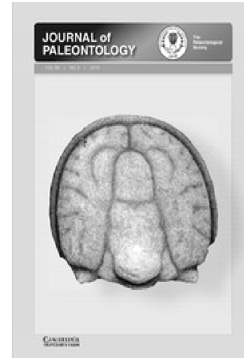

Cambrian series 3 agnostoid trilobites *Ptychagnostus sinicus* and *Ptychagnostus atavus* from the Machari Formation, Yeongwol Group, Taebaeksan Basin, Korea

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Journal of Paleontology / Volume 89 / Issue 03 / May 2015, pp 377 - 384
DOI: 10.1017/jpa.2015.30, Published online: 11 September 2015

Journal of Paleontology, 89(3), 2015, p. 377–384

0022-3360/15/0088-0906
doi: 10.1017/jpa.2015.30

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

Cambrian series 3 agnostoid trilobites *Ptychagnostus sinicus* and *Ptychagnostus atavus* from the Machari Formation, Yeongwol Group, Taebaeksan Basin, Korea

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Abstract.—This paper reports the successive occurrence of *Ptychagnostus sinicus* Lu, 1957 and *Ptychagnostus atavus* (Tullberg, 1880) from the lower part of the Machari Formation, Yeongwol Group, Korea. Morphometric approaches of using the landmark and principal component analyses make it possible to differentiate *P. sinicus* from *P. atavus* with clarity: pygidia of *P. sinicus* have a relatively narrow M1, a transverse F2, and a weakly developed M2 tubercle, whereas those of *P. atavus* are characterized by a broadly arching M1, a chevron-shaped F2, and a prominent M2 tubercle. Recognition of *P. atavus*, for the first time in Korea, allows the determination of the base of the Drumian Stage in Korea and aids correlation with other parts of the world.

Introduction

The Machari fauna of Korea has been well known to paleontologists in yielding abundant invertebrate fossils of Cambrian age (Kobayashi, 1962). The Machari fauna denotes the macroinvertebrate fossil assemblage from the Machari Formation of the Yeongwol Group, Taebaeksan Basin, Korea, and comprises diverse trilobites of Cambrian Series 3 to Furongian, with some inarticulate brachiopods, monoplacophorans, gastropods, and hyoliths. It was partly introduced by Kobayashi (1935) and later was comprehensively dealt with by him (Kobayashi, 1962). The Machari fauna has been intensively studied during the past two decades, with studies including taxonomic revision, biostratigraphy, and paleogeographic reconstructions (Lee and Choi, 1994, 1995, 1996; Choi and Lee, 1995; Hong et al., 2003a, 2003b; Choi et al., 2004, 2008; Choi and Kim, 2006). A total of ten trilobite biozones have been established in the Machari Formation, and in ascending order, comprise the *Tonkinella*, *Lejopyge armata*, *Glyptagnostus stolidotus*, *G. reticulatus*, *Proceratopyge tenuis*, *Hancrania brevilimbata*, *Eugonocare longifrons*, *Eochuangia hana*, *Agnostotes orientalis*, and *Pseudoyuepingia asaphoides* zones (Choi and Chough, 2005).

First appearance data of agnostoid trilobite species offer precise reference points for high-resolution global correlation in the upper half of the Cambrian System. For instance, *Ptychagnostus* Jaekel, 1909, includes such types of cosmopolitan species that occur in ascending order in the lower to middle interval of the traditional middle Cambrian (Robison, 1982, 1984): namely, *Ptychagnostus praecurrens* (Westergård, 1936), *Ptychagnostus gibbus* (Linnarsson, 1869), *Ptychagnostus atavus* (Tullberg, 1880), and *Ptychagnostus punctuosus* (Angelin, 1851). Of these, *P. atavus* exhibits a global distribution, and consequently has been selected by the International Subcommission on Cambrian Stratigraphy to define the Global Stratotype Section and Point (GSSP) of the middle stage of the tripartite Cambrian Series 3, i.e., the Drumian Stage (Babcock et al., 2007).

In this study, we report, for the first time in eastern Asia, the successive occurrences of *Ptychagnostus sinicus* Lu, 1957 and *P. atavus* from the lower part of the Machari Formation, in a newly discovered section in the western part of Yeongwol. This study also attempts to evaluate the species concept of *P. sinicus* and to reveal how it differs significantly from *P. atavus*.

General geology and fossil locality

The Taebaeksan Basin occupies the mid-eastern region of the Korean Peninsula and comprises the Cambrian-Ordovician Joseon Supergroup and the Carboniferous-Permian Pyeongan Supergroup, which are separated by a ~140-myr-long hiatus (Chough et al., 2000). The Joseon Supergroup is a mixed carbonate-siliciclastic succession of shallow marine origin and has been divided into the Taebaek, Yeongwol, Yongtan, Pyeongchang, and Mungyeong groups (Choi, 1998; Choi and Chough, 2005).

