Ventral exoskeletal morphology of the trilobite *Neodrepanura premesnili* from the Cambrian Kushan Formation, Shandong, China

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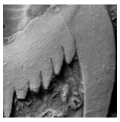

The polymerid trilobite *Neodrepanura* (family Damesellidae) is one of the most famous and abundant fossils from the Kushan Formation (Cambrian) of the North China Platform. Recent discovery of the first known complete exoskeleton of *Neodrepanura premesnili*, together with additional material, allows further description of the butterfly-shaped hypostome and wide doublure in this species. These new materials suggest that *N. premesnili* had a carnivorous feeding habit. • Key words: Trilobita, *Neodrepanura*, *Drepanura*, hypostome, doublure, Cambrian, China.

LIU, Q., LEI, Q. & OU, Q. 2011. Ventral exoskeletal morphology of the trilobite *Neodrepanura premesnili* from the Cambrian Kushan Formation, Shandong, China. *Bulletin of Geosciences 86(3)*, 659–664 (3 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received March 4, 2011; accepted in revised form July 11, 2011; published online July 27, 2011; issued September 30, 2011.

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Neodrepanura, which is one of the most famous polymerid trilobites from China, is locally abundant in the Kushan Formation (Cambrian) of the North China Platform (*e.g.*, Zhang 2003, Peng 2007). Known as the "bat-stones", the *Neodrepanura*-bearing rocks had been first mentioned in a Chinese ancient dictionary (Guo ~300 A.D.) dated back to the 4th century, and this comment also represents the oldest written reference to trilobites (Chang 1927, Needham 1959, St. John 2007). The first scientific study of "*Neodrepanura*" was by the French palaeontologist Bergeron in 1899, who initially proposed the name *Drepanura* for this genus. As the name was preoccupied by an insect genus of Family Entomobryidae (Schoett 1891), Özdikmen (2006) replaced the junior homonym with *Neodrepanura*.

The first known complete exoskeleton of *Neodrepanura premesnili* (Bergeron 1899), the type species of the genus, was recently reported and described by Liu & Lei (2010). The new description, highlighting the features of dorsal morphology, helps to correct previous misconceptions of *N. premesnili* introduced by Kobayashi (1942), based on incomplete material, and widely cited for more than half a century.

Since the publication of our article on the exoskeletal morphology of *N. premesnili*, additional material, including some hypostomes and specimens exhibiting the doublure, has been collected. The additional specimens permit us to describe and interpret the ventral exoskeletal morphology of this species.

Systematic palaeontology

Repository. – Type and figured materials described in this paper are housed in the Early Life Evolution Laboratory of China University of Geosciences, Beijing (prefix ELEL).

Order Lichida Moore, 1959
Superfamily Dameselloidea Kobayashi, 1935
Family Damesellidae Kobayashi, 1935
Subfamily Drepanurinae Hupé, 1953

Genus *Neodrepanura* Özdikmen, 2006

***Neodrepanura premesnili* (Bergeron, 1899)**
Figures 1–3

1899 *Drepanura premesnili* Bergeron, p. 509, pl. 13, fig. 8.
1902 *Drepanura premesnili* Bergeron. – Airaghi, p. 10, pl. 1, figs 31, 32.

DOI 10.3140/bull.geosci.1271

1992 *Drepanura premesnili* Bergeron. – Zhu, p. 355, pl. 119, figs 1, 4.
1996 *Drepanura premesnili* Bergeron. – Guo *et al.*, p. 129, pl. 10, fig. 12.
2004 *Drepanura premesnili* Bergeron. – Peng *et al.*, p. 129, pl. 45, fig. 1.
2010 *Neodrepanura premesnili* (Bergeron). – Liu & Lei (see this reference for a detailed synonymy).

Lectotype. – A pygidium on the upper left of the Bergeron's rock slab (E.N.S.M. 9000), figured as pl. 13, fig. 8 by Bergeron (1899); selected by Peng *et al.* (2004, p. 129).

