Geosciences Journal
Vol. 12, No. 3, p. 227 − 231, September 2008
DOI 10.1007/s12303-008-0023-8

Taxonomic revisions of Upper Cambrian *Granatodontus* Chen et Gong, 1986 of the *Dasytodus* Lineage (Conodonta)

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ABSTRACT: The Upper Cambrian conodont taxa of the *Dasytodontus* Lineage is particularly useful to divide strata near Cambrian-Ordovician boundary. This lineage known only in Korea, China and Australia include many coniform paraconodonts and euconodonts with granulose, spinose or nodose ornaments, comprising *Granatodontus* Chen et Gong, 1986. The generic and specific concepts of *Granatodontus* are reviewed herein, with comments on its evolution, paleoecology and geographic distribution. Two new species are erected: *Granatodontus asymmetrica* sp. nov. and *Granatodontus multicorrugata* sp. nov.

Key words: Upper Cambrian, conodont taxonomy, *Granatodontus* of *Dasytodus* Lineage

1. INTRODUCTION

Relatively little has been known about the evolutionary development of the Cambrian conodonts until mid 1970's. Bengtson (1976, 1983a,b) proposed a conodont evolutionary model on protoconodonts to paraconodonts to euconodonts. Miller (1980) documented the Upper Cambrian euconodont evolutionary relationships, and suggested two important lineages: *Teridontus* and *Proconodontus* lineages. The *Teridontus* Lineage includes *Hirsutodontus, Clavohamulus, Semiacontiodus, Monocostodus* and *Utahconus.* The *Proconodontus* Lineage includes *Cambrooistodus, Eoconodontus* and *Cordylodus*. Miller (1984) erected one more lineage viz. *Fryxellodontus* Lineage previously regarded as a part of the *Proconodontus* Lineage (Miller, 1980).

Afterwards, Chen and Gong (1986) added one more lineage, the *Dasytodus* Lineage. They suggested that *Dasytodus* Chen et Gong, 1986 is derived from *Granatodontus* Chen et Gong, 1986.

The paraconodont and euconodont elements with papillose surface texture include *Rotundoconus*, *Granatodontus*, and *Dasytodus*. These are endemic ones which occur only in Korea, China and Australia, whereas *Hirsutodontus* and *Clavohamulus* are cosmopolitan genera which occur in North America, South America, Australia, Asia and Antarctica. The genera and species of *Dasytodus* Lineage as well as *Teridontus* and *Fryxellodontus* lineages are excellent tools for the zonation of worldwide uppermost Cambrian.

In Korea, *Rotundoconus* An et Zhang, *Granatodontus* Chen et Gong and *Dasytodus* Chen et Gong are abundant in Upper Cambrian Hwajeol Formation of Taebaeksan Basin (Lee, 1989a,b, 1990, 1992, 2002a,b, 2001a,b, 2004; Lee, B. S. and Lee, H. Y., 1988; Lee, B. S. and Lee, J. D., 1993). However, *Hirsutodontus* Miller is very rare (Lee, 2004), and *Clavohamulus* Furnish has been not recovered yet.

During last two decades, the similarity of the Lower Paleozoic environment has been given rise to serious complications between conodont specialists of Korea and China in nomenclature of the *Dasytodus* Lineage, particularly in taxonomy of endemic genus *Granatodontus*. Some unknown number of names of the Lower Paleozoic conodonts of China have been based on a single specimen. Fortunately, recent systematic studies reduced most of sustaining taxonomic feud.

The present study aims to re-evaluate and build on the definition of the genus *Granatodontus*, a member of the *Dasytodus* Lineage, and to describe new species, with comments on its evolution, paleoecology and paleogeographic distribution.

2. PREVIOUS WORK

The taxa of the *Dasytodus* Lineage of Chen and Gong (1986) are characterized by granulose surface ornaments. Two member of this lineage is *Rotundoconus* and *Granatodontus.* These taxa appear to be closely related in taxonomy with spinous and nodose members of *Teridontus* lineage: *Hirsutodontus*, *Clavohamulus* and *Dasytodus nodus*.

Rotundoconus has granulose surface with bulbous tip, *Granatodontus* has granulose and/ or tiny spinose surface with sharp tip, *Hirsutodontus* has rather robust spines mainly on its anterior surface, and *Clavohamulus* is relatively small and is covered with many strong spines except posterior side. Four genera except *Rotundoconus* are euconodonts with cusp filled with white matter.

