J. Paleont., 82(4), 2008, pp. 842–850
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0022-3360/08/0082-842$03.00

THE OLDEST KNOWN STALK-EYED TRILOBITE, *PARABLACKWELDERIA* KOBAYASHI, 1942 (DAMESELLINAE, CAMBRIAN), AND ITS OCCURRENCE IN SHANDONG, CHINA

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ABSTRACT—*Parablackwelderia* is the oldest known stalk-eyed trilobite and thrived during the middle–late Cambrian (Guzhangian Age) in eastern Gondwanaland. The elongated palpebral lobe extends outward and forward from the anterior corner of the cranidium and shows positive allometry, becoming markedly longer and relatively thinner in large specimens. The animal occurred in muddy environments and may have been a predator that burrowed for concealment. Stalked-eyes were independently derived in several trilobite clades, but whenever they appeared were restricted to small numbers of taxa and thus do not appear to have served as a key innovation that promoted extensive diversification of species bearing the structure. The stalk-eyed condition in trilobites has a striking modern analog in the hypercephaly of diopsinid flies, where it is commonly associated with mate recognition and mate selection. We document the first occurrence of *Parablackwelderia* in Shandong, North China and describe a new species, *Parablackwelderia luensis* sp. nov.

INTRODUCTION

THE OLDEST eyes known in the geological record are those of trilobites, a clade of early euarthropods whose evolutionary history is richly chronicled in the fossil record due to their biomineralized calcitic exoskeleton. The visual surface of the trilobite eye was made of calcite, the optical properties of which have been studied extensively and provide elegant examples of functional inferences that can be drawn from extinct organisms (e.g., Clarkson, 1966, Towe 1973, Clarkson and Levi-Setti, 1975, Clarkson 1997, Clarkson et al., 2006). Not only can the optics of individual lenses be understood, but the size and outline form of individual lenses within the eye can be used to infer the levels of illumination to which the eye was adapted (McCormick and Fortey, 1998). Results can then be tested against other kinds of evidence of ecology, such as geographic distribution and facies preference, to make cogent arguments for particular life habits (e.g., Fortey, 1985). In this paper we describe the earliest example of a different but striking morphological feature associated with the trilobite eye, the development of stalked eyes that elevated the visual surface high above the remainder of the dorsal exoskeleton. Remarkably, stalked eyes of similar form appeared repeatedly and evidently independently during trilobite evolution, occurring in trilobites of disparate morphology and distant phylogenetic relationship. To date, all documented examples have been trilobites of post-Cambrian age and belong to derived clades known for complex morphological embellishments (Hughes, 2007). In this paper we describe the occurrence of stalked eyes in a middle-late Cambrian trilobite that, although displaying a quite complex morphology, is relatively basal within the clade as a whole. We also review the form and occurrence of stalked eyes throughout Trilobita and evaluate what inferences can be made as to their likely function.

CASES OF THE STALK-EYED CONDITION IN TRILOBITES

Parablackwelderia Kobayashi, 1942 is the oldest known stalk-eyed trilobite, being the only Cambrian trilobite known to possess this structure. It thrived during the Guzhangian Stage, which lasted from about 503 to about 499 Ma ago, in rocks traditionally considered of late middle to early late Cambrian age, and it occurs widely in China, Australia, India, N. Korea, and Kazakhstan.

Post-Cambrian stalk-eyed trilobites are also uncommon, with only a few species assigned to families Asaphidae, Encrinuridae, and Odontopleuridae, (belonging to the orders Asaphida, Phacopida, and Lichida respectively) of which the well-known stalk-eyed trilobites include *Asaphus* (*Neoasaphus*) *kowalewskii* Lawrow, 1856 from the Middle Ordovician near St. Petersburg, Russia, *Cybellela rex* (Nieszkowski, 1857) from the Upper Ordovician of Estonia, both of which occur in light colored micritic limestones, and *Miraspis mira* (Barrande, 1846) from the Wenlockian (Silurian) of Bohemia, which occurs in a dark colored, organic-rich siltstone. The sporadic appearance of the feature and considerable phylogenetic distance between all of these taxa (Fortey, 1997) confirm that occurrence of the stalked eye was independently derived in each major clade. In each case stalked eyes characterize either single species or single genera. This suggests that although the structure arose convergently in several major groups of trilobites, in no case did its evolution serve as an adaptive ''key innovation'' that resulted in a notably species-rich clade characterized by possession of the structure. Although the structure was consistently associated with fine-grained sediments, the pattern of taxonomic occurrence might imply that the structure was adaptively advantageous only in rather specific settings, a conclusion supported by occasional co-occurrence in the same beds of stalked-eye-bearing trilobites belonging to disparate clades (for example, *Asaphus* (*Neoasaphus*) *kowalewskii* Lawrow, 1856, and *Cybele panderi* Schmidt, 1907 in the Middle Ordovician Wolchow bei Obuchowo locality near St. Petersburg).

The proportional length of the stalked eye in *Parablackwelderia* is greater than in any other stalk-eyed trilobite, as its palpebral lobe is elevated as much as 1.5 times the length of the cephalon or twice to three times the height of the maximum convexity of the cephalon judging from a cranidium of *Parablackwelderia* cf. *huabeiensis* preserved in a dark colored argillaceous limestone (Peng et al., 2004, pl. 31, figs. 8–12). The asaphids *A.* (*Neoasaphus*) *kowalewskii* and *Ectenaspis beckeri* (Slocum, 1913), which are from the Middle and Upper Ordovician respectively, are also long stalk-eyed trilobites, but the palpebral lobe is elevated only to a height about that of the cephalic length in the former and half of the cephalic length in the latter (excluding the anterior projection in that species). *Ectenaspis beckeri* occurs within light colored carbonate-rich mudstones. In *A.* (*Neoasaphus*) *kowalewskii*, the palpebral lobe is elevated probably about twice the maximum height of the rest of the cephalon (Woodward, 1868, pl. 21, figs. 4, 5). Most of the stalk-eyed trilobites have their eyes modestly elevated, with a height usually no more than half of the glabella length or even shorter, as seen in the late Ordovician and Silurian odontopleurid and encrinurid genera bearing the eye stalk. A faked long stalk-eyed species of *Calymene* (Calymenidae), *Calymene ceratophthalma*, was described from the Silurian formation at Dudley, England (Woodward, 1868), and was actually an artificially enhanced specimen of *C. blumenbachii* (Mikulic and Kluessendorf, 2007).