Material. – Figured specimens include two incomplete exoskeletons (ELEL-LW100020, ELEL-LW100025), four hypostomes (ELEL-LW100014, ELEL-LW100015, ELEL-LW100017, ELEL-LW100018), three librigenae (ELEL-LW100013, ELEL-LW100023, ELEL-LW100024), three cranidia (ELEL-LW100016, ELEL-LW100021, ELEL-LW100026), a thoracic segment (ELEL-LW100019) and a pygidium (ELEL-LW100022). The complete exoskeleton (ELEL-LW100010) is refigured to show anterior morphology of cephalon.

Additional diagnosis. – To the diagnosis of dorsal morphology (see Liu & Lei 2010), the following characters of ventral morphology are added: Librigenal doublure wide and flat in the genal region, but narrowing and increasingly incurved anteriorly, pleural doublure wide (transverse) and extends under entire pleural spines, pygidial doublure particularly wide. Hypostome butterfly-shaped, shoulders widely spread laterally with sharp ends, posterior border with a pair of deep depressions and a pair of broad marginal spines.

Description. – To the description of dorsal morphology (see Liu & Lei 2010), the additional description of ventral morphology is given as follows:

Hypostome butterfly-shaped (Figs 1C, D, 2A–D), smooth, noticeably wider (transverse) than long (sagittal). Anterior margin slightly convex medially, but straight abaxially, anterior wings subtriangular. Anterior lobe of middle body sub-ovate and strongly inflated, posterior lobe of middle body crescent and gently convex, short (sagittal & exsagittal), and slightly wider (transverse) than anterior lobe; middle furrow shallow medially and deepening abaxially. Shoulders large and widely spread laterally as subtriangular extensions with sharp ends. Posterior border inconspicuous medially, widening (exsagittal) abaxially, where it bears a pair of deep depressions and a pair of broad marginal spines projecting strongly rearward, posterior margin gently arched (Figs 2A, B, 3B). Hypostomal doublure smooth, covering most of the shoulders and the posterior border with flexuous inner margin (Figs 2C, D, 3C).

Cephalic doublure consisting of two parts: 1) librigenal doublure, wide (transverse) and flat in the genal region, increasingly incurved and narrow anteriorly (Figs 2E, F, H, 3A), with weak terrace ridges (Fig. 2G, I); 2) occipital doublure, broad medially and narrow abaxially, maximum width (sagittal) occupying about 0.6 width of occipital ring (Fig. 2J). Cranidium without anterior border, without preglabellar field (Fig. 2K–M), rostral plate absent (Fig. 1A, B).

