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Cambrian–Ordovician trilobite family Missisquoiidae Hupé, 1955: Systematic revision and palaeogeographical considerations based on cladistic analysis

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Abstract

The missisquoiids are among the most important trilobites in the Cambrian–Ordovician boundary interval of Laurentia and Gondwana. This study deals with a systematic review of the family Missisquoiidae based on a cladistic analysis and explores their palaeobiogeographical history. A total of 22 missisquoiid species were selected for cladistic analysis. The cladistic results demonstrate that the family Missisquoiidae includes *Parakoldinioidia*, *Pseudokoldinioidia*, *Tangshanaspis*, and *Tasmanocephalus*; *Lunacrania* and *Hardyia* are included with reservation. The well-known genus *Missisquoia* is treated as a junior synonym of *Parakoldinioidia*. Based on the distribution of the missisquoiids, six palaeogeographical areas are recognised: Sino-Korea, Yangtze, Australia, southern Laurentia, northwestern Laurentia, and northeastern Laurentia. Palaeogeographical analyses show that the missisquoiids originated in Gondwana and continued to expand their geographical range within the continent and eventually expanded into the Laurentia. Optimisation results of geographical area transitions demonstrate that there were transitions between the two continents, and evolution of the Laurentian missisquoiids appears to have been strongly influenced by the Gondwanan counterparts. We suggest that dispersal of non-fossilised egg stage probably transported by oceanic currents may have been responsible for these inter-continental transitions.

Keywords: Trilobites; Cambrian; Ordovician; Palaeogeography; Gondwana; Laurentia

1. Introduction

The family Missisquoiidae is an important group of Furongian (late Cambrian) and early Ordovician trilobites in eastern Gondwana and Laurentia. The type genus *Missisquoia* Shaw, 1951 was long employed as an index taxon for defining the base of the Ordovician in Laurentia (Winston and Nicholls, 1967; Stitt, 1971, 1977; Ross et al., 1982; Loch et al., 1993; Ross et al., 1997). More recently, the Global Stratotype Section and Point for the base of the Ordovician was ratified at the slightly younger level at the lowest occurrence of a conodont species, *Iapetognathus fluctivagus* Nicoll et al., 1999 (Cooper et al., 2001). Nonetheless, the stratigraphical importance of *Missisquoia* has not been weakened, as the trilobite faunal change across the boundary between the *Eurekia apopsis* Zone and the *Missisquoia* Zone is conspicuous in Laurentia (Westrop, 1989; Ross et al., 1997; Miller et al., 2003).

Missisquoia was limited to Laurentia, until *Missisquoia perpetis* Zhou and Zhang, 1985 was reported in North China. The recognition of *Missisquoia* in North China apparently enhanced its stratigraphical value for correlation between eastern Gondwana and Laurentia: e.g., the *M. perpetis* Zone of North China was correlated with the *Missisquoia* Zone of Laurentia with confidence (Shergold, 1988; Geyer and Shergold, 2000).

In recent investigations on the lower Palaeozoic Taebaek Group of the Taebaeksan Basin, Korea (Choi et al., 2003, 2004), several fossiliferous horizons were located in the Cambrian–Ordovician boundary interval that yielded relatively diverse and abundant trilobites. Of note is the occurrence of *Missisquoia* sp. (Choi et al., 2003, Fig. 2) in a thin interval (less than 1 m thick) in the lowermost part of the Dongjeom Formation. The trilobite

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faunal assemblage was correlated with the *Missisquoia perpetis* Zone of North China and *Missisquoia* Zone of Laurentia (Choi et al., 2003). Subsequent examination of better preserved specimens reveals that *Missisquoia* sp. is referable to *M. perpetis*, but more importantly that *M. perpetis* is morphologically distinct from the typical *Missisquoia* species of Laurentia and can be better referred to *Pseudokoldinioidia* Endo, 1944 (Lee and Choi, 2007). This requires that the inter-continental correlations based on *Missisquoia* should be reassessed and that all the missisquoiid species should be examined from the phylogenetic and palaeogeographical viewpoints. Accordingly, this report aims to compile all the available data on the species assigned to the Missisquoiidae, to analyze their morphology by cladistic methods to determine phylogenetic relationships, and then to examine their palaeobiogeographical history based on the phylogenetic relationships.

2. Review of missisquoiid trilobites

Hupé (1955) erected the family Missisquoiidae based on *Missisquoia* and questionably included three genera in the family (*Inouyina* Poletayeva, 1936; *Chakasskia* Poletayeva, 1936; and *Kaolishania* Sun, 1924). However, *Missisquoia* was the only genus listed under the family Missisquoiidae in the Treatise on Invertebrate Paleontology (Lochman–Balk in Moore, 1959). Species of *Missisquoia* have since been widely documented in Laurentia (Winston and Nicholls, 1967; Hu, 1971; Stitt, 1971; Hu, 1973; Taylor and Halley, 1974; Dean, 1977; Stitt, 1977; Ludvigsen, 1982; Fortey et al., 1982; Westrop, 1986; Ludvigsen et al., 1989;Dean, 1989; Loch et al., 1993).

