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Wang, L, Wignall, PB, Sun, Y et al. (3 more authors) (2017) New Permian-Triassic conodont data from Selong (Tibet) and the youngest occurrence of Vjalovognathus. *Journal of Asian Earth Sciences*, 146. pp. 152-167. ISSN 1367-9120

<https://doi.org/10.1016/j.jseaes.2017.05.014>

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Accepted Manuscript

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PII: S1367-9120(17)30232-8

DOI: <http://dx.doi.org/10.1016/j.jseaes.2017.05.014>

Reference: JAES 3079

To appear in: *Journal of Asian Earth Sciences*

Received Date: 4 November 2015

Revised Date: 9 May 2017

Accepted Date: 9 May 2017

Please cite this article as: Wang, L., Wignall, P.B., Sun, Y., Yan, C., Zhang, Z., Lai, X., New Permian-Triassic conodont data from Selong (Tibet) and the youngest occurrence of *Vjalovognathus*, *Journal of Asian Earth Sciences* (2017), doi: <http://dx.doi.org/10.1016/j.jseaes.2017.05.014>

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New Permian-Triassic conodont data from Selong (Tibet) and the youngest occurrence of *Vjalovognathus*

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Abstract:

The controversial biostratigraphy of the well-known Permo-Triassic (P-T) boundary section at Selong, South Tibet is reinvestigated based on large conodont samples. The conodont data in this study confirm that the upper part of Selong Formation and the *Waagenites* Bed in the lower part of Kangshare Formation as Changshingian age. Just above the *Waagenites* Bed, the *Otoceras latilobatum* Bed is assigned to the basal Triassic due to the presence of *H. parvus* Zone. The discovery of *Vjalovognathus* (a cool-temperature tolerant form) in Changshingian strata allows the youngest *Vjalovognathus* species (*V. carinatus* sp. nov.) to be described, and a possible Permian *Vjalovognathus* evolutionary trend proposed: in ascending order this is, *V. australis* (late Sakmarian-early Artinskian), *V. shindyensis* (early Kungurian), *V.*

nicolli (late Kugurian-Early Roadian) and ultimately *V. carinatus* sp. nov. (Changshingian). The last species *V. carinatus* sp. nov. is also found in the pre-mass extinction beds at Guryul Ravine, Kashmir allowing correlation with South Tibet.

Key Words: Himalaya; Induan; *Vjalovognathus*; mass extinction; biostratigraphic correlation.

1. Introduction

The Permian-Triassic (P-T) boundary interval records the biggest mass extinction, with more than 90% of marine species lost at the time. Numerous studies have been conducted to understand this event in the Palaeo-Tethys and Panthalassan regions (Erwin, 1994; Retallack, 1995; Renne et al., 1995; Isozaki, 1997; Knoll et al. 2007; Brayard et al., 2009; Wignall et al., 2010; Grasby et al., 2011; Jochimscki et al., 2012; Payne and Clapham, 2012; Sun et al., 2012; Yin et al., 2013; Clarkson et al., 2015; Xie et al., 2017). The Perigondwanan margin is a major research area for the P-T boundary because of the distinctive history of the crisis in the region (Wignall et al., 1996; Retallack et al., 1998; Wignall and Newton, 2003; Waterhouse, 2004; Shen et al., 2006; 2010; Shi and Waterhouse, 2010; Hermann et al., 2010; Clarkson et al., 2013; Metcalfe et al., 2013; Waterhouse and Shi, 2013). Precise conodont biostratigraphic control in Perigondwana underpins these research efforts.

Selong is one of the best-known Perigondwanan P-T boundary sections (Jin et al., 1996; Wignall and Newton, 2003; Shen et al., 2006), and it is vital for correlating between Perigondwana and other P-T boundary records because of the presence of both conodonts and ammonoids including the biostratigraphically-significant

conodont *Mesogondolella sheni* and ammonoid *Otoceras*. This conodont species is first found in the Selong section and is regarded as a key latest Permian indicator (Mei, 1996; Shen and Shi, 2002; Shen et al., 2003b; Shen et al., 2006). A Late Permian, temperature sensitive (“cold water”) conodont *Vjalovognathus* is reported from the Salt Range, Pakistan; Manang, central Nepal; Guryul Ravine, Kashmir and this is believed to be the youngest occurrence of this genus (Wardlaw and Pogue, 1995; Nicora and Garzanti, 1997; Brookfield and Sun, 2015). Furthermore, Selong has been at the centre of the debate concerning the relative timing of the P-T mass extinction between equatorial and higher latitudes (Wignall and Newton, 2003; Shen et al., 2006). In order to address the considerable evolutionary complexity of *Vjalovognathus* in the later Permian, we sampled at Selong (in 2010) and present a new study of its conodonts.

2. Geological setting

The Selong section is situated in the northwest of Selong in Nyalam County and is about 700 km southwest of Lhasa, Tibet, China (Fig. 1). P-T strata in southern Tibet accumulated in the inner shelf seas along the passive continental margin of Indian Perigondwana (Jin et al., 1996). The P-T boundary beds at Selong are composed of the Coral Bed at the top of the Selong Group (Rao and Zhang, 1985; Wang et al., 1989; Jin et al., 1996) and then, at the base of the overlying Kangshare Formation, the Caliche Bed, the *Waagenites* Bed, the *Otoceras* Bed and the *Ophiceras* Bed (Jin et al., 1996; Wignall and Newton, 2003) (Fig. 2). The *Otoceras* Bed has been further subdivided into an upper *Otoceras woodwardi* Bed and a lower *Otoceras latilobatum* Bed (Wang and He, 1976).

Although the P-T boundary strata have undergone detailed conodont

biostratigraphic study (Xia et al., 1992; Orchard et al., 1994; Mei, 1996; Jin et al., 1996; Shen et al., 2003a, 2006), the precise ages of the Permian Selong Group and the mostly Triassic Kangshare Formations are controversial.

The Coral Bed is the uppermost part of Selong Formation (Jin et al., 1996) and was assigned a pre-Changhsingian age based on its rugose corals (Wang et al., 1989). The uppermost 6 m of the Selong Formation was described in detail by Jin and colleagues (1996). Discontinuously developed at the formational contact, the Caliche Bed is composed of travertine-like layers with gypsum intergrowths and grey-green shale clasts (Jin et al., 1996; Wignall and Newton, 2003). The presence of the shale clasts indicates that a sedimentary unit has been removed that is no longer present and therefore indicates erosion at this level (Wignall and Newton, 2003). However, Shen et al.'s (2006) conodont study suggests only a brief hiatus at the level of the Caliche Bed within a single conodont zone. Regardless of the duration of the hiatus all studies consider the formational contact to be a disconformity (e.g. Wang et al., 1989; Xia and Zhang, 1992) that Shen and Jin (1999) considered to coincide with the P-T boundary. However, the *Waagenites* Bed (called the *Tethyochonetes* Bed by Chen et al., 2000) contains a diverse Permian fauna, especially brachiopods (Chen et al., 2005) and subsequent conodont studies have placed the P-T boundary at the top of the *Waagenites* Bed (Fig. 2; Shen et al., 2006).

3. Materials and Methods

A total of 31 large conodont samples from Selong, weighing 176 kg (Table 1), were collected from 3.51 m of strata straddling the Permian-Triassic boundary. The samples were processed using the acetic acid dissolution method (Jiang et al., 2007) in the conodont laboratory of the China University of Geosciences (Wuhan). A total of

13 samples yielded 4746 conodonts, including 4124 P1 elements (2834 of them were broken) and 622 ramiform elements. No conodont was found in sample SL-6a-1 or in the samples below this level. In total there were 1290 well-preserved P1 elements belonging to *Hindeodus* (*H.*), *Clarkina* (*C.*), *Mesogondolella* (*M.*), *Jinogondolella* (*J.*) and *Vjalovognathus* (*V.*) (Figs. 3-9, Table1).

4. Results

4.1 Conodont fauna

4.1.1 Coral Bed (Bed 10)

Significant new conodont finds were obtained from the Coral Bed: *C. meishanensis*, *M. sheni*, *M. idahoensis*, *M. lamberti* and one new species *V. carinatus* sp. nov. that are described below.

M. sheni was first established as *C. sheni* by Mei (1996) but then assigned to *Mesogondolella* by Henderson and Mei (2000). *M. sheni* is considered a useful Changshingian marker species and it has been widely used when correlating within the Himalayan region, such as the Selong and Qubu sections of South Tibet and the Manang section of central Nepal (Mei, 1996; Shen et al., 2003; Shen et al., 2006). *M. idahoensis* was originally described from Idaho (Youngquist et al., 1951) and it has been widely reported from Gondwana [Australia (Nicoll and Metcalfe, 1998), New Zealand (Ford et al., 1999)], northwest Pangea [e.g. the Phosphoria Basin (Youngquist et al., 1951), British Columbia (Chung, 1993; Orchard and Forster, 1988), Panthalassa Japan (Igo, 1981)], western palaeo-Tethys [Sicily (Catalano et al., 1991)] and eastern palaeo-Tethys [South China, Wang and Wang, (1981); Zhang et al., (2010); Sun et al., 2017] as a Kungurian zonal conodont. However, the associated taxa in the Selong

assemblage clearly indicate a Changshingian age, therefore the presence of Kungurian *M. idahoensis* most likely reveals the presence of reworked conodonts in the Coral Bed (Fig. 8).