The Yeongwol Group is divided, in ascending order, into the Sambangsan, Machari, Wagok, Mungok, and Yeongheung formations (Yosimura, 1940; Kobayashi, 1966; Choi, 1998; Choi and Chough, 2005). The lowermost Sambangsan Formation is composed exclusively of siliciclastic sediments, whereas the upper four formations are dominated by carbonates. The base of the Machari Formation comprises thick-bedded bioclastic grainstone/packstone beds that contain well-preserved middle Cambrian trilobites belonging to the genera *Tonkinella*, *Olenoides*, *Dorypyge*, and *Peronopsis*.

These beds are succeeded by dark gray dolomitic limestone and black shale in the lower part of the formation. The middle part is characterized by laminated dark gray to black shale with occasional intercalations of thin dolomitic limestone layers and yields diverse trilobites of Furongian age (Lee and Choi, 1994, 1995, 1996; Choi et al., 2004, 2008). The upper part displays a conspicuous banded appearance, composed of alternating units of thin-bedded, light gray dolomitic limestone and black shale layers. The banded structure becomes obscure in the uppermost part of the formation and grades upward into massive dolostone of the overlying Wagok Formation. The lower and middle parts of the Machari Formation are richly fossiliferous, whereas the upper part is generally poorly fossiliferous.

The newly discovered Deoksang section (37°16'50"N, 128°22'40"E), is located at a road cut about 13 km northwest from Yeongwol (Fig. 1) where the Sambangsan Formation and the lower part of the Machari Formation occur in superpositional order. The lowermost 10 m thick interval of the Machari Formation is particularly well exposed: the lower 6 m thick interval of massive bioclastic grainstone beds yields well-preserved trilobites of the *Tonkinella* Zone and the overlying 4 m thick interval is characterized by alternating units of dark gray wacke- to packstone and black shale. This upper interval yields well preserved trilobites belonging to Cambrian Stage 5 to the Paibian Stage. *Ptychagnostus sinicus* occurs at three fossil horizons, 6 m, 6.8 m, and 6.9 m above the base of the formation, whereas *P. atavus* is restricted to one fossil horizon 7.0 m above the base of the formation. *Ptychagnostus sinicus* is associated with *Peronopsis taitzuhoensis* Lu (1957) at the lowermost horizon, whereas *P. atavus* is associated with *Yakutiana ovale* (Yang, 1982).

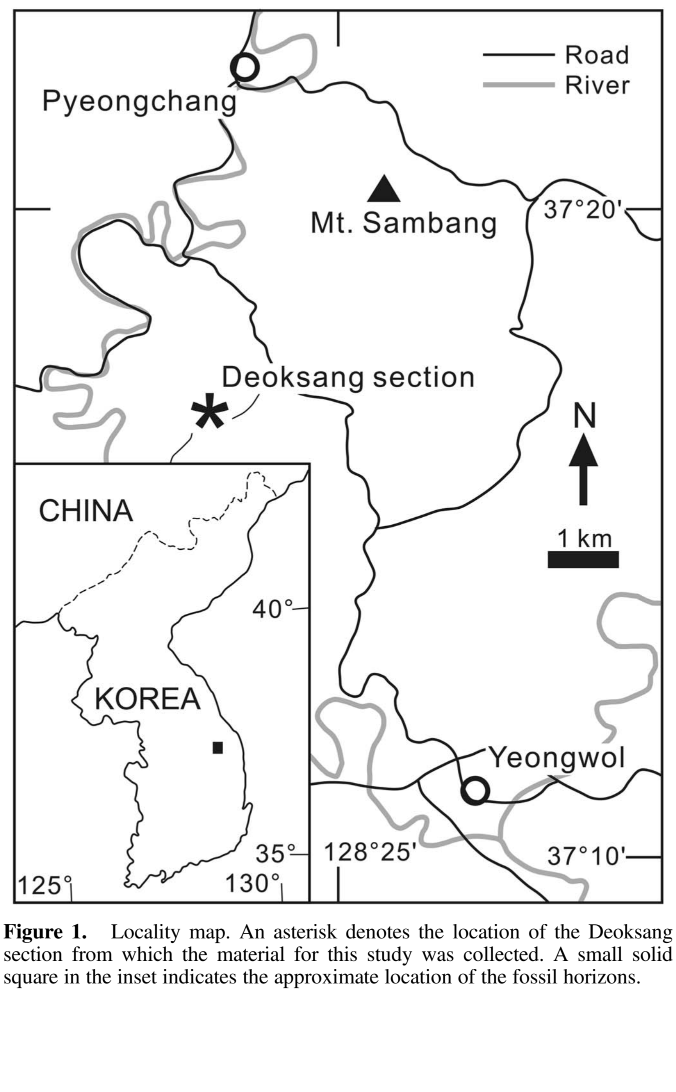

Figure 1. Locality map. An asterisk denotes the location of the Deoksang section from which the material for this study was collected. A small solid square in the inset indicates the approximate location of the fossil horizons.

