M2) are similar in specimens from northwestern Hunan and Quebec. Likewise, there appear to be no consistent differences in the expression and orientation of the F2 glabellar furrows, the F1 and F2 pygidial axial furrows, expression of the preglabellar furrow, and the terminal nodes on the posteroglabella and pygidial posteroaxis. There can be little doubt that the new material from Hunan is conspecific with *L. americanus* because it all shows features used in the diagnosis of *L. americanus* by Westrop *et al.* (2011) or, when variability is present, similar variability is evident in the material from Quebec that is assigned to the species.

Following restudy of *L. americanus* material illustrated by Billings (1860, figs 1a, b) and illustrated or mentioned by Rasetti (1944, pl. 36, figs 1, 2; see Westrop *et al.* 2011, figs 5D–F, 6A–D), Westrop *et al.* (2011, p. 578) provided a new, and very restricted, diagnosis of *L. americanus*. That diagnosis is: “*Lotagnostus* with weakly scrobiculate cephalon partly effaced externally but with weakly convex glabella well defined on internal mould; short basal glabellar lobes terminate well short of level of axial node. Distinct median indentation of acrolobe at anterior tip of preglabellar median furrow. Pygidial acrolobe gently constricted. F1 furrows not connected across axis. Posteroaxis long; trisection weakly developed, with intranotular axis recognizable primarily by change in slope medially, and may be absent altogether in small individuals.”

Variation in cephalic scrobiculation exists on cephalon of *L. americanus* from Quebec (Westrop *et al.* 2011, figs 5D–G, 6). Scrobiculation varies in expression from weak to moderately expressed. Westrop *et al.* (2011, p. 578) mentioned the presence of faint scrobiculation on the topotype cephalon but did not provide a description of the range of variation in this character among the topotypes. From published photographs (Rasetti 1944, pl. 36, fig. 1; Westrop *et al.* 2011, fig. 6F), moderately developed scrobiculation, comparable to that on some specimens

Figure 2. *Lotagnostus americanus* (Billings, 1860) from the Shenjiawan Formation, Wa’ergang section, Taoyuan, northwestern Hunan, South China, showing morphologic variation related in part to ontogeny; collecting levels in meters (m) above the base of the Huaqiao Formation are indicated. • A, C, E (= Fig. 1B, G, H respectively) – holaspide exoskeletons, anterolateral view. • B, D, F (= Fig. 1A, C, E respectively) – posterior, posterior and anterior views. • G (= Fig. 1D) – incomplete exoskeleton in dorsal view. • H – cephalon in dorsal view, 696.63 m, NIGP 159595. • I – cephalon, dorsal view, 695.55 m, NIGP 159596. • J – cephalon, dorsal view, 692.2 m, NIGP 159597. • K–N – cephalon in dorsal, lateral, anterolateral, and posterior views, 689.9 m, NIGP 159598. All scale bars = 1 mm.



from northwestern Hunan, is present on a topotype cephalon.

Landing *et al.* (2010, p. 18) argued that a topotype cephalon of *L. americanus* illustrated by Rasetti (1944) should be excluded from the species, stating that “there is no evidence that effaced and furrowed cephalon co-occur or intergraded, or that the cephalon figured by Rasetti (1944) and Billings’ paratype cephalon are conspecific.” In addition, the same authors stated that “there are insufficient data to revise *L. americanus*, and even the correct sclerite association are essentially nonexistent” (Landing *et al.* 2010, p. 18). These statements are incorrect. Specimens refigured by Westrop *et al.* (2011) provide confirmation that the topotype cephalon figured by Rasetti (1944) and Billings’s (1860) topotype (“paratype cephalon”) fall within the range of variation of *L. americanus*, and indicate that they are conspecific with the species. The specimens refigured by Westrop *et al.* (2011) also tend to confirm that the sclerite association made by Rasetti (1944) is correct.

Landing *et al.* (2010, p. 18) assigned *Lotagnostus* sclerites from the Rabbitkettle Formation, northern Canada (illustrated by Westrop 1995, figs 17–20) to *L. obscurus*, but this assignment was not followed by Westrop *et al.* (2011). The more recent images of a cephalon first illustrated by Rasetti (1944, pl. 36, fig. 1) show that *L. americanus* includes not only gently effaced but also distinctly scrobiculate or “furrowed” cephalon (Westrop *et al.* 2011, fig. 6E–G). Westrop *et al.* (2011) explained that scrobiculation evident on Rasetti’s (1944) photo was exaggerated by “harsh lighting”, but the explanation seems farfetched.

Westrop *et al.* (2011, fig. 5D–F) figured an exfoliated cephalon of *L. americanus* with faint furrows on the genal field to show the faint scrobiculation in the species. This cephalon is almost completely identical in size, in scrobiculation and furrowing, and in the shape of the terminal node, with a testate cephalon illustrated here (Fig. 2K–N) from northwestern Hunan.

Comparison of *Lotagnostus asiaticus* with *L. americanus*

Peng & Babcock (2005) synonymized a number of specific or subspecific taxa as junior synonyms of *Lotagnostus americanus* (Billings, 1860), including *L. asiaticus* Troedsson, 1937. Later, Westrop *et al.* (2011, pp. 570, 577, 580) excluded *L. asiaticus* from the synonymy using a restricted concept of *L. americanus*. *L. asiaticus* has been shown to vary in the cephalic scrobiculation from smooth to well furrowed (Troedsson 1937, pl. 1, figs 10–16; Lu & Lin 1989, pl. 6, fig. 13, pl. 7, figs 1–3). However, Westrop *et al.* (2011, p. 582) indicated that *L. asiaticus* was differentiated by having a “greater development of the trisection of the posteroaxis, which includes deeper notular furrows that, in

the latter, are augmented by conspicuous notulae”. They did not discuss any further differences between the concepts of *L. asiaticus* and *L. americanus* except for citing the discussion of Ludvigsen & Westrop (1989, p. 12), who stated that *L. americanus* is differentiated by “possessing much shorter basal glabellar lobes”. Landing *et al.* (2011, p. 624) also cited longer basal lobes in *L. asiaticus*.

The type material of *Lotagnostus asiaticus* Troedsson, 1937 shows intergradation spanning nearly the full range of character states for the species concepts of *L. americanus* and *L. asiaticus*. The species concepts overlap considerably, and any perceived “differences” between *L. americanus* and *L. asiaticus* seem to be related primarily to intraspecific variation. Troedsson (1937, pp. 25–29) described a large collection of dorsal exoskeletons, cephalon, and pygidia of *L. asiaticus* from the Torsuqtag Formation at a single locality, Charchaq Ridge (loc. 22), Kuruktag (Quruq tagh), Xinjiang, China. His type material is part of his “great many specimens” now housed in the Nanjing Institute of Geology and Palaeontology. The type specimens show wide variation in cephalic and pygidial scrobiculation and in the expression of the trisection of the posteroaxis in the species. All available figured specimens of Troedsson (1937) have been rephotographed and are refigured here except for his specimens in figs 13 and 14, which seem to be lost.

The holotype of *L. asiaticus* is a dorsal exoskeleton (Troedsson 1937, pl. 1, figs 10a, b; Zhao 1963, pl. 5, figs 3, 4; Lu *et al.* 1965, pl. 3, figs 4, 5; Peng & Babcock 2005, fig. 2.12; here Figs 4, 5A–F) with the cephalon rotated clockwise because it is compressed over a larger cephalon of the same species. As noted by Troedsson (1937), the holotype “is unweathered and has been prepared out of the rock by needle.” Examination of the holotype shows that most of it was prepared free from rock. Some areas of the cephalon including the left genal area and areas raised above the main bedding surface of the slab, where the scrobiculation becomes faint, appear to have been exposed to weathering. Most of the cephalon is exfoliated, but the right genal area is testaceous and shows faint scrobiculation. The thorax and pygidium are testaceous and were prepared out from the slab. The cephalon of the holotype is 5.90 mm long (and the entire exoskeleton is 13.98 mm long), nearly the same size as a topotype cephalon of *L. americanus* (Westrop *et al.* 2011, fig. 6F), which is calculated to be 5.78 mm long. The cephalon beneath the holotype is not fully prepared out of matrix but is clearly larger in size. It has an estimated length of nearly 9 mm, which is much larger than the 6.88 mm length calculated for the holotype pygidium of *L. americanus* (Westrop *et al.* 2011, fig. 5A).

For comparison, the holotype exoskeleton of *L. asiaticus*, the holotype pygidium of *L. americanus*, and a topotype cephalon of *L. americanus* are illustrated in Fig. 5. We

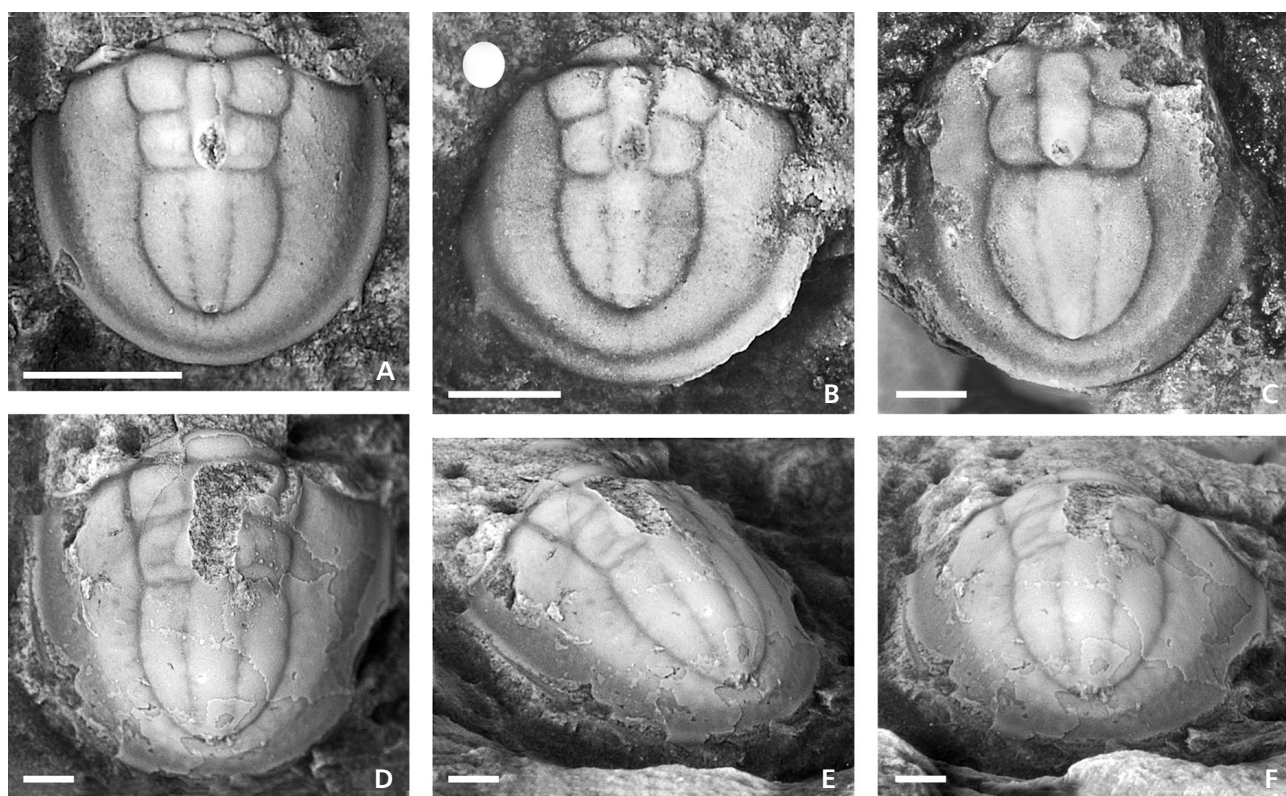


Figure 3. *Lotagnostus americanus* (Billings, 1860) from the Shenjiawan Formation, Wa'ergang section, Taoyuan, northwestern Hunan, South China, showing morphologic variation related in part to ontogeny. All holaspide pygidia; collecting levels in meters (m) above the base of the Huaqiao Formation are indicated. • A–C – dorsal views, 696.63 m, 695.55 m, 692.2 m, NIGP 159599–159601; B – latex cast, retrodeformation showing inferred strain ellipse. • D–F – dorsal, posterolateral, and posterior views, 696.63 m, NIGP 159602. All scale bars = 1 mm.

cannot find any significant difference between the type specimens from China and Canada. The reasons used by Westrop *et al.* (2011) and Ludvigsen & Westrop (1989) to differentiate *L. asiaticus* from *L. americanus* are not supported by these specimens.

Trisection of posteroaxis. – Ludvigsen & Westrop (1989, p. 12) noted that the pygidia of *L. asiaticus* and *L. americanus* were indistinguishable, but Westrop *et al.* (2011) stated that the pygidium of *L. asiaticus* has better developed trisection of the posteroaxis. Restudy of the original material of Troedsson (1937) has verified the conclusion of Ludvigsen & Westrop (1989). On the holotype of *L. asiaticus* (Fig. 5A–C, E), trisection on the posteroaxis is almost identical in convexity with that of the holotype pygidium of *L. americanus* (Westrop *et al.* 2011, fig. 5A–C; here Fig. 5H–J, reproduced from Westrop *et al.* 2011). The new image of the holotype of *L. asiaticus* (Fig. 5A–E) suggests that Troedsson's (1937) figures were retouched, making the notular furrows more conspicuous. The notular furrows on the holotype of *L. asiaticus* look slightly darker in our photographs, but this is an artifact of the photographic technique, as the specimen was blackened with ink and then coated with white magnesium oxide. As shown in

photos published by Zhao (1963, pl. 5, figs 3, 4) and Lu *et al.* (1965, pl. 1, figs 4, 5), which were made without blackening, the notular furrows on the holotype of *L. asiaticus* appear “shallower” than those on the holotype of *L. americanus*.

