PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2009, v. 24, p. 473–477
Research Note
DOI: 10.2110/palo.2008.p08-105r

A JUVENILE REDLICHIID TRILOBITE CAUGHT ON THE MOVE: EVIDENCE FROM THE CAMBRIAN (SERIES 2) CHENGJIANG LAGERSTÄTTE, SOUTHWESTERN CHINA

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ABSTRACT

A trace fossil with its putative *in situ* maker, a redlichiid juvenile of *Eoredlichia intermedia* Lu, 1940 from the lower Cambrian (Series 2) Chengjiang fauna, southwestern China, is reported here. Evidence for biogenetic linkage of the trail to the trilobite includes their close, integrated association, *in situ* preservation, and consistent dimensions. Analysis from Scanning Electron Microscopy further strengthens this argument. Preservation mechanism and fidelity loss in the trail are considered. In light of functional morphology, a nektonic-benthic transition in modes of life is inferred for meraspides of *Eoredlichia*.

INTRODUCTION

Trace fossils, the fossilized behaviors of ancient life, are commonly acknowledged to be most significant in accessing the onset and early evolution of bilaterians (Glaessner, 1969; Jensen, 1990, 2003; Droser et al., 2002; Jensen et al., 2005; Weber et al., 2007). The prime reason for this is that body fossils of earliest bilaterians in the onset of the Cambrian radiation are poorly preserved because of the lack of biomineralization. Trilobite trace fossils otherwise play an important role in sedimentary facies analysis (e.g., Glaessner, 1969; Seilacher, 1967; Crimes, 1975, 1994). Ichnological genera *Cruziana* and *Rusophycus*, which are common in Paleozoic deposits, are generally recognized as trilobite-attributed traces. *Cruziana* trails putatively indicate plowing and foraging processes of trilobites, and *Rusophycus* excavations imply their resting or hunting activities with more confidence (e.g., Seilacher, 1967, 2007; Crimes, 1975; Jensen, 1990; Fortey and Seilacher, 1997).

Herein we describe an exquisitely preserved redlichiid trilobite *Eoredlichia intermedia* Lu, 1940, from the lower Cambrian (Series 2) Chengjiang deposit of southwesterm China that perished while producing an associated trail. The Chengjiang deposit is a Burgess Shale–type Konservat-Lagerstätte that serves as a so-called Rosetta Stone to understand the initiation and innovation of Phanerozoic metazoans and body plans (Steiner et al., 2005), which includes the earliest true vertebrates and such extinct phyla as Vetulicolia (Shu et al., 1999, 2001). The Chengjiang Lagerstätte can also provide novel insights into the ichnofabric of the early Cambrian benthos (Luo et al., 1994; Weber et al., 2007; Zhang et al., 2007). For instance, remarkable cases of infaunal priapulid worms, such as *Cricocosmia jinningensis* Hou and Sun, 1988 (Hu, 2005; Han et al., 2004, 2007), *Palaeopriapulites parvus* Hou et al., 1999 (Han et al., 2004, 2007), and *Maotianshania cylindrical* Sun and Hou, 1987 (Zhang et al., 2006; Han et al., 2007), are exceptionally found situated within their burrows.

Trilobites caught on the move, that is, their body fossils found within their own ichnofossils, are almost unknown from the Paleozoic. Preservation of this kind has special significance in both paleoecology and paleoethology of trilobites. Only in rare cases were trilobites preserved within their *Rusophycus* trace fossils. The Late Ordovician Phacopid trilobite *Flexicalymene meeki* Foerste, 1910, from the Cincinnati area was described and interpreted as the cubichnia tracemaker of *Rusophycus pudicum* Hall, 1852 (Osgood, 1970). Two other Ordovician asaphids (*Ogygyinus armoricanus* and *Lycophron sp.*) were also reported preserved *in situ* within their *Rusophycus* burrows (Draper, 1980; Fortey and Owens, 1999). Burrowing asaphid trilobites (*Asaphus raniceps* Dalman, 1827) of Middle Ordovician age from the Holen Limestone Formation, Sweden, were observed within tunnel-like trace fossils assigned to *Thalassinoides* and presumed to be the tracemakers, which was unusual ethology for trilobites (Cherns et al., 2006). Apart from these examples, to date few others have been reported with respect to trilobite body fossils found within elongated, horizontal trails or tracks.