Systematic paleontology

Morphological terms used herein are adopted from Whittington and Kelly (1997) and from Peng and Robison (2000). Specimens are stored at the Seoul National University in Korea with designated SNUP numbers.

Class Trilobita Walch, 1771
Order Agnostida Salter, 1864
Family Ptychagnostidae Kobayashi, 1939
Genus *Ptychagnostus* Jaekel, 1909

Type species.—*Agnostus punctuosus* Angelin, 1851 from the *P. punctuosus* Zone of the Alum Shale (Drumian), Sweden (by original designation). Official ruling on the conservation of accepted usage of *A. punctuosus* as the type species was given by the International Commission on Zoological Nomenclature, 1993.

Remarks.—There are disparate views on the taxonomy of the genus *Ptychagnostus* and its relationship with other genera or subgenera that include *Acidusus* Öpik (1979), *Triplagnostus* Howell (1935), *Yakutiana* Özdikmen (2009) among others. Monophyly of these taxa had been rejected (Westrop et al., 1996) or accepted (Laurie, 2008), presumably due to differences in morphological characters selected for analyses. A complete taxonomic assessment of *Ptychagnostus* is beyond the scope of this study, and a more broad definition of *Ptychagnostus* suggested by Peng and Robison (2000) is herein followed.

Ptychagnostus atavus (Tullberg, 1880)
Figure 2.1–2.8

1880 *Agnostus atavus* Tullberg, p. 14, pl. 1, figs. 1a–1d.
1880 *Agnostus intermedius* Tullberg, p. 17, pl. 1, figs. 4a–4b.
1909 *Ptychagnostus atavus*; Jaekel, p. 400.
1980 *Ptychagnostus intermedius*; Ergaliev, p. 69–70, pl. 1, figs. 18–20.
1988 *Acidusus atavus*; Laurie, p. 180, fig. 5.
2000 *Ptychagnostus atavus*; Peng and Robison, p. 69–70, fig. 52.
2006 *Acidusus atavus*; Fletcher, pl. 34, figs. 43, 44.
2007 *Ptychagnostus atavus*; Ahlberg, Axheimer, and Robison, p. 710–713, figs. 2.1–2.12 (for additional synonymy).
2007 *Ptychagnostus atavus*; Babcock, Robison, Rees, Peng, and Saltzman, figs. 6B–6D, 7B.
2008 *Ptychagnostus atavus*; Høyberget and Bruton, p. 49–50, pl. 7, figs. G–M.
2009 *Acidusus atavus*; Weidner and Nielsen, p. 259–260, figs. 8A–8D, 10A, 10B.
2014 *Acidusus atavus*; Weidner and Nielsen, p. 32–35, figs. 9, 10A–D, 11A–H, 12F–H.