LIFE HABITS

A recurrent attribute of trilobites bearing stalked eyes is their occurrence in fine-grained muddy sediments, whether carbonate or clastic. This setting is concordant with interpretations of the morphology that suggest a life habit partially submerged beneath a blanket of mud. Ingham (1968) considered the stalk-eye-bearing *Cybeloides* had a burrowing habit on the basis of its elevated eyes and the form of the marginal spines on the trunk. *Cybeloides* is an Ordovician encrinurid characterized by having short stalked eyes, a thorax with the last six segments bearing long pleural spines, and a pygidium bearing slender marginal spines. The stalked eyes were inferred to remain above the sediment surface as the animal buried into sediment. The macropleural spines on the sixth segment were considered to be partly stabilizing in function, and they may have prevented excessive lateral rolling during flexure of the thorax while burrowing, whereas backward directed spines were possibly protective in function. Although we cannot evaluate the details of this interpretation, the consistent and repeated relationship between muddy substrates and the occurrence of stalked eyes suggests that elevation of the eye above the remainder of the exoskeleton was advantageous in such settings.

Parablackwelderia had an analogous overall morphology to *Cybeloides* and thus likely had similar life habits. Both genera shared a stalk-eyed cephalon of similar overall shape and convexity. The pygidium of *Parablackwelderia*, which bears two pairs of macropleural segments and four pairs of lateral spines placed between the macropleural spines, is comparable in a general way to the posterior half of the trunk (i.e., the posterior thoracic segments and the pygidium) of *Cybeloides*. This exoskeletal structure suggests that *Parablackwelderia* was probably also a burrower and used periscopic vision via stalked eyes when the main body of the animal was immersed in soft sediment. However, the eyes of *Parablackwelderia* are much more elevated than those of *Cybeloides*, which would have allow the former vision while being buried more completely in muddy or argillaceous sediment. In the only known thorax of *Parablackwelderia*, that of *P. sheridanorum*, all thoracic segments bear spines at the tip, which are moderately long, and backward curved but do not extend beyond the width of the cephalon. The morphology and direction of the spines on the thoracic segments are consistent with a protective function and they would have provided little resistance as the animal progressed forward. Ingham's (1968) postulated stabilizing function of the macropleural spines during burrowing for the stalk-eyed *Cybeloides* could also apply to *Parablackwelderia*.

Parablackwelderia is most commonly recovered from shales deposited on the shallow water platform in North China, and in argillaceous limestones deposited on the relatively deeper slope of South China. Its lithofacies preference is consistent with the inference of a soft sediment burrowing habit inferred from the morphology. The well preserved stalked eye bears a large, rounded extremity, which is about half as long as the glabella (excluding occipital ring) and indicates that a large eye was situated on the librigenal (abaxial) side of the eye stalk. The relatively large eyes might suggest that this animal was adapted to a dim environment, possibly associated with fluidized mud near the sediment-water interface. *Parablackwelderia* probably ingested relatively bulky food (such as prey items), because the animal had a modified hypostome characterized by its strong posterior border consisting of a pair of wing-shaped lobes and bearing an anterior curvature medially (Peng et al., 2004, pl. 30, fig. 11). The hypostome was held in the rigid, conterminent condition (Jell and Hughes, 1997, pl. 32, figs. 6, 7). The modified posterior margin and rigidly attachment of the hypostome suggests a predatory habit (Fortey and Owens, 1999), and the relatively large exoskeletons of the largest *Parablackwelderia* compared to those of other trilobites in the Guzhangian trilobite faunal assemblages of South and North China could be consistent with this inference. Large holaspid pygidia of *Parablackwelderia* are some 20 mm in length (excluding spines) (Peng, 1987, pl. 9, fig. 1; Peng et al., 2004, pl. 30, fig. 13) and, based on the pygidial proportions in the complete exoskeleton (Jell and Hughes, 1997), the animal is estimated to be over 100 mm in length. If this was so, the burrowing habit of *Parablackwelderia* may have allowed the animal to watch prey surreptitiously.

FIGURE *1*—Dorsal view of the anterior part of the body of a diopsinid fly, genus and species undetermined, from Nam Tok Tat Man (Tat Man waterfall), Pua District, Nan Province, Thailand, showing stalked eyes and bearing antennae on the anterior of eye stalk, near the visual surface, UCRC ENT144617, ×13.

The eye of *Parablackwelderia* is not only elevated compared to the condition in most trilobites: the distance between the eyes is also markedly expanded. Possible adaptive reasons for this condition are considered below.

LIVING ANALOGS

Although a flexible stalked eye is quite common among living decapod crustaceans, the condition in that group is different because the trilobite stalked eye was rigid and immobile. A rigid eye stalk is seen in several groups of insects, and that which is most similar to the condition in trilobites characterizes the diopsinid flies (Warren and Smith, 2007) (Fig. 1), although these animals are much smaller than mature stalk-eyed trilobites. In the Diopsinae both eye and antennae lie at the ends of the eye stalks (Fig. 1) and stalked-eye condition, known as hypercephaly, is present in all members of the subfamily, which comprises over 11 genera and 160 species. Our argument that the stalk-eyed condition in trilobites was related, at least in part, to elevating the eye above the remainder of the exoskeleton to attain conditions of higher light intensity apparently has no direct analog among the diopsinids, although physiological analysis suggests optical advantages for diopsinid eye stalks in certain lighting conditions (Burkhardt, 1972, Buschbeck and Hoy, 1998). It has been postulated that increased separation of the eyes of diopsinids increases the near field distance (the distance from the animal at which at point object is seen by at least one ommatidium in each eye) (Burkhardt and de la Motte, 1988). For *Crytodiopsis whitei* this distance is estimated to be 400–800 mm, many times that of a fly without eye stalks.