On the pygidium of the holotype of *L. asiaticus*, the notulae of the notular furrows are obscure (at best), or may be absent. The notulae were not reported from the holotype pygidium of *L. americanus*, but images published by Ludvigsen & Westrop (1989, pl. 1, fig. 15) and Westrop *et al.* (2011, fig. 5A, here Fig. 5H) indicate that they are equally obscure.

The extent to which trisection is defined in the type series of *L. asiaticus* varies widely from faint to well-defined with rather distinct notular furrows (Fig. 6). On a paratype (Troedsson 1937, pl. 1, fig. 17; here Fig. 6B–D), which is nearly the same size as the holotype (Fig. 5A–F), trisection is obscure or faint and the notular furrows are extremely faint. Trisection is well defined on some other paratype pygidia (Fig. 6G–I), however, and in these examples, the notulae are also better developed.

We were unable to gain access to the holotype pygidium of *L. americanus* for a direct comparison between it and the specimens from Hunan because the holotype was

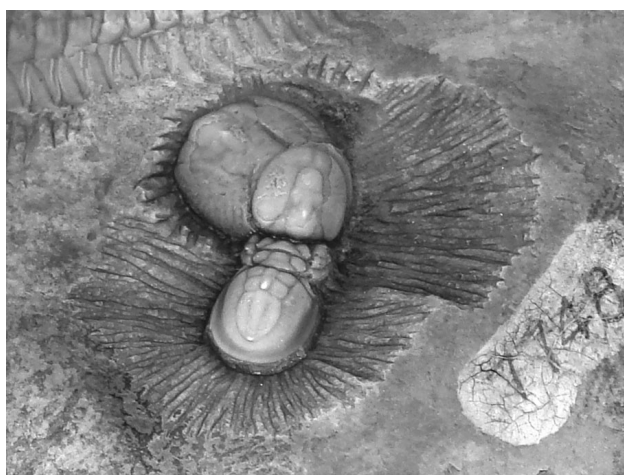


Figure 4. *Lotagnostus americanus* (Billings, 1860). Original slab bearing holotype exoskeleton of *L. asiaticus* of Troedsson (1937, pl. 1, figs 10a, b; NIGP 7748), and a cephalon of *L. americanus* beneath the holotype, showing the preservation and the preparation state for this specimen. In the left upper of the image is a portion of the nearly complete holotype exoskeleton of *Westergaardites pelturaeformis* Troedsson, 1937 (see Troedsson 1937, pl. 8, fig. 1).

on loan and unreturned. Certainly the expression of trisection on the holotype of *L. americanus* falls within the range expressed in the type series of *L. asiaticus*. Even if there is a minor difference in the expression of trisection between the holotypes of *L. americanus* and *L. asiaticus*, there is little justification for regarding it as a species-level diagnostic feature.

Length of basal lobe. – Ludvigsen & Westrop (1989, p. 12) differentiated both *L. asiaticus* and *L. punctatus* from *L. americanus* on the basis of a longer basal glabellar lobe. There is no basis for that conclusion. Measurements show that the length of the basal lobe in *L. asiaticus* is almost identical with that of *L. americanus*. The basal lobe on the holotype of *L. asiaticus*, which is well preserved (Fig. 5B, C), occupies 36.1% of the length of the posteroglabella. Expressed as a ratio, the basal lobe length to posteroglabellar length (BLL : PGL) ratio of this specimen is 0.361. The BLL : PGL ratio on a paratype exoskeleton of *L. asiaticus* (Fig. 6B) is 0.367, and the ratio on a paratype cephalon (Fig. 6F) is 0.362. As discussed above, the ratios for the topotype cephalon of *L. americanus* are 0.363, ~0.328, ?0.346,

and ~0.349 (based on Westrop *et al.* 2011, figs 5D, 6C, F, H respectively). Although the lengths of the basal lobes in the material from the Lévis Formation of Quebec appear to be variable, the most reliable ratio obtained from any of these specimens is that of the topotype, 0.363, which is nearly identical with the 0.361 value obtained from the holotype of *L. asiaticus*.

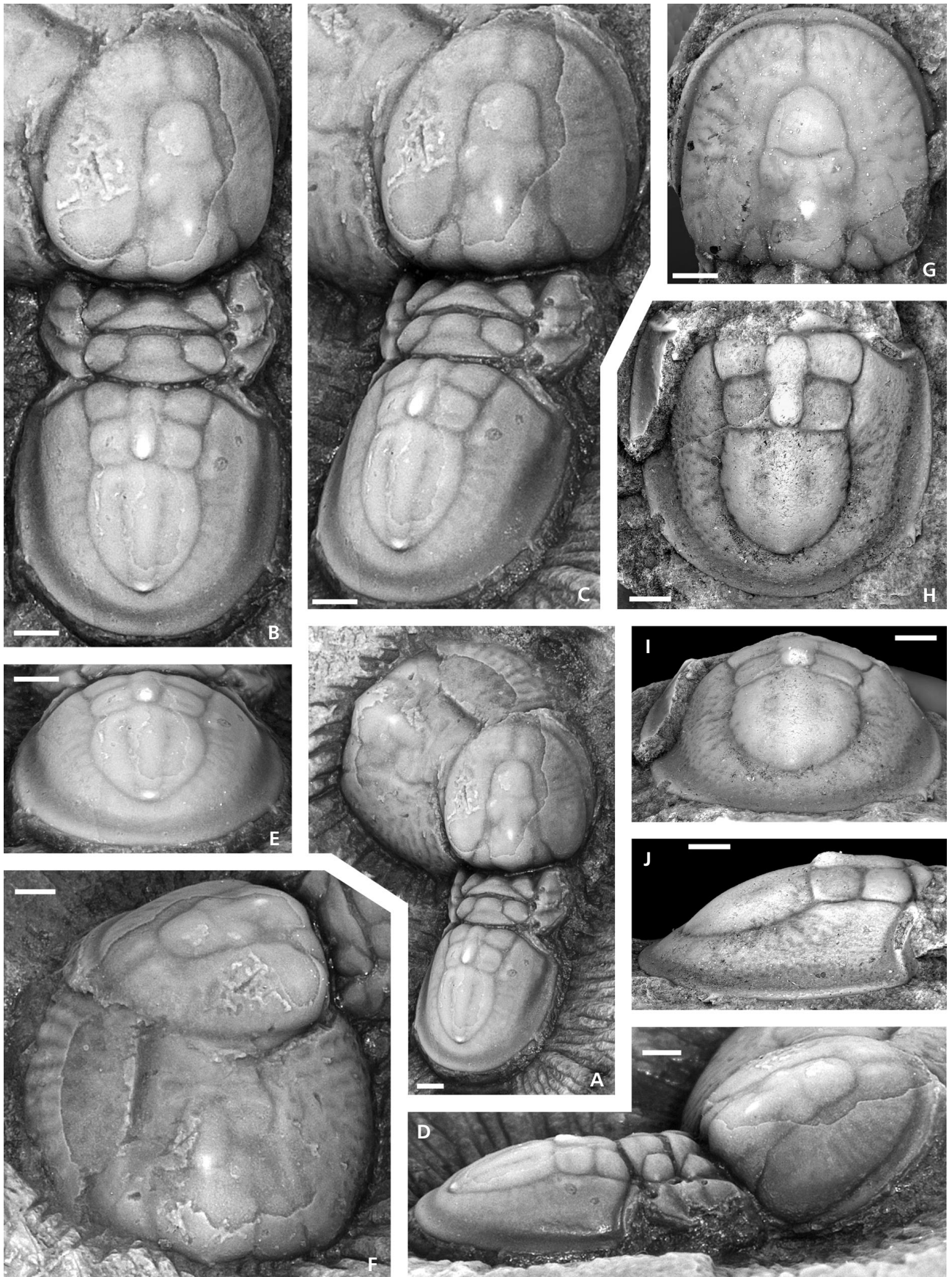
Some illustrated specimens assigned to either *L. asiaticus* or *L. punctatus* do have slightly longer basal glabellar lobes, but they are not much beyond the range inferred for the illustrated specimens of *L. americanus* from Quebec. A cephalon assigned to *L. asiaticus* by Lu & Lin (1980, pl. 1, fig. 6; here Fig. 7F), has a BLL : PGL ratio of 0.378. In two dorsal exoskeletons preserved in shale, the holotype of *L. punctatus* (Lu 1964, pl. 5, fig. 5; here Fig. 9B), and another specimen illustrated by Lu & Lin (1980, pl. 1, fig. 5), the basal lobes appear to be elongated more than they are because the narrow (tr.) lateral portions of the M2 glabellar lobe almost look to be incorporated in the basal lobes, giving the illusion that the basal lobes are more than half the length of the posteroaxis (see discussion below under *L. punctatus* and *L. trisectus*). The BLL : PGL ratio for the holotype of *L. punctatus* (Lu 1964, pl. 5, fig. 5) is 0.357, and for the specimen illustrated by Lu & Lin (1980, pl. 1, fig. 5), the ratio is 0.375. Both values are close to the BLL : PGL ratio obtained from the topotype cephalon of *L. americanus*.

Scrobiculation. – In addition to the expression of trisection on the posteroaxis and the length of the basal lobe, Westrop *et al.* (2011) also used the expression of genal and pygidial scrobiculation as a species-level character state for *Lotagnostus*. Excluded from their concept of *L. americanus* were “strongly furrowed” *Lotagnostus* sclerites, such as the types of *L. asiaticus* and *L. punctatus* from China, *L. trisectus* (as assigned by Westergård 1922) from Sweden, and *L. trisectus* (as assigned by Pegel 2000) from Siberia.

The extent of scrobiculation varies among specimens in collections of *Lotagnostus*. Scrobiculation ranges from smooth and effaced to deeply scrobiculate. Also, in individual dorsal exoskeletons, the expression of scrobiculation normally varies between the cephalon and pygidium, as it does in the type material of *L. asiaticus*.

Westrop *et al.* (2011) were inconsistent in their determinations of scrobiculation. As illustrated in Fig. 5A–C,

Figure 5. *Lotagnostus americanus* (Billings, 1860). Comparison of holotype exoskeleton of *L. asiaticus* Troedsson, 1937 with the holotype pygidium and a topotype cephalon of *L. americanus* (Billings, 1860). • A–E – holotype exoskeleton of *L. asiaticus* Troedsson, 1937 (pl. 1, figs 10a, b); dorsal, dorsal, dorsal, lateral, and posterior views, NIGP 7748, from the Torsuqtag Formation, Quruq tagh, Xinjiang, China. Specimen overlies a topotype cephalon (F, NIGP 7757 newly assigned) that was not illustrated by Troedsson (1937). • G–J – from the Lévis Formation, North Ridge, Lévis, Quebec, Canada, topotype cephalon (G), dorsal view, GSC134620 (previously illustrated by Rasetti 1944, pl. 36, fig. 1 and by Westrop *et al.* 2011, fig. 6E–G); and holotype pygidium by monotype (H–J), dorsal, posterior, and lateral views, GSC 859; original of Billings (1860, fig. 1a), Ludvigsen & Westrop (1989, pl. 1, fig. 15), and Westrop *et al.* (2011, fig. 5A–C). All scale bars = 1 mm.



scrobiculation on the cephalon of the holotype of *L. asiaticus* is shallower, not more deeply incised, than on the topotype of *L. americanus* (Westrop *et al.* 2011, fig. 6F; here Fig. 5G). Also, pygidial scrobiculation on the holotype exoskeleton of *L. asiaticus* appears to be fainter than on the holotype of *L. americanus*. The holotypes of both species bear short bar-like radial furrows around the posteroaxis and densely scattered pits on the pleural field. Scrobiculation on the holotype of *L. asiaticus* is similar to that on the topotype of *L. americanus* (Westrop *et al.* 2011, fig. 6C). Overall, specimens originally assigned to *L. asiaticus* from Xinjiang, China, do not differ significantly from specimens of *L. americanus* from Quebec in the expression of genal and pleural scrobiculation.

Troedsson (1937) stated that deeper furrowing in *L. asiaticus* material from Xinjiang was the result of weathering, but we regard it as the result of intraspecific variation. Collections from limestone in South China, and assigned to either *L. asiaticus* or *L. punctatus*, include a number of unweathered sclerites that bear strong scrobiculation (Lu & Lin 1989, pl. 6, fig. 9, pl. 7, fig. 1; Peng 1984, fig. 1, 1992, fig. 6B, E, G; here Fig. 2J). Similarly, some unweathered sclerites from Siberia (Lazarenko *et al.* 2008a, b; 2011; here Fig. 9B–E) and Sweden (Ahlberg & Terfelt 2012) also show strong scrobiculation.

Conclusion. – Comparisons between the holotype of *L. asiaticus* and the holotype pygidium and topotype cephalon of *L. americanus* (Fig. 5) show that these species are almost indistinguishable. Both are essentially identical in terms of their weakly scrobiculate genal field on the cephalon, lengths of the basal lobes, shapes of the glabellar furrows, positions of the glabellar nodes, proportional lengths of the pygidial axes, inflation of the intranotular axis, tripartite M1 and M2 of the pygidia with the middle portion merged, and in having both a distinct axial node at the end of M2 and a prominent terminal node at the end of axis. The only notable difference is in the transglabellar furrow (F3) of the holotype of *L. asiaticus*: it is nearly transverse, rather than gently curved backward as it is on the topotype cephalon of *L. americanus*. This feature, however, is variable in the type suite of *L. asiaticus*, and backward curvature is present in some cephalon (Troedsson 1937, pl. 1, fig. 14; Lu & Lin 1989, pl. 7, fig. 1). In our opinion, *L. asiaticus* should be regarded as a junior subjective synonym of *L. americanus*.

Variation in cephalic scrobiculation of *L. americanus*

Landing *et al.* (2010, p. 18) stated: “There is no evidence that effaced and furrowed cephalon co-occur or intergrade”. This statement contradicts the information published by a variety of previous authors, and contradicts the evidence from collections of *Lotagnostus* made from numerous localities.