4.1.2 *Waagenites* Bed (Bed 11)

No conodonts were recovered from the Caliche Bed. They were also scarce in the *Waagenites* Bed samples; we found only *M. sp.* and *C. sp.*, which could not be assigned to any species. Previous studies have identified *M. spp.* (Orchard et al., 1994), *C. meishanensis?*, *C. zhejiangensis*, *M. sheni*, *H. praeparvus*, *H. cf. latidentatus* (Shen et al., 2006), *C. orchardi*, *H. typicalis* (Mei, 1996; Shen et al., 2006) and *C. tulongensis* (Mei, 1996) in this bed (Fig. 2).

C. orchardi was established by Mei (1996) and has been reported in Changshingian strata belonging to the *C. taylorae*-*C. zhejiangensis*-*C. yini* zone in the Chaotian section, northern Sichuan (Ji, et al., 2007) and also in Bed 27 of the Tulong Formation at Qubu, South Tibet where it co-occurs with *C. tulongensis* and *C. taylorae* (Shen, 2006). However, *C. orchardi* is also known from the Griesbachian *Neoclarkina krystyni* zone in Daxiakou section (Zhao et al., 2013) and the Gaomao section in South China (Yang et al., 2012). In the GSSP (Global Boundary stratotype Section and Point) of the P-T boundary at Meishan, South China, *C. orchardi* shows a relatively longer range from the *C. meishanensis* zone to the *C. krystyni* zone (Orchard and Krystyn, 1998). The reports of *M. sheni* and *C. orchardi* indicate that the *Waagenites* Bed is of Changhsingian age. Foraminifers also appear in this level that are typical of genera encountered in lower palaeolatitude Changhsingian sites (Wignall and Newton, 2003).

The biostratigraphic evidence suggests the *Waagenites* Bed is of Changhsingian age, but it is unclear if the sharp contact with the overlying *Otoceras* Bed is conformable.

4.1.3 *Otoceras* Bed (Bed 12-13)

Conodonts become common and diverse in the lower part of *Otoceras* Bed. We found *H. typicalis*, *H. pisai*, *H. latidentatus*, *H. parvus*, *H. praeparvus*, *C. zhejiangensis*, *M. sheni*, *C. deflecta*, *C. tulongensis*, *C. orchardi*, *C. taylorae* and *C. planata*. The first appearance of *H. parvus* indicates an earliest Triassic (Fig. 10). In the *Otoceras latilobatum* Bed (Bed 12), these Triassic conodonts co-occur with the older Permian species previously noted by Xia and Zhang, (1992), *C. liangshanensis* (Plate 2, fig.7.8 in Xia and Zhang, 1992), *M. rosenkrantzi* (Plate 2, fig.11-12 in Xia and Zhang, 1992), *M. phosphoriensis* (14 in Fig. 8, this paper) and *M. omanensis* (4 in Fig. 7; 6-8 in Fig. 8, this paper). Additionally we found other Permian conodonts, namely *J. granti*, *C. postbitteri*, *C. hongshuiensis* and *M. sp.*

M. omanensis was established as a short-ranging species in the late Wordian to Wordian-Capitanian boundary in Oman by Kozur and Wardlaw (2010). It is characterised by having a high anterior blade and elongate subtriangular platform and is considered to be the successor of *M. siciliensis*. This species currently is only reported from the Perigondwana region (e.g. Oman and South Tibet). *J. granti* is a zonal index for the late Capitanian and was first established by Mei and Wardlaw (1994) from Laibin, South China. *Jinogondolella* is regarded as a conodont with an equatorial, warm water distribution during the Guadalupian (Mei et al., 1999 a, b; Mei and Henderson, 2001). *J. granti*'s reported occurrence from Oman, where it is associated with *Mesogondolella* species, shows the species was more widespread than

previously thought (Kozur and Wardlaw, 2010). The occurrence of *Jinogondolella* at Selong increases this distribution. *M. phosphoriensis* is a Roadian-Wordian conodont and was first described in the Phosphoria Basin by Youngquist et al. (1951). It has also been found from the Canadian Arctic, Nepal and South China (Garzanti, 1994; Wang, 1999; Henderson and Mei, 2000; Wardlaw, 2001; Beauchamp et al., 2009). *C. postbitteri* is a zonal conodont of early Wuchiapingian age and *C. hongshuiensis* is generally used to indicate a late Capitanian age (Jin et al., 1998; Baud et al., 2012) and is widely distributed in equatorial Tethyan locations in South China (Jin et al., 1998). The presence of these older conodonts might indicate a substantial Permian stratigraphy was present at Selong that was eroded prior to the earliest Triassic.

Taxonomic notes

Family Vjalovognathidae Shen, Yuan and Henderson, 2015

Genus *Vjalovognathus* (Kozur, 1977)

Type species: *Vjalovognathus shindyensis* Kozur and Mostler, 1976.

Vjalovognathus carinatus Wang, Lai and Sun

sp. nov.

(Figs. 3-4; 1, 2 of Fig. 5)

2015 V. sp. Sun and Brookfield: Fig. 2

Holotype: P1 element, 3 of Fig. 3, w12-4-022.

Paratype: P1 element, 2 of Fig. 3, Y22-035.

Material: 8 P1 elements (1-3 of Figs. 3; 1-3 of Fig. 4; 1-2 of Fig. 5)

Derivation of name: From Latin “carinatus” meaning keeled, referring to its distinguished longitudinal ridge.

Diagnosis: The P1 element of *V. carinatus* sp. nov. has a deeply excavated basal cavity, the cusp is located in the posterior part of the element and posteriorly inclined. The denticles are spaced tightly, and their tops have been truncated to a flat curve in lateral view. The truncated denticle tips are normally round-ovate shape. A distinctive longitudinal ridge developed in the carina.

Description: The segminiscaphate P1 element is almost rectangular in lateral view, can have up to 13 denticles on the carina which are posteriorly inclined, the top of the denticles form a regular curved surface. One terminal cusp is located on the posterior end of the cup and pointed 45° posteriorly along the length of the element body. Older elements have more tightly spaced denticles. Generally, the anterior denticles are more spaced comparing with the posterior ones. In oral view, the tip of the denticles is truncated in a rounded or lens shape, the central area forms a trough or is even voided by removing of the white matter. The base of each denticle is expanded and a slightly inflated area occurs in its connecting area with the cup. A longitudinal ridge is developed within adjacent denticles. The basal cavity is large and deeply excavated, even reaching the base of the denticles, the widest part is the posterior end of the cup and narrows anteriorly.

Comparison: The P1 element of *Vjalovognathus* is distinguished by its deeply excavated basal cavity along the whole element and a significant truncation section developed on most of the denticles in the carina. Species are distinguished by the

shape of the truncated denticle section in upper view, or the development in the denticle of an anterior groove, or the presence of a median ridge between adjacent denticles.

Late Kungurian-early Roadian *V. nicolli* differ from *V. carinatus* sp. nov. by their more compressed denticles, although they have a longitudinal ridge. Early Permian *V. australis* and *V. shindyensis* have a distinctive anterior groove rather than a longitudinal ridge seen within adjacent denticles.

Remarks: The main characters of the truncated cross section of *Vjalovognathus* are shown in Fig. 11. The Sakmarian-Artinskian *V. australis* is ovate-kidney-bean shaped and linearly compressed at its base with an anterior groove on the denticles. The Kungurian *V. shindyensis* is distinguished by the absence of anterior groove but it develops a weak axial ridge on the posterior part of the denticles. Late Kungurian *V. nicolli* develops a prominent axial ridge which straddles the carina and is slightly appressed in the base of the denticles. *V. sp. nov. X* has a round-ovate shaped cross-section of the denticles and is more thick-walled compare to *V. nicolli* (Zheng et al. 2007; Nicoll and Metcalfe 1998). The precise age of this species was not given by Zheng et al. (2007). The new specimens we report from Changhsingian differ from previously reported species by their well-developed linear ridge between denticles, absence of groove and a basal cavity that is more excavated. The denticles are not compressed compared with the older *V. australis* and *V. shindyensis*.

Occurrence: Changhsingian; South Tibet, Kashmir.