Hypercephaly in diopsinids is evidently promoted by both direct and indirect sexual selection (Warren and Smith, 2007). It is possible that the stalk-eyed condition in trilobites was the subject of sexual selection, and the positive allometry of the eye stalk might be consistent with this interpretation, as has recently been argued for the anterior cephalic spine of raphiophorid trilobites (Knell and Fortey, 2005). However, making a strong case for recognizing secondary sexual characters and sexual dimorphism in trilobites is challenging, and few, if any, cases are strongly supported (Hughes and Fortey, 1995, Fortey and Hughes, 1998). Regardless of the relative importance of natural and sexual selection in the evolution of prominent eye stalks in trilobites, the challenges of both constructing and maintaining stalked eyes requires considerable resource investment by the maker, and in some situations this may limit the prevalence of the condition (Buschbeck and Hoy, 1998). As in trilobites, the stalked-eye condition occurs convergently among insect clades, and the condition is rare among the group as a whole.

GENERIC CONCEPT OF *PARABLACKWELDERIA*

Until recent clarification (Peng et al., 2004, p. 101), the generic concept of *Parablackwelderia* was long ambiguous because of poor preservation and inadequate illustration of the type material of *Blackwelderia spectabilis* Resser and Endo (Endo and Resser, 1937, p. 188, pl. 52), the type species from the Kushan Formation, Liaoning, northeast China (Kobayashi, 1942). Further hindrances included inaccurate reconstruction of the type species by Kobayashi (1942, plate 21, fig. 4) in the paper in which the genus *Parablackwelderia* was erected. The stalked eyes of *Parablackwelderia* are rarely preserved in most circumstances, particularly in limestones, because of their fragility, but the lack of such an important feature has impeded the correct assignment of specimens in many cases. All these factors lead to the creation of a number of junior synonyms of *Parablackwelderia* (see Peng et al., 2004, p. 101) and, on the other hand, led others to regard the genus as a junior synonym of *Blackwelderia* (Zhang and Jell, 1987). The discovery of stalk-eye bearing cranidia from Tarim and South China (Zhang, 1981, pl. 65, fig. 3; Peng et al., 2004, pl. 29, fig. 5, pl. 30, fig. 6; pl. 31, figs. 8, 11) permitted Peng et al. (2004) to revive *Parablackwelderia* as a valid genus based on the possession of stalked eyes, anteriorly placed palpebral lobes, a subtriangular-shaped glabella, long posterolateral projections of the fixigenae, and a pygidium with macropleural spines on the first and fifth segments, and to emend the generic diagnosis by suppression a number of genera as junior synonyms of *Parablackwelderia*. However, neither the complete eye stalks nor eyes were known for *Parablackwelderia* at that time. Shortly following the appearance of Peng et al. (2004), Duan et al. (2005) published significant newly recovered material of *Parablackwelderia* from Liaoning, northeast China, which revealed not only complete stalked eyes but also, for the first time, the visual surface in position (Duan et al., 2005, pl. 38, fig. 8). Although poorly preserved, the lens arrangement appears to have been holochroal, and the species presumably lacked a circumocular suture.

The new material described in this paper was collected from the transition interval between the Changhia and Kushan formations at two localities in central Shandong Province, China. It includes the most complete stalked-eye bearing specimens of both mature and juvenile forms available to date, and represents an undescribed species of *Parablackwelderia*. *Parablackwelderia* has been recorded previously from nearly 20 localities in south (Anhui, Guizhou, Hunan, Jiangsu), northeast China (Liaoning, Jilin), and northwest (Tarim) China, but had not been recorded from Shandong, north China, and no specimen described previously from this region can be reassigned to the genus. This find of *Parablackwelderia* in Shandong extends the geographic distribution of the genus to the classical region for study of North China-type Cambrian formations, including the Changhia and Kushan formations.

Peng et al. (2004, p. 101–103) clarified the generic concept of *Parablackwelderia* and its differentiation from *Blackwelderia* Walcott, 1906, which is closely similar. They suppressed *Damesops* Chu, 1959, *Meringaspis* Öpik, 1967, *Paradamesops* Yang *in* Lu et al., 1974, and questionably also *Guancenshania* Zhang and Wang, 1986, as junior synonyms of the genus. Duan et al. (2005) accepted the synonymy of *Damesops* Chu. Here, we follow the generic concept as outlined by Peng et al. (2004). The material found recently from Liaoning (Duan et al., 2005) and from Shandong, described herein, adds new information on the morphology of the eye stalk, the eye, and the nature of the posterior border between posterolateral spines on the pygidium. The stalked eye, omitted on the reconstructions of *Parablackwelderia* species by Peng et al. (2004, text-fig. 11, Fig. 2), is long and slender, with a bulb-like extremity extending far beyond the margins of the cranidium; the compound eye is relatively large and is positioned on the outer side of the extremity of stalk, i.e., at the top of the inner portion of the librigena, and the posterior pygidial border bears a pair of short but broad spines. The posterior pygidial border is known to vary markedly within the genus. It may bear a pair of long and thin spines, a single long and broad projection, or lack spines entirely (Peng et al., 2004, text-fig. 11). A complete holaspid specimen of *P. sheridanorum* (Jell and Hughes, 1997) from India has a thorax comprising 12 segments.