The type suite of *L. asiaticus* (Troedsson 1937, explanation of pl. 1) includes weakly and distinctly scrobiculate (or “furrowed”) cephalon (Fig. 6A–F, I). According to Troedsson (1937), “it was impossible to keep those variant forms separated”. These specimens are from a single locality, but whether they were collected from a single bed is uncertain.

Specimens assigned to *L. asiaticus* by Lu & Lin (1980, pl. 1, figs 6, 7, 1989, pl. 6, fig. 13, pl. 7, figs 1–3; here Fig. 7) are from a single bed (collecting level GC26a) in the middle part of Bed 14 of the Siyanshan Formation, Siyanshan section, Changshan, Zhejiang, China. Together, the specimens display a wide range of intraspecific morphologic variation in cephalic and pygidial scrobiculation. They clearly show that effaced and “furrowed” forms do co-occur and intergrade. Included in the collection are specimens having smooth genal fields and pygidial pleural fields (Fig. 7A, B), faint cephalic and pygidial scrobiculation (Fig. 7C–E), well-incised cephalon (Fig. 7F–G), and weakly incised pygidia (Fig. 7H–J).

Specimens of *L. americanus* from the Khos-Nelege River section, Siberia, Russia (Fig. 8), show considerable variation in cephalic scrobiculation from weak to strong and show intergradation of scrobiculation. *L. americanus* has a reported stratigraphic range of about 100 m in the section, extending from Bed 47 through Bed 53 of the Ogon’or Formation (Lazarenko *et al.* 2008a, b, 2011), and, in general, specimens show stronger scrobiculation up-section. The cephalon illustrated here were collected from between 322 m and 398 m above the base of the Ogon’or Formation. The largely effaced cephalon (Fig. 8A) and the moderately scrobiculate fragmental cephalon (Fig. 8B) are from Bed 47 at levels 335.6 m and 339 m above the base of the formation, respectively. The other three cephalon (Fig. 8C–E), all of which exhibit greater scrobiculation, are from higher stratigraphic positions. The specimen illustrated in Fig. 8C is from Bed 48 at a level of 357.6 m. The specimens in

Figure 6. *Lotagnostus americanus* (Billings, 1860) from the Torsuqtug Formation, Quruq tagh, Xinjiang, China. • A – original slab of Troedsson (1937), showing some paratypes and how they are preserved; small capital letters indicate designations in this composite figure. • B–D – paratype of *L. asiaticus*, dorsal exoskeleton, NIGP 7749, dorsal, lateral, posterior views; original of Troedsson (1937, pl. 1, fig. 11). • E – cephalon, dorsal view, NIGP 159603 (previously unfigured specimen, number newly assigned). • F – paratype cephalon of *L. asiaticus*, dorsal view, NIGP 7753; original of Troedsson (1937, pl. 1, fig. 15). • G, H – paratype pygidium of *L. asiaticus*, dorsal, posterolateral views, NIGP 7754; original of Troedsson (1937, pl. 1, fig. 16). • I – paratype of *L. asiaticus*, exoskeleton, dorsal view, NIGP 7750; original of Troedsson (1937, pl. 1, fig. 12). All scale bars = 1 mm.

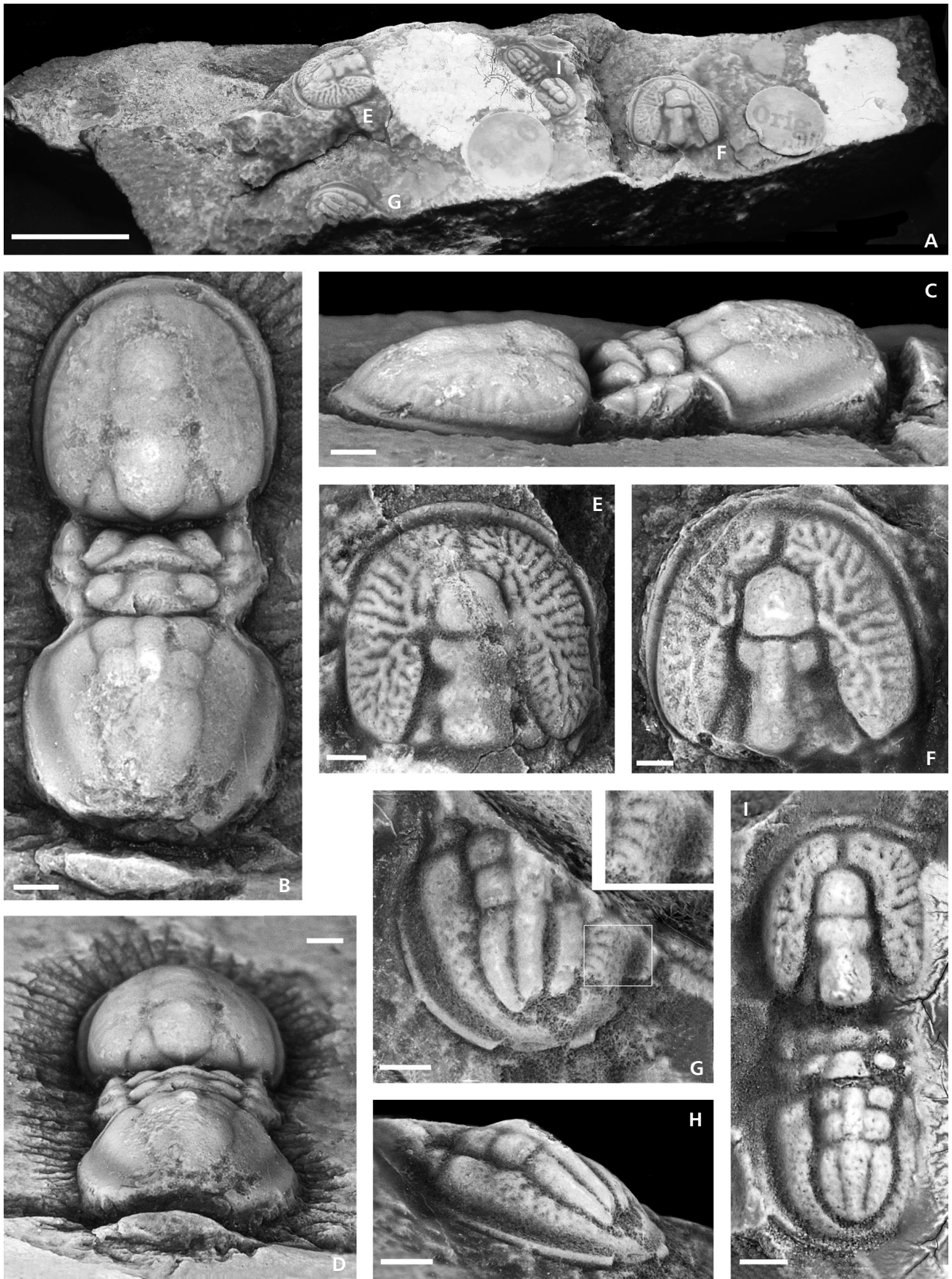


Fig. 8D and E are from Bed 51 at levels of 397.5 m and 398 m respectively.

The microevolutionary pattern shown in the cephalic scrobiculation of holaspid *L. americanus* from Siberia follows the same trend (effaced to increasingly scrobiculate) as the ontogenetic pattern shown in new material of the species from northwestern Hunan.

Comparison of *Lotagnostus punctatus* with *L. americanus*

Westrop *et al.* (2011, pp. 570, 577, 580) advocated the use of a restricted concept of *L. americanus*, and in so doing, excluded *L. punctatus* as a junior synonym. These authors used the same criteria to differentiate *L. punctatus* from *L. americanus* as they used to differentiate *L. asiaticus* from *L. americanus*: “greater development of trisection on posteroaxis” and longer basal glabellar lobes. They stated that *L. punctatus* has even more distinct trisection than *L. asiaticus*.

Similar to the type suite of *L. asiaticus*, specimens assigned to *L. punctatus* vary greatly in the expression of notular furrows and in the development of trisection on the posteroaxis. Illustrated pygidia assigned to *L. punctatus* by Lu & Lin (1984, pl. 3, figs 9–11) and Peng & Babcock (2005, figs 2.22, 2.23), and the pygidium of a dorsal exoskeleton figured by Lu & Lin (1989, pl. 6, fig 12; here Fig. 9C), all collected from shale, either have faint or weak notular furrows, shallow but distinct notular furrows, obscure notulae, or they lack notulae altogether. This variation results in variable convexity of the intranotular portion of the trisection (Fig. 9I–M). The statement of Westrop *et al.* (2011) on the expression of trisection in *L. punctatus* seems to be based primarily on the holotype exoskeleton (Fig. 9B), in which trisection is defined by incised notular furrows. However, even among specimens preserved in shale, the strength of the notular furrows varies greatly.

There are no consistent differences between *L. punctatus* and *L. asiaticus*. The paratypes of *L. asiaticus* (Fig. 6G–I) and specimens of *L. punctatus* show similar deep notular furrows on the posteroaxis and similar pitted scrobiculation on the pleural fields of the pygidium. Also there are no consistent differences between *L. punctatus* and *L. americanus*, including in the expression of trisection on the posteroaxis. The pygidium of a young holaspid exoskeleton assigned to *L. punctatus* by Lu & Lin (1984, pl. 3, fig. 11) closely resembles the holotype pygidium of *L. americanus* in the nature of trisection, including the presence of obscure notular furrows. The cephalon of this specimen has genal scrobiculation closely similar to a topotype cephalon of *L. americanus* (Westrop *et al.* 2011, fig. 6F).

The holotype of *L. punctatus* (Lu 1964, pl. 5, fig. 5; Lu *et al.* 1965, pl. 4, fig. 8, 1974, pl. 1, fig. 1; here Fig. 9B) appears to have a long basal lobe, which was considered to be a key feature used to differentiate the species from *L. americanus* by Ludvigsen & Westrop (1989), Westrop *et al.* (2011) and Landing *et al.* (2011). The holotype is a flattened dorsal exoskeleton preserved in shale, and the elongate appearance of the basal lobe resolves to be a taphonomic effect. Specimens compressed in shale commonly, although not always, show incorporation of the narrow (tr.) lateral portion of the M2 glabellar lobe (Figs 9–11, lp) and the true basal lobe (Figs 9–11, b). A specimen illustrated by Lu & Lin (1989, pl. 6, fig. 12; here Fig. 9C) does not show this pattern. However, some specimens display the pattern on both basal lobes (Lu & Lin 1989, pl. 6, fig. 11) or on one basal lobe (Lu 1964, pl. 5, fig. 5; here Fig. 9B, left basal lobe, Fig. 9C, left basal lobe) and not the other. Well-preserved, inflated specimens of *L. punctatus* preserved in limestone (*e.g.*, Peng 1984, pl. 1, fig. 1; here Fig. 9A; Lu & Lin 1984, pl. 3, fig. 8; here Fig. 9D, E, 1989, pl. 6, fig. 8; here Fig. 9H) reveal greater distinction between the M2 glabellar lobe and the basal lobe and rarely show an “elongated” basal lobe. The lateral portion of M2 is clearly separated from the true basal lobe by a short, transverse furrow and from the M2 lobe (main part) by a longitudinal (exsag.) furrow (see also discussion of *L. trisectus*, below). This longitudinal furrow is evidently not the anterior part of the basal furrow, although the two may appear to be connected, because it is less incised than the basal furrow (see Fig. 9A). It is noteworthy that Shergold *et al.* (1990, p. 34) and Shergold & Laurie (1997, p. 341) recognized incorporation of the narrow (tr.) portion of the M2 glabellar lobe and the basal lobe in their revised diagnosis of *Lotagnostus*.

Analogous examples in which the lateral portion of the M2 lobe has become at least partly isolated from the main part of the M2 lobe by a longitudinal furrow include specimens of *Glyptagnostus reticulatus* (Shergold *et al.* 1990, fig. 10.2a), *Agnostus inexpectans* (Shergold & Laurie 1997, fig. 217.6a; Peng & Robison 2000, figs 7.1–7.3, 7.8), and *Agnostotes orientalis* (Choi *et al.* 2004, fig. 10.1–10.4; here Fig. 11A–D). In some specimens of *Agnostus inexpectans*, *Glyptagnostus stolidotus*, and *G. reticulatus* (Peng & Robison 2000, figs 7, 71, 72), the lateral portion of the M2 lobe is completely isolated. When the lateral portion of the M2 lobe is incorporated with the true basal lobe, the two parts are still distinguishable and the feature does not constitute a new structure. This seems to contrast with the pattern observed in *Ptychagnostus*, which has either an entire or a divided basal lobe that does not incorporate with M2 (see Öpik 1979, figs 27–29; Robison 1982, text-fig. 2, pl. 1, figs 1, 2, pl. 2, fig. 13).