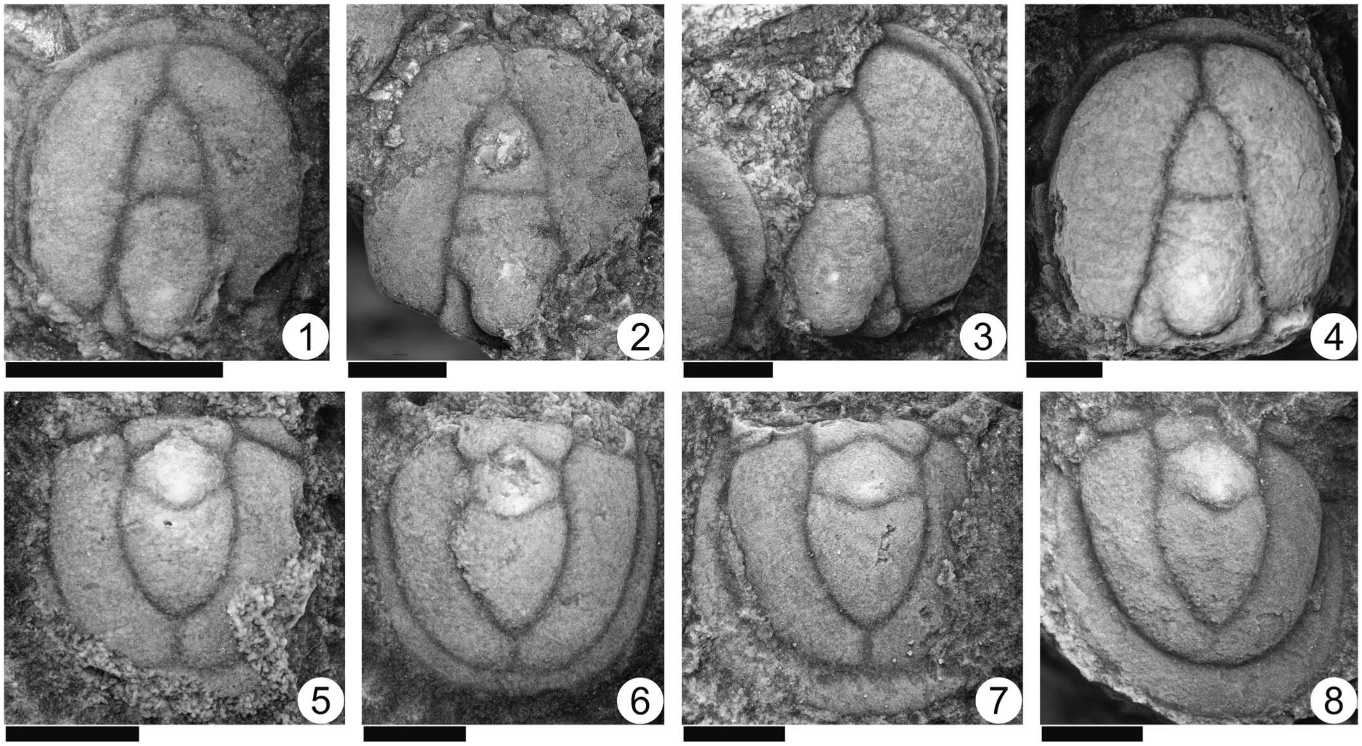

Figure 2. *Ptychagnostus atavus* (Tullberg, 1880) from the lower part of the Machari Formation in the Deoksang section, Yeongwol, Korea. (**1–4**) cephala, SNUP6311–6314; (**5–8**) pygidia, SNUP6315–6318. All scale bars represent 1 mm.

Occurrence.—Ten cephala and 22 pygidia from the horizon 7.0 m above the base of the Machari Formation at the Deoksang section.

Remarks.—The first appearance datum of *P. atavus* defines the base of the Drumian Stage of Cambrian Series 3 (Babcock et al., 2007), and this species has been thoroughly treated by Peng and Robison (2000) and Ahlberg et al. (2007).

Ptychagnostus atavus differs from other species of *Ptychagnostus* in lacking cephalic and pygidial spines and surface granules, and in having a hexagonal M2 on the pygidial axis. Although variations in the degree of scrobiculation on the genae have been known to range from smooth to moderately scrobiculate (Robison, 1982, pl.1. figs. 1–9; 1984, fig. 11), all the specimens from the Deoksang section are uniformly smooth. In addition, the width of the pygidial border is variable.

Ptychagnostus sinicus Lu, 1957
Figure 3.1–3.16

1954 *Ptychagnostus richmondensis* (Walcott); Palmer, p. 61–62, pl. 13, fig. 5 (part).
1957 *Ptychagnostus sinicus* Lu, p. 259, pl. 137, figs. 17–19.
1965 *Ptychagnostus sinicus*; Lu, Chang, Chu, Chien, and Hsiang, p. 37–38, pl. 3, figs. 16–18.
1979 *Ptychagnostus* (*Ptychagnostus*) *idmon* Öpik, p. 95–96, pl. 43, figs. 5–8.
1979 *Ptychagnostus* (*Ptychagnostus*) *intermedius*; Öpik, p. 95, pl. 41, fig. 8.
1979 *Ptychagnostus* (*Ptychagnostus*) *scarifatus* Öpik, p. 96–97, pl. 44, figs. 1–5, pl. 58, fig. 2.
1979 *Ptychagnostus* (*Ptychagnostus*) sp. aff. *scarifatus* Öpik, p. 97, pl. 44, fig. 6.
1980 *Ptychagnostus sinicus*; Nan, p. 484, pl. 200, figs. 7, 8.
1980 *Ptychagnostus atavus*; Ergaliev, P. 67–69, pl. 1, figs. 13–17.
1982 *Ptychagnostus intermedius*; Robison, 1982, p. 143–145, pl. 3, figs. 1–9.
1982 *Ptychagnostus intermedius*; Rowell, Robison, and Strickland, p. 161–182.
non 1983 *Ptychagnostus sinicus*; Qiu, Lu, Zhu, Bi, Lin, Zhou, Zhang, Qian, Ju, Han, and Wei, p. 37, pl. 12, fig. 15 (? = *P. atavus*).
1984 *Ptychagnostus intermedius*; Robison, p. 25–28, figs. 15.1–15.7.
1988 *Ptychagnostus intermedius*; Lisogor, Rozov, and Rozova, p. 56–57, pl. 4, figs. 1–4.
1988 *Zeteagnostus scarifatus*; Laurie, p. 178, figs. 4A–H.
1989 *Ptychagnostus sinicus*; Sun, p. 76–77, pl. 4, figs. 9–21.
1994 *Ptychagnostus intermedius*; Robison, p. 56–57, figs. 27.7, 27.8.
1996 *Ptychagnostus sinicus*; Guo, Zan, and Luo, p. 50, pl. 1, figs. 1–6.
1999 *Ptychagnostus sinicus*; Luo, pl. 7, figs. 1, 2.
2000 *Ptychagnostus intermedius*; Peng and Robison, p. 80.