Peng et al. (2004, p. 101–102) accommodated 10 species in the genus. Subsequently Duan et al. (2005) added a new species *Parablackwelderia acuticonica* and a species in open nomenclature to the genus, which is based on a single cranidium and is here referred to *Parablackwelderia luensis* sp. nov. In addition, Duan et al. (2005) transferred *Dorypygella alastor* Walcott, 1905 (Walcott, 1913, pl. 9, fig. 7a, b) and *Stephanocare fuxiangensis* Guo and Luo (*in* Guo et al., 1996, pl. 10, figs. 4–6 only) to *Parablackwelderia*. Both the assignments are rejected herein. *Dorypygella alastor* was questionably referred to *Damesops* by Zhang and Jell (1987, p. 216), however the relatively large and posteriorly placed palpebral lobes, the long preglabellar field, the postaxial ridge-bearing pygidial axis and the flattened lateral pygidial spines firmly suggest a species of *Tienistion*. The transfer of *S. fuxiangensis* also violates nomenclatural rules because the holotype cranidium of the species (Guo et al., 1996, pl. 10, fig. 2) (and one paratype pygidium, Guo et al., 1996, pl. 10, fig. 1) remained untransferred. It should also be noted that none of the above pygidia that Duan et al. (2005) reassigned to *Parablackwelderia fuxiangensis* belong to the genus because they all have subequally sized pygidial spines. A total 12 species can now be assigned to *Parablackwelderia*, including: *Blackwelderia chiawangensis* Chu, 1959, *Damesops convexus* Chu, 1959, *Meringaspis meringaspis* Öpik, 1967, *Paradamesops jimaensis* Yang *in* Lu et al., 1974, *Paradamesops laterilobatus* Yang *in* Zhou et al., 1977, *Meringaspis huabeiensis* Zhang *in* Qiu et al., 1983, *Paradamesops triangularis* Guo and Luo *in* Guo, et al., 1996, *Damesops sheridanorum* Jell and Hughes 1997, *Parablackwelderia acuticonica* An and Duan *in* Duan and An, 2005, *Parablackwelderia* sp. cf. *P. huabeiensis* (Zhang *in* Qiu et al., 1983), *Parablackwelderia* sp. sensu Peng et al., 2004, and *Parablackwelderia luensis* sp. nov.

All these species likely had long stalked eyes, which are preserved completely in *Parablackwelderia acuticonica* and *P. luensis* sp. nov. and, as an exceptional case of preservation in limestone, almost completely in *Parablackwelderia* cf. *huabeiensis*. Stalked eyes are largely or entirely broken off or damaged in available specimens of other species but the presence of elevated palpebral lobes could be determined confidently in all.

STRATIGRAPHIC SETTING OF *PARABLACKWELDERIA*

As synonymized (Peng et al., 2004) *Parablackwelderia* is endemic to eastern Gondwana, being known from China, Australia, India, North Korea, and Kazakhstan, and occurring exclusively in strata assigned to the Guzhangian Stage (previously the informal Cambrian Stage 7 as defined by Peng and Babcock, 2005 and Babcock et al., 2005). In China *Parablackwelderia* is among a small number of polymerid genera found in three major Cambrian

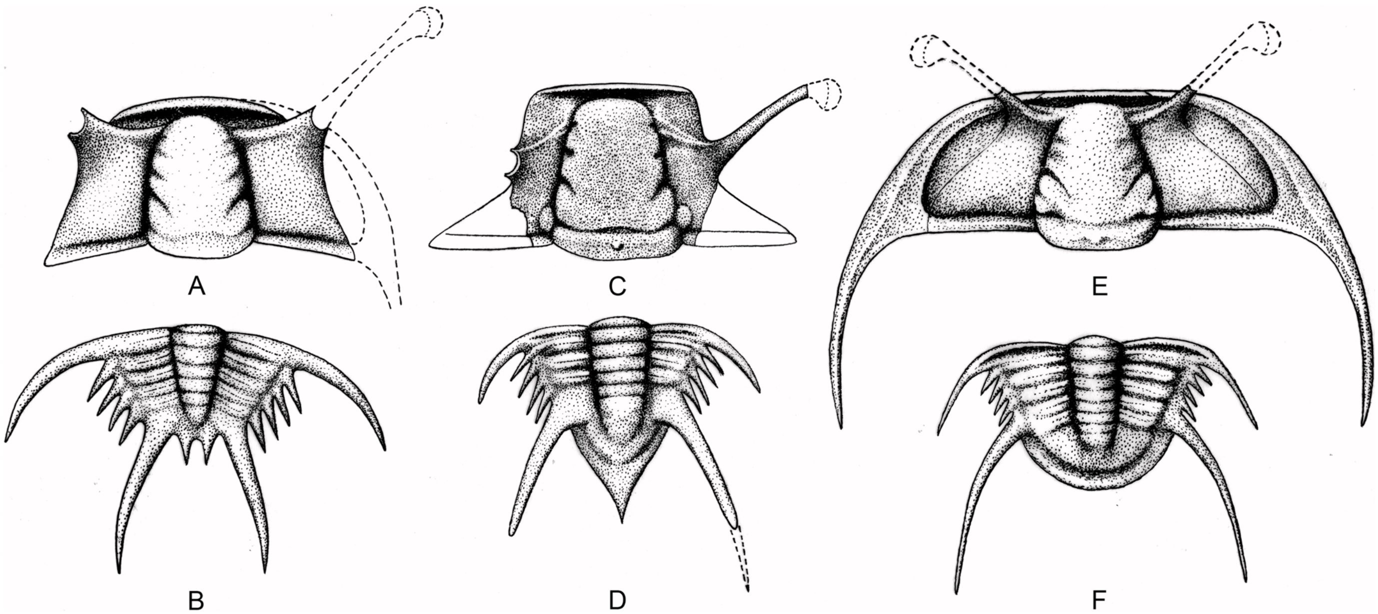
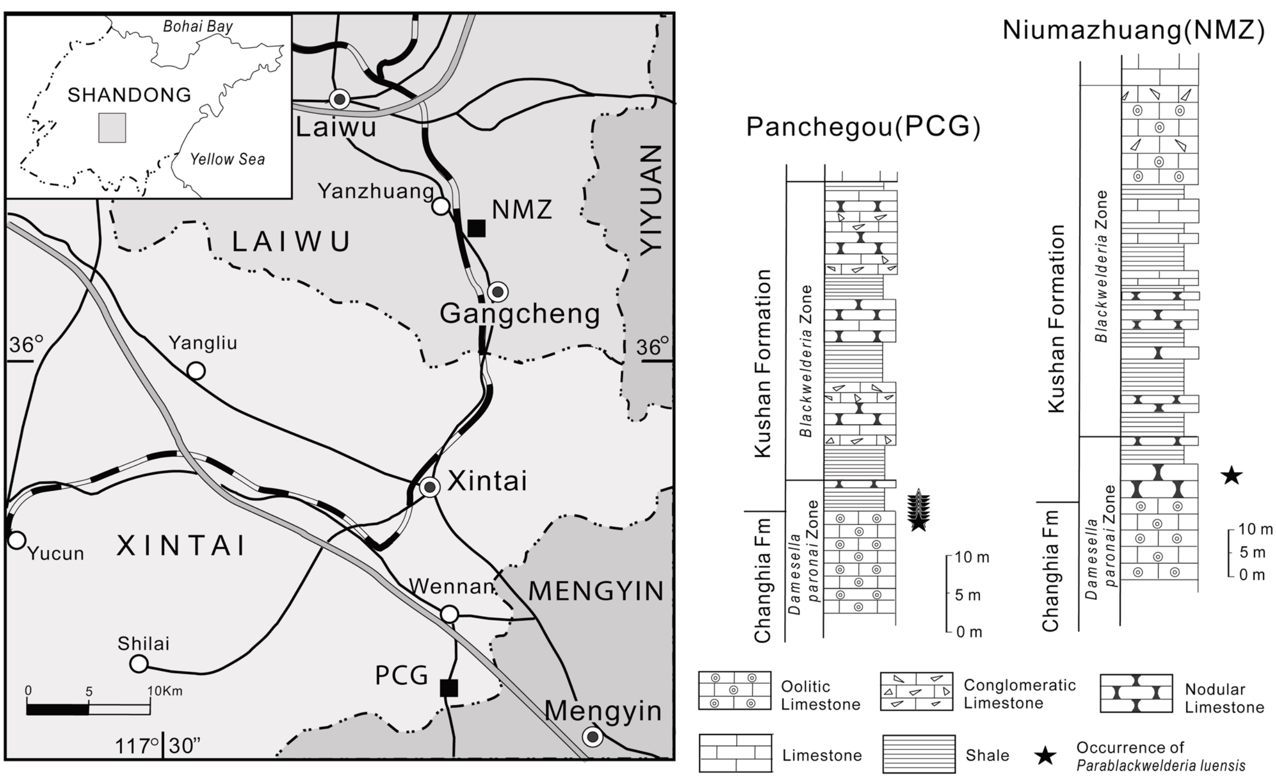