The example of “elongate” basal lobes in cephalo of *Agnostotes orientalis* (Kobayashi, 1935) from the Machari

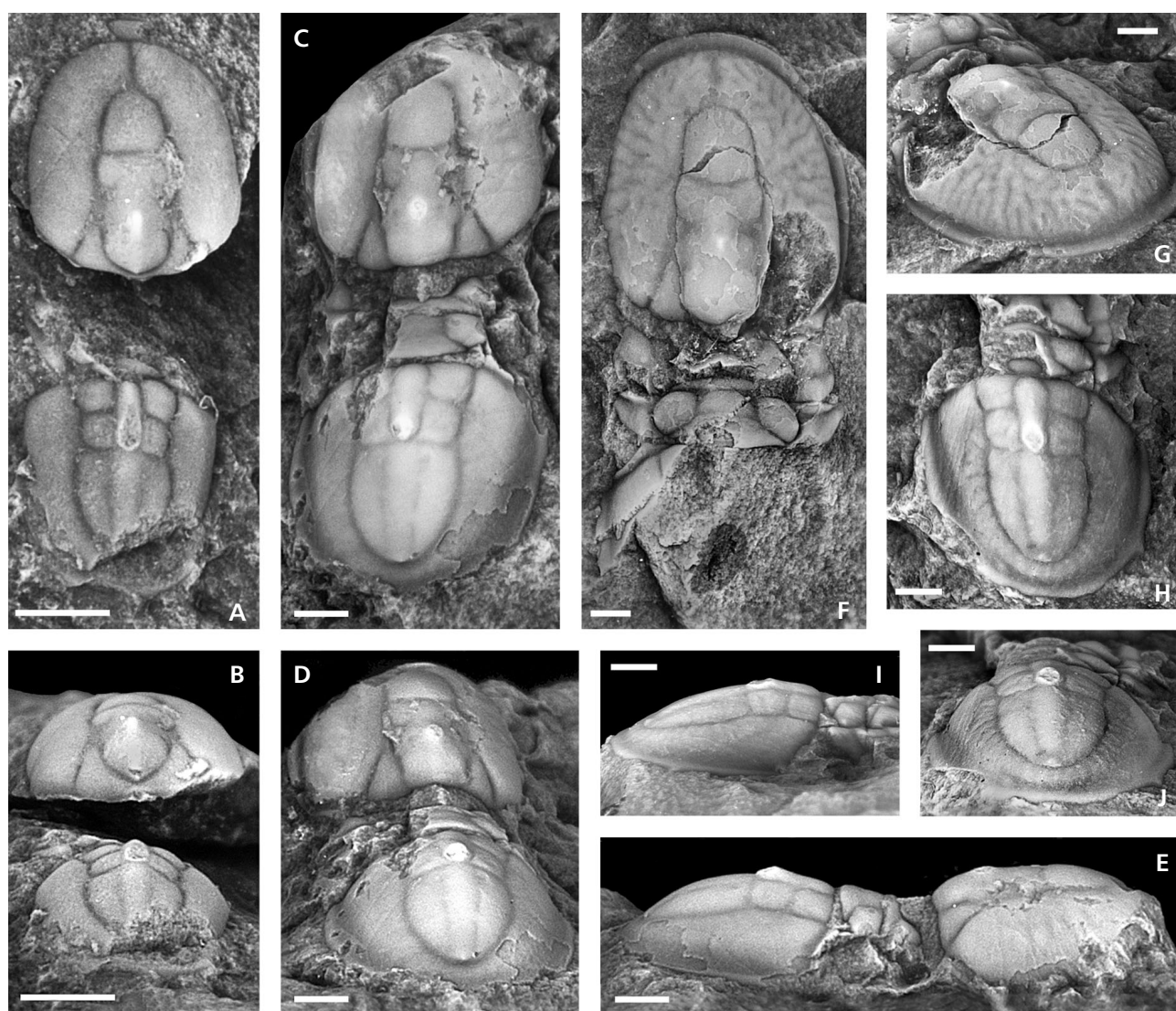


Figure 7. *Lotagnostus americanus* (Billings, 1860) from Siyanshan Formation, collecting level GC26a, Siyanshan section, Changshan, Zhejiang, China, previously assigned by Lu & Lin (1980, 1989) to *L. asiaticus* Troedsson, 1937, showing the co-occurrence of weakly and well furrowed cephalo of *L. americanus*. • A, B – incomplete exoskeleton, dorsal, posterior views, NIGP 66249 (previously illustrated by Lu & Lin 1989, pl. 7, fig. 3). • C–E – nearly complete exoskeleton, dorsal, posterior and lateral views, NIGP 66248 (previously illustrated by Lu & Lin 1989, pl. 7, fig. 13). • F, G – incomplete exoskeleton, dorsal and anterolateral views, NIGP 61554 (previously illustrated by Lu & Lin 1980, pl. 1, fig. 6, 1989, pl. 7, fig. 1). • H–J – incomplete exoskeleton, dorsal, lateral, posterior views, NIGP 61553 (previously illustrated by Lu & Lin 1980, pl. 1, fig. 7, 1989, pl. 7, fig. 2). All scale bars = 1 mm.

Formation, Yongwol, South Korea, is a particularly noteworthy analogy with the basal lobes in *L. punctatus*. The Korean specimens are flattened in shale (Choi *et al.* 2004, fig. 10.1–10.4; here Fig. 11A–D) and the basal lobes all appear to be elongate. However, two illustrated cephalo reveal that the true basal lobes are subtly separated from the lateral portions of the M2 glabellar lobe (Fig. 11C, D). Comparative cephalo preserved three-dimensionally in limestone from the Huayansi Formation, Duibian B section, Zhejiang, South China, show that the basal lobes are short, that the poorly defined lateral portions of the M2 lobe are narrow (tr.), and that the lateral areas of the M2

lobe do not connect with the basal lobe (Peng *et al.* 2012c, fig. 9A–D; Fig. 11E–H).

After exclusion of the lateral portion of the M2 lobe from the taphonomically elongated basal lobe, the ratios of basal lobe length to posteroglabellar length (BLL : PGL) are 0.336 (holotype, Fig. 9B), 0.348 (Fig. 9A), 0.364 (Fig. 9C), 0.356 (Fig. 9D), 0.345 (Fig. 9F), 0.389 (Fig. 9G), and 0.376 (Fig. 9H). These values are within the range of variation described above for specimens described as *L. americanus* and *L. asiaticus*. On this basis, there appears to be no consistent differences between the species concepts of *L. americanus*, *L. asiaticus*, and *L. punctatus*.

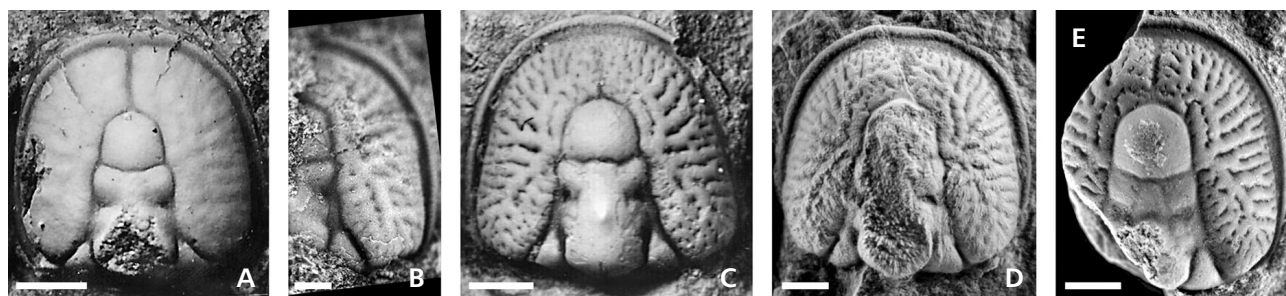


Figure 8. *Lotagnostus americanus* (Billings, 1860) from the Ogon'or Formation, Khos-Nelege River section, Siberia, Russia. All cephalons are in dorsal view; collecting levels in meters (m) above the base of the Ogon'or Formation are indicated. • A – from Bed 47, 335.6 m; illustrated as *Lotagnostus hedini* by Lazarenko *et al.* 2008a, pl. 21, fig. 1; also illustrated as *Lotagnostus (Eolotagnostus) agnostiformis* by Lazarenko *et al.* 2011, fig. 9D. • B – from Bed 47, 339 m (original of Lazarenko *et al.* 2008b, pl. 1, fig. 6). • C – from Bed 48, 357.6 m (original of Lazarenko *et al.* 2008a, pl. 23, fig. 1, 2008b, pl. 1, fig. 1, 2011, fig. 9F). • D – from Bed 51, 397.5 m (original of Lazarenko *et al.* 2008b, pl. 1, fig. 3, 2011, fig. 9H). • E – from Bed 51, 398 m (original of Lazarenko *et al.* 2008b, pl. 1, fig. 4, 2011, fig. 9J). All scale bars = 1 mm.

Comparison of *Lotagnostus trisectus* with *L. americanus*

Rushton (2009, p. 273) agreed with Peng & Babcock (2005) in synonymizing the *Lotagnostus trisectus* (Salter, 1864), described from the United Kingdom, with *L. americanus*, but preferred to retain it as a subspecies of *L. americanus* because *L. trisectus* “cephala appear to differ slightly (e.g. *L. trisectus* has larger basal glabellar lobes than *L. americanus*)”. According to Rushton (2009, p. 276), *L. trisectus* is indistinguishable from *L. americanus* in the pygidium. Westrop *et al.* (2011, pp. 580, 582) considered *L. trisectus*, along with *L. asiaticus* and *L. punctatus*, to be “entirely separate species from *L. americanus*”. Sclerites from Avalonian Canada (Nova Scotia), which were referred to *L. trisectus* by Hutchinson (1952), were partly referred by Westrop *et al.* (2011, figs 2, 3) to *L. cf. L. trisectus*.

For reasons discussed above, we judge the elongate appearance of the basal lobes of *L. trisectus* to be a taphonomic effect. Specimens of *L. trisectus* from the White-leaved Oak Shale of Malvern, United Kingdom, are flattened in shale, and all specimens that we have examined in The Natural History Museum, London, UK, and the Oxford University Museum of Natural History, Oxford, UK, show incorporation of the lateral parts of the M2 glabellar lobe with the true basal lobes. Rushton (2009, pp. 276–277) stated that the basal lobes in *L. trisectus* are 50% to 60% of the length of the posteroglabella, but we obtained values of about 30% to 40% for specimens that could be confidently measured. The White-leaved Oak Shale is a low-grade metasedimentary rock (soft black shale or mudrock), and many of the cephalons have been compacted or otherwise gently distorted. Similar to what we have observed in *L. punctatus*, not all specimens assigned to *L. trisectus* (or *L. americanus trisectus*), even if preserved in mudrock or shale, have taphonomic “elongation” of the basal lobes. A specimen from Belt's (1867)

collection (illustrated by Rushton 2009, fig. 2D) from the Dolgellau Formation in North Wales shows a true basal lobe separated from the M2 glabellar lobe.

Cephalons of *Lotagnostus* (and assigned to *L. trisectus*, *L. americanus*, or *L. americanus trisectus*) from the Alum Shale Formation in Scania and Västergötland, Sweden, show the same pattern in the basal lobes as observed elsewhere (Babcock *et al.* 2012). Specimens preserved three-dimensionally in limestone (e.g., Westergård 1922, pl. 1, fig. 11; Rushton 2009, fig. 2E, F; Ahlberg & Terfelt 2012) do not show elongation of the basal lobes, whereas specimens flattened in shale do tend to show such “elongation”. Also a limestone cephalon from Cerro Pelado, Argentina, which was described originally as *Goniagnostus verrucosus* by Rusconi (1951, fig. 5) but subsequently referred to *L. trisectus* by Shergold *et al.* (1990, fig. 9.7a, 1995, pl. 1, fig. 12), does not show the elongation of the basal lobes.

If “elongation” of the basal lobes of the glabella is regarded as a feature of taphonomic origin, then there are no consistent morphologic differences that can be used to differentiate *L. trisectus* from *L. americanus*. For this reason, we consider *L. trisectus* to be a junior subjective synonym of *L. americanus*.

Morphologic variation in other agnostoids

Morphologic variation among holaspide individuals and through ontogeny, microevolution within a species, and taphonomically related differences, especially between flattened and three-dimensional sclerites of the same species, have commonly been observed in agnostoids. Variation of the types discussed above for *Lotagnostus americanus* are consistent with the types of variation described in *Agnostus pisiformis*, *Ptychagnostus atavus*, *Glyptagnostus reticulatus*, *Lejopyge laevigata*, and *Agnostotes orientalis*, among others.