MATERIAL AND METHODS

A single specimen of *Eoredlichia intermedia* (ELI-EOM001) with its associated trail (Fig. 1) was excavated from the Erjie section, Jinning, a locality ~40 km west of the classic Maotianshan section in the vicinity of the Chengjiang area, Yunnan, southwestern China. Stratigraphically, this specimen was preserved in the Yu'anshan Member, Heilinpu (formerly Qiongzhusi) Formation, lower Cambrian (ca. 518 Ma), within the *Eoredlichia–Wutingaspis* Zone. All specimens reported here are reposited in the Early Life Institute, Northwest University, Xi'an, China.

Scanning Electron Microscopy (SEM) at extremely high magnification enabled examination of uncoated fossils. Elemental scanning via EDX (Energy Dispersive X-Ray Spectroscopy) is efficient for determining the relative abundance of elements in various parts of the fossil and the adjacent matrix. Results from this analysis were used for the interpretation of the anatomy and taphonomy of the trilobite. These techniques were accomplished using an FEI Quanta 400-FEG in the State Key Laboratory of Continental Dynamic, Northwest University, Xi'an, China. In addition, a Zeiss Stemi 2000-C stereomicroscope was used for optical observation in the Early Life Evolution Laboratory, China University of Geosciences, Beijing, China.

DESCRIPTION

The specimen is preserved in weathered yellowish argillaceous mudstone. In high contrast against the matrix, the pink to pale brown trilobite is situated at the terminus of the trail and parallel to bedding. The disproportionately sized, semicircular cephalon, elongate, crescent ocular lobes, opisthoparian facial sutures, and slightly forward-tapering glabella characterize the trilobite specimen (Shu et al., 1995). Deducing from its strikingly prolonged first (mutilated) and second thoracic pleural spines and cephalic features, combined with the sagittal cephalic length of ~1.6 mm (Fig. 1–2), we infer that the trilobite was in meraspid (juvenile) degree 11 (Lu, 1940), with the sagittal tergite length ~3.0–3.3 mm (Fig. 3A). The remaining five thoracic segments and a miniature pygidium are lacking (Fig. 1).