FIGURE 2—Revision with stalked eye of the reconstruction text-figure 11 of Peng et al., 2004, for some species of *Parablackwelderia* Kobayashi, 1942. A, B. *Parablackwelderia spectabilis* (Resser and Endo *in* Resser and Endo, 1937), the type species; C, D. *Parablackwelderia meringaspis* (Öpik, 1967), note the eye stalk for this species is based on that of *P*. sp. cf. *P. huabeiensis* (Zhang *in* Qiu et al., 1983; see Peng et al., 2004, pl. 31, figs. 8, 11, 12) which closely resembles *P. meringaspis* in cranidial morphology; E, F. *Parablackwelderia jimaensis* (Yang *in* Lu et al., 1974).



Dameslla
paronia Zone

FIGURE 3—Location of the stratigraphic sections (solid square) yielding *Parablackwelderia luensis* sp. nov. in central Shandong province (PCG: Penchegou section; NMZ: Niumazhuang section), and the stratigraphic occurrences of the species in the measured sections.

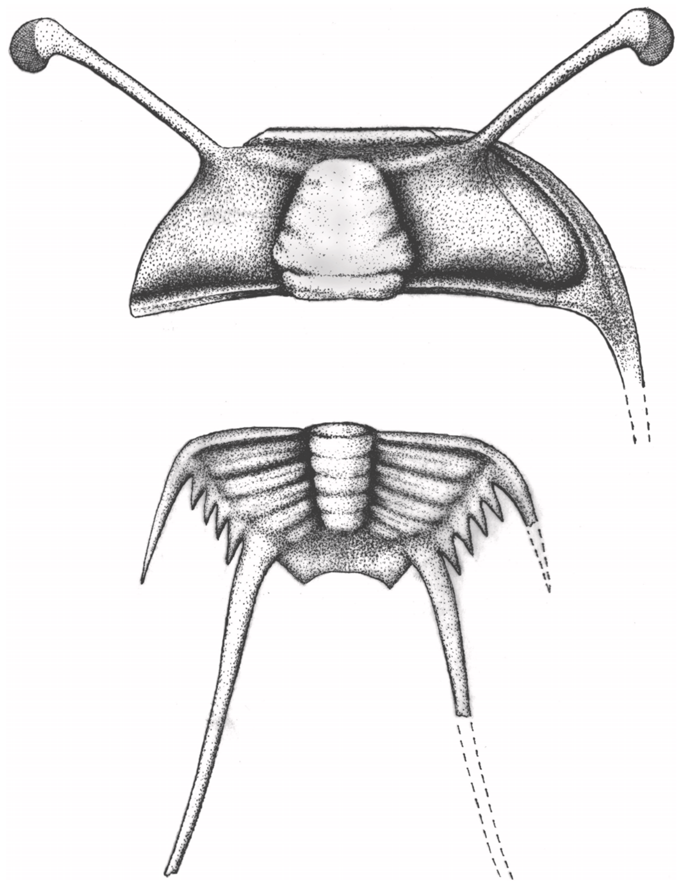


FIGURE 4—Reconstruction of *Parablackwelderia luensis* sp. nov. The cranidium (above) is based on NIGP140550 (Fig. 5.1, 5.2, 5.6), the librigena is based on DA0629 and DA630 (Duan et al., 2005, pl. 38, figs. 2, 9), and the eye is based on that of *P. acuticonica* Duan et al., 2005, pl. 38, fig. 8, DA0639; the pygidium (below) is based on NIGP140556 and NIGP140558 (Fig. 5.11, 5.13).