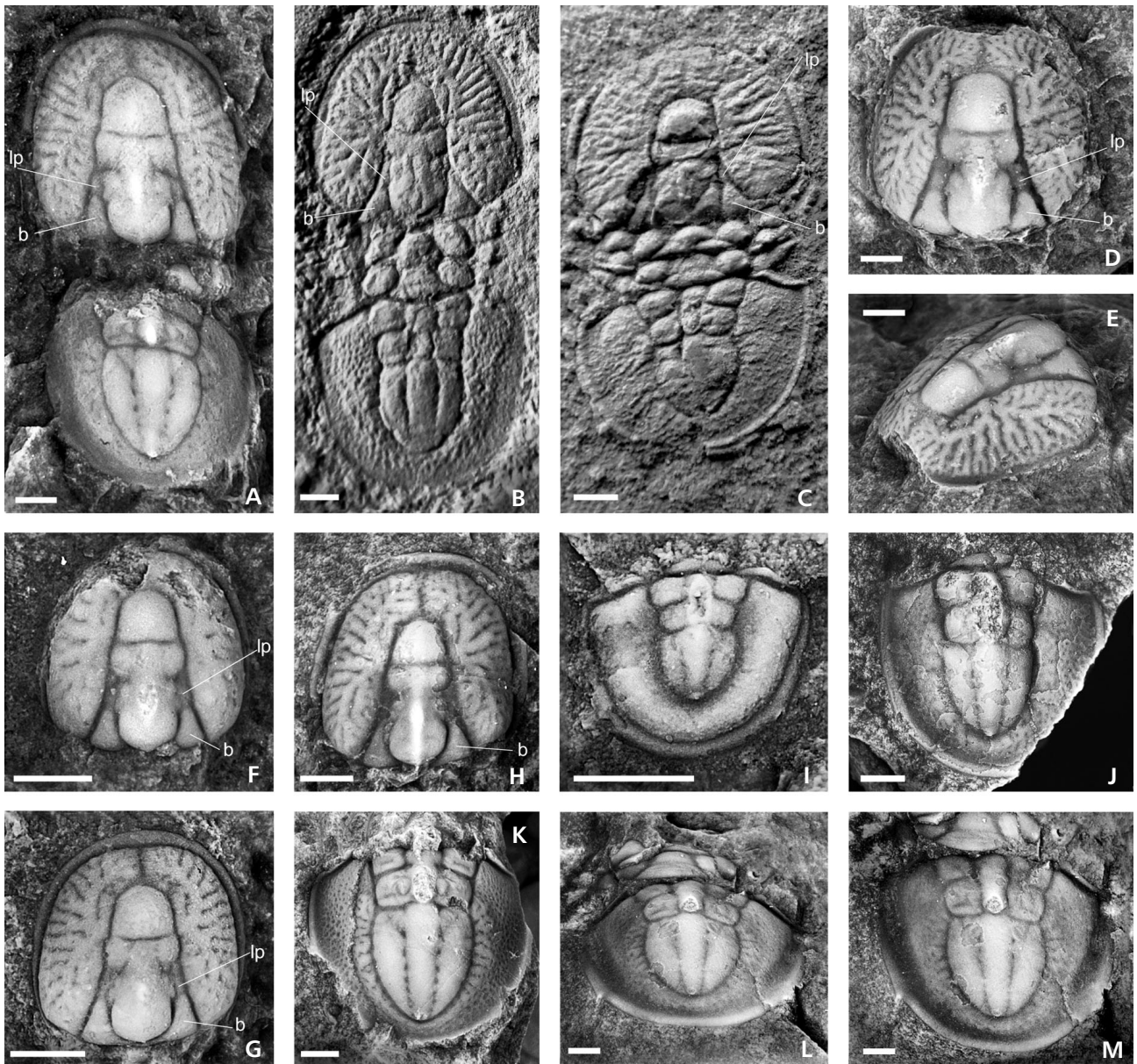


Figure 9. *Lotagnostus americanus* (Billings, 1860) assigned previously to *L. punctatus* Lu, 1964, indicating lateral portion of M2 glabellar lobe (lp) and basal lobe (b). • A, F, G, I – from the Shenjiawan Formation, Shenjiawan, Cili, northwestern Hunan, China. • B–E, H, J–M – from the Siyangshan Formation, western Zhejiang, China. • A – exoskeleton, dorsal view, TT51, NIGP 83022 (original of Peng 1984, pl. 1, fig. 1). • B – exoskeleton, dorsal view, NIGP 23711 (holotype of *L. punctatus*, original of Lu 1964, pl. 5, fig. 5). • C – exoskeleton, dorsal view, CB167, NIGP 66247, Dachen, Jiangshan (original of Lu & Lin 1989, pl. 6, fig. 12). • D, E – cephalon, dorsal, anterolateral views, KDS6, NIGP 88427, Duibian, Jiangshan (original of Lu & Lin 1984, pl. 3, fig. 8). • F – cephalon, dorsal view, TT51, NIGP 94909 (original of Peng 1992, fig. 6C). • G – cephalon, dorsal view, TT51, NIGP 83022 (original of Peng 1984, pl. 1, fig. 2). • H – cephalon, dorsal view, GC24, Siyangshan, Changshan, NIGP 66243 (original of Lu & Lin 1989, pl. 6, fig. 8). • I – pygidium, dorsal view, TT51, NIGP 94912 (original of Peng 1992, fig. 6F). • J – pygidium, dorsal view, GC24, NIGP 66244, Siyangshan, Changshan (original of Lu & Lin 1989, pl. 6, fig. 9). • K, L – pygidium, dorsal, posterior views, KDS6, NIGP 88428, Duibian, Jiangshan (original of Lu & Lin, 1984, pl. 3, fig. 9). • M – pygidium, dorsal view, CX119, NIGP 88429, Sanbeiling, Changshan (original of Lu & Lin 1984, pl. 3, fig. 10). All scale bars = 1 mm.

The wide variation expressed in scrobiculation, the length of the frontal sulcus, the axial furrows, and the notular furrows, and the pervasiveness of such variation among agnostoids, indicates that these character states should be accorded little taxonomic significance. Westrop *et al.* (2011), however, expressed the opposite view, and

accorded these features high taxonomic significance in *Lotagnostus*. Using features that we consider to reflect intraspecific variation resulted in an extremely narrow species concept for *Lotagnostus americanus*, and unjustified taxonomic splitting. If similar narrow species concepts were applied to other agnostoids, their inferred value for

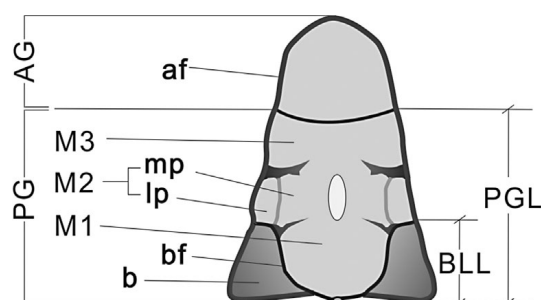


Figure 10. Diagram showing selected morphological terminology used in this paper for the glabella of *Lotagnostus americanus* and *Agnostotes orientalis* and measurements taken on specimens. Abbreviations: af – axial furrow; AG – anteroglabella; b – basal lobe; bf – basal furrow; BLL – length of basal lobe; lp – lateral portion of M2 glabellar lobe; mp – main portion of M2 glabellar lobe; M1, M2, M3 – designations of axial divisions of glabella; PG – posteroglabella; PGL – posteroglabellar length.

interregional correlation in the Cambrian would be significantly reduced.

In *Agnostus pisiformis* from Sweden, Norway, and the United Kingdom, Westergård (1922, pl. 1, figs 1–3), Henningsmoen (1958, pl. 5, figs 1–12), Rushton (1978, pl. 24, figs 15–19), and Høyberget & Bruton (2008, pl. 1, figs G–N) observed variation in scrobiculation on the genal fields ranging from smooth to distinct. The species usually has a smooth genal field, but “in some cases the ordinary smooth-cheeked cephalons are associated with cephalons with grooved cheeks” (Henningsmoen 1958, p. 181). All those authors regarded such differences as intraspecific variation.

In *Ptychagnostus atavus* (Tullberg, 1880), the key species for identifying the base of the Drumian Stage, the cephalic scrobiculation varies widely (e.g. Ahlberg *et al.* 2007). Some cephalons have smooth genal fields (Robison 1982, pl. 1, figs 2, 8, 1984, figs 11.1, 11.8), whereas others are either weakly scrobiculate (Robison 1982, pl. 1, figs 1, 6, 7, 1984, fig. 11.2; Peng & Robison 2000, figs 52.1, 52.4) or strongly scrobiculate (Robison 1982, pl. 1, fig. 9; Peng & Robison 2000, figs 52.3, 52.5).

Peng & Robison (2000) and Peng *et al.* (2004, fig. 8) illustrated variation in the scrobiculation of *Glyptagnostus reticulatus* (Angelin, 1851), which is used to identify the base of the Paibian Stage and Furongian Series. Some exoskeletons are only partly reticulate, with scrobiculation being concentrated in either the posterior genal field of the cephalon or the anterior pleural field of the pygidium (Peng & Robison 2000, figs 71.1, 71.2; Peng *et al.* 2004, fig. 8C–E), whereas other exoskeletons show reticulation on both the cephalon and pygidium (Peng & Robison 2000, figs 71.3, 71.4; Peng *et al.* 2004, fig. 8F, G). Peng & Robison (2000, p. 88) described microevolution in the reticulation within these species. Individuals tend to become more reticulate upsection.

In *Lejopyge laevigata* (Dalman, 1828), which is used to identify the base of the Guzhangian Stage, intraspecific variation is shown in the expression of pygidial axial furrows, in genal scrobiculation, and in the presence or absence of marginal spines on the pygidium. In most specimens, the axial furrows define only the anteroaxis of the pygidial axis, either fully or partly with variable incision (Robison 1984, fig. 23; Peng & Robison 2000, fig. 60), but in some specimens, faint axial furrows also define the posteroaxis (Westergård 1946, pl. 13, figs 23, 26; Daily & Jago 1975, pl. 62, figs 7, 9; Shergold & Laurie 1997, fig. 224.5a). Scrobiculation of the genal field in this species varies from smooth to weak (Westergård 1946, pl. 13, fig. 22; Daily & Jago 1975, pl. 62, fig. 10; Axheimer *et al.* 2006). Normally, the pygidium of *L. laevigata* has a smooth uninterrupted pygidial margin, but rare specimens have a pair of tiny marginal spines (Daily & Jago 1975, pl. 62, fig. 6; Peng & Robison 2000, fig. 60.7).

In *Agnostotes orientalis* (Kobayashi, 1935), which is used to identify the base of the Jiangshanian Stage, intraspecific variation exists in the shape of the anteroglabella, in scrobiculation of the pygidium, and in the axial furrows of the pygidium. The most notable variation is in the frontal sulcus of the anteroglabella. In the earliest examples of the species, or the ones having the lowest stratigraphic occurrences, the sulcus is a short (sag.), notch-like furrow (Fig. 11A, C, E), but in successively younger examples, the sulcus extends increasingly rearward until finally developing into a longitudinal furrow. In the stratigraphically youngest examples, the longitudinal furrow divides the anteroglabella into two lobes (Fig. 11D, G, H). Commonly, the pleural field of *A. orientalis* is moderately scrobiculate and the axial furrows are distinctly incised, resulting in clear definition of the posteroaxis (Peng *et al.* 2012c, fig. 9E). However, in some variants the pleural field is densely scrobiculate and the part of the posterior axial furrow that defines the posteroaxis is effaced (Peng *et al.* 2012c, fig. 9F).

As illustrated particularly by Westergård (1946) and Peng & Robison (2000), a number of other agnostoid species show morphologic variability that can be attributed to ontogenetic changes or microevolution. Among them are *Tomagnostus fissus* (Lundgren in Linnarsson, 1879), *Lejopyge armata* (Linnarsson, 1869), *Clavagnostus calensis* Rusconi, 1950, *Aspidagnostus lunulosus* (Kryskov in Borovikov & Kryskov, 1963), *Oidagnostus trispinifer* Westergård, 1946, *O. changi* (Lu, 1964), *Ptychagnostus punctuosus* (Angelin, 1851), and *Tomagnostella sulcifera* (Wallerius, 1895).

Revised synonymy of *L. americanus*

We follow longstanding practice in regarding axial characters, morphology of the acrolobe, and morphology of the

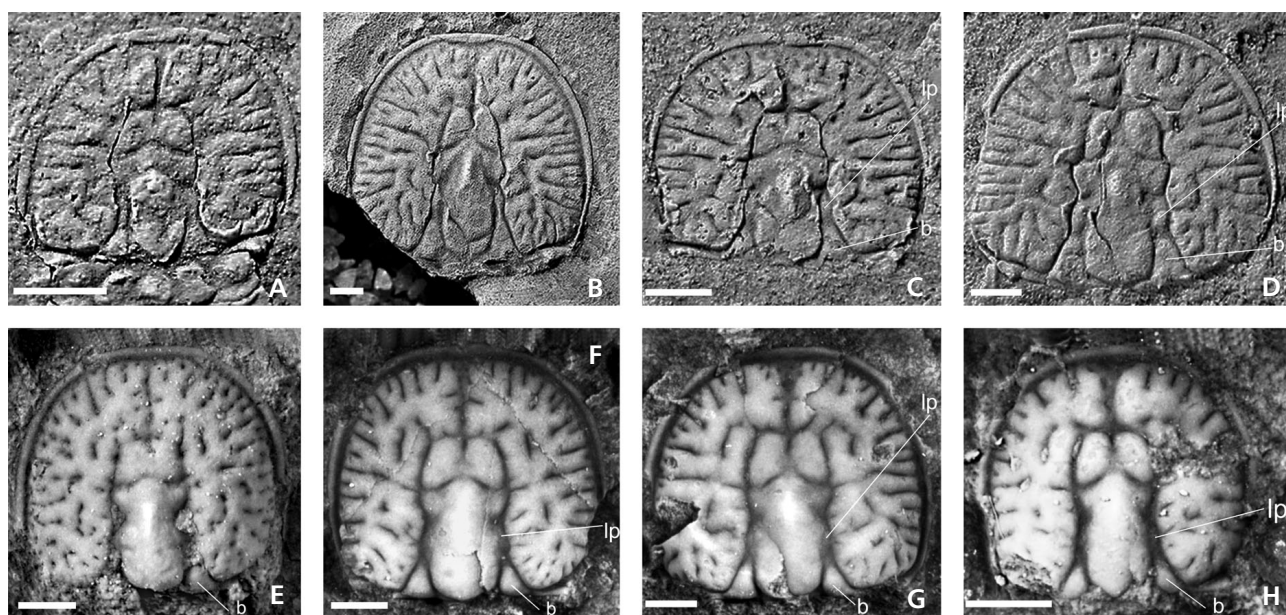


Figure 11. *Agnostotes orientalis* (Kobayashi, 1935) showing taphonomically altered cephalata preserved in shale and three-dimensional cephalata preserved in limestone. Basal lobes (b) on cephalata preserved in limestone are small and short, whereas in specimens flattened in shale they are incorporated with the lateral portions of the M2 glabellar lobe (lp). • A–D – specimens from shale of the *Agnostotes orientalis* Zone, Machari Formation, Konggiri section, Yongwol, South Korea (originals of Choi *et al.* 2004, fig. 10.1–10.4). Note that two cephalata (C, D) show short basal lobes separated from the lateral portions of the M2 glabellar lobe by a short transverse furrow. • E–G – specimens preserved in limestone from the basal part of the Huayansi Formation, Duibian B section, Zhejiang, South China, at 108.12 m, 119 m, 119 m, and 119.5 m above the base of Huayansi Formation (originals of Peng *et al.* 2012c, fig. 9A, D, C, G). All scale bars = 1 mm.

border and border furrows as being of highest value for diagnosing agnostoid species (*e.g.*, Peng & Robison 2000 and references therein). In *L. americanus*, diagnostic characters of the cephalon include a distinctly tapered and clearly defined glabella with a subpentagonal anterior lobe; well incised F2 furrows; a glabellar node lying near the center of the posteroglabella and immediately behind F2; a simple, short, triangular basal lobe; and a clearly defined preglabellar median furrow. Diagnostic characters of the pygidium are a subequally trisected anteroaxis with the lateral portions subdivided subequally by the F1 furrow, a laterally conterminous medial portion of the axis; a subequally trisected posteroaxis bearing a well developed terminal node; and a variably developed acrolobe defined by a generally faint border furrow.