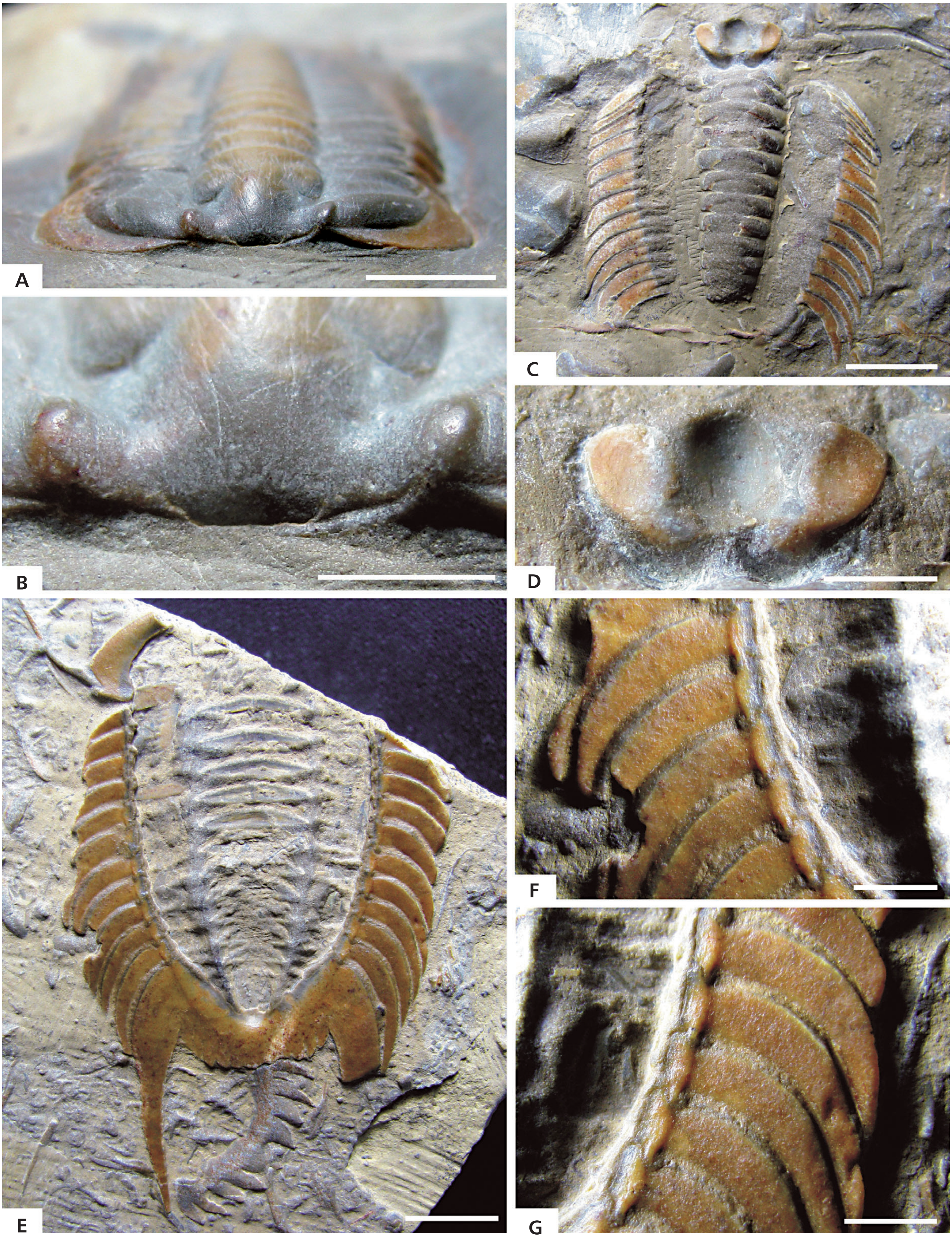
Thoracic doublure consisting of two parts: 1) pleural doublure, wide and smooth, extending under entire pleural spines, ending adaxially into a bar-like structure under fulcrum (Figs 1E, 3A), which comprises a fulcral process anteriorly and a fulcral socket posteriorly (Figs 1F, G, 2O); 2) axial doublure, wide medially and narrowing abaxially, maximum width (sagittal) occupying about 0.5 width of axial ring (Fig. 2N).

Pygidial doublure very wide, extending under pygidial spines, most of the pleural field, and the entire post-axial field as well as a small part of terminal piece, where it forms a depressed area (Figs 2P, Q, 3A). Thin and densely-packed terrace ridges run subparallel to the margin (Fig. 2Q).

Occurrence. – From limestone in the upper part of the Kushan Formation, *Neodrepanura* Zone, uppermost Guzhangian Stage (Cambrian), Laiwu, Shandong, China.