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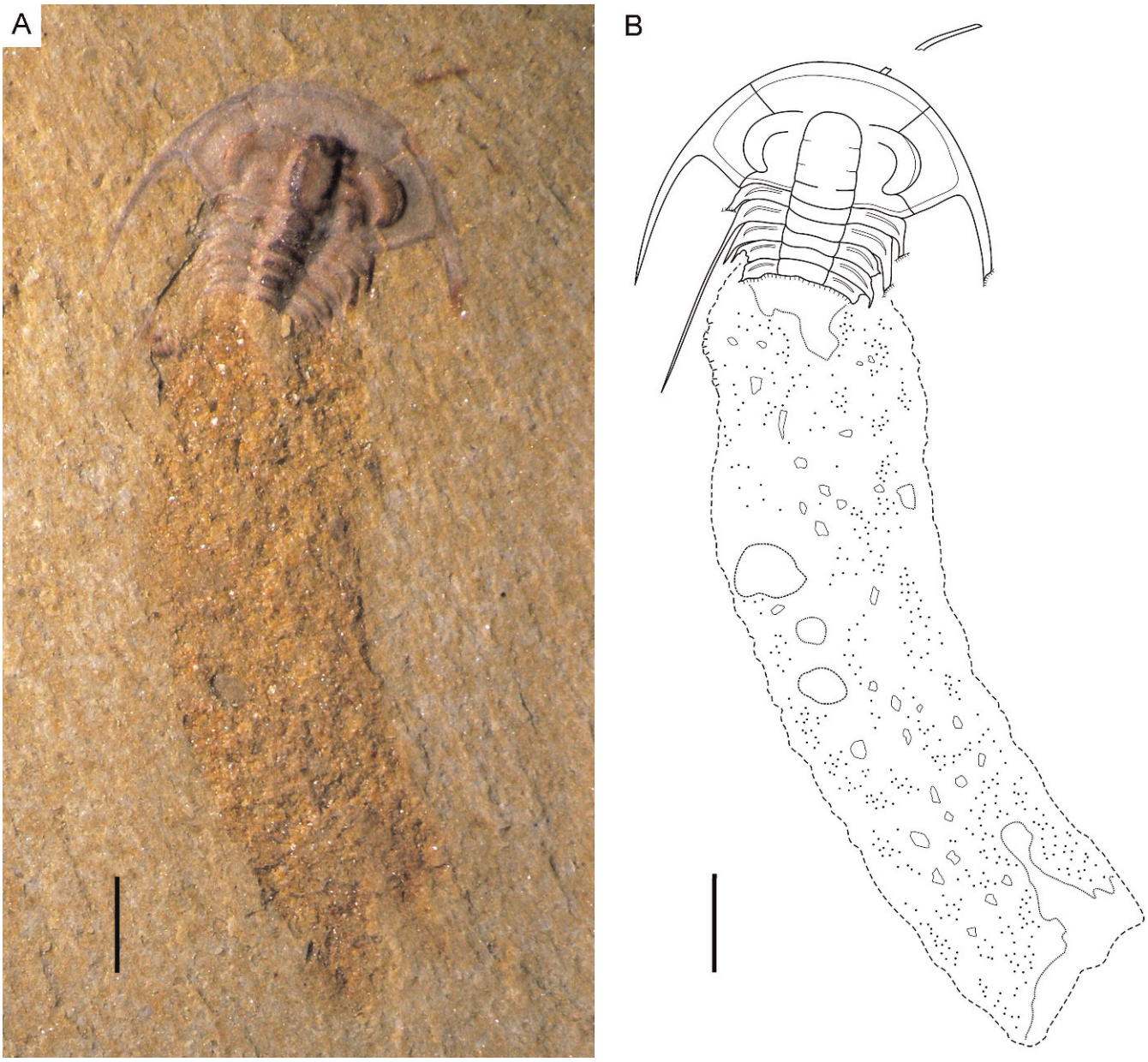

FIGURE 1—A) Juvenile of *Eoredlichia intermedia* Lu, 1940 (ELI-EOM001) and associated trail from Heilinpu Formation, lower Cambrian, southwestern China; B) camera-lucida drawing of specimen. Inequilateral polygon = muscovite flakes; small dot = coarse felsic minerals; scale bar = 1 mm.

The horizontal, slightly curved trail behind the trilobite appears to be pale orange, forming a distinct contrast to the matrix (Fig. 1). The trail is ~8.1 mm long and ~2.2 mm wide on average, exhibiting the clockwise locomotion of its maker (Fig. 1). Such biogenic details as scratches or furrows were not recorded, or they are not visible and likely preserved within the matrix on underside of the trail. Optical microscopic observation reveals that the surface of the trail is slightly uneven. Crystallization of coarse quartz and feldspar and muscovite flakes render localized positive relief, in association with a few comparatively smooth areas similar to the matrix.

SEM imaging further clarifies such anatomical features of the trilobite as the long paired spines formed by extensions of the first and second thoracic pleurae and two pairs of glabellar furrows, as well as the faintly defined occipital ring (Fig. 2). Elemental mapping reveals that, relative to the sedimentary matrix, the trilobite exhibits minor elevated concentrations of Si, Al, and O, whereas the trail shows depleted Si and Al concentrations and relative enrichments of Fe (Figs. 2; Si, Al, O, Fe). The trail can be distinguished by the enrichment of Fe element. On the contrary, the trilobite displays a lack of Fe on the surface, apart from an area on the axial ring of the fourth thoracic segment (Fig. 2; Fe). Both the trail and the surrounding matrix are composed mainly of aluminosilicate minerals, whereas the trail has coarser crystals of aluminosilicates and a higher content of iron oxide.