Intraspecific variability is expressed in a number of characters in *L. americanus*. The genal and pleural fields range from smooth through weakly scrobiculate to well scrobiculate. In some specimens, the pleural fields are also pitted. In the cephalic axis, the anterior end of the anteroglabella is pointed or acutely curved anteriorly; the transglabellar furrow (F3) is transverse or gently curved backward; the M2 glabellar lobe is entire or subdivided faintly by a longitudinal (exsag.) auxiliary furrow; the intranotular axis is variably convex, and the notular furrows are weak or faint, bearing notulae that are variable in depth and number.

The morphologic variation that we have observed on the new material of *L. americanus* from South China, combined with that which we have observed in material from elsewhere, and observations on variation in other agnostoids leads us to modify the species concept of *L. americanus* only slightly. We include as junior subjective synonyms all the species synonymized by Ludvigsen & Westrop (1989), Peng & Babcock (2005), and Rushton (2009) except *L. obscurus* Palmer, 1955. *Lotagnostus tri-sectus*, *L. asiaticus*, and *L. punctatus*, which were regarded by Westrop *et al.* (2011, p. 580) as “entirely separate species from *L. americanus*” are here regarded as junior synonyms, as all represent grades of variation that are expressed within single collections of *L. americanus*.

Ludvigsen & Westrop (1989) first synonymized *L. obscurus* Palmer, 1955 with *L. americanus*, and this synonymy was followed by Westrop (1995) and Peng & Babcock (2005). Restudy of the types of *L. obscurus* from Nevada, USA, led Westrop *et al.* (2011) to recognize it as a distinct species, and that conclusion is followed here. *L. obscurus* is mostly effaced. The glabella and posteroaxis of the pygidium are poorly defined, and evidence of trisection in the M2 pygidial lobe is nearly lacking.

Some specimens assigned to *Lotagnostus hedini* (Troedsson, 1937) appear to be *L. americanus* (Lazarenko *et al.* 2008a, pl. 21, figs 1, ?5), although the holotype is not a synonym (see synonymy list below). *L. hedini* is distinct

from *L. americanus* mainly in having a broad V-shaped F3 glabellar furrow, a more posteriorly positioned glabellar node, a much longer pygidial axis, and an anteroaxis that is trisected transversely and longitudinally (*i.e.*, the medial portions of the M1 and M2 pygidial lobes are not incorporated). Westrop *et al.* (2011, p. 580) diagnosed the species as having a “non-trisected posteroaxis”, but as emphasized by Lu & Lin (1980, p. 124, 1989, p. 216), on the well preserved specimens from Zhejiang, China, the posteroaxis bears obscure notular furrows, described as “the anterior portion [of the posteroaxis] marked by two shallow, broad, longitudinal furrows”. It was this character state that led Lu & Lin (1980, pl. 1, fig. 8, 1989, pl. 7, fig. 5) to transfer the species from *Agnostus* to *Lotagnostus*. *L. hedini* (Troedsson, 1937) is essentially a smooth species (Troedsson 1937, pl. 1, figs 6–8; Lu & Lin 1984, pl. 1, figs 12, 13, 1989, pl. 7, figs 4, 5, 7, 8; Apollonov *et al.* 1984, pl. 14, figs 1, 2, 4, 5, 7, 8; Ludvigsen & Westrop 1989, pl. 1, figs 9–11, ?1–8, 12–14), but some sclerites from Kazakhstan and China bear weak to strong scrobiculation in cephalon (Apollonov *et al.* 1984, pl. 14, figs 3, 6; Lu & Lin 1989, pl. 7, fig. 6), providing good examples of intraspecific variation in cephalic scrobiculation in another species of *Lotagnostus*.

Westrop *et al.* (2011, p. 570) assigned exfoliated and nonscrobiculate cephalon and pygidia from the Rabbitkettle Formation, Mackenzie Mountains, Canada, to *Lotagnostus* sp. indet. Previously, Westrop (1995) identified them as *Lotagnostus americanus* but Peng & Babcock (2005) failed to list them in their synonymy of the species. The cephalon from the Mackenzie Mountains are similar to the obscurely scrobiculate cephalon from Quebec (Westrop *et al.* 2011, fig. 5D; Fig. 2C, I). In the pygidium, the middle portion of the anteroaxis does not appear to be subdivided and the posteroaxis seems to be obscurely trisected. These specimens from the Rabbitkettle Formation are here questionably assigned to *L. americanus* pending the discovery of testate specimens that will help clarify their identification.

Additions to the synonymy of *L. americanus* (see Peng & Babcock 2005) are as follows:

- 1954 *Lotagnostus* sp. – Lu, p. 126, pl. 1, fig. 4.
- 1976 *Lotagnostus trisectus* (Salter, 1864) (closely related). – Taylor & Cook, p. 208, text-fig. 29F.
- 1978 *Lotagnostus sanduensis* Lu & Chien in Yin & Lee, p. 387, pl. 144, fig. 28.
- 1983 *Lotagnostus sanduensis* Lu & Chien. – Lu & Qian (Chien), p. 17, pl. 1, fig. 1, 2.
- 1983 *Lotagnostus* sp. – Lu & Qian, p. 18, pl. 1, fig. 3.
- 1983 *Lotagnostus* (*Eolotagnostus*) cf. *agnostiformis* Apollonov & Chugaeva, p. 67, text-fig. 2, pl. 7, fig. 1.
- 2005 *Lotagnostus americanus* (Billings, 1860). – Peng & Babcock, pp. 110–113, fig. 2 (see for additional synonyms except for *L. obscurus* Palmer, 1955).

- 2008a *Lotagnostus hedini* (Troedsson, 1937). – Lazarenko *et al.*, p. 124, pl. 21, figs 1, ?5.
- 2008a *Lotagnostus americanus* (Billings, 1860). – Lazarenko *et al.*, p. 128, pl. 23, figs 1, 2, ?figs 5, 5a.
- 2008b *Lotagnostus americanus* (Billings, 1860). – Lazarenko *et al.*, p. 56, pl. 1, figs 1–4, 6–8, ?figs 5, 5a, 5b.
- 2009 *Lotagnostus americanus trisectus* (Salter, 1864). – Rushton, pp. 274–277, figs 1A–I, P, 2.
- 2009 *Lotagnostus americanus americanus* (Billings, 1860). – Rushton, p. 274, figs 1J–O.
- 2011 *Lotagnostus* (*Eolotagnostus*) cf. *agnostiformis* Apollonov & Chugaeva, 1983. – Lazarenko *et al.*, p. 563, fig. 9D, ?E.
- 2011 *Lotagnostus* (*Lotagnostus*) *americanus* (Billings, 1860). – Lazarenko *et al.*, p. 563, fig. 9F–K.
- 2011 *Lotagnostus* cf. *L. trisectus* (Salter, 1864). – Westrop *et al.*, p. 572, figs 2, 3.
- 2011 *Lotagnostus germanus* (Matthew, 1901). – Westrop *et al.*, p. 577, fig. 4.
- 2011 *Lotagnostus americanus* (Billings, 1860). – Westrop *et al.*, p. 578, figs 5, 6.
- ?2011 *Lotagnostus* sp. indet. – Westrop *et al.*, p. 578, figs 11A–I.
- 2012 *Lotagnostus americanus* (Billings, 1860). – Babcock *et al.*, p. 155.
- 2012a *Lotagnostus americanus* (Billings, 1860). – Peng *et al.*, p. 182.
- 2012 *Lotagnostus americanus* (Billings, 1860). – Ahlberg & Terfelt, p. 1006, fig. 4a–f.
- 2014 *Lotagnostus americanus* (Billings, 1860). – Peng *et al.*, p. 210, fig. 5A–F.

First Appearance Datum (FAD) of *Lotagnostus americanus*

In their discussion of the stratigraphic and paleogeographic distribution of *Lotagnostus*, Landing *et al.* (2011, pp. 261–262) concluded that the first local occurrences of *Lotagnostus*, and by implication, *L. americanus*, were diachronous on separate paleocontinents. There is little or no evidence to support this claim, which appears to be rooted in splitting *L. americanus* into a series of narrowly defined species, most of which are geographically restricted, and either reliance on outdated stratigraphic information or misinterpretation of stratigraphic information. As recognized herein, the first occurrence of *L. americanus* in South China, western North America, Sweden, Russia (Siberia), Kazakhstan, and the United Kingdom all seem to be synchronous or at least below the limits of our present stratigraphic resolution. Some species of *Lotagnostus*, such as *L. obscurus* (which is here excluded from synonymy with *L. americanus*), may have different ranges from *L. americanus*, but that does not negate the conclusion that

L. americanus makes its first appearance globally within a time interval so narrow that it essentially defines a time plane.

Lotagnostus americanus has a cosmopolitan distribution around the margins of Cambrian paleocontinents, and a relatively narrow stratigraphic range. The first appearance of *L. americanus* is tightly constrained by multiple chronostratigraphic tools (agnostoid biostratigraphy, polymerid biostatigraphy, $\delta^{13}\text{C}$ chemostratigraphy, and sequence stratigraphy) in a number of regions, and all available evidence points to the conclusion that the species makes its first appearance in open-shelf deposits at the same, or very nearly the same, time.

As with other agnostoids in the upper half of the Cambrian (e.g., *Ptychagnostus gibbus*, *Ptychagnostus atavus*, *Lejopyge laevigata*, *Glyptagnostus reticulatus*, and *Agnostotes orientalis*), *L. americanus* makes its first appearance on multiple paleocontinents in association with a significant eustatic rise in sea level (see Babcock et al. 2007; Peng et al. 2012b, c). Each of these taxa appears in open-shelf deposits in the lower part of a transgressive systems tract (TST), and the point of appearance on each paleocontinent is as close to synchronous as our present stratigraphic resolution allows us to determine. On each paleocontinent where these agnostoids are recorded, we have observed a lithologic change (usually to an organic-rich lithofacies, either dark gray limestone, dark gray calcareous shale, dark gray shale, or black shale). The lithologic change normally precedes the first occurrence of the agnostoid. The transgressive surface just below the FAD of *L. americanus* corresponds to the last large-scale cycle (inferred to be a second- or third-order sequence boundary) in the Cambrian, and it is correlative with the onset of a small, unnamed positive $\delta^{13}\text{C}$ excursion (see Peng et al. 2012b). The same stratigraphic pattern is exemplified in South China, western North America, Sweden, Siberia, Kazakhstan, and the United Kingdom, and there can be little doubt that the first appearance of *L. americanus* in each of these places was coeval within the limits of stratigraphic resolution.

After a review of the literature, and accounting for changes in information, there is little evidence to suggest that the first appearances of *L. americanus* in collections of reasonable size (i.e., more than two or three specimens) are diachronous. Existing evidence strongly supports that the interpretation that the lowest local occurrences around the world are close to coeval.

Landing et al. (2011, p. 626) stated that *L. americanus* appears in the *Ctenopyge spectabilis* Subzone (or Zone) in Sweden, and that the lowest occurrence of the species coincides with a relatively abrupt change in polymerid faunas. In their view, the first recorded appearance of *L. americanus* in Sweden “may not accurately record an origination” because it appears immediately above a “faunal dis-

continuity (Landing et al. 2011). This argument was based on information carried forward from older literature (e.g., Ahlberg 2003, Terfelt et al. 2011). However, based on a review of all known occurrences of *Lotagnostus* in Västergötland and Skåne, Sweden, the lowest observed occurrence of *L. americanus* in Sweden is near the base of the *Ctenopyge tumida* polymerid zone (Babcock et al. 2012). The *C. tumida* Zone overlies the *C. spectabilis* Zone. This revised information brings the first occurrence of *L. americanus* closer to its expected first occurrence based on its stratigraphic distribution outside Scandinavia (see discussion above), and eliminates the argument that the first occurrence of *L. americanus* in Sweden is associated with a “faunal discontinuity”.

Landing et al. (2011) based their conclusion on the presumed diachroneity of *L. americanus* in Sweden partly on the occurrences of *Pseudoagnostus rugosus* in Kazakhstan, Sweden, and South China (Ergaliev 1980, Peng 1992, Lu & Lin 1989, Terfelt & Ahlberg 2010). The conclusion is erroneous as they followed an incorrect interpretation of the species' occurrence in northwestern Hunan, China (see Terfelt & Ahlberg 2010). *P. rugosus* was reported from the *Eolotagnostus decorus*-*Kaolishaniella* Zone of Hunan (Peng 1992), which correlates with the *Eolotagnostus scrobicularis*-*Jegorovaia* Zone (previously the *Agnostus scrobicularis* Zone) of Kazakhstan (Peng 1992, p. 10, fig. 5). *P. rugosus* occurs in the *Eolotagnostus scrobicularis*-*Jegorovaia* Zone of Kazakhstan (Ergaliev 1980, p. 112). Polymerid trilobite fossils co-occurring with *P. rugosus*, such as *Jegorovaia* and *Chekiangaspis*, provide further support for a correlation of the *E. scrobicularis*-*Jegorovaia* Zone of Kazakhstan (Ergaliev 1980) with the *E. decorus*-*Kaolishaniella* Zone of South China (Peng 1992).

The presence of *P. rugosus* in the lower *L. americanus* Zone (or *Ctenopyge tumida* Zone of polymerid zonation) in Sweden is nearly identical to its position in the *L. americanus* Zone of Zhejiang, South China. Using the Furongian stratigraphic record of South China (Peng 1992) as a guide (and recognizing stratigraphic condensation in Sweden), suggests that occurrences of *P. rugosus* in northwestern Hunan and Kazakhstan represent the lower part of the species' range, whereas occurrences in Sweden and Zhejiang, China, represent the upper part of the species' range. The species may span a total of three trilobite zones in Hunan (Peng 1992), i.e., the *E. decorus*-*Kaolishaniella* Zone, the *Probilacunaspis nasalis*-*Peichashania hunanensis* Zone, and the *Lotagnostus americanus* Zone, and its last occurrence datum (LAD) can be used to constrain the first occurrence of *L. americanus*.