Discussion. – Several hypostomes were assigned by Monke (1903, pl. 8, figs 7–9) to *Neodrepanura premesnili* shortly after its establishment. However, the hypostomes described by Monke were erroneously assigned to this species. Walcott (1913, pl. 10, fig. 2e) and Zhang & Jell (1987, pl. 106, fig. 6) described the correct hypostome of *N. premesnili*, but it was an incomplete specimen in which the anterior wings were broken off. Kobayashi (1942, pl. 2) published a reconstruction of *N. premesnili* that included not only the dorsal exoskeleton, but also the hypostome, and this reconstruction has been widely cited for more than half a century (*e.g.*, Moore 1959, p. 318, fig. 235). Kobayashi's reconstruction of the hypostome was based on the specimens assigned by Monke (1903, pl. 8, figs 10, 11) to *Stephanocare richthofeni*. Although these specimens might

Figure 1. *Neodrepanura premesnili* (Bergeron, 1899), from the Kushan Formation in Laiwu, Shandong, China. • A, B – ELEL-LW100010, complete exoskeleton in obliquely anterior view and close-up of partial cephalon. • C, D – ELEL-LW100020, incomplete exoskeleton in dorsal view and close-up of anterior portion of exoskeleton. • E–G – ELEL-LW100025, incomplete exoskeleton in ventral view, close-up of left part of pleural portion and close-up of right part of pleural portion; scale bars 8 mm in A, C, E and 3 mm in B, D, F, G.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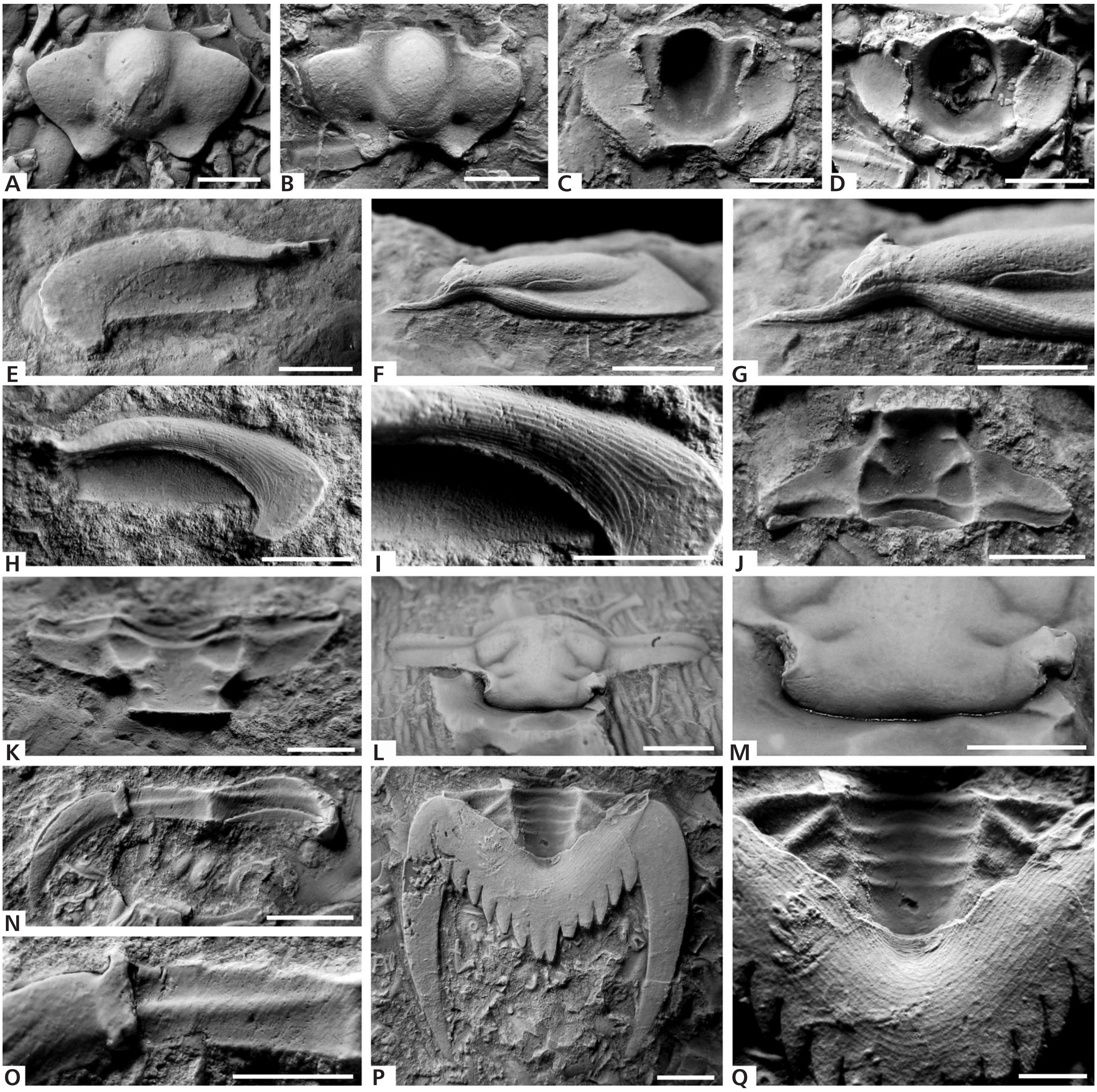