An and Yang (1980) first described a coniform conodont, *Hirsutodontus primitivus* An et al., without a differentiated cusp from the Upper Cambrian Fengshan Formation, China.

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An et al. (1983) described two coniform conodonts: *Hirsutodontus bulbousus* (Miller, 1969) with granulose surface and bulbousus tip, and *Hirsutodontus* aff. *primitivus* An et al., 1983 with granulose or spinous surface. Lee and Lee (1988) described some species of *Hirsutodontus* for the first time in Korea: *H. primitivus*, *H*. n. sp. A, *H*. n. sp. B and *H*. n. sp. C. They also reassigned *Proconodontus transmutatus* An et al., 1983 to *Teridontus transmutatus* (Xu et Xiang, 1983) on the ground of its sectional similarity to the latter genus. Chen and Gong (1986) reassigned *Teridontus nakamurai nodus* An et al., 1983 and *Proconodontus transmutatus* An et al., 1983 to the species under the genus *Dasytodus* Chen et Gong, 1986, because they have differentiated cusp and base, oval to rounded cross section, and nodose and spinose surfaces. They also reassigned *Hirsutodontus*? *ani* Wang, 1985 to the new genus *Granatodontus* Chen et Gong, 1986 due to the lack of true cusp. Lee (2002) proposed two new species of *Hirsutodontus hwajeolensis* Lee, 2002 for the specimens of *Hirsutodontus* sp. nov. A of Lee and Lee (1988) and *Rotundoconus bulousus* Lee, 2002.

Elements of the *Dasytodus* Lineage range from the *Proconodontus* to *Cambrooistodus minutus* zones, but are dominant in the *Proconodontus tenuiserratus* Zone, China (An et al., 1983; Chen and Gong, 1986), and *Proconodontus* Zone, Korea (Lee and Lee, 1988; Lee, 2002, 2004).

3. EVOLUTION, PALEOECOLOGY AND GEOGRAPGIC DISTRIBUTION

General evolutionary trends of Upper Cambrian conodonts include differentiation of the posterior edge of elements, shortening of basal cavities, development of white matter and thickening of walls with reduction of basal cones. Differentiation of the posterior edge of elements represents development of keels, costae, and adenticulate and denticulate processes.

Evolutionary relationships among early euconodont genera of Upper Cambrian are now well understood, and have been useful in generic classification. However, those among paraconodonts including *Granatodontus* are still poorly understood.

Major changes in euconodont evolution, as well as biofacies adaptation and development of provincialism, coincided with sea-level fluctuations near the end of the Cambrian. However, paraconodonts such as *Westergaardodina, Furnishina* and *Granatodontus* were flourished before this environmental changes, and then gradually disappeared and were replaced by new pelagic genus like *Cordylodus*.

Evolutionary relationships of Upper Cambrian conodonts are studied by some authors (Miller, 1980, 1984; An and Mei, 1994; Dong, 1997). Miller (1980, 1984) studied mainly on the euconodont lineage as stated above (see introduction), An and Mei (1994) studied on paraconodont lineages, and the derivation of euconodonts from paraconodonts. Dong (1997) studied on two paraconodonts of *Gapparodus* and *Westergaardodina.*

An and Mei (1994) are trailblazers in documentation on evolution of Cambrian conodonts. They proposed three paraconodont lineages viz. the *Laiwugnathus-Westergaardodina, Dolabrodus-Furnishina* and *Prooneotodus* lineages, and explained that early euconodonts are derived polyphyletically from genus *Prooneotodus*. Particularly, *Hirsutodontus* (=*Granatodontus*) *ani* is evolved from *Prooneotodus* by the granulation of the unit surface. Chen and Gong (1986) pointed out that *Dasytodus* was derived from *Granatodontus* on the ground of stratigraphic relationship and morphologic linkage.

In conclusion, *Granatodontus* was derived from *Prooneotodus,* and *Granatodontus* evolved into *Dasytodus*, and probably into *Hirsutodontus* through the acquisition of spines and white matter in Late Cambrianon time. This recognition came from a number of the observation of Korean specimens from the Sesong Slate (lower Upper Cambrian), Hwajeol (middle to upper Upper Cambrian) and Machari (upper Middle Cambrian to middle Upper Cambrian) formations (Lee, B. S. and Lee, H. Y., 1988; Lee, 1989a,b, 1990, 1992, 2001a,b, 2002a,b, 2004; Lee, B. S. and Lee, H. Y., 1988; Lee et al., 1991; Lee, B. S. and Lee, J. D., 1993). This morphologic continuity among Korean specimens can be easily verificated by images (Fig. 1).