Landing et al. (2011, p. 626) discussed occurrences of the polymerid trilobite *Hedinaspis regalis*, which co-occurs with *L. americanus* in western Nevada, USA (Taylor & Cook 1976), in order to provide support for

the interpretation of diachroneity in the first occurrences of *L. americanus*. However, the information provided is misleading or incomplete. In China, *H. regalis* is known from Xinjiang, Northwest China, and Hunan and Zhejiang, South China. In each region, *H. regalis* co-occurs with *L. americanus*.

In the Tybo Canyon section, Hot Creek Range, Nevada, a complete dorsal exoskeleton of *L. americanus* (Taylor & Cook 1976, text-fig. 29F, assigned as “closely related to *L. trisectus*”; Taylor 1976, p. 673, text-fig. 3) was reported to be associated with *H. regalis* and *Charchaia norini* in collection USGS 7130-CO from the basal part of the Hales Limestone. The section is from a shelf-margin setting and includes allochthonous limestone layers yielding resedimented shallow shelf trilobites interspersed between autochthonous layers of thin-bedded deep water carbonates (Taylor & Cook 1976, text-fig. 15). The biostratigraphic guides Landing *et al.* (2011) used to correlate derive from the allochthonous shelf fauna rather than the autochthonous fauna of the basin. For example, *Irvingella angustilimbata*, which Landing *et al.* (2011, p. 626) used to constrain the occurrence of *H. regalis*, occurs in layers of allochthonous trilobite sclerites in the Hales Limestone (Taylor & Cook 1976, Taylor 1976). Resedimented sclerites of *I. angustilimbata* in the Hales Limestone are considerably older than the thin-bedded background sediments with which they have been subsequently intercalated. Normally *I. angustilimbata* first appears at the base of the Jiangshan Stage, which is well below Cambrian Stage 10, and its FAD is used as a secondary tool for constraining the base of the Jiangshan Stage (Peng *et al.* 2012c).

Lotagnostus americanus, *Hedinaspis regalis*, and *Charchaia norini* commonly co-occur in upper Furongian formations of South China, Northwest China and Kazakhstan (Troedsson 1937, Ergaliev 1983, Lu & Lin 1989, Peng 1992). The discovery of this same assemblage in autochthonous limestone beds of the Hales Limestone in Nevada (Taylor & Cook 1976, Taylor 1976) indicates that the occurrence of *L. americanus* in western North America is coeval with its occurrences in China and Kazakhstan.

An erroneous reference to correlation has led to misunderstanding of the stratigraphic position of *L. americanus* in North and South China. Landing *et al.* (2011, p. 262) stated: “Peng (1991) also correlated the base of the *Lotagnostus punctatus*-*Hedinaspis regalis* Zone into the *Ptychaspis-Tsinania* Zone of North China”. The 1991 date, both in the text and the reference list was a misprint. It should have been listed as Peng (1990). However, in the 1990 paper, Peng did not discuss the stratigraphic correlation of the two regions. Instead, a correlation was indicated in a figure within a later paper (Peng 1992, fig. 5). Peng (1992) correlated the basal part of the *L. americanus* (previously referred to as *L. punctatus*-*H. regalis* Zone) to the

upper part of the *Ptychaspis-Tsinania* Zone of North China. According to Sohn & Choi (2007), the basal part of the *L. americanus*-*H. regalis* Zone is equivalent to the upper part of the *Asioptychaspis* Zone of South Korea, but not to the entire zone. The *L. americanus*-*H. regalis* Zone of South China was later revised by Peng & Babcock (2008) and Peng *et al.* (2012b). As revised, it correlates to the *Sinosaukia impages* Zone of Australia, which, according to Sohn & Choi (2007), overlies the *Asioptychaspis* Zone of South Korea. It also correlates to the upper part of the *Saukiella junia* Zone or its equivalent, the *Saukiella pyrene-Rasettia magna* Zone of Laurentia (Peng & Babcock 2008, Peng *et al.* 2012b). The *Saukiella junia* Zone overlies the *Ellipsocephaloides* Zone. Miscorrelation of the *Ellipsocephaloides* Zone led Landing *et al.* (2011) to the erroneous conclusion that the FAD of *L. punctatus* is “significantly older than all of the other species” of *Lotagnostus* that they discussed.

Conclusions

New material of *Lotagnostus americanus* from northwestern Hunan, and existing collections from other localities in the world, including the species’ type area, indicate that *L. americanus* has a moderately wide morphologic variability, contrary to the narrow concept of *Lotagnostus* species advocated by Westrop *et al.* (2011). Reexamination of collections and published illustrations indicates that the species concept promulgated by Ludvigsen & Westrop (1989) and later emended slightly by Peng & Babcock (2005) is reasonable if *L. obscurus* Palmer, 1955 is excluded from synonymy. *L. americanus*, as revised, is a distinctive species with no known taxonomic problems. It has a cosmopolitan distribution around the margins of Cambrian paleocontinents, and a narrow stratigraphic range. The first appearance of *L. americanus* is tightly constrained by multiple chronostratigraphic tools (agnostoid biostratigraphy, polymerid biostatigraphy, $\delta^{13}\text{C}$ chemostratigraphy, and sequence stratigraphy) in a number of regions, and its first appearances in South China, western North America, Sweden, Russia (Siberia), Kazakhstan, and the United Kingdom all seem to be synchronous or as close to synchronous as our present stratigraphic resolution allows. Arguments raised by Landing *et al.* (2010, 2011) on the diachroneity of *L. americanus* are contrary to current information.

Agnostoids are the leading group of fossils for defining global stages in the upper half of the Cambrian, and *L. americanus* provides the same favorable characteristics as other agnostoids such as *Ptychagnostus atavus*, *Lejopyge laevigata*, *Glyptagnostus reticulatus*, and *Agnostotes orientalis*, which are key tools used in the definition of the bases of global stages. So far as known, the lowest occurrence of *L. americanus* in sections around the world are as

close to coeval as we can determine with present day techniques, which makes the First Appearance Datum (FAD) of *L. americanus* one of the most readily recognizable levels in the Cambrian. As such, the FAD of *L. americanus* stands as an excellent marker horizon for defining the base of the uppermost Cambrian stage (provisional Stage 10). No other proposed level, either trilobite- or conodont-based, has been shown to be superior to the FAD of *L. americanus*.

Acknowledgments

Yuan Daojun of the Museum of the Nanjing Institute of Geology and Palaeontology loaned specimens of Troedsson (1937), Lu & Lin (1984, 1989) and Peng (1984, 1992). Claire Mellish granted access to specimens at The Natural History Museum, London, and Louise Howlett arranged the loan of specimens from the Oxford University Museum of Natural History. Tatyana V. Pegel, Siberian Research Institute of Geology, Geophysics, and Mineral Resources, Russia, and Duck K. Choi, Seoul National University, Korea, provided images of sclerites from Russia and Korea, respectively. Two anonymous reviewers provided valuable comments, leading to improvement of this paper. This work was supported by grants to S. Peng from the Chinese Natural Science Foundation (41290260, 41221001, 41330101), the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) (20091103, 20121101), and the National Commission on Stratigraphy of China.

References

- AHLBERG, P. 2003. Trilobites and international tie points in the Upper Cambrian of Scandinavia. *Geologica Acta* 1, 127–134.
- AHLBERG, P., AXHEIMER, N. & ROBISON, R.A. 2007. Taxonomy of *Ptychagnostus atavus*: A key trilobite in defining a global Cambrian stage boundary. *Geobios* 40, 709–714. DOI 10.1016/j.geobios.2007.01.004
- AHLBERG, P. & TERFELT, F. 2012. Furongian (Cambrian) agnostoids of Scandinavia and their implications for intercontinental correlation. *Geological Magazine* 149, 1001–1012. DOI 10.1017/S0016756812000167
- ANGELIN, N.P. 1851. *Palaeontologia Suecica, pars I: Iconographia Crustaceorum Formationis Transitionis*. 24 pp. Weigel, Lund.
- APOLLONOV, M.K. & CHUGAEVA, M.N. 1983. Some trilobites from the Cambrian-Ordovician boundary deposits in the Batyrbai Valley of the Lesser Karatau, 66–90. In APOLLONOV, M.K., BANDALETOV, S.M. & IVSHIN, N.K. (eds) *The Lower Palaeozoic Stratigraphy and Palaeontology of Kazakhstan*. Nauka, Alma-Ata. [in Russian]
- APOLLONOV, M.K., CHUGAEVA, M.N. & DUBININA, S.V. 1984. *Trilobites and conodonts from the Batyrbai section (Uppermost Cambrian – Lower Ordovician) in Malyi Karatau Range (Atlas of palaeontological plates)*. 48 pp. Nauka, Alma-Ata. [in Russian]
- AXHEIMER, N., ERIKSSON, M.E., AHLBERG, P. & BENGTTSSON, A. 2006. The middle Cambrian cosmopolitan key species *Lejopyge laevigata* and its biozone: new data from Sweden. *Geological Magazine* 143, 447–455. DOI 10.1017/S0016756806002007
- BABCOCK, L.E., ROBISON, R.A., REES, M.N., PENG, S. & SALTZMAN, M.R. 2007. The Global boundary Stratotype Section and Point (GSSP) of the Drumian Stage (Cambrian) in the Drum Mountains, Utah, USA. *Episodes* 30, 85–95.
- BABCOCK, L.E., AHLBERG, P., PENG, S., TERFELT, F. & ERIKSSON, M.E. 2012. Morphologic variation, taphonomy and biostratigraphic range of the agnostoid *Lotagnostus* (Cambrian: Furongian) from Sweden. *Journal of Guizhou University (Natural Sciences)* 29 (Sup. 1), 154–155.
- BELT, T. 1867. On some new trilobites from the Upper Cambrian rocks of North Wales. *Geological Magazine* 4, 294–295. DOI 10.1017/S0016756800205748
- BILLINGS, E. 1860. On some new species of fossils from the limestone near Point Levi, opposite Quebec. *Canadian Naturalist and Geologist* 5, 301–324.
- BOROVNIKOV, L.E. & KRYSKOV, L.N. 1963. Cambrian deposits in the Kendyktas Mountains (South Kazakhstan). *Material on Geology and Mineral Deposits of Altai and Kazakhstan. Trudy Vsesoyuznogo nauchno-issledovatelyeskogo geologicheskogo instituta (VSEGEI), New Series* 94, 266–280. [in Russian]
- CHOI, D.K., LEE, J.G. & SHEEN, B.C. 2004. Upper Cambrian agnostoid trilobites from the Machari Formation, Yongwol, Korea. *Geobios* 27, 159–189. DOI 10.1016/j.geobios.2003.02.004
- CLARK, T.H. 1924. The paleontology of the Beekmantown Series at Lévis, Quebec. *Bulletins of American Paleontology* 10, 1–134.
- DAILY, B. & JAGO, J. B. 1975. The trilobite *Lejopyge* Hawle and Corda and the Middle-Upper Cambrian boundary. *Palaeontology* 18, 527–550.
- DALMAN, J.W. 1828. *Nya Svenska Paleader. Årsberättelse om Nyare Zoologiska Arbeten och Upptäckter*, 134–135. Kongliga Svenska Vetenskaps-Akademiens Handlingar.
- ERGALIEV, G.K. 1980. *Middle and Upper Cambrian trilobites of the Malyi Karatau Range*. 211 pp. Nauka, Alma-Ata. [in Russian]
- ERGALIEV, G.K. 1983. Some trilobites from the Upper Cambrian and Lower Ordovician of the Greater Karatau and Ulutau, 35–66. In APOLLONOV, M.K., BANDELETOV, S.M. & IVSHIN, N.K. (eds) *The Lower Paleozoic Stratigraphy and Paleontology of Kazakhstan*. Nauka, Alma-Ata. [in Russian]
- HENNINGSMOEN, G. 1958. The Upper Cambrian fauna of Norway. *Norsk Geologisk Tidsskrift* 38, 179–196.
- HØYBERGET, M. & BRUTON, D.L. 2008. Middle Cambrian trilobites of the suborders Agnostina and Eodiscina from the Oslo Region, Norway. *Palaeontographica* A286, 1–87.
- HUTCHINSON, R.D. 1952. The stratigraphy and trilobite faunas of the Cambrian sedimentary rocks of Cape Breton Island, Nova