Genus *Clarkina* (Kozur, 1989)

Type species: *Clarkina leveni* Kozur, Mostler and Pjatakova, 1975

Diagnosis: see Kozur, 1989

***Clarkina hongshuiensis* (Henderson and Mei, 2001)**

(12 in Fig. 8)

2006, *C. postbitteri*, Sun et al., Plate 1, Figs. 4-10.

2007, *C. postbitteri hongshuiensis*, Jin et al., Plate 1, Figs. 1,6-10,13-16.

2007, *C. postbitteri*, Zhang et al., Plate 1, Figs. 19-21, 23, 26, 29-30; Plate 2, Figs. 1-2, 5-6, 10, 21; Plate 2, Figs. 1-2, 5-6, 10, 21.

2017 *Clarkina hongshuiensis* Sun et al. Plate 6, Fig. 16.

Diagnosis: A species of *Clarkina* that exhibits a wide range of morphotypes, generally with tear shape, but always has smooth anterior margins, a narrow brim and high, fused anterior denticles on blade. The platform margins tend to be flat and the adcarinal furrows indistinct. The number of denticles is variable and mostly discrete, but some are closely spaced to fused. In most of the specimens there is a gap between the posterior denticle and the cusp.

Remarks: *C. hongshuiensis* was a subspecies of *C. postbitteri*, and was ranked as species by Lambert et al. (2010). It is widely known in South China (e.g., Sun et al., 2017). The specimens found in Selong have a slim platform parallel in both sides and narrow abruptly in the anterior third of the platform. The denticles on the carina are discrete with a distinctive cusp located at the end of the platform without a brim. As illustrated in original description, a brim is diagnostic, but the many specimens of *C. hongshuiensis* in Jin's collection do not possess this character.

Occurrence: South China, South Tibet.

***Clarkina postbitteri* Mei and Wardlaw (1994)**

(4 in Fig. 8)

2006, *C. postbitteri*, Jin et al., 2–5 in Fig. 7.

2006, *C. postbitteri*, Sun et al., Plate 1, Figs. 11-13.

2007, *C. postbitteri*, Zhang et al., Plate 2, Figs. 3-4, 11, 15, 22-26; plate 3, Figs. 9-10;

Plate 2, Figs. 3-4, 11, 15, 22-26; Plate 3, Figs. 9-10.

2010 *C. postbitteri*, Sun et al., Plate 1, Fig. 14.

Diagnosis: The P1 elements of *C. postbitteri* have widely spaced and consistently discrete denticles; the anterior platform narrows abruptly.

Remarks: the specimen found in Selong section have an obvious terminal cusp, compare to *C. hongshuiensis*, *C. postbitteri* have more spaced denticles in the carina, the anterior quarter of the platform narrows suddenly.

Occurrence: South China, South Tibet.

Genus *Jinogondolella* Mei and Wardlaw, 1994.

Type Species: *Gondolella nankingensis* Ching, 1960.

Diagnosis: See Mei and Wardlaw (1994).

***Jinogondolella granti* (Mei, 1998)**

(5 in Fig. 8)

1998 *J. granti*, Mei, Plate3, Figs. 1-4,10-14; Plate 7, Figs. 8,9,12,15-24; Plate 3, Figs. 24-26.

2007 *J. granti*, Zhang et al., Plate 1, Figs. 7-9, 27-28.

2010 *J. granti*, Wardlaw and Nestell, Plate 10, Figs 2,5-6,9;Plate 15, Fig. 13.

Diagnosis: “A species of *Jinogondolella* characterised by a P1 element that has an elongate and slender platform, usually with nearly paralleled platform margins on its posterior part. The platform narrows gradually to the anterior part, and has a

symmetric and rounded posterior area. The cusp is high and terminal located, and the carina is tightly denticulated but nearly fused in its middle part.” (p. 62-63, Mei, 1998).

Remarks: The anterior serration is well preserved in the specimens in our collection. A distinctive cusp is located in the posterior end of the platform which has parallel sides and gradually narrows anteriorly. Carina is high in the anterior blade, and decreases posteriorly. In the middle part of the carina, the denticles are fused. A constriction occurs in the middle to anterior portion of the platform.

Occurrence: South China, South Tibet.

Genus *Mesogondolella* Kozur, 1990

Type species: *Mesogondolella bisselli* (Clark and Behnken, 1971))

Diagnosis: See Kozur, 1990

***Mesogondolella idahoensis* (Youngquist, Hawley et Miller)**

(17 in Fig. 7)

2001 *M. idahoensis* Wardlaw , Fig. 1, 8-11

1951 *M. idahoensis* Youngquist et al., Plate 54, Fig. 1-3,14,15

Diagnosis: A species of *Mesogondolella* characterised by a P1 element with a high, elongate cusp located at the posterior end of the platform and roughly parallel in 2/3 of the posterior lateral margin without a brim.

Remarks: A well preserved specimen is found in the upper part of Selong Formation, the posterior end of the element is a blunted square.

Occurrence: US, Japan, Sicily, South China, South Tibet.

***Mesogondolella omanensis* Kozur and Wardlaw, 2010**

(4 in Fig. 7; 6-8 in Fig. 8)

2010 *M. omanensis* n. sp. nov. Kozur and Wardlaw, Plate 2, Figs. 2, 11-14, 16; Plate 3, Figs. 1-7, 9, 10, 15

Diagnosis: The platform of the species is large and has an elongate subtriangular outline. Normally, one side of the platform is straight and the other side is slightly convex in two-thirds of the platform. The carina is composed of tightly spaced posterior denticles and low to moderately high anterior blade whose denticles are highly fused.

Remarks: The *M. omanensis* found in this paper closely accord with the original description of Kozur and Wardlw (2010). However, the specimens at Selong have more bluntly rounded posterior end, and the anterior denticles on the blade are higher but tightly fused as Oman specimens.

Occurrence: Oman, South Tibet (Selong).

***Mesogondolella phosphoriensis* (Youngquist, Hawley et Miller)**

(14 in Fig. 8)

1951 *M. phosphoriensis* (Youngquist et al., 1951) Plate 54, Figs. 10-12.

2001 *M. phosphoriensis* (Wardlaw, 2001), Fig. 1, 15-17.

Diagnosis: *M. phosphoriensis* is characterised by a bluntly rounded to square posterior margin, a generally triangular shape, a prominent longitudinally elongate cusp, prominent carinal denticles that increase in size anteriorly and are discrete to partially fused with low, short partially fused denticles on the blade and indistinct furrows (Youngquist et al., 1951; Wardlaw, 2001).

Remarks: Our specimens normally have a triangular shape, and a distinct cusp located in the posterior portion of the element, possess a *M. phosphoriensis* feature

also in aboral view as illustrated by Youngquist et al. (1951). The escutcheon is bounded by distinct flanges and becomes very narrow anteriorly. The extreme anterior end of the element is terminated by a small, narrowly grooved keel. The posterior denticles in our specimens are only weakly fused in contrast to those found in the Phosphoria Formation of Idaho. *M. phosphoriensis* is differentiated from *M. omanensis* by its lower anterior blade. When comparing with *M. idahoensis*, it was more deeply excavated in the attached surface. Both of *M. phosphoriensis* and *M. idahoensis* have a larger cusp (Kozur and Wardlaw, 2010).

Occurrence: Western US, South Tibet.

5. Discussion

5.1 Changhsingian *Vjalovognathus* and its evolution during Permian

Vjalovognathus was first established by Kozur and Mostler (1976) and is characterised by an octomembrate apparatus (Yuan et al., 2015). It was used to establish the family Vjalovognathidae by Shen et al. (2015). It has been considered a cool water conodont typical of the Perigondwanan region especially during the Early Permian (Nicoll and Metcalfe, 1998; Mei et al., 1999a, b; Lai and Mei, 2000; Yuan et al., 2015) (Table 2). Five species have been assigned to *Vjalovognathus* (Fig. 11). The earliest member of the *Vjalovognathus* group is *V. australis*, reported from Timor (Indonesia) and Western Australia where it ranges from late Sakmarian to early Artiskian (Van den Boogaard, 1987; Reimers, 1991; Nicoll and Metcalfe, 1998). The second species *V. shindyensis* is known from Kungurian or Roadian strata in the Pamirs (Kozur and Mostler, 1976), Western Australia (Nicoll and Metcalfe, 1998) and Shiquanhe, Tibet (Zheng et al., 2007). A third species *V. nicolli* was reported in the late Kungurian strata from Western Australia (Nicoll and Metcalfe, 1998) and the

central Lhasa block (Yuan et al., 2015). The youngest *Vjlovognathus* was reported from Changhsingian strata: the upper part of the Chhidru Formation in the Salt Range, Pakistan (Wardlaw and Pogue, 1995) and the basalmost of Khunamuh Formation at Guryul Ravine, Kashmir (Brookfield and Sun, 2015) but had not been described. At Selong, eight broken specimens with the distinctively truncated denticles described here are considered the same species as those from Guryul Ravine and the Salt Range.