blocks (the North China, South China and Tarim blocks), having been reported from Liaoning, Jinin, Hebei, Shandong, Henan, Anhui, Jiangsu, Hunan, Guizhou, Yunnan, and Xinjiang provinces (Endo and Resser, 1937; Chu, 1959; Lu et al., 1974; Luo, 1974; Nan, 1976; Yang, 1978; Zhang, 1981; Qiu et al., 1983; Peng, 1987; Zhu and Wittke, 1989; Yang et al., 1991; Zhang et al., 1995; Guo et al., 1996; Peng et al., 2004; Duan et al., 2005). Although the stratigraphic occurrence of *Parablackwelderia* in most literature is based on a single species and is simply referred to formations of either traditional middle or late Cambrian age (i.e., the Kushan, the Huaqiao, and the Mohershan formations), a composite stratigraphic range that is precisely constrained by occurrences of key agnostoids has been recorded for 4 species of *Parablackwelderia* recently in a measured section at Paibi, northwestern Hunan (Peng et al., 2004). In the section, the oldest species *Parablackwelderia* sp. occurs somewhat above the base of the *Lejopyge laevigata* Zone whereas the youngest species, *P. jimaensis*, has its last occurrence close to the base of the *Glyptagnostus stolidotus* Zone. This indicates that in western Hunan the genus has a local range embracing three successive global agnostoid zones, namely the *Lejopyge laevigata* Zone, the *Proagnostus bulbus* Zone, and the *Linguagnostus reconditus* Zone. *Parablackwelderia* is reported in association with *Lejopyge armata* and *Ptychagnostus aculeatus* in India (Jell and Hughes, 1997) and with *Damesella* and *Blackwelderia* in N. Korea (Kim, 1987): these taxa occur exclusively within the range of *Parablackwelderia* in the Paibi section, Hunan. In Kazakhstan and in Australia only a single species has been reported occurring within that range (Ergaliev, 1980) or extending upward into the *Glyptagnostus stolidotus* Zone (Öpik, 1967), which is also a globally applicable zone lying in succession above the *Linguagnostus reconditus* Zone. Thus, *Parablackwelderia* has an observed range spanning all the 4 zones of the Guzhangian Stage. Although the evolutionary relationships of existing species of *Parablackwelderia* remain uncertain, morphological changes observed in certain species from northwestern Hunan show that the species occurring in younger horizons, i.e., *P. jimaensis*, which is commonly from the *Proagnostus bulbus* and *Linguagnostus reconditus* zones, bears less widely separated stalked-eyes, a narrower anterior cranidial border, and longer posterolateral projections than those of *P. laterilobata*, which occurs in the older *Lejopyge laevigata* Zone.

In summary, the relatively short stratigraphic range occurrence and wide geographical distribution suggest that *Parablackwelderia* can be used as valuable tool for the recognition of Guzhangian strata and for their correlation on interregional and intercontinental scales.

FOSSIL LOCALITY OF THE NEW SPECIES

The shale and micritic limestone specimens used in this study were collected respectively from two sections in the boundary interval of the Changhia and Kushan Formations, measured along a highway near Penchegou Village, 15 km south of Wennan township, or 35 km south of Xintai, and on the side of a railway at Niumazhuang, 4 km south of Yanzhuang, both in central Shandong (Fig. 3). Xintai (Sin-T'ai) and Yanzhuang (Yenchuang) are two of the districts where Willis and Blackwelder (Blackwelder, 1907) investigated the Cambrian during the early years of the last century, and has often since been visited by Chinese geologists for the study of litho- and biostratigraphy of the North China-type Cambrian. The collection of Willis and Blackwelder formed the base of Walcott's (1913) monumental work on Chinese Cambrian trilobites. However, the locations studied herein were beyond the scope of Willis and Blackwelder's investigation. The studied interval in the Panchegou section is about 59 m thick, with the lower 14 m occupied by massive oolitic limestone belonging the uppermost Changhia Formation, which is overlain conformably by the Kushan Formation (up to 93 m thick in the Wennan area) that is composed mainly of shale and nodular limestone in the lower part, and thin-bedded limestone and conglomeratic limestone in the upper part. This section is well exposed in