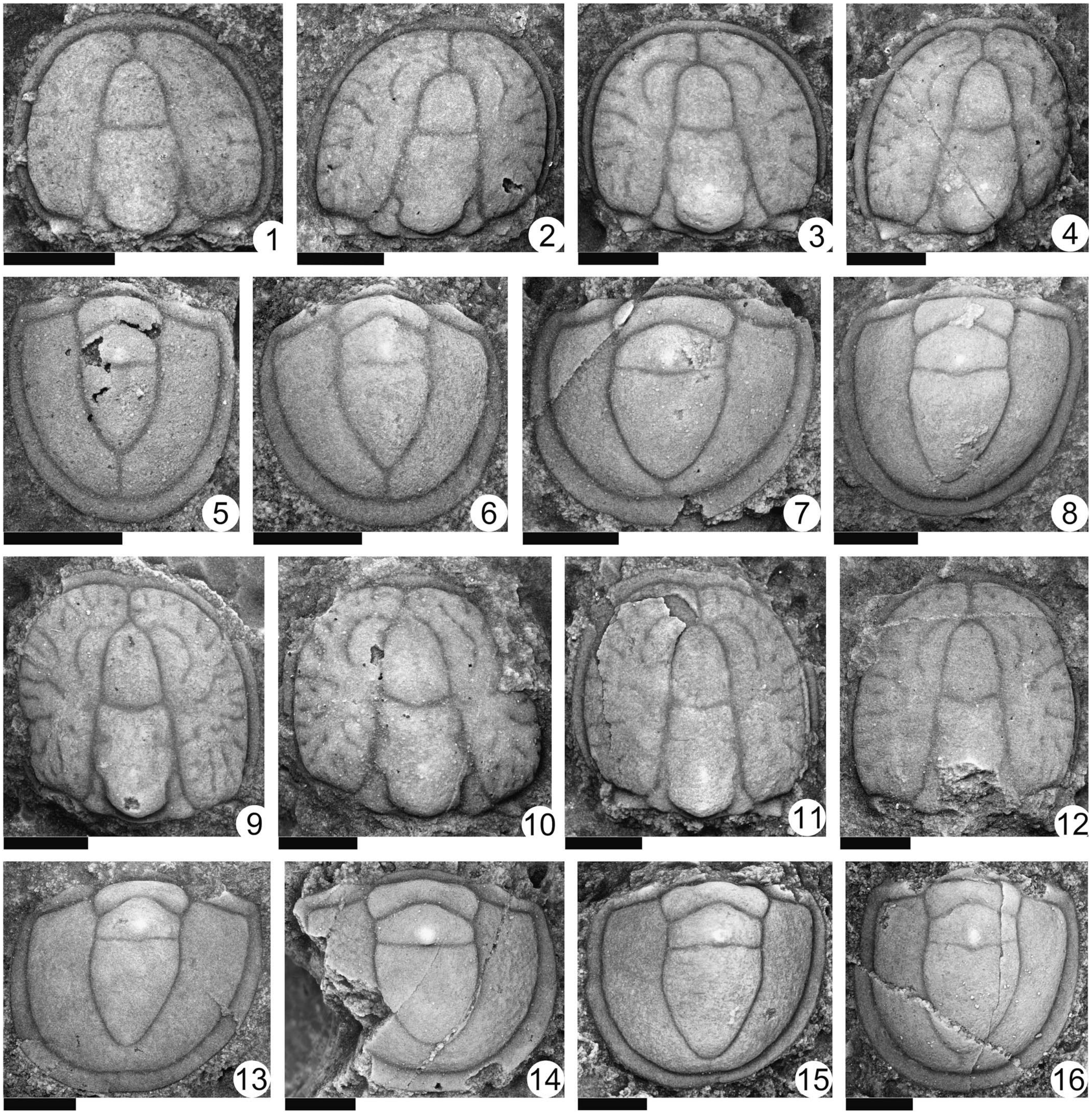

Figure 3. *Ptychagnostus sinicus* Lu, 1957 from the lower part of the Machari Formation in the Deoksang section, Yeongwol, Korea. (**1–4, 9–12**) cephala, SNUP6319–6322, SNUP6327–6330; (**5–8, 13–16**) pygidia, SNUP6323–6326, SNUP6331–6334. All scale bars represent 1 mm.

2007 *Ptychagnostus sinicus*; Ahlberg, Axheimer, and Robison, p. 712.

2007 *Ptychagnostus intermedius*; Bordonaro and Banchig, figs. 2N–P.

2008 *Ptychagnostus intermedius*; Bordonaro, Banchig, Pratt, and Raviolo, p. 121, figs. 4N–P.

2012 *Ptychagnostus* (*Acidusus*) *sinicus*; Yuan, Li, Mu, Lin, and Zhu, p. 62–63, pl. 4, figs. 1–16, pl. 5, figs. 1–4.

Types.—A cephalon from the Tangshih Formation in Benxi, east-central Liaoning, North China (Lu, 1957, pl. 137, fig. 17; re-illustrated by Lu et al., 1965, pl. 3, fig. 16) has been selected as the lectotype by Yuan et al. (2012, p. 63).