DISCUSSION

Biogenetic Linkage

Trilobites previously reported associated with their traces are exclusively preserved in semi-infaunal burrows or shallow excavations (e.g., Osgood, 1970; Fortey and Owens, 1999), or in infaunal tunnels (Cherns et al., 2006). Until now, direct field evidence has been lacking to confirm trilobites as originators of horizontal repichnia or fodinichnia traces.

The redlichiid trilobite *Eoredlichia intermedia* is likely the *in situ* maker of this trace fossil. This juvenile trilobite was aligned within the

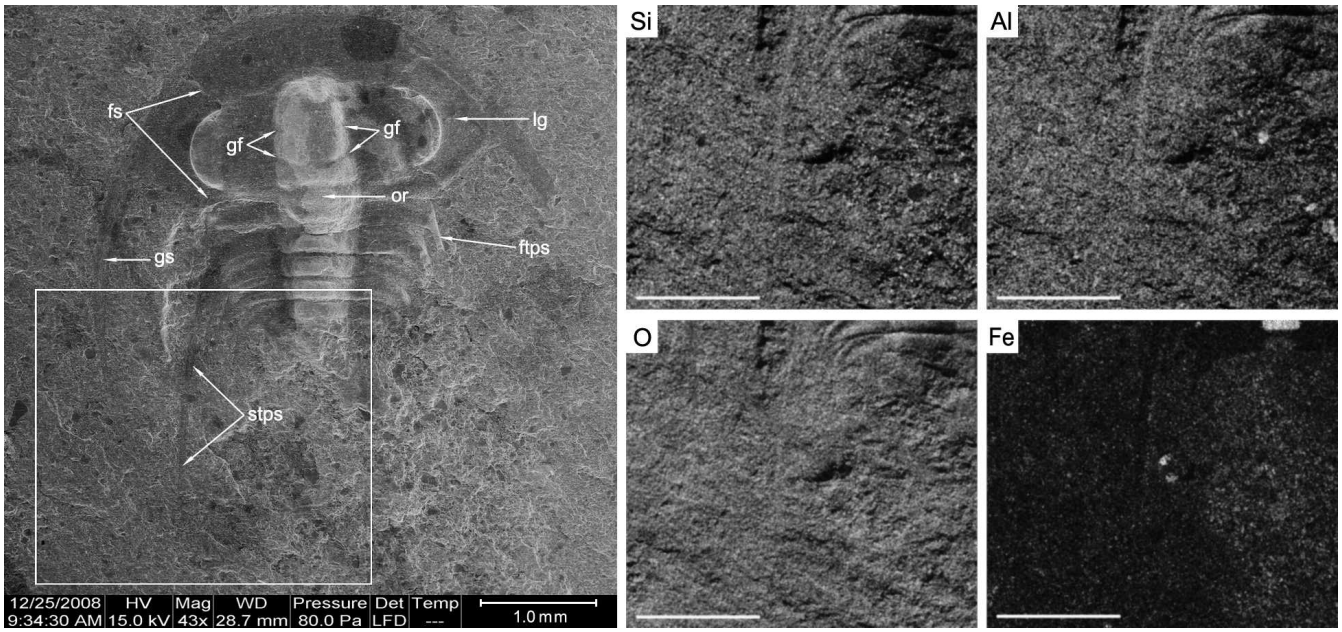

FIGURE 2—SEM image and elemental maps of *Eoredlichia intermedia* Lu, 1940, with part of trail (ELI-EOM001). Si, Al, O, and Fe elemental maps display relative abundance of available element in terms of contrasts in brightness—the brighter, the more abundant—indicated by inset on SEM image. ftps = first thoracic pleural spine; fs = facial suture; gf = glabellar furrow; gs = genal spine; lg = librigena; or = occipital ring; stps = second thoracic pleural spine; scale bar = 1 mm.

trail with its cephalon trending forward. The trilobite is articulated, with the attached librigenae, an exquisitely preserved antenna, and extremely elongate pleural spines. The transverse length of the trilobite's thorax matches the width of the trail. The trilobite also exhibits a dorsoventrally oriented life posture. Still noteworthy is that elemental mapping shows that the Fe-rich trail stretches continuously into the thorax (Fig. 2; Fe). The slightly clockwise orientation of the trail may imply a locomotive preference of its maker, albeit opposite to those left by *Cruziana semiplicata* Salter, 1854, from the Cambrian Andam Formation, Oman (Fortey and Seilacher, 1997). All evidence suggests that this specimen represents an *in situ* body fossil rather than molted exuviae and, thus, indicates the biogenetic linkage of the trace to the juvenile of *Eoredlichia intermedia*.