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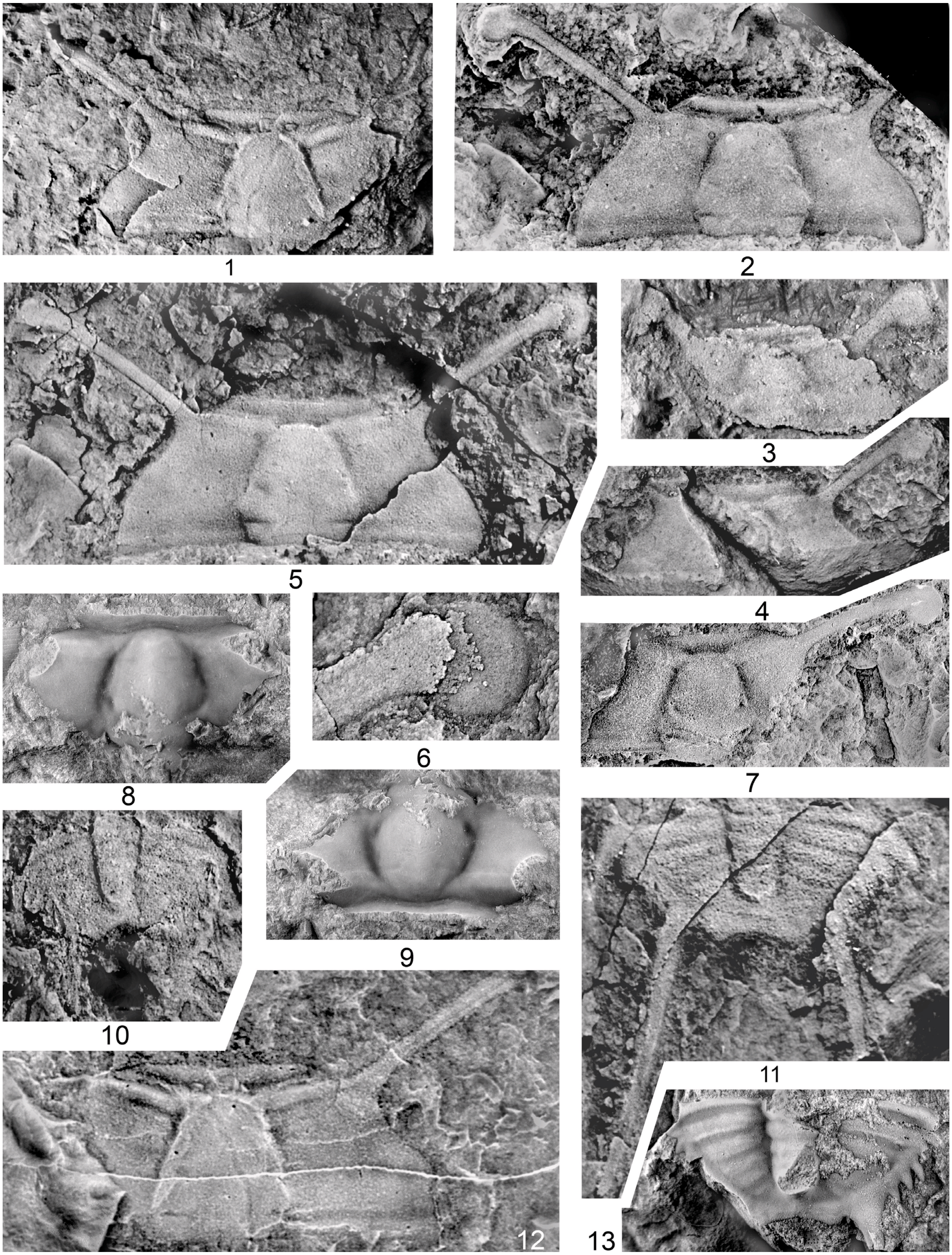
FIGURE 5—*1–13. Parablackwelderia luensis* sp. nov., all from the topmost part of the Changha Formation at Panchegou, Wennan (*1–7, 10–12*) and Niumazhuang, Gangcheng (*8, 9, 13*), central Shandong; all shale specimens unless otherwise stated. Image polarity reversed in *2, 4,* and *11. 1,* cranidium with recrystallized shield, paratype, NIGP140549, dorsal view, ×4.6; *2, 5, 6,* cranidium, external and internal (with partially recrystallized shield) molds and partial enlargement of the extreme of stalked-eye in *5* respectively, note the outer side of extremity of stalked-eye in *6* is probably the imprint of visual surface, holotype, NIGP140550, dorsal views, ×4.0, ×4.3; *3,* juvenile cranidium with recrystallized shield, paratype, NIGP140551, dorsal view, ×8.5; *4,* damaged cranidium, internal mold, paratype, NIGP140552, ×4.8; *7,* cranidium, external mold, paratype, NIGP140553, dorsal view, ×4.7; *8, 9,* micritic limestone cranidium, paratype, NIGP140554, in dorsal and oblique anterior views, ×4.5; *10,* juvenile pygidium, internal mold, paratype, NIGP140555, dorsal view, ×10; *11,* juvenile pygidium internal mold, paratype, NIGP140556, dorsal view, ×8.9; *12,* cranidium, external mold, paratype, NIGP140557, dorsal view, ×5.7; *13,* micritic limestone pygidium, paratype, NIGPA140558, dorsal view, ×5.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a road-cut and richly fossiliferous throughout. It embraces two zones: the *Damesella paronai* Zone, which occupies the measured Changhia Formation and the basal 5 m of the Kushan Formation, and the *Blackwelderia* Zone that occupies the succeeding interval of the measured section. Both are Guzhangian in age as used globally or Upper Wangcunian and Youshuian in age as used in South China (Peng and Babcock, 2005, Babcock et al., 2005). The zonal boundary is defined by the appearance of *Blackwelderia* sp. Specimens from the Panchegou section, figured and unfigured, are from 6 horizons within an interval of 1.6 m in the *Damesella paronai* Zone of the Kushan Formation in the Panchegou section (i.e., at 1, 1.1, 1.2, 1.3, 1.4 and 1.6 m above the base of the formation), whereas the uppermost part of underlying Changhia Formation yields also specimens assignable to *Parablackwelderia*. Specimens from the Niumazhuang section are from a single collection in the Changhia Formation, 1 m to the top of the formation. *Damesella paronai* is the most common form of the zone bearing its name, but species assigned to *Parablackwelderia*, *Cyclolorenzella*, *Ajacicrepida* and *Yabeia* also characterize the zone in both sections.

SYSTEMATIC PALEONTOLOGY

Type and figured material in this paper is held in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (prefix NIGP), and in the University of California, Riverside Museum of Entomology (prefix UCRC ENT).

Family DAMESELLIDAE Kobayashi, 1935
Subfamily DAMESELLINAE Kobayashi, 1935
Genus PARABLACKWELDERIA Kobayashi, 1942
[=*Damesops* Chu, 1959; =*Meringaspis* Öpik, 1967;
=*Paradamesops* Yang *in* Lu et al., 1974;
?=*Guancenshania* Zhang and Wang, 1986]

Type species.—*Blackwelderia spectabilis* Resser and Endo *in* Endo and Resser, 1937, from the Kushan Formation, Changxingdao Island, Liaoning; by original designation.

Diagnosis.—Glabella broadly conical, with rounded or acutely rounded front; palpebral lobe long, stalk-like, extending outward and forward far beyond the sides of cranidium with base lying anterior to midlength of glabella (excluding occipital ring) and bulb-like extremity bearing eye on outer side; eye ridge usually well-defined; preglabellar field narrow (sag., exs.) or absent; posterior branch of facial suture straight or gently curved, enclosing long (exs.), triangular posterolateral projection. Thorax of 12 segments. Pygidium with six pairs of lateral border spines of unequal length; pygidial margin with variable shape.

Remarks.—The diagnosis of Peng et al. (2004) is slightly emended on the basis of the new materials found recently from Northeast China (Duan et al., 2005) and from Shandong described herein.