Kozur and Mostler (1976) suggested that *Vjalovognathus* was derived from *Neostreptognathodus pequopensis* through the fusion of the two opposite rows of denticles. However, *N. pequopensis* first appears in the late Artinskian (Magginetti et al., 1988; Jin et al., 1997) which postdates the first occurrence of *V. australis*, suggesting that the relationship proposed by Kozur and Mostler (1976) is unlikely. Yuan et al. (2015) proposed a possible relationship between *Vjalovognathus* and Gondolellidae (Nicoll and Metcalfe, 1998) by the similarity of the blade-like P1 element (cf. von Bitter & Merrill 1980). However, more data are clearly needed to establish the evolutionary relationship between *Vjalovognathus* and other conodont genera.

5.2 Reworked (?) or unexpected occurrences of Permian conodonts in the Triassic

Permian fauna previously reported from the basal part of Kangshare Formation at Selong have been regarded as “*in situ*”, because the hiatus between Selong Formation and Kangshare Formation is short and the preservation quality of the Permian taxa is good (Shen et al., 2006). The occurrence of *Mesogondolella* and *Jinogondolella* associated with *Clarkina* and *Hindeodus* in the Kangshare Formation could represent a mixture of biofacies similar to the co-occurrence of *Mesogondolella* and

Jinogondolella in Oman (Kozur and Wardlaw, 2010; Wardlaw and Nestell, 2010). However, the Permian conodonts (Xia and Zhang, 1992; Orchard, 1994; Wang and Wang, 1995; this study) have a different preservation status (Fig. 12) and we suggest that they were eroded from Permian strata before incorporation in the P-T boundary beds. For example, “*in situ*” conodonts, such as *C. changxingensis* and *C. tulongensis* have recrystallised surfaces that contrast with the smoother surfaces of older conodont such as *M. omanensis* (Fig. 12), suggesting a different diagenetic history. The better preservations of the older Permian conodonts contrast with other conodonts found in the *Otoceras* Bed (e.g. the *Hindeodus* specimens in figure 9 and most *Clarkina* in figures 7 and 8). Thus, the occurrence of *M. phosphoriensis* and *M. omanensis*, in the *O. latilobatum* Bed, are associated with *J. granti*–*C. postbitteri*–*C. hongshuiensis* of the Guadalupian Series. Similar mixture of conodonts in the Nepal region, is suggested by the presence of *V. shindyensis*?, *Gondolella* cf. *phosphoriensis* and *Gullodus* cf. *sicilianus* in the topmost biocalcarene beds from the Braga and Manang sections, which also contains the basal Triassic *H. parvus* (Nicora and Garzanti, 1997). The Nepal sections have a black shale horizon, of presumed Changhsingian age, underlying the biocalcarene beds. This lithology is not seen in Selong although the presence of shale clasts included within the stromatolitic layer at the base of the Kangshare Formation hint at its former presence (Wignall and Newton, 2003). The Kungurian conodont *M. idahoensis* was also found in the Coral Bed at Selong indicating that substantial parts of the Permian stratigraphy might have been removed prior to the P-T boundary interval.

5.3 Correlation with other sections in the Himalayan region

The age of Selong conodont fauna has been much discussed (Orchard et al., 1994;

Wang 1995; Orchard and Krystyn, 1998; Shen et al., 2000; Shen et al., 2001; Shen et al., 2006; this paper). The presence of *M. sheni* in association with *C. meishanensis*, *C. zhejiangensis*, *H. praeparvus* and *H. cf. latidentatus*, in the upper part of Selong Formation and the lower part of the Kangshare Formations indicates a late Changshingian age for these levels. *H. parvus* together with other earliest Triassic conodonts places the *Otoceras latilobatum* Bed in the earliest Triassic (Fig. 13).

The Changshingian strata at Selong can be correlated with the Marsyangdi Formation of Nepal based on the presence of the conodont *M. sheni*, *C. taylorae* and the brachiopods *Retimarginifera xizangensis* and *Spiriferella rajah* (Shen et al., 2003a,b; Waterhouse, 2010). Also, the lower *Marginalosia-Composita* brachiopod assemblage and an upper *Chonetella nasuta* brachiopod assemblage from Selong Group could correlate well with those of Kalabagh Member of the Wargal and Chhidru formations in the Salt Range, Pakistan (Shen et al., 2000). The negative carbon isotope excursions (Shen et al., 2003; 2006; Brookfield, 2010; Yoshida et al., 2014) seen in all four sections provides independent age confirmation and shows that latest Changshingian strata were widespread in Himalaya area.

Vjalovognathus has been reported in the four Perigondwana sections: Selong, South Tibet, Guryul Ravine, Kashmir, the Salt Range, Pakistan and Manang, Nepal (Fig. 13). The presence of *V. carinatus* from the Selong Formation reported in this paper and from the pre-mass extinction Bed (20 mm from the base of Khunamuh E1 Formation) at Guryul Ravine (Brookfield and Sun, 2015), suggests that it can be used for regional correlation. The *Vjalovognathus* reported in Wardlaw and Pogue (1995) from Pakistan and Manang by Nicora (1997) are probably also this youngest *Vjalovognathus* species.

5.4 Temperature change based on conodont data in the Selong section

Various elements of the fauna found at Selong provide evidence for temperature trends in the Permian and P-T boundary interval. The appearance of Tethyan brachiopods, foraminifers and sponges in the *Waagenites* Bed and the *Otoceras latilobatum* Bed has been used to infer a rapid and major warming in the P-T interval (Wignall and Newton, 2003; Shen et al., 2006). Prior to this, the Changhsingian temperature was cool as indicated by the presence of the cool-water conodont *V. carinatus* and *Mesogondolella* in the Coral Bed. The *Vjalovognathus* found in beds 45 and 47 of the Zewan and Khumamuh members in Kashmir disappeared prior to this warming event (Brookfield and Sun, 2015), consequently, the extinction of *Vjalovognathus* in late Permian coincided with the onset of a warming trend in Perigondwana.

6. Conclusions

We have investigated the conodonts from the Permian-Triassic Boundary interval at Selong, South Tibet and present a study on the youngest occurrence of *Vjalovognathus* enabling us to establish an evolutionary lineage. The oldest Triassic conodont assemblages contain substantial numbers of Permian elements most likely indicating substantial erosion of pre-Changhsingian strata in the region. Kungurian, Guadalupian and Wuchiapingian strata were probably originally present in the region. The Perigondwanan Selong section records the presence of cool-water conodonts for much of the Kungurian-Changhsingian interval. This was punctuated by the brief appearance of warmer conditions in the late Capitanian and at the end of the Permian. The disappearance of *Vjalovognathus* in the latest-Changhsingian coincides with appearance of a warm-water Tethyan fauna in the Perigondwanan region.

Acknowledgements

This study is supported by the Natural Science Foundation of China (grant no. 41572002, 41272044), the National Key Research and Development Program of China (grant no. 2016YFA0601104), the “111” project (grant B08030), the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (GBL11202), the Scientific Research Foundation of Hebei GEO University (BQ2017014). We thank Haishui Jiang, Robert Nicoll and Shuzhong Shen for their very useful comments and Dr. Ling kang Chen for his assistance in the field work and Dr. Muhui Zhang for his scanning of *J. granti* using MicroCT. We are also grateful to two anonymous reviewers and Charles Henderson for their constructive comments for improving this manuscript

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Figure and table captions

Figure 1, A, Palaeogeographic reconstruction of the Permian-Triassic world (from Stampfli and Borel, 2004); B, Location of Selong section, South Tibet, China.

Figure 2 Summary of previously reported conodont occurrences at Selong in the Permian-Triassic boundary interval (Coral Bed is Bed 10; Caliche Bed: the black line is between Bed 10 and Bed 11; the *Waagenites* Bed is Bed 11; the *Otoceras* Bed is Bed 12-13).

Figure 3 SEM images of Permian conodonts of the Selong section.

All specimens are preserved in the Faculty of Earth Science, China University of Geosciences, Wuhan, Hubei Province, P. R. China.

1-3, *V. carinatus* sp. nov., 1a, lateral view, 1b, upper view, 1c, magnification of the anterior 2 denticles, from bed 10e of Selong Fm. (Coral bed), Y22-032; 2a, lateral view, 2b, upper view, 2c, magnify of the 2-3 posteriorly denticles, from bed 10e of Selong Fm. (Coral bed), Y22-035; 3a, lateral view, 3b, upper view, 3c, magnify of the 4-6 denticles anteriorly, from bed 10f of Selong Fm. (Coral bed), w12-4-022.

Figure 4 SEM images of Permian conodonts of the Selong section.