Diagnosis.—A species of *Ptychagnostus* with pentagonal pygidial M2, smooth acrolobe surfaces without pustules or granules, and no border spines on the cephalon or pygidium.

Occurrence.—Eighty-two cephala and more than one hundred pygidia were collected from three horizons, 6.0 m, 6.8 m, and 6.9 m above the base of the Machari Formation in the Deoksang section. Aside from the type locality in east-central Liaoning, occurrences in North China include the *Bailiella* Zone (Nan, 1980; Sun, 1989) and the *Crepicephalina* Zone (Guo et al., 1996) of the Hsuchuang Formation, southern Liaoning, and the upper *Tonkinella flabelliformis*–*Poriagraulos nanus* Zone and the lower *Bailiella lantenoisi* Zone of the Changhsia Formation, central Shandong (Yuan et al., 2012). This species has also been known to occur in the *P. intermedius* Zone in the Kyrshabakty section of Malyi Karatau, Kazakhstan (Ergaliev, 1980; Lisogor et al., 1988; Ergaliev et al., 2008); *P. atavus* and *Euagnostus opimus* zones of the Inca Formation, Queensland, Australia (Öpik, 1979); *P. gibbus* Zone of the Wheeler Formation and coeval formations in Utah and Nevada, USA (Palmer, 1954; Robison, 1982; Babcock et al., 2007); the Henson Gletscher Formation, northern Greenland (Robison, 1984, 1994); and the Alojamiento Formation, Precordillera, Argentina (Bordonaro and Banchig, 2007).

Description.—Cephalon semielliptical, with narrow border and border furrow, without posterolateral spines. Acrolobe unconstricted; genal field scrobiculate, with a pair of crescent-shaped furrows opposite anteroglabella, without pustules or granules; median preglabellar furrow well developed. Glabella about four-fifths of cephalic length; anteroglabella about two-fifths of glabellar length, subtriangular in outline; F3 posteriorly curved medially; posteroglabella tapering forward, constricted near F3; F2 weakly impressed near axial furrow; axial glabellar node, small, circular, positioned posterior to M2 mid-length. Basal lobe elongate, weakly divided.

Pygidium semielliptical, with moderately broad border and narrow border furrow, without posterolateral spines. Acrolobe unconstricted; pleural field smooth, without pustules or granules; postaxial median furrow moderately to weakly developed. Axis about one-third of pygidial width, constricted across M2, with maximum width at anterior quarter of posteroaxial length; anteroaxis about two-fifths of axial length; M1 arched, of even length (sag., exsag.) or slightly shorter medially; F1 anteriorly curved, of even depth or slightly shallower medially; M2 pentagonal in outline; median tubercle small, circular, positioned near F2; F2 straight to slightly flexed toward posterior; posteroaxis with pointed to rounded posterior end.

Remarks.—*Ptychagnostus sinicus* and *P. atavus* differ from all other species of the genus in having smooth acrolobe surfaces without pustules or granules and in lacking border spines on the cephalon and pygidium. However, it has been difficult to differentiate the two species, because *P. atavus* has been known to display a wide range of variation in morphological characters such as scrobiculation of the genal region, whether arcuate scrobicules are present opposite anteroglabella, position of the median node on glabellar M2, and relative width of the pygidial border (Robison, 1982; Ahlberg et al., 2007).

Morphological variation in the pygidial F2 of *P. atavus* has been responsible for the taxonomic confusion of the species with other species including *P. intermedius*, *P. sinicus*, and *P. affinis* (Brøgger, 1878). *Ptychagnostus atavus* and *P. intermedius* were established by Tullberg in 1880 among the collections from the *P. atavus* Zone of the Alum Shale in the Andrarum area of southern Sweden. Tullberg (1880) differentiated the two species based on the difference in the course of the pygidial F2 furrow. As is clear from the plates of Tullberg (1880) and illustrations of Tullberg's syntypes by Westergård (1946), *P. atavus* possesses a V-shaped F2 furrow, whereas F2 furrow of *P. intermedius* is more or less straight. Accordingly, *Ptychagnostus* species with comparatively straight F2 documented subsequently in Laurentia, Australia, Kazakhstan, and Argentina were referred to as *P. intermedius*. However, re-examination of Tullberg's original collections by Ahlberg et al. (2007) revealed that the degree of flexure of the F2 furrow in specimens assigned to *P. intermedius* is well within the range of variation of *P. atavus*. Tullberg's hand-drawn figures of *P. intermedius* did not show the true degree of the curvature, and re-illustration of the original collections by Westergård (1946) widely referenced by subsequent researchers were found to be retouched to emphasize the straightness of the F2 furrow (Ahlberg et al., 2007, p. 712). In addition, original materials of *P. atavus* and *P. intermedius* by Tullberg (1880) were collected from the *P. atavus* Zone (Ahlberg et al., 2007), whereas non-Baltic specimens assigned previously to *P. intermedius* all occur in zones equivalent to the *P. gibbus* Zone that lies immediately below the *P. atavus* Zone. The relatively less known species, *P. sinicus*, was established by Lu in 1957 from the *Bailiella* Zone (approximately equivalent to the *P. gibbus* Zone) of the Tangshih Formation of Liaoning, China. It is characterized by a straight F2 furrow on the pygidium and hence non-Baltic specimens that were previously assigned to *P. intermedius* should be reassigned to *P. sinicus*.