Figure 2. *Neodrepanura premesnili* (Bergeron, 1899), from the Kushan Formation in Laiwu, Shandong, China. • A – ELEL-LW100014, B – ELEL-LW100018, hypostome in ventral view; C – ELEL-LW100017, D – ELEL-LW100015, hypostome in dorsal view; E – ELEL-LW100023, librigena in ventral view; F, G – ELEL-LW100013, librigena in lateral view and close-up of anterior portion; H, I – ELEL-LW100024, librigena in ventral view and close-up of posterior portion of the doublure; J – ELEL-LW100016, cranidium in ventral view; K – ELEL-LW100026, cranidium in ventral and obliquely anterior view; L, M – ELEL-LW100021, cranidium in obliquely anterior view and close-up of anterior portion; N, O – ELEL-LW100019, thoracic segment in ventral view and close-up of anterior portion; P, Q – ELEL-LW100022, pygidium in ventral view and close-up of middle area. Scale bars 5 mm in F, L, N, P and 3 mm in A–E, G–K, M, O, Q.

belong to *N. premesnili*, our new materials demonstrate that Kobayashi's (1942) reconstruction is inaccurate, as the shoulders are reconstructed narrow (transverse) and rounded at the ends rather than sharp.

A rostral plate is lacking in some representatives of the order Asaphida, being replaced by a ventral median suture or conjoining ventrally (Fortey & Chatterton 1988, Fortey 1990, Park & Choi 2009). Our new materials demonstrate that the rostral plate is absent in *N. premesnili*; anteriorly, the doublures of the librigenae narrow and become increasingly incurved, reaching each other medially. This condition is rather unusual for a dameselloidean trilobite.

Although no specimens with articulated hypostomes have been observed, it seems from disarticulated material that the hypostomal condition of *N. premesnili* is of the conterminent condition described by Fortey (1990). The hypostome is inferred to have attached to the anterior librigenal doublure, and aligned with the anterior edge of the glabella.

Remarkable variety of trilobite exoskeletal shapes, particularly in the cephalon, can be explained as a response to the adoption of specific feeding habits. *N. premesnili* shows exoskeletal features that Fortey & Owens (1999) and Babcock (2003) described as consistent with a carnivorous (predator/scavenger) feeding habit. The conterminant hypostomal condition in *N. premesnili* may stabilize the hypostome against the cephalic exoskeleton, which would aid in processing prey. Lack of a rostral plate could lead to a strengthened anterior cephalic doublure. A pair of marginal spines on the hypostome of *N. premesnili*, which is similar to the fork present in some asaphids (Fortey & Owens 1999, Babcock 2003), may have been used as an aid to process bulky food and help prevent prey escape. Furthermore, the relatively expanded glabella of *N. premesnili* may have served to accommodate more food.