1-3, *V. carinatus* sp. nov., 1a, lateral view, 1b, upper view, 1c, magnify of the 2-4 anterior denticles, from bed 10f of Selong Fm. (Coral bed), 13-1-018; 2a, lateral view, 2b, upper view, 2c, magnification of the abraded denticles, from bed 10f of Selong Fm. (Coral bed), Y22-026; 3a, lateral view, 3b, upper view, 3c, magnification of the abraded denticles, from bed 10f of Selong Fm. (Coral bed), y22-029.

Figure 5 SEM images of Permian conodonts of the Selong section.

1-2, *V. carinatus* sp. nov., 1a, lateral view, 1b, upper view, 1c, magnify of the abrasive denticles, from bed 10f of the Selong Fm. (Coral Bed), 13-1-018; 2a, lateral view, 2b, upper view, 2c, magnify of the abrasive denticles, from bed 10f of Selong Fm.(Coral bed), Y22-024; 3, *V. sp.*, 3a, lateral view, 3b, upper view, 3c, magnify of the denticles, from bed 10f of Selong Fm. (Coral Bed), Y22-030;
4, *V. sp.*, upper view, from bed 10d of Selong Fm. (Coral bed), w12-4-026.

Figure 6 SEM images of Permian conodonts of the Selong section

1-2,6,8 *C. meishanensis* (Zhang, Lai, Ding and Liu, 1995) 1a, upper view, 1b, lower view, from bed 10f of Selong Fm., w12-4-019; 2, upper view, from bed 10f of Selong Fm., sl-a-024; 6a, upper view, 6b, lower view, from bed 10e of Selong Fm., 13-1-006; 8, upper view, from bed 10c of Selong Fm., sl-a-004;
4,9, *M. sheni* Mei, 1996, 4a, upper view, 4b, lower view, from bed 10e of Selong Fm., 13-1-003; 9, upper view, from bed 10b of Selong Fm., 13-1-002;

3,7, *M. lamberti* Mei et Henderson 2002, upper view, from bed 10f of Selong Fm., sl-a-014; 7a, upper view, 7b, lower view, from bed 10d of Selong Fm.,

5, *M. phosphoriensis* (Youngquist, Hawley and Miller 1951), 5a, upper view, 5b, lower view, from bed 10e of Selong Fm., 13-4-004;

6, *M. sp.*, 6a, upper view, 6b, lower view, from bed 10e of Selong Fm., 13-1-006;

10, *C. sp.*, 11a, upper view, 11b, lower view, from bed 11 of Kangshare Fm. (Waggenites Bed), w12-4-011;

11, *C. sp.*, 10a, upper view, 10b, lower view, from bed 10a of Selong Fm., 13-4-001;

Figure 7. SEM images of Permian conodonts from the Selong section

1,7,13,16 *C. changxingensis* Wang et Wang 1981, 1, upper view, from bed 12 of Kangshare Fm., w12-2-019; 7, upper view, from bed 12 of Kangshare Fm., sl-a-032; , 13, upper view, from bed 12 of Kangshare Fm., sl-a-043; 16a, upper view, 16b, lower view, from bed 12 of Kangshare Fm., w12-1-042;

2, 6, *C. tulongensis* Tian 1982, upper view, from bed 12 of Kangshare Fm., sl-a-035; 6, upper view, from bed 13 of Kangshare Fm., sl-a-038;

3, *M. sp.*, 2a, upper view, 2b, lower view, from bed 12 of Kangshare Fm., 13-1-02

4, *M. omanensis* Kozur and Wardlaw, 2010, 4a, the upper view, 4b, the lower view, from bed 12 of Kangshare Fm., 13-1-035;

5, *C. sp.*, 4a, upper view, 4b, lower view, from bed 12 of Kangshare Fm., 13-4-026;

8,18,19 *C. taylorae* Orchard 1994 upper view, from bed 13 of Kangshare Fm., w12-3-030; 15a, upper view, 16a, lower view, from bed 12 of Kangshare Fm.,

w12-1-041; 19, lateral view, from bed 12 of Kangshare Fm., sl-a-039;

9, *C. deflecta* Wang and Wang 1981, upper view, from bed 12 of Kangshare Fm., sl-a-057;

11,15, *C. orchardi* Mei 1996, upper view, from bed 13 of Kangshare Fm., sl-b-093;

15a, upper view, 15b, lower view, from bed 12 of Kangshare Fm., w12-1-040;10,12,14, *C. planata* (Clark 1959), 10, upper view, from bed 12 of Kangshare Fm., Y22-017; 12, upper view, from bed 12 of Kangshare Fm., Y22-019;

14, upper view, from bed 12 of Kangshare Fm., sl-a-059;

17, *M. idahoensis* (Youngquist, Hawley and Miller 1951), 17a, upper view, 17b, lower view, from bed 10f of Selong Fm., 13-1-017;

20, *C. carinata* (Clark 1959), lateral view, from bed 12 of Kangshare Fm., sl-a-039;

Figure 8. SEM images of Permian conodonts from the Selong section

1,15, *C. changxingensis*, Wardlaw and Collision 1979, 1a, upper view, 1b, lower view, from bed 12 of Kangshare Fm., 13-1-031; upper view, from bed 12 of Kangshare Fm., Y22-018;

2, *C. sp.*, upper view, from bed 12 of Kangshare Fm., Y22-014;

3, *C. cf. changxingensis* Wardlaw and Collision 1979, 3a, upper view, 3b, lateral view, from bed 12 of Kangshare Fm., 13-4-007;

5, *J. granti* Mei and Wardlaw 1994, 5a, upper view, 5b, lateral view, 5c, upper view of micro-CT photo, from bed 12 of Kangshare Fm., w12-1-045;

6-8, *M. omanensis* Kozur and Wardlaw, 2010 6a, upper view, 6b, lower view, from

Bed 12 of Kangshare Fm., 13-4-028; 7a, upper view, 7b, lower view, from Bed 12 of Kangshare Fm., 13-4-027; 8a, upper view, 8b, lateral view, from Bed 12 of Kangshare Fm., sl-a-047;

4, *C. postbitteri* Mei and Wardlaw 19944a, upper view, 4b, lower view, from Bed 12 of Kangshare Fm., 13-4-030;

9-11 *C. zhejiangensis* Mei 1996, 9a, upper view, 9b, lower view, 9c, magnify of the abnormal area of this specimens, from bed 12 of Kangshare Fm.; 10a, upper view, 10b, lower view, from Bed 12 of Kangshare Fm., 13-1-036; 11a, upper view, 11b, lower view, from Bed 12 of Kangshare Fm., 13-4-029;

12, *C. hongshuiensis* (Henderson and Mei, 2001) 12a, upper view, 12b, lower view, 11c, lateral view, from Bed 12 of Kangshare Fm., w12-1-048;

13, *M. sp.* 12a, upper view, 12b, lower view, from Bed 12 of Kangshare Fm., w12-1-046;

14 *M. phosphoriensis* (Youngquist, Hawley and Miller 1951), 14a, upper view, 14b, lower view, from Bed 12 of Kangshare Fm., 13-1-037;

Figure 9. SEM images of Permian conodonts of the Selong section

1,3,5,8,11,13,14, *H. praeparvus* (Kozur, 1996), 1, lateral view, from Bed 12 of Kangshare Fm., sl-b-001; 3, lateral view, from Bed 13 of Kangshare Fm., sl-b-057; 5, lateral view, from Bed 12 of Kangshare Fm., sl-b-018; 8, lateral view, from Bed 12 of Kangshare Fm., sl-b-022; 11, lateral view, from Bed 12 of Kangshare Fm., sl-b-023; 13, lateral view, from Bed 12 of Kangshare Fm., sl-b-032; 14, lateral view, from Bed

12 of Kangshare Fm., sl-b-029;

2,4,9,10,16 *H. typicalis* (Sweet 1970), 2, lateral view, Bed 12 of Kangshare Fm.,

sl-b-002; 4, lateral view, from Bed 12 of Kangshare Fm., sl-b-007; 9, lateral view.

From Bed 12 of Kangshare Fm., w12-1-036; 10, lateral view, from Bed 12 of

Kangshare Fm., sl-b-021; 16, lateral view, from Bed 12 of Kangshare Fm., sl-b-031;

16, lateral view, from Bed 12 of Kangshare Fm.,sl-b-032;

6, *H. inflatus* Nicoll et al. 2002, 6a, lateral view, 6b, upper view, from Bed 12 of

Kangshare Fm., 13-1-025;

7,15,17, *H. parvus* (Kozur and Pjatakova) 1976, lateral view, from bed 13 of

Kangshare Fm., sl-b-052; 15, lateral view, from Bed 12 of Kangshare Fm.,sl-b-027;

17, lateral view, from Bed 12 of Kangshare Fm., w12-1-019 ;

12, *H. latidentatus* (Kozur, Mostler and Tahimi-Yazd 1975), lateral view, from bed 12

of Kangshare Fm., sl-b-024;

Figure 10. Conodont species ranges at the Permian-Triassic boundary, Selong. The

solid line marks the P-T boundary and the dashed line the Caliche Bed. The older

conodonts of Bed 12 are not shown. Note that *Mesogondolella* and *Clarkina* were

recovered from Bed 11 (the *Waagenites* Bed) but they were too poorly preserved for

species identification. (Coral Bed is Bed 10; Caliche Bed: the black line between Bed

10 and Bed 11; *Waagenites* Bed is Bed 11; *Otoceras* Bed is Bed 12-13).