Landmark-based geometric morphometrics were used to test the significance of shape differences between *P. atavus* and *P. sinicus*. Nine landmarks were selected on the M1 and M2 of the pygidium that correspond to right/left, antero-/postero-lateral corners and three axial points of M1 and M2 (Fig. 4.1). A total of 66 specimens were digitized using the NIH ImageJ software (Abràmoff et al., 2004) and all analytical processes were performed with the IMP software series (Sheets, 2012): three specimens of *P. atavus* and 13 specimens of *P. sinicus* from the Deoksang section, and 28 specimens of *P. atavus* and 22 specimens of *P. sinicus* from illustrations of previous studies (see Supplementary Data 1). Superimposition of the mid-point landmark of the F2 furrow displays the visual difference between the two species (Fig. 4.2). Regressions of partial Procrustes distance against the natural logarithm of the centroid size for both species did not identify any significant shape changes with size increase, and suggest that shape variations present in the dataset is not due to ontogeny. The amount of shape deviation for each specimen can be quantified by assessing the displacement vectors of landmarks from the reference form (in this case, the consensus of all configurations in a partial Procrustes superimposition). Following the thin-plate spline method, the deviation matrix of all specimens are first decomposed into mathematically independent styles of deformation (warps) and its contribution to each deformation (warp scores), and then the principal component analysis is performed on the warp scores to examine the structure of the shape variations present in a dataset (Webster and Sheets, 2010).