Comparisons and Fidelity Loss

The trace *Cruziana* commonly found in Paleozoic deposits is hypothetically ascribed, albeit not exclusively, to feeding behaviors of trilobites, despite opposing opinions (e.g., Whittington, 1980). Many other early marine arthropods with biramous appendages could equally be the candidates. *Cruziana* is characterized by a series of V-shaped scratches and a pair of parallel marginal grooves, presumably produced by limbs and by genal spines respectively (Seilacher, 2007). The bilobate, coffee-bean–shaped *Rusophycus* is featured by a deep median furrow and symmetrical lobes transversely wrinkled by anterolaterally directed striae (Osgood, 1970).

This trail from the Chengjiang Lagerstätte is comparable to *Cruziana* in terms of their horizontal, elongate, and curved geometry. The specimen contrasts clearly with typical *Cruziana* that exhibit scratches and medial groove and *Rusophycus* that commonly show distinctive semi-reliefs. Without the *in situ* maker, the trail would be difficult to assign to an arthropod (Valentine, 2004). Our interpretation for the lack of ichnological details remains speculative. One possibility is that since the trilobite was in the meraspid period with a sagittal cephalic length of merely 1.7 mm, its feeble endopodites and genal spines could barely produce very delicate striations on the sediment, which could not survive the postmortem diagenetic compaction and cementation. Another reason for the loss of fidelity is the lithological consistency of the Chengjiang mudstone: details of arthropod traces are best preserved as convex hyporeliefs in sediments of silt size underlain by argillaceous rocks (e.g., Osgood, 1970; Crimes, 1975).

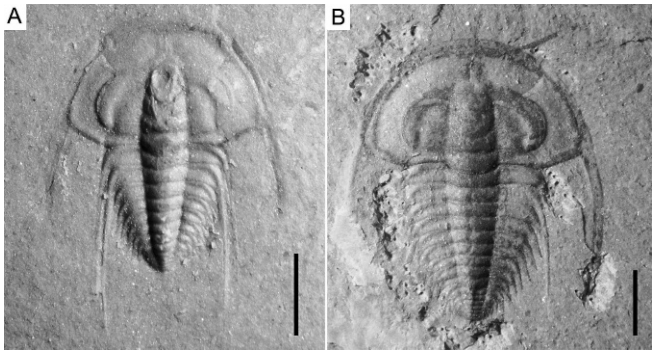

FIGURE 3—Comparison of two other meraspides (*Eoredlichia intermedia*) from same locality in different ontogenetic stages. A) Meraspid degree 11 (ELI-EOM002); B) late meraspid degree 14~15 (ELI-EOM003). Note reduction of thoracic pleural spines and proportion of cephalon to thorax. A rudiment of axial spine developed in (B); scale bar = 1 mm.

Preservation

We reason that the presence of organic materials within the trail is fundamental for its preservation. We postulate that the trilobite lost its pygidium as well as partial thorax after a predatory attack. It then trudged on the sea bottom for refuge, leaving a trail of body fluid and debris oozing from the wound, soon after which the trilobite and the organic-rich trail were caught in and entombed by a sudden mudflow. Arguments include:

1. The elevated concentration of Fe on the trail. The permeation of body fluid and residue secreted from the injured trilobite into the sediment may have produced a favorable environment for Fe- and S-reducing anaerobic bacteria, whose subsequent activities may have enhanced the precipitation of authigenic pyrite as well as Fe- and Al-rich silicates (Orr et al., 1998; Gabbott et al., 2004). Moreover, the organic secreta themselves are rich in Fe and have also the nature of absorbing ambient iron element (Zhang, 2001).