Figure 11. Evolutionary trend of Permian *Vjalogognathus*. Scale bars represent 20µm.

A. *V. australis* is characterised by a groove in the anterior of the denticles, indicated

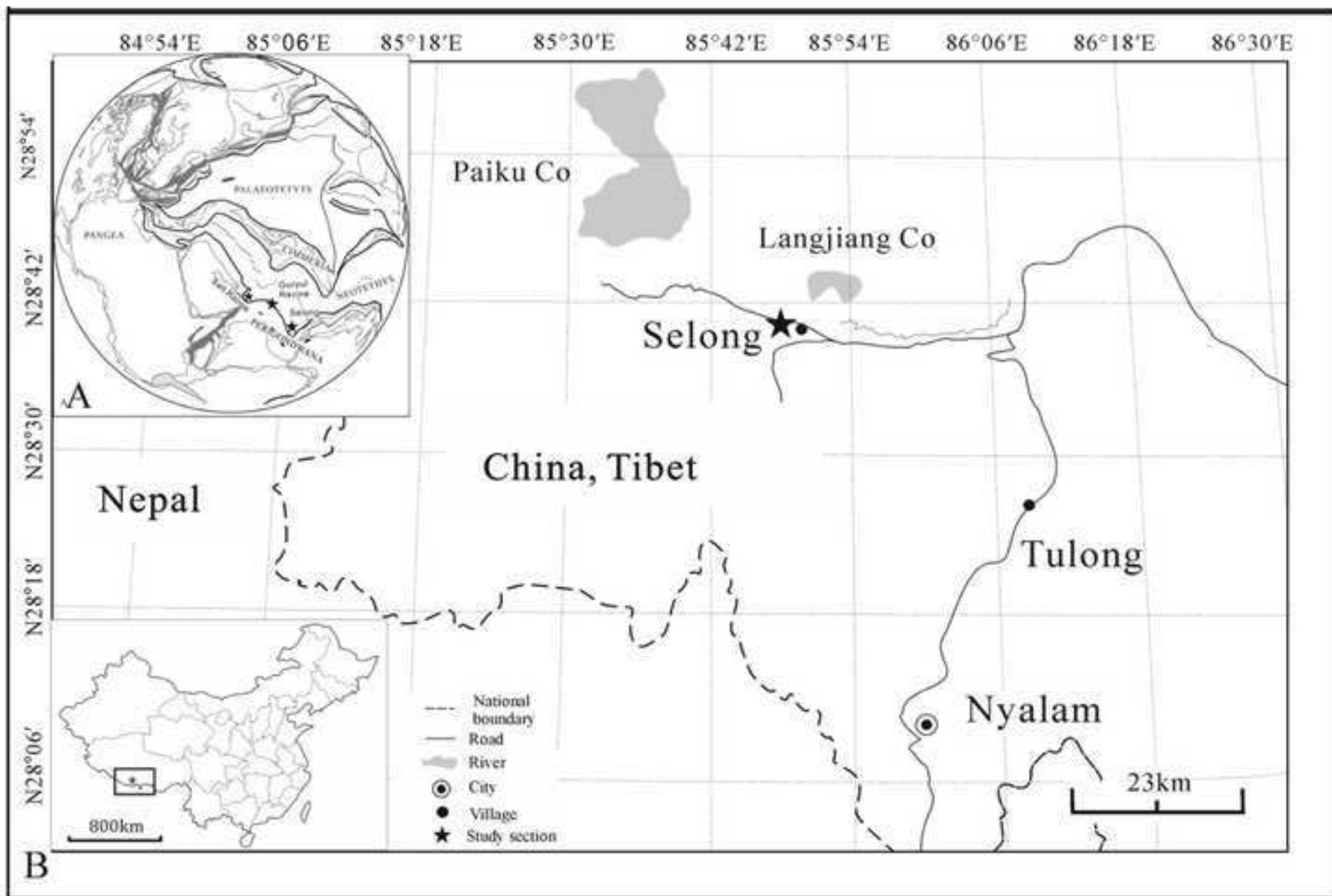
by a white dashed line; *B. V. shindyensis* is distinguished from *V. australis* by its weak axial ridge in the posterior part of the denticle (A, B, photos after Nicoll and Metcalfe, 1998); *C. V. nicolli* has well developed axial ridges shown in the Fig. connecting the adjacent denticles, the cross section for the denticles is ovate-diamond in shape (photo from Yuan et al., 2015); *V. sp.X* is from Zheng et al., 2007; E, F, *V. carinatus* sp. nov. from Coral Bed, Selong section, which develop very conspicuous axial ridge.

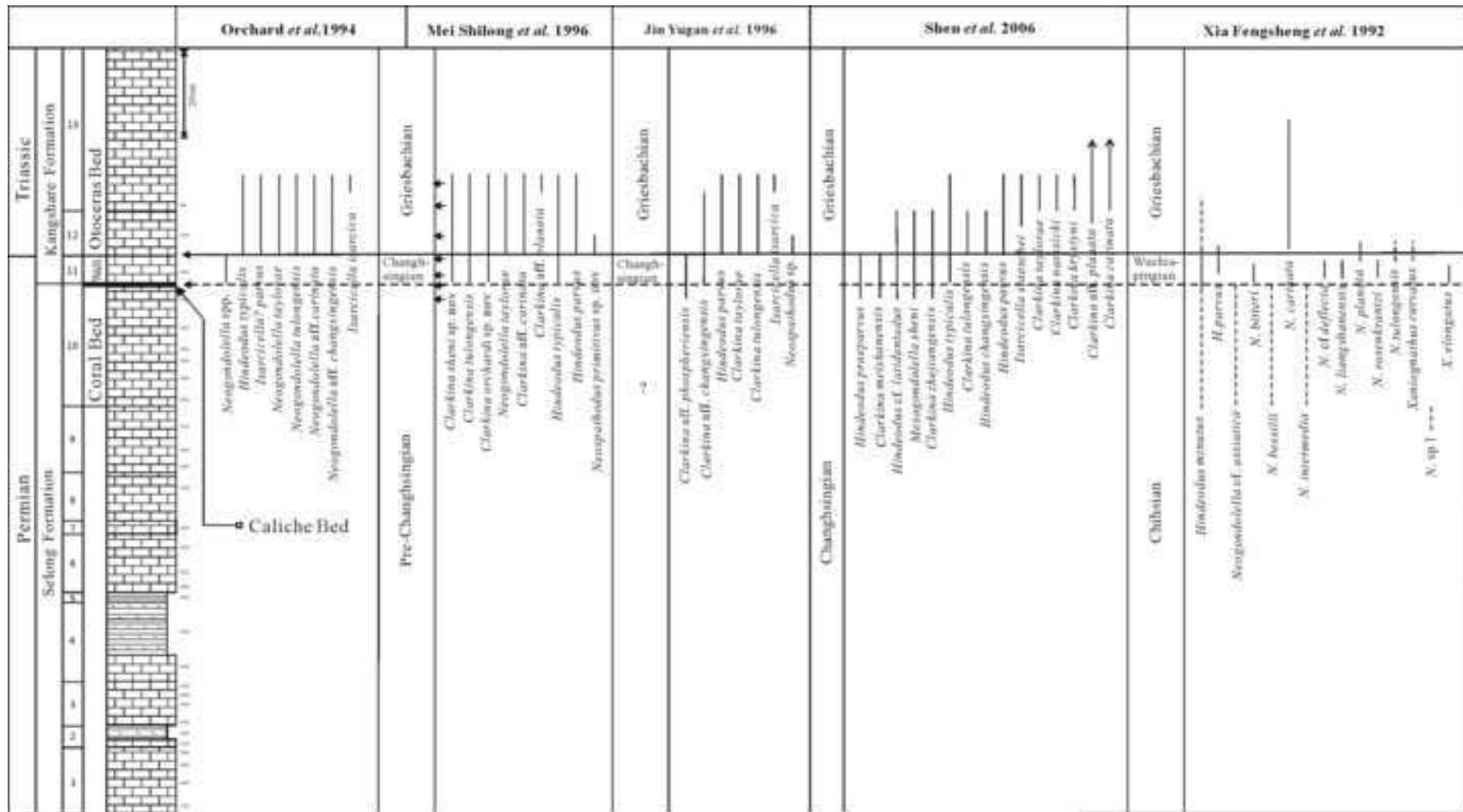
Figure 12. Different preservation shown by *C. changxingensis* (1), *C. tulongensis* (2) and *M. omanensis* (3). The platform surface of *Clarkina* conodonts are covered with crystal overgrowths that mostly covers micro-ornamentation (except in circled area). In contrast, *M. omanensis* shows well preserved denticles on the carina, and the micro-ornamentations on the platform (indicated by a white arrow).