Protoconodonts and paraconodonts were probably pelagic and cosmopolitan based on the geographic distribution doc-

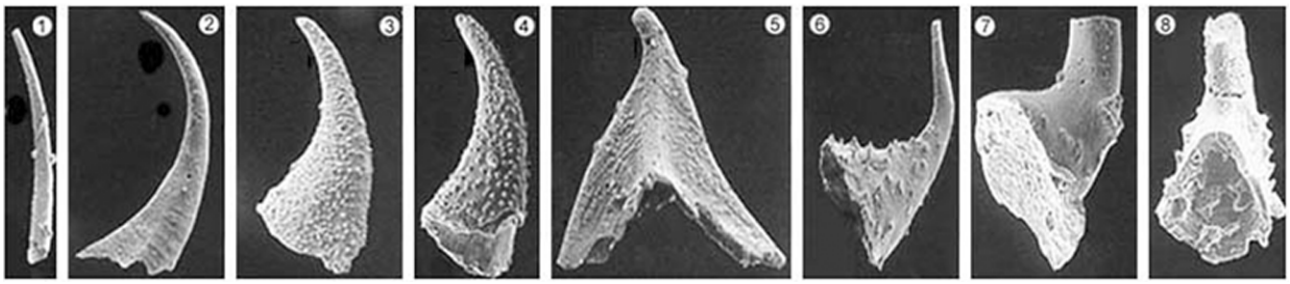

Fig. 1. Some Upper Cambrian conodonts showing evolutionary trend (from left to right). All specimen from Hwajeol Formation: 1, *Phakelodus tenuis*, x100; 2, *Prooneotodus rotundatus*, x75; 3-4, *Granatodontus ani*, x160; 5, *Rotundoconus jingxiensis*, x86; 6, *Dasytodus transmutatus*, x90; 7, *Dasytodus nodus*, x180; *Hirsutodontus hirsutus*, x80 (Lee and Lee, 1988; Lee, 2004).

umented by most of the reports on the Cambrian conodonts (Müller, 1959, 1973; Müller, and Hinz, 1991; Miller, J. F., 1969, 1982, 1984; Druce and Jones, 1971; Miller, R. H. and Paden, E. A., 1976; An, 1982, 1987; An et al., 1983; Chen and Gong, 1986). However, the *Dasytodus* Lineage including *Granatodontus* has been recorded only in Asia (Korea, China) and Australia. Particularly, *Granatodontus* has been occurred only in Korea and China, and so is endemic.

Paraconodonts are common in the Swedish "stinkstones" (Müller, 1959) deposited under anoxic conditions. From this environment, it can be deduced that the mode of life of paraconodonts were pelagic, tolerant of wide variations in water temperature or possibly depth, but were probably intolerant of elevated salinity.

Most of depositional environments containing paraconodonts including *Granatodontus* are from platform facies (Warm Water Realm of Miller, 1984, 1988), although challenge is raised (Landing et al., 2007). Conodonts from the Warm Faunal Realm are high in abundance and diversity compared with those from the Warm faunal Realm (Miller, 1988). The paleogeographic settings of the Hwajeol Formation, Korea and Fengshan Formation, China are very similar to each other. Two areas are located within the Sino-Korean Carbonate Flatform at a paleolatitude of 30°N approximately (Chen et al., 1986), and the lithofacies consists mainly of a rhythmical sequence of fine-grained carbonates deposited in a moderately deep outer shelf environment of quiet water below the normal storm wave base.

4. SYSTEMATIC PALEONTOLOGY

Conodont elements described herein were recovered from the Hwajeol Formation in the Seokgaejae section, Taebaeksan Basin. See Lee and Seo (2008) for conodont-related data.

Genus *Granatodontus* Chen et Gong, 1986

Type species.- *Hirsutodontus*? *ani* Wang in Chen et al., 1985

Granulose coniform paraconodonts with single elemental apparatus. Base and cusp are not differentiated, lacking white matter. Entire surface is sculptured with numerous granules (minute warts). Base is widely expanded, particularly posteriorly in lower part. Basal cavity is wide and deep, extending nearly to the tip of cusp. Cross sections of the units are variable: oval to rounded, subtriangular, or multicarinated by modifying additional lateral carina (e), resulting in increase of asymmetricity of the element.

Granatodontus asymmetrica sp. nov.

Plate 1, Figures 2-3

Holotype.- Plate 1, Figure 3.

Derivation of name.- After its asymmetrical cross section.