- Scotia. *Geological Survey of Canada Memoir* 263, 1–124. DOI 10.4095/101599
- JAGO, J.B. & COOPER, R.A. 2007. Middle Cambrian trilobites from Reilly Ridge, northern Victoria Land, Antarctica. *Memoirs of the Australasian Association of Palaeontologists* 34, 473–487.
- KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen, Palaeontology. Part 3, Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo, Section II* 4(2), 49–344.
- LANDING, E., WESTROP, S.R. & ADRAIN, J.M. 2011. The Lawsonian Stage – the *Eoconodontus notchpeakensis* FAD and HERB carbon isotope excursion define a globally correlatable terminal Cambrian stage. *Bulletin of Geosciences* 86(3), 621–640. DOI 10.3140/bull.geosci.1251
- LANDING, E., WESTROP, S.R. & MILLER, J.F. 2010. Globally practical base for the uppermost Cambrian (Stage 10) – FAD of the conodont *Eoconodontus notchpeakensis* and the Housian Stage, p. 18. In FATKA, O. & BUDIL, P. (eds) *Prague 2010, the 15th Conference of the Cambrian Stage Subdivision Working Group, International Subcommission on Cambrian Stratigraphy; Abstracts and Excursion Guide*. Czech Geological Survey, Prague.
- LAZARENKO, N.P., GOGIN, I.Y., PEGEL, T.V. & ABAIMOVA, G.P. 2011. The Khos-Nelege River section of the Ogon'or Formation: a potential candidate for the GSSP of Stage 10, Cambrian System. *Bulletin of Geosciences* 86(3), 555–568. DOI 10.3140/bull.geosci.1270
- LAZARENKO, N.P., GOGIN, I.Y., PEGEL, T.V., SUKHOV, S.S., ABAIMOVA, G.P., EGOROVA, L.I., FEDOROV, A.B., RAEVSKAYA, E.G. & USHATINSKAYA, G.T. 2008a. Excursion 1b. Cambrian stratigraphy of the northeastern Siberian Platform and potential stratotype of lower boundaries of proposed Upper Cambrian Chekurovian and Nelegerian stages in the Ogon'or Formation section at the Khos-Nelege River; the boundaries are defined by the FAD of *Agnostotes orientalis* and *Lotagnostus americanus*, 61–139. In ROZANOV, A.Y. & VARLAMOV, A.I. (eds) *The Cambrian System of the Siberian Platform, Part 2: North-East of the Siberian Platform*. PIN RAS, Moskva & Novosibirsk.
- LAZARENKO, N.P., PEGEL, T.V., SUKHOV, S.S., ABAIMOVA, G.P. & GOGIN, I.Y. 2008b. Type section of Upper Cambrian of Siberian Platform – Candidate of stage stratotype of International stratigraphic scale, 3–58. In BUDNIKOV, I.V. (ed.) *Cambrian sections of Siberian Platform – candidates of stratotype subdividing International Stratigraphic Scale (Stratigraphy and Paleontology); Material for 13th International Field Conference of Cambrian Stage Subdivision Working Group*. SB RAS Press, Novosibirsk. [in Russian]
- LINARSSON, J.G.O. 1869. Om Vestergötlands cambriska och siluriska aflagringar. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 8(2), 1–89.
- LINARSSON, J.G.O. 1879. Om faunan i kalken med *Conocoryphe exsulans* ("coronatuskalken"). *Sveriges Geologiska Undersökning, Series C* 35, 1–31.
- LU, Y. 1954. Upper Cambrian trilobites from Santu, southeastern Kueichou. *Acta Palaeontologica Sinica* 2(2), 117–152. [in Chinese with English summary]
- LU, Y. 1964. Trilobites, 31–41. In WANG, Y. (ed.) *Index Fossils of South China*. Science Press, Beijing. [in Chinese]
- LU, Y., CHANG (ZHANG), W., CHU (ZHU), C. (Z.), CHIEN (QIAN), Y. & HSIANG (XIANG), L. 1965. *Trilobites of China*. 1–362 + 363–766 pp. Science Press, Beijing. [in Chinese]
- LU, Y., CHU (ZHU), C.(Z.), CHIEN (QIAN), Y., LIN, H., ZHOU, Z. & YUAN, K. 1974. Bio-environmental control hypothesis and its application to the Cambrian biostratigraphy and palaeozoogeography. *Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 5, 27–116 [in Chinese]
- LU, Y. & LIN, H. 1980. Cambro-Ordovician boundary in western Zhejiang and the trilobites contained therein. *Acta Palaeontologica Sinica* 19, 118–135. [in Chinese]
- LU, Y. & LIN, H. 1984. Late Cambrian and earliest Ordovician trilobites of Jiangshan-Changshan area, Zhejiang, 45–143. In NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, ACADEMIA SINICA (ed.) *Stratigraphy and Palaeontology of Systemic Boundaries in China, Cambrian-Ordovician Boundary, Volume I*. Anhui Science & Technology Publishing House, Hefei.
- LU, Y. & LIN, H. 1989. The Cambrian trilobites of western Zhejiang. *Palaeontologia Sinica, Whole Number 178, New Series B*, 25, 1–287.
- LU, Y. & QIAN (CHIEN), Y. 1983. Cambro-Ordovician trilobites from eastern Guizhou. *Palaeontologia Cathayana* 1, 1–105.
- LUDVIGSEN, R. & WESTROP, S.R. 1989. Systematic Paleontology, 11–63. In LUDVIGSEN, R., WESTROP, S.R. & KINDLE, C.H. 1989 *Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada*. *Palaeontographica Canadiana* 6, 1–175.
- MÜLLER, K.J. & WALOSSEK, D. 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils and Strata* 19, 1–124.
- ÖPIK, A.A. 1979. Middle Cambrian agnostids: systematics and biostratigraphy. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 172, 1–188.
- PALMER, A.R. 1955. Upper Cambrian Agnostidae of the Eureka district, Nevada. *Journal of Paleontology* 29, 86–101.
- PEGEL, T.V. 2000. Evolution of trilobite biofacies in Cambrian basins on the Siberian platform. *Journal of Paleontology* 74, 1000–1019. DOI 10.1666/0022-3360(2000)074<1000:EOTBIC>2.0.CO;2
- PENG, S. 1984. Cambrian-Ordovician boundary in the Cili-Taoyuan border area, northwestern Hunan, 285–405. In NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, ACADEMIA SINICA (ed.) *Stratigraphy and paleontology of systemic boundaries in China, Cambrian and Ordovician boundary 1*. Anhui Science and Technology Publishing House, Hefei.
- PENG, S. 1990. Upper Cambrian in the Cili-Taoyuan area, Hunan, and its trilobite succession. *Journal of Stratigraphy* 14, 261–276. [in Chinese with English abstract]
- PENG, S. 1992. Upper Cambrian biostratigraphy and trilobite faunas of the Cili-Taoyuan area, northwestern Hunan. *Memoirs of the Association of Australasian Palaeontologists* 13, 1–119.

- PENG, S. & BABCOCK, L.E. 2005. Two Cambrian agnostoid trilobites, *Agnostotes orientalis* (Kobayashi, 1935) and *Lotagnostus americanus* (Billings, 1860): Key species for defining global stages of the Cambrian System. *Geosciences Journal* 9, 107–115. DOI 10.1007/BF02910573
- PENG, S. & BABCOCK, L.E. 2008. Cambrian Period, 37–46. In OGG, J., OGG, G. & GRADSTEIN, F.M. (eds) *The Concise Geologic Time Scale*. 177 pp. Cambridge University Press, Cambridge.
- PENG, S., BABCOCK, L.E. & AHLBERG, P. 2012a. Morphologic variation of *Lotagnostus americanus* from China and Russia. *Journal of Guizhou University (Natural Sciences)*, 29 (Sup. 1), 182–183.
- PENG, S., BABCOCK, L.E. & COOPER, R.A. 2012b. The Cambrian Period, 437–488. In GRADSTEIN, F.M., OGG, J.G., SCHMITZ, M.D. & OGG, G.M. (eds) *The Geologic Time Scale 2012 (2 volumes)*. 1144 pp. Elsevier BV, Amsterdam, Boston, Heidelberg.
- PENG, S., BABCOCK, L.E., ROBISON, R.A., LIN, H., REES, M.N. & SALTZMAN, M.R. 2004. Global Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). *Lethaia* 37, 365–379. DOI 10.1080/00241160410002081
- PENG, S., BABCOCK, L.E., ZUO, J., LIN, H., ZHU, X., YANG, X., ROBISON, R.A., QI, Y., BAGNOLI, G. & CHEN, Y. 2009. The global boundary stratotype section and Point (GSSP) of the Guzhangian Stage (Cambrian) in the Wuling Mountains, northwestern Hunan, China. *Episodes* 32, 41–55.
- PENG, S., BABCOCK, L.E., ZUO, J., ZHU, X., LIN, H., YANG, X., QI, Y., BAGNOLI, G. & WANG, L. 2012c. Global Standard Stratotype-section and Point (GSSP) for the base of the Jiangshanian Stage (Cambrian: Furongian) at Duibian, Jiangshan, Zhejiang, Southeast China. *Episodes* 35, 462–477.
- PENG, S., BABCOCK, L.E., ZHU, X., ZUO, J. & DAI, T. 2014. A potential GSSP for the base of the uppermost Cambrian stage, coinciding with the first appearance of *Lotagnostus americanus* at Wa'ergang, Hunan, China. *GFF* 136, 208–213. DOI 10.1080/11035897.2013.865666
- PENG, S. & ROBISON, R.A. 2000. Agnostoid biostratigraphy across the Middle–Upper Cambrian boundary in Hunan, China. *Paleontological Society Memoir* 53 (supplement to *Journal of Paleontology* 74), 1–104.
- PRATT, B.R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana* 9, 1–179.
- RASETTI, F. 1944. Upper Cambrian trilobites from the Lévis Conglomerate. *Journal of Paleontology* 18, 229–258.
- ROBISON, R.A. 1972. Mode of life of agnostid trilobites. 24th International Geological Congress, Montreal, Session 7, 33–40.
- ROBISON, R.A. 1982. Some Middle Cambrian agnostoid trilobites from western North America. *Journal of Paleontology* 56, 132–160.
- ROBISON, R.A. 1984. Cambrian Agnostida of North America and Greenland, Part I: Ptychagnostidae. *University of Kansas Paleontological Contributions, Paper* 109, 1–59.
- ROBISON, R.A. 1994. Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 169, 25–77.
- ROWELL, A.J., ROBISON, R.A. & STRICKLAND, D.K. 1982. Paleontology and chronocorrelation of a potential series boundary within the Cambrian. *Journal of Paleontology* 56, 161–182.
- RUSCONI, C. 1950. Trilobitas y otros organismos del Cambrico de Canota. *Revista del Museo de Historia Natural de Mendoza* 4, 71–84.
- RUSCONI, C. 1951. Trilobitas Cambricos del Cerro Pelado (Mendoza). *Boletín Paleontológico de Buenos Aires* 24, 1–4.
- RUSHTON, A.W.A. 1978. Fossils from the middle-upper Cambrian transition in the Nuneaton district. *Palaeontology* 21, 245–283.
- RUSHTON, A.W.A. 2009. Revision of the Furongian agnostoid *Lotagnostus trisectus* (Salter). *Memoirs of the Association of Australasian Palaeontologists* 37, 273–279.
- SALTER, J.W. 1864. Figures and descriptions illustrative of British organic remains. Decade 11, Trilobites (chiefly Silurian). *Memoirs of the Geological Survey of the United Kingdom*, 1–64.
- SHERGOLD, J.H. & LAURIE, J.R. 1997. Agnostina, 331–383. In KAESLER, R.L. (ed.) *Treatise on Invertebrate Paleontology, Part O. Arthropoda 1. Trilobita, Revised*. Geological Society of America & University of Kansas Press, Boulder & Lawrence.
- SHERGOLD, J.H., LAURIE, J.R. & SUN, X. 1990. Classification and review of the trilobite Order Agnostida Salter, 1864: an Australian perspective. *Bureau of Mineral Resources, Geology and Geophysics, Australia, Report* 296, 1–93.
- SOHN, J.W. & CHOI, D.K. 2007. Furongian trilobites from the *Asioptychaspis* and *Quadraticephalus* zones of the Hwajeol Formation, Taebaeksan Basin, Korea. *Geosciences Journal* 11, 297–314. DOI 10.1007/BF02857047
- TAYLOR, M.E. 1976. Indigenous and redeposited trilobites from Late Cambrian basinal environments of central Nevada. *Journal of Paleontology* 50, 668–700.
- TAYLOR, M.E. & COOK, H.E. 1976. Continental shelf and slope facies of the Upper Cambrian and lowest Ordovician of Nevada. *Brigham Young University Geology Studies* 23, 181–214.
- TERFELT, F. & AHLBERG, P. 2010. *Pseudagnostus rugosus* Ergaliev, 1980: a key agnostoid species for intercontinental correlation of upper (Cambrian) Furongian strata. *Geological Magazine* 147, 789–796. DOI 10.1017/S0016756810000282
- TERFELT, F., AHLBERG, P. & ERIKSSON, M.E. 2011. Complete record of Furongian polymerid trilobites and agnostoids of Scandinavia – a biostratigraphical scheme. *Lethaia* 44, 8–14. DOI 10.1111/j.1502-3931.2009.00211.x
- TERFELT, F. & AHLGREN, J. 2007. *Macropyge* (*Promacropyge*) *scandinavica* new species; the first macropyginid trilobite recorded from the Furongian of Baltica. *Journal of Paleontology* 81, 1516–1522. DOI 10.1666/06-020R.1
- TERFELT, F., ERIKSSON, M.E., AHLBERG, P. & BABCOCK, L.E. 2008. Furongian Series (Cambrian) biostratigraphy of Scandinavia – a revision. *Norwegian Journal of Geology* 88, 73–87.

- TROEDSSON, G.T. 1937. On the Cambro-Ordovician faunas of western Quruq Tagh, eastern Tien-Shan. *Palaeontologia Sinica B2*, 1–74.
- TULLBERG, S. 1880. Om Agnostus-arterna i de kambriska aflagringarne vid Andrarum. *Sveriges Geologiska Undersökning C42*, 1–38.
- WALLERIUS, I.D. 1895. *Undersökningar öfver zonen med Agnostus laevigatus i Vestergötland: Jämte en inledande öfversikt af Vestergötlands samtliga Paradoxideslager*. 72 pp. Hjalmar Möller, Lund.
- WESTERGÅRD, A.H. 1922. Sveriges olenidskriffer. *Sveriges Geologiska Undersökning Ca 18*, 1–205.
- WESTERGÅRD, A.H. 1946. Agnostidea of the Middle Cambrian of Sweden. *Sveriges Geologiska Undersökning C477*, 1–141.
- WESTROP, S.R. 1995. Sunwaptan and Ibexian (Upper Cambrian-Lower Ordovician) trilobites from the Rabbitkettle Formation, Mountain River region, northern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana 12*, 1–75.
- WESTROP, S.R., ADRAIN, J.M. & LANDING, E. 2011. The Cambrian (Sunwaptan, Furongian) agnostoid arthropod *Lotagnostus Whitehouse*, 1936, in Laurentian and Avalonian North America: systematics and biostratigraphic significance. *Bulletin of Geosciences 86*(3), 569–594. DOI 10.3140/bull.geosci.1256
- YIN, G. & LEE (LI), S. 1978. Trilobita, 385–595. In GUIZHOU WORKING TEAM ON STRATIGRAPHY AND PALAEONTOLOGY (ed.) *Palaeontological Atlas of Southwest China, Guizhou Province (1): Cambrian-Devonian*. Geological Publishing House, Beijing. [in Chinese]
- ZHAO, J. (ed.) 1963. *Handbook of Index fossils of China, Xibei (Northwest China) Region*. 179 pp. Science Press, Beijing. [in Chinese]