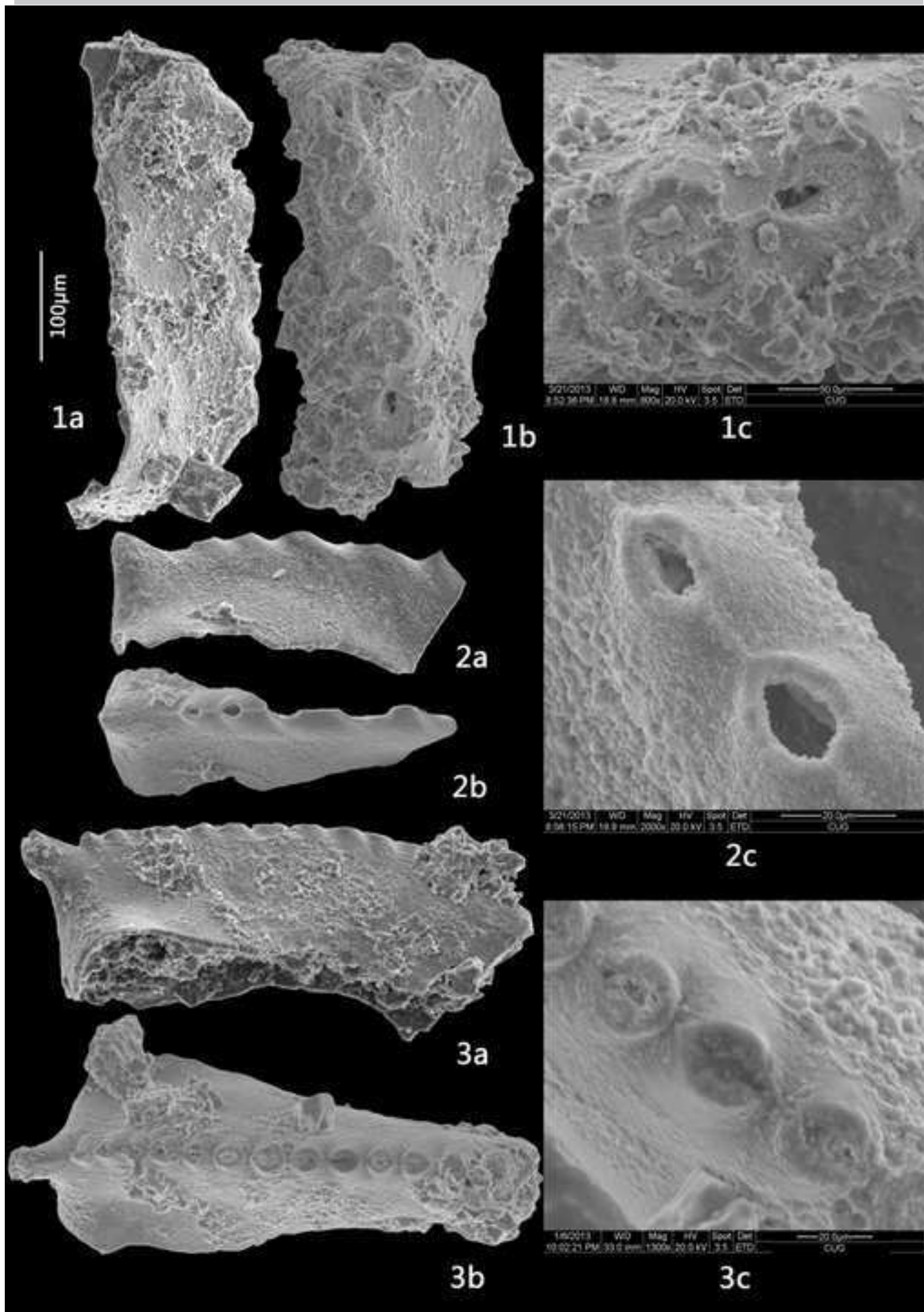
Figure 13 Correlation chart of the Permo-Triassic in the Himalayan region (modified from Waterhouse et al., 2010). The Griesbachian correlation is based on the first appearance datum of *H. parvus* and *Otoceraswood wardi*. Changshingian age criteria are based on the occurrence of *V. carinatus* sp. nov., *C. meishanensis*, *M. sheni*. Selong (Wignall and Newton, 2003; Shen et al., 2003; 2006; this paper), Guryul Ravine (Brookfield et al., 2003; 2013 Brookfield and Sun, 2015), Salt Range (Wardlaw and Pogue, 1995; Shen et al., 2003), Manang (Nicora, 1997; Yoshida et al., 2014)

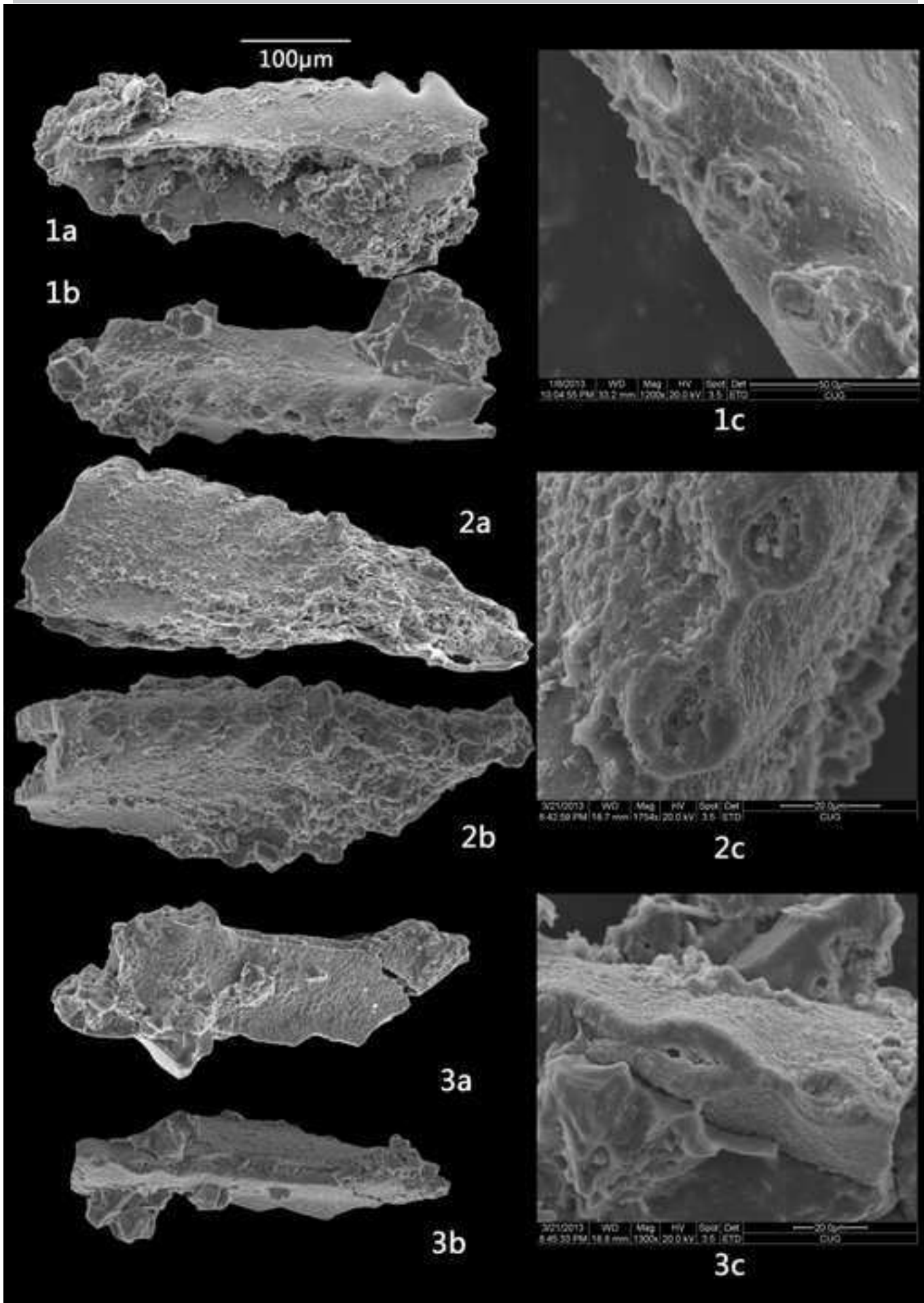
Table 1. Conodont P₁ elements of key species found at Selong Section, South Tibet. Only samples that yielded conodonts are listed.