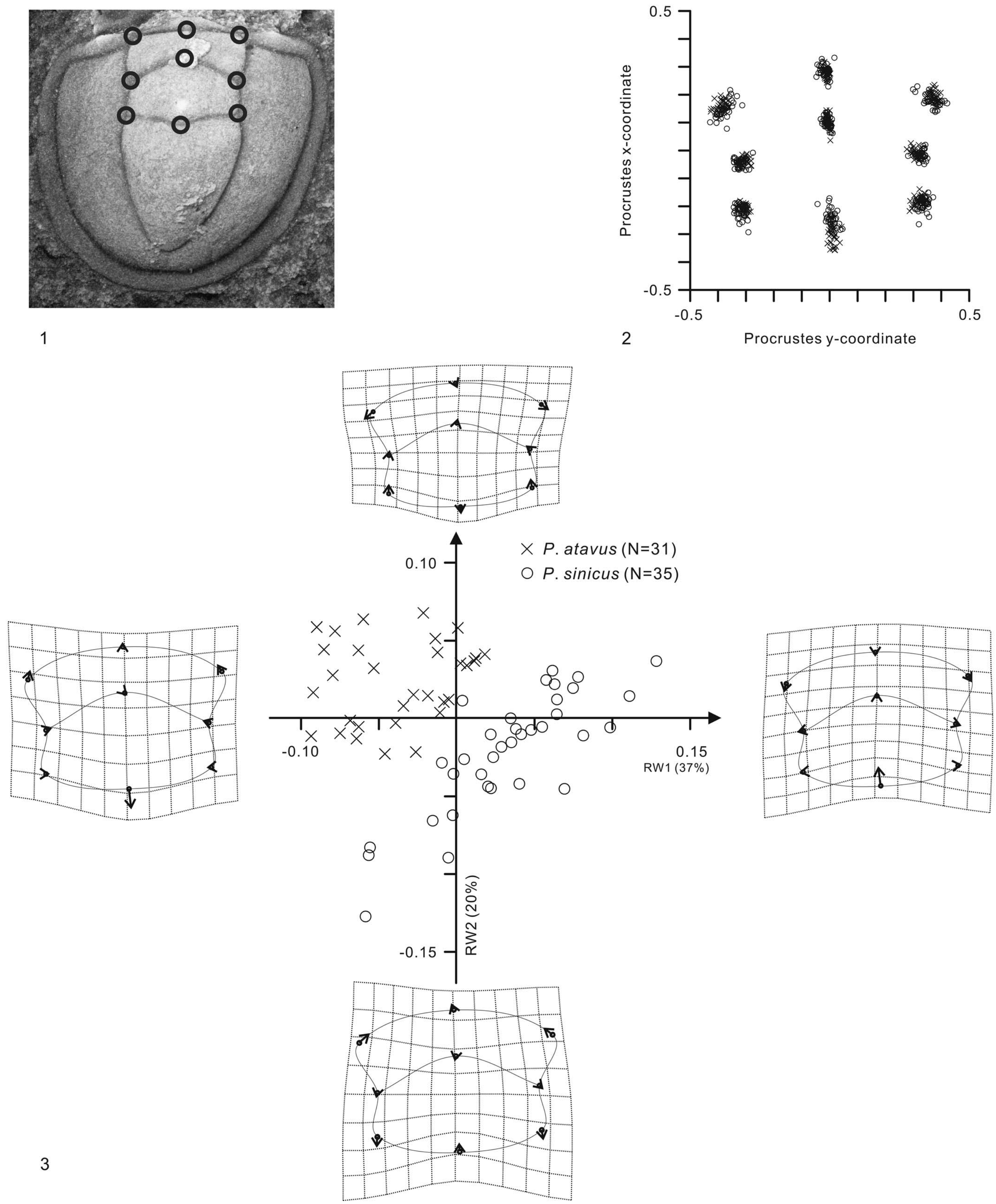

Figure 4. Landmark data analyses employing 31 pygidia of *Ptychagnostus atavus* (Tullberg, 1880) and 35 pygidia of *Ptychagnostus sinicus* Lu, 1957. (**1**) location of nine landmarks recorded from each pygidium at dorsal view; (**2**) partial Procrustes superimposition of 66 specimens; (**3**) bivariate plot of the specimens on the first two relative warps RW1 and RW2 from the principal component analysis of warp scores; RW1 and RW2 explain 37% and 20% of the total shape variance, respectively; thin-plate spline deformation grids depict shape variation along each relative warp; and arrows on landmarks of thin-plate spline deformation grids express relative displacements (Zelditch et al., 2004).

Results (Fig. 4.3) show that the first and second principal components (termed relative warps) account for 37% and 20% of the total shape variance, respectively, and that the two species are significantly different with the degree of flexure of the pygidial F2 furrow being the major component in the morphological variations, and with abaxial-widening and posteriorly-arching of the anterolateral regions of the pygidial M1 being the second component. Although variations in the pygidial F2 furrow of the two species overlap (Fig. 4.2), the two species are clearly differentiated when the information on the shape of anterolateral regions of the pygidial M1 (Fig. 4.3) is considered.

In summary, *P. atavus* and *P. sinicus* can be distinguished on the basis of the shape of M1 and the course of pygidial F2 furrow in association with the median tubercle on the pygidial M2: *P. atavus* has a broadly-arching M1, a chevron-shaped pygidial F2, and a prominent median tubercle that medially flexes the posterior margin of M2, whereas *P. sinicus* is characterized by having a relatively narrow M1, a transverse pygidial F2, and a weakly developed tubercle on M2.

Biostratigraphic significance

Ptychagnostus sinicus and *P. atavus* occur successively and do not overlap in their stratigraphic distribution in the Deoksang section. Such occurrences have also been documented in Kazakhstan (Ergaliev, 1980; Ergaliev et al., 2008) and North America (Robison, 1982; Babcock et al., 2007). However, in Kazakhstan and North America *P. sinicus* has been known to occur in association with *P. gibbus*. The co-occurrence of *P. sinicus* and *P. gibbus* has also been reported in Australia (Öpik, 1979) and Greenland (Robison, 1984, 1994). In Australia, Öpik (1979) reported the occurrences of *Ptychagnostus* from the Inca Formation of the Georgina Basin in which one locality (M208) yielded *P. sinicus*, *P. gibbus*, and *P. atavus*, whereas three localities (M149, M170, and M176) produced *P. sinicus* and *P. gibbus*.

In North America, *P. sinicus* and *P. gibbus* first appeared in the *P. gibbus* Zone (Robison, 1982, 1984; Babcock et al., 2007): *P. sinicus* is restricted to the *P. gibbus* Zone, while *P. gibbus* is extendeds into the overlying *P. atavus* Zone. In North China, *P. sinicus* occurs in the *Tonkinella flabelliformis*-*Poriagraulos nanus* and *Bailiella lantenoisi* zones in Shandong province, both of which can be correlated with the *P. gibbus* Zone of South China (Yuan et al., 2012). Therefore, it can be concluded that the stratigraphic occurrences of *P. sinicus* appear to be restricted within an age equivalent to the *P. gibbus* Zone and can be used as a guide fossil for intercontinental correlation. In Korea, the boundary between the Cambrian Stage 5 and the Drumian Stage can be confidently drawn at the *P. atavus*-yielding horizon, 7 m above the base of the Machari Formation at the Deoksang section.

Acknowledgments

We are grateful to John Laurie, Steve Westrop, and an anonymous reviewer for their constructive suggestions and linguistic corrections. Thanks are extended to Sangmin Lee, Seung-bae Lee, Jusun Woo, Tae-yoon Park, Ji-hoon Kihm, Dong Yeong No, and Seungyun Kim for discussions during this work and for their help in the field. Xuejian Zhu and Yang Zhang helped us providing with references. This work was supported by a grant (Grant No. 2011–0013164) from the National Research Foundation of Korea. This paper is a contribution of the BK21 Project of the School of Earth and Environmental Sciences, Seoul National University.

Supplemental data

Supplemental data deposited in Dryad data package: http://dx.doi.org/10.5061/dryad.j0fc6

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Accepted 7 July 2015