2. The librigenae are more likely to detach from the cranidium than the thoracic tergite is from the middle. The mutilation (equally exhibited on the counterpart), therefore, is more likely to have resulted from a predatory attack.

3. The width of the trail is consistent to the transverse length of the thorax but not the genae. Provided that the trilobite ploughed (in a foraging process, for instance) through the sediment, the breadth of trail would be isometric to the span of the genae.

The pale orange hue of the trail (Fig. 1A) resembles those observed on escape trails left by priapulid worms from similar horizons (Han et al., 2007), implying that secreting mucus (Zhang et al., 2006) seems not to be a prerequisite for the worms to produce such trails (Han et al., 2007), whereas microbial activity may have favored their formation. Organic stains commonly found behind *Marrella splendens* Walcott, 1912, from the Burgess Shale (e.g., Whittington, 1985; Briggs et al., 1994; Conway Morris, 1998), representing the leaking of decay products out of the carcass, definitely differ from the present locomotory trail in essence.

Lifestyle

We propose a nektobenthic locomotory style for juvenile redlichiids of *Eoredlichia intermedia*. In the case described here, the extra broad cephalon, paired prominent genal spines, and extremely prolonged first and second pleural spines (Figs. 1, 3A) may have functioned for buoyancy, balancing, or steering in the water column, reminiscent of meraspides of *Paradoxides pinus* (Bergström, 1972). A robust, long median axial tergal spine is presumed to have germinated during meraspid degree 9 (Fig. 3B) in light of its location on the tergite and the timing of thoracic tagmosis. The axial spine, analogous to the terminal telson of extant *Limulus*, presumably acted as a back brace that assists in shoveling the cephalon down into the sediment in search of food or otherwise has been used to lever the trilobite and generate a jump forward. It is noteworthy that the proposed self-made trail of the juvenile in part is evidence of their vagrant benthic locomotion. The development of the axial spine, therefore, may mirror a turn from nektonic to benthic style of predominant locomotion for juveniles of *Eoredlichia*. In the early holaspid (adult) period (after meraspid degree 15), *Eoredlichia* sheds its long pleural spines, and its cephalon becomes proportionate to the thorax (Lu, 1940). This further substantiates the predominant bottom-living habit in adults, albeit the possibility of occasional swimming, as seen in *Limulus*.

It seems appropriate to infer that during the early meraspid period, juveniles of *Eoredlichia intermedia* were free-swimming planktivores in the water column, as were their pelagic larvae. Later on they may have grown into organic particle feeders foraging on soft sediments, or, more likely, scavengers or predators (Fortey and Owens, 1999), in light of their stout, spinose endopod bases in common with naraoiids (Ramsköld and Edgecombe, 1996), indicative of gnathobase, as well as their spinose, conterminant hypostomes (Shu et al., 1995).

CONCLUSIONS

A juvenile of *Eoredlichia intermedia* from the Chengjiang fauna is proposed to be responsible for a trace fossil defined by slight differences in chemistry and lithology from the matrix. A predation event is inferred to have played a crucial role in the preservation of this rare case. Functional morphology of the trilobite, combined with its putative trace, suggests a nektobenthic lifestyle for juvenile redlichiids of *Eoredlichia intermedia*.

ACKNOWLEDGMENTS

This paper benefited from valuable discussions and correspondence with Robert W. Scott (University of Tulsa, Oklahoma, United States). Simon Conway Morris (University of Cambridge, London, UK) commented on the early draft of the manuscript. Thanks also are due to Gong Hujun (State Key Laboratory for Continental Dynamics, Northwest University, Xi'an, China) for use of scanning electron microscope facilities; and Zhai Juanping, Cheng Meirong, and Yao Yanchun (Early Life Institute, Northwest University, Xi'an, China) for both field and lab work. Financial support for this study was provided by the National Natural Science Foundation of China (Grant No. 40830208, 32070207, and 04062003), the National 973 Project (Grant No. 2006CB806401), and the Program for Chengjiang Scholars and Innovative Research Team in University (PCSIRT).

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ACCEPTED FEBRUARY 27, 2009