Diagnosis.- Asymmetrical coniform paraconodonts with granulose surface and very deep basal cavity, lacking white matter.

Description.- Granulose asymmetrical paraconodonts with very deep basal cavity, extending nearly to the tip of apex. Cross section is asymmetrical, particularly in lower part. Coniform conodonts, lacking white matter.

Remarks.- This new species is characterized by asymmetrical cross section. It can be easily distinguishable among species under the genus: *Granatodontus ani* Wang, 1985 has oval to rounded cross section, and *Granatodontus multicorrugata* sp. nov. has four or more carinated cross section.

Occurrence.- *Proconodontus* Zone to *Cambrooistodus minutus* Zone of the Hwajeol Formation, Seokgaejae section, Taebaeksan Basin.

Material.- Thirty four elements.

Granatodontus multicorrugata sp. nov.

Plate 1, Figures 4-5

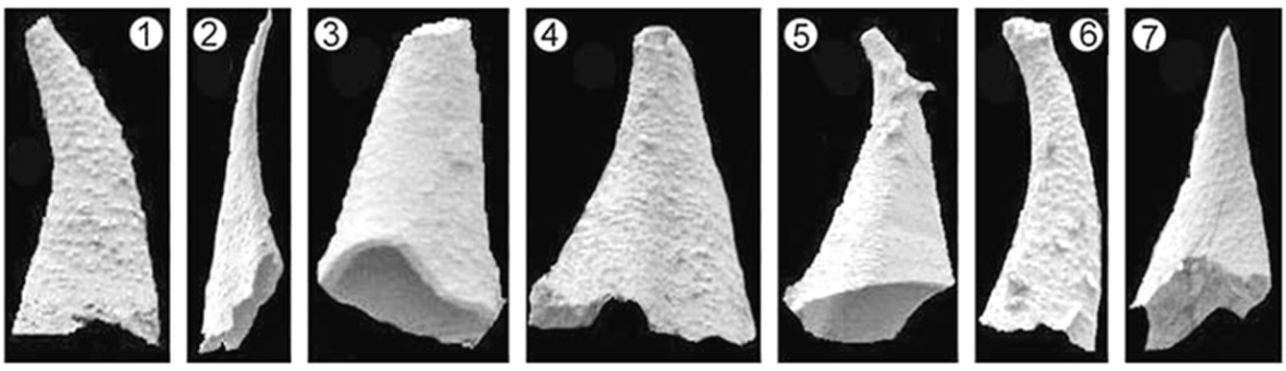

Plate 1. SEM micrographs of selected conodonts from the Hwajeol Formation in the Seokgaejae section, southeast Taebaeksan Basin (Lee and Seo, 2008). (1) lateral view of *Granatodontus ani* (Wang, 1985), KH 13 (x50). (2-3) lateral and posterolateral views of *Granatodontus asymmetrica* sp. nov. KH 4 (x50), KH 14 (x100). (4-5) posterolateral and lateral views of *Granatodontus multicorrugata* sp. nov., KH 4 (x50), KH 5 (x75). (6) lateral view of *Rotundoconus bulbousus* Lee, 2002, noncarinate element (KH 14, x100). (7) posterior view of *Granatodontus hwajeolensis* (Lee, 2002), KH 4 (x50).

Holotype.- Plate 1, Figure 5.

Derivation of name.- Latin *multi*, many, and *corrugate*, fold, after the many carinated cross section.

Diagnosis.- Asymmetrical coniform paraconodonts with four or more carinae and very deep basal cavity.

Description.- Granulose, symmetrical to asymmetrical paraconodonts, lacking white matter. Base moderately expanded bilaterally. Cross section is tetracarinated or multicarinated by modifying additional lateral carina (e), giving usually asymmetrical appearance. Basal cavity is very deep, extending nearly to the tip of apex.

Remarks.- This newly erected species is characterized by tetracarinated or multicarinated cross section. The differentiation of the species under the genus is documented under the description of *Granatodontus asymmetrica* sp. nov.

Occurrence.- *Proconodontus* Zone to *Eoconodontus notchpeakensis* Zone of the Hwajeol Formation, Seokgaejae section, Taebaeksan Basin.

Material.- Nine elements.

ACKNOWLEDGMENTS: The writer would like to thank Miss Park, N. R. (KNU) for her assistance in laboratory work. We are grateful to anonymous reviewers for their constructive comments and suggestions.

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Manuscript received January 16, 2008
Manuscript accepted August 11, 2008