Most trilobites were capable of enrollment (*e.g.*, Moore 1959, Bergström 1973, Babcock 2003). Enrollment is complete when a posterior portion of the thorax or the pygidium was bought into contact with the ventrally or inwardly facing inner surfaces of the cephalic doublure (Clarkson & Whittington 1997). Among dameselloidean trilobites, many enrolled specimens of *Damesella* have been found (*e.g.*, Kobayashi 1942, pl. 5, figs 3–5). However, articulated sclerites of *N. premesnili* are so rare that no enrolled specimens have been discovered so far. Based on available material of *N. premesnili*, most of which is disarticulated, we infer that the fulcral structures in *N. premesnili* allowed for enrollment of the body, but the exoskeleton could not fully close laterally because the pleural spines would project around a lateral gap similar to that described in *Remopleurides* (Nikolaisen 1983, pl. 5; Chatterton & Campbell 1993, fig. 4).

Hypostomal morphology is of taxonomic significance in drepanurid trilobites. The hypostome of *N. premesnili* appears similar to that of *Palaeadotes hunanensis* (Peng *et al.* 2004, pl. 39, figs 3–5; pl. 57, figs 10–13). Hypostomes of the two species differ slightly in size and in proportions of the posterior lobe of the middle body. The posterior lobe is wider than the anterior lobe in *N. premesnili* but narrower in *P. hunanensis*. Hypostomes of two other drepanurid species, *Paradamesella typica* (Peng *et al.* 2004, pl. 42, fig. 5; pl. 43, fig. 2) and *Paradamesella peculiaris* (Peng *et al.* 2004, pl. 44, fig. 8) exhibit many more differences from the hypostome of *N. premesnili*. They are subquadrate in outline, the shoulders are very narrow (transverse) rather than wide (transverse), and the posterior marginal spines are short and blunt rather than sharp. These comparisons suggest *Neodrepanura* may be phylogenetically closer to *Palaeadotes* than to *Paradamesella*.

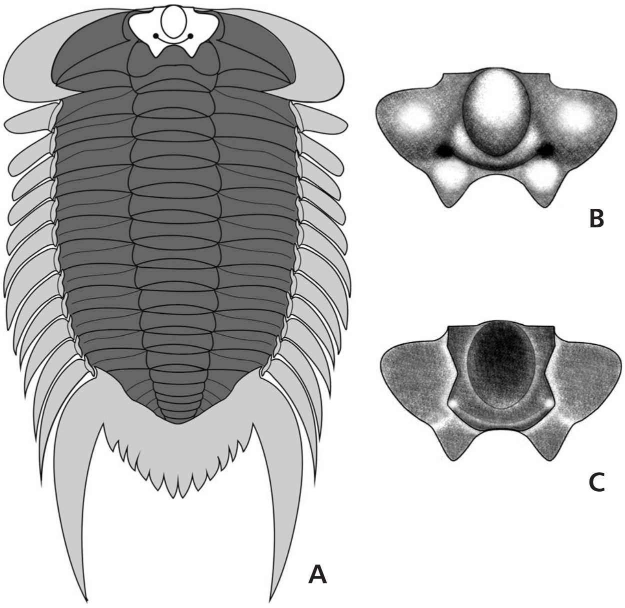

Figure 3. Reconstruction of *Neodrepanura premesnili* (Bergeron, 1899). • A – complete exoskeleton in ventral view; B – hypostome in ventral view; C – hypostome in dorsal view.

Acknowledgments

We particularly thank Shanchi Peng (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) for his great help with this study. We are grateful to Loren E. Babcock (The Ohio State University, Ohio, USA) and Frédéric B.M. Jacques (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) for providing helpful comments. We thank Haichun Zhang, Christopher Richard Hill, Jun Wang (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) and Robert W. Scott (University of Tulsa, Oklahoma, USA) for all their kindly help. The comments of the reviewers Rudy Lerosey-Aubril (Senckenberg Research Institute, Frankfurt am Main) and Jih-Pai Lin (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) are greatly acknowledged. Many thanks to the teachers, colleagues and friends who helped us in the writing process.

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