In the 1970s and 1980s, considerable attention was paid to the Missisquoiidae, mainly because *Missisquoia* and related genera were known to have a stratigraphical value in recognising the Cambrian–Ordovician boundary. Hu (1973) erected the genus *Paranumia* from South Dakota specimens; but it was later suggested to be synonymous with *Missisquoia* by Ludvigsen (1982) or *Lunacrania* Kobayashi, 1955 by Fortey (1983). Shergold (1975) documented *Parakoldinioidia* Endo in Endo and Resser, 1937 in Australia and assigned it to the Missisquoiidae under the superfamily Leiostegiacea. Dean (1977), based on a detailed account of *Missisquoia*, proposed that *Lunacrania*, *Macroculites* Kobayashi, 1955, and *Rhamphopyge* Kobayashi, 1955 from the southern Canadian Rocky Mountains are junior subjective synonyms of *Missisquoia*. Zhou and Zhang (1978) established the missisquoiid genus *Tangshanaspis* from the *Mictosaukia* Zone of Hebei Province, China. Ludvigsen (1982), however, synonymised *Lunacrania*, *Macroculites*, *Rhamphopyge*, *Paranumia*, and *Tangshanaspis* with *Missisquoia*; this left only two genera, *Missisquoia* and *Parakoldinioidia*, in the family Missisquoiidae. On the other hand, Fortey et al. (1982) argued that *Lunacrania* can be differentiated from *Missisquoia* by its anteriorly-placed small eyes and longer triangular postocular cheeks. Fortey (1983) went further to suppress *Missisquoia* as a junior synonym of *Parakoldinioidia*. Most of the missisquoiids were known from Furongian strata, but Jell and Stait (1985) recognised *Tasmanocephalus* Kobayashi, 1936 from the lower Arenigian of Tasmania as a member of the Missisquoiidae, and also suggested that *Parakoldinioidia* has a nomenclatural priority over *Missisquoia* and *Lunacrania*.

In the late 1980s, missisquoiid trilobites were frequently described in China. Zhou and Zhang (1985) proposed the species *Missisquoia perpetis* from North China and emphasised that *Tangshanaspis* is a missisquoiid genus distinct from *Missisquoia*. Qian (1985) revived *Pseudokoldinioidia* by erecting a new species *Pseudokoldinioidia bifurcata* from Anhui Province, China, but it was Duan et al. (1986) who first assigned *Pseudokoldinioidia* to the Missisquoiidae and established two species (*P. taiziheensis* and *P. huinanensis*) and a subspecies (*P. perpetis wennanensis*) from Liaoning and Shandong provinces. Duan et al. (1986) also recorded another missisquoiid species, *Parakoldinioidia wennanensis* Duan and An in Duan et al. (1986). Lu and Zhou (1990) documented two new species of *Pseudokoldinioidia*, *P. expansa* and *P. encrinuroides*, from Guizhou Province for the first time in South China and proposed the subfamily Pseudokoldinioidiinae under the family Encrinuridae and suborder Cheirurina. More recently Zhang and Peng (1998) proposed *Fuzhouwania* based on two cranidia from the *Kaolishania pustulosa* Zone of Shandong and Liaoning provinces, North China, and assigned it to the Missisquoiidae.

Shergold et al. (1988), in a comprehensive discussion of the Missisquoiidae, included *Parakoldinioidia*, *Missisquoia*, *Tangshanaspis*, *Lunacrania*, and *Pseudokoldinioidia* in the family, but favored an assignment of *Tasmanocephalus* to the Styginidae. Jell and Adrian (2003) listed six genera under the family Missisquoiidae: *Fuzhouwania*, *Hardyia*, *Lunacrania*, *Parakoldinioidia*, *Pseudokoldinioidia*, and *Tasmanocephalus*. *Paranumia* was treated as a junior synonym of *Lunacrania*, and *Macroculites*, *Rhamphopyge*, *Tangshanaspis*, and *Missisquoia* were synonymised with *Parakoldinioidia*. Thus, there have been considerable disagreements or confusions about the taxonomy of the Missisquoiidae. To sum up, eleven genera have been assigned to the family and 47 species, including nine species in open nomenclature, have been described (Appendix 1).

Based on cranidial similarities of the Missisquoiidae with the Leiostegiidae, Shergold (1975, p. 195) assigned the family to the superfamily Leiostegiacea. On the other hand, Ludvigsen (1982, p. 119) noted the similarities between *Missisquoia depressa* Stitt, 1971 and *Perischoclonus capitalis* Raymond, 1925 (cf. Whittington, 1963) and suggested that the family should be ancestral to the Styginidae, which in turn appears to be ancestral to the Illaenidae and Scutelluidae (see also Jell and Stait, 1985; Shergold et al., 1988). Lane and Thomas (1983, p. 155) however contradicted Ludvigsen's view and claimed that the Missisquoiidae have more similar cephalic morphology to the Cambrian Corynexochina than post-Cambrian Scutelluina (= Illaenina of Fortey in Whittington et al., 1997).

3. Stratigraphical and geographical distribution of the missisquoiids

The occurrences of the missisquoiid trilobites can be grouped into two palaeogeographically widely separated regions—Laurentia and eastern Gondwana. In eastern Gondwana,