PARABLACKWELDERIA LUENSIS new species
Figures 4, 5.1–5.13

Parablackwelderia spectabilis (RESSER and ENDO *in* ENDO and RESSER, 1937); DUAN et al., 2005, p. 182, pl. 38, figs. 1a, 2, 9, 10, 11a, 11b.
Parablackwelderia sp.; DUAN et al., 2005, p. 183, pl. 38, fig. 12.

Diagnosis.—Glabella slightly longer than wide, broadly rounded anteriorly with S1 and S2 furrows shallow to fully effaced and baccula obscurely defined; ocular ridge nearly as wide as occipital ring; posterior branches of facial suture diverging at an angle about 60 degrees. Pygidium with axis 0.75 of pygidial length; w-shaped posterior margin defining a pair of broad and short marginal spines.

Description.—Cranidium trapezoidal, half as long as wide with anterior margin gently concave rearward. Glabella subtriangular, nearly as wide as long, broadly rounded anteriorly, with S1 furrow shallow or largely effaced and S2 weakly-incised to fully effaced; baccula obscurely defined, not completely isolated from glabella; occipital furrow shallow, deepening abaxially; occipital ring short, slightly narrower than preoccipital lobe. Preglabellar field absent; anterior border flat and short (sag.), gently upturned. Eye ridge belt-like, gently oblique forward, as wide as the glabellar width at S1. Palpebral lobe stalk-like, with base opposite glabellar front, extending outward and forward. The stalked eye is rather thick and short (equal to glabellar length) in a younger cranidium (Fig. 5.3), becoming thin and long (two times glabellar length) in later holaspid cranidia (Fig. 5.1, 5.2, 5.5, 5.10). In both growth stages, the abaxial end of stalked eye is expanded into a large, bulb-like extremity where the compound eye should be placed on the opposite side. Anterior branches of facial suture strongly convergent forward at an angle of about 120 degrees; posterior branches of gentle curvature, moderately convergent rearward, enclosing narrow (tr.) and long triangular posterolateral projection occupying about half of posterior width of fixigena. Posterior border furrow transverse and shallow, defining short posterior border.

Pygidium inverted trapeze (excluding posterolateral spine), twice as wide as long, with slightly rearward tapering axis bearing 5 rings and a short terminal piece. Borders defined by weakly impressed border furrows, bearing 6 pairs of lateral spines, of which the first pair of moderate length and the sixth pair strong and long (twice pygidial length), and a pair of short and broad posterior spines.

The limestone specimens show that the surface of glabella and fixgena are smooth or bear finely wrinkled ornamentation (Duan et al., 2005, pl. 38, fig. 1).

Etymology.—From Lu, the abbreviated form for Shandong Province in Chinese, referring to the first record of *Parablackwelderia* from the province.

Types.—Holotype, a nearly complete, largely exfoliated cranidium, NIGP140550, Panchegou (Fig. 5.2. 5.5, 5.6); paratypes, five cranidia and three pygidia, NIGP140549, 140551–140553, 140555–140557, Panchegou; NIGP140554, 140558, Niumazhuang.

Occurrence.—*Damesella paronai* Zone, the topmost part of Changhia Formation and basal part of Kushan Formation, Panchegou, Wennan, Xintai and the basal of Kushan Formation, Niumazhuang, Gangcheng, Leiwu, central Shandong. It is also known from the *Damesella paronai* Zone, Changhia Formation, Changxingdao Island, southern Liaoning and Liuhe and Fumintun, Huinan, southern Jilin.

Discussion.—In having a proportionally smaller glabella and widely spaced palpebral lobes, *Parablackwelderia luensis* sp. nov. resembles *Parablackwelderia laterilobata* (Yang *in* Zhou et al., 1977, p. 189, pl. 59, figs. 1, 2; also see Yang, 1978, pl. 13, figs. 3–5; Peng et al., 2004, pl. 31, figs, 1–5) from the Huaqiao Formation, Huaqiao, Hunan, South China. However, *P. laterilobata* has a strongly furrowed glabella with S1 and S2 furrows deeply incised and a well-defined baccula that is fully isolated from the glabella by a clearly impressed basal furrow. *P. laterilobata* is further differentiated by having a more strongly divergent posterior branch of the facial suture that embraces a much wider posterolateral projection of the fixigena and a pygidium without posterior border spines.

In comparison to *Parablackwelderia spectabilis* (Resser and Endo, 1937), the type species (refigured by Zhang and Jell, 1987, pl. 102, figs. 8, 9; pl 103, figs. 3, 4, 5?) which has a similarly effaced glabella, the new species has a much more forward tapered and proportionally longer glabella, more widely spaced palpebral lobes, and a pair of longer and more slender posterior pygidial spines. *Parablackwelderia acuticonica* An and Duan (2005, p. 182, pl. 38, figs. 3–8, 13, 14) from the top of the Taizi Formation, Jilin differs in having a glabella with an acutely rounded front and deeply impressed S1and S2 furrows, and less widely spaced palpebral lobes. With respect of the pygidium, *P. acuticonica* has a longer pygidial axis reaching onto the posterior border furrow.

The limited ontogenetic material for *Parablackwelderia luensis* sp. nov. reveals that the peduncle of the stalked eye grew at a faster rate than the compound eye (and the extremity of the stalk), which became relatively smaller in proportion during the ontogeny. On the other hand, the remaining cranidial features show few, if any, significant changes in proportion during ontogeny.

ACKNOWLEDGMENTS

We acknowledge support from the Chinese Academy of Sciences (KZCX2-YW-122) and the Ministry of Science and Technology of China (2006FY120300, 2006CB806400). The Chinese National Natural Science Foundation grant (40332018) and the U.S. National Science Foundation grants (EAR-0543868 and EAR-0616574) facilitate this collaboration. David Rudkin and Sandro Minelli kindly alerted us to relevant trilobite and dipterid literature. Douglas Yanga and John Heraty of the University of California Riverside Entomology Department facilitated the production of Fig. 1. We are grateful to the reviewers and to editor Pratt for helpful suggestions.

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ACCEPTED 25 MARCH 2008