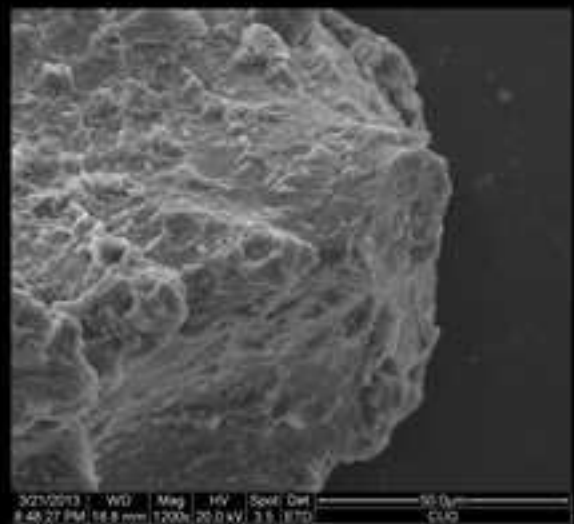
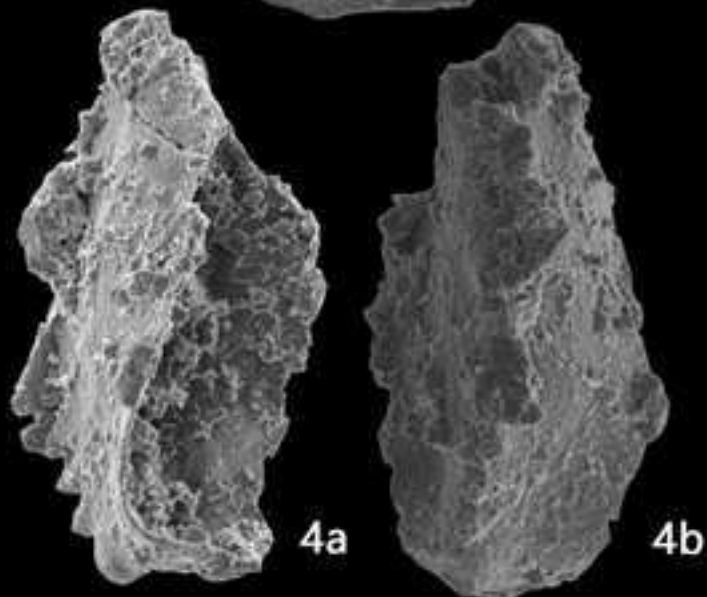
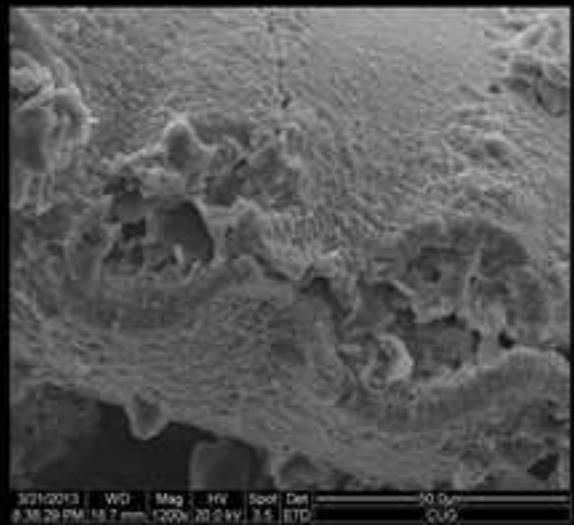
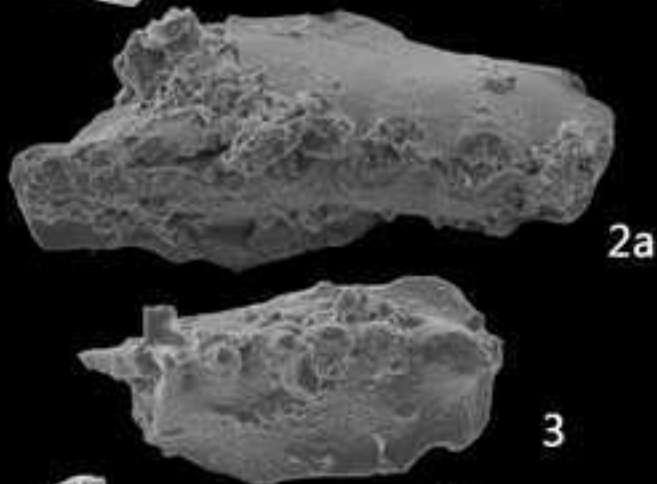
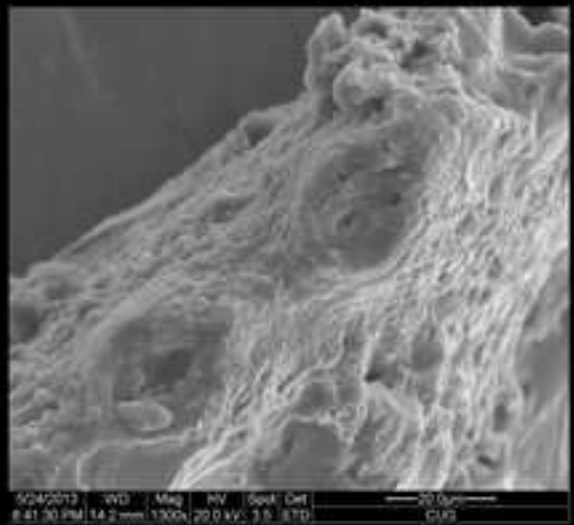
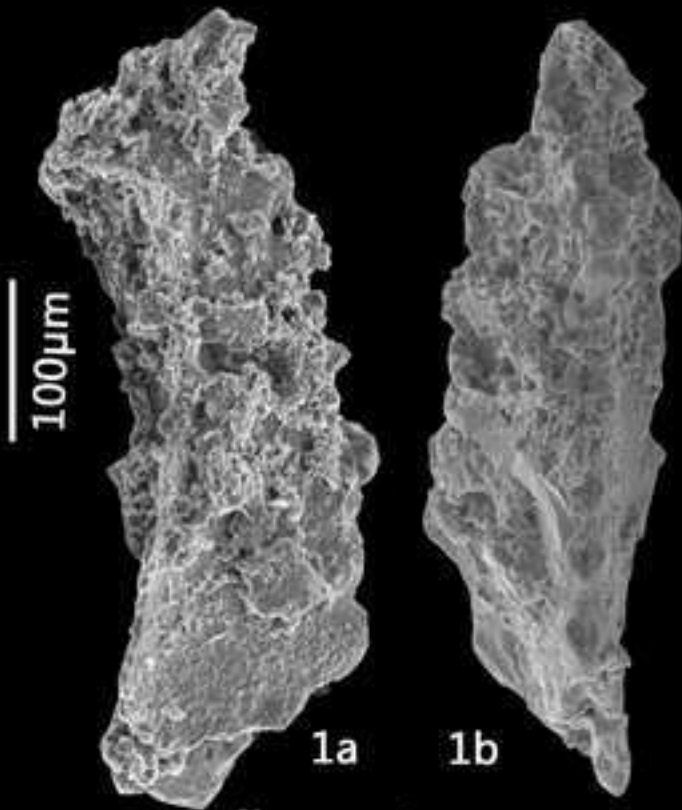
Sample No.	Taxa	<i>Mesogon dolella</i> P1 elements	<i>Jinogon dolella</i> P1 elements	<i>Clarkina</i> P1 elements	<i>Hindodus</i> P1 elements	<i>Vjalovogonathus</i> P1 elements	broken Gondolleid P1 elements	broken Hindoeidid P1 elements	Ramiform elements	Total
	Weight(Kg.)									
SL-13	3.3			443	83		2062	32	442	3062
SL-12	4.3	10 (reworked)	2 (reworked)	531	175		459	106	164	1447
SL-11	6.58	3 (reworked)					50			53
SL-10f	6.1	12(10 reworked)				6	47		11	76
SL-10e	5.5	4(reworked)				3	19		4	30
SL-10d	5.5	7(reworked)				1	40			48
SL-10c	3.5						2		1	3
SL-10b	6	4(3 reworked)					2			6
SL-10a	6,48	2(reworked)					6			8
SL-9b	10.7	1(reworked)								1
SL-8	13	1(reworked)								1
SL-6b	7	1(reworked)					6			7
SL-6a-2	5.48	1(reworked)					3			4
Total	175.74	46	2	974	258	10	2696	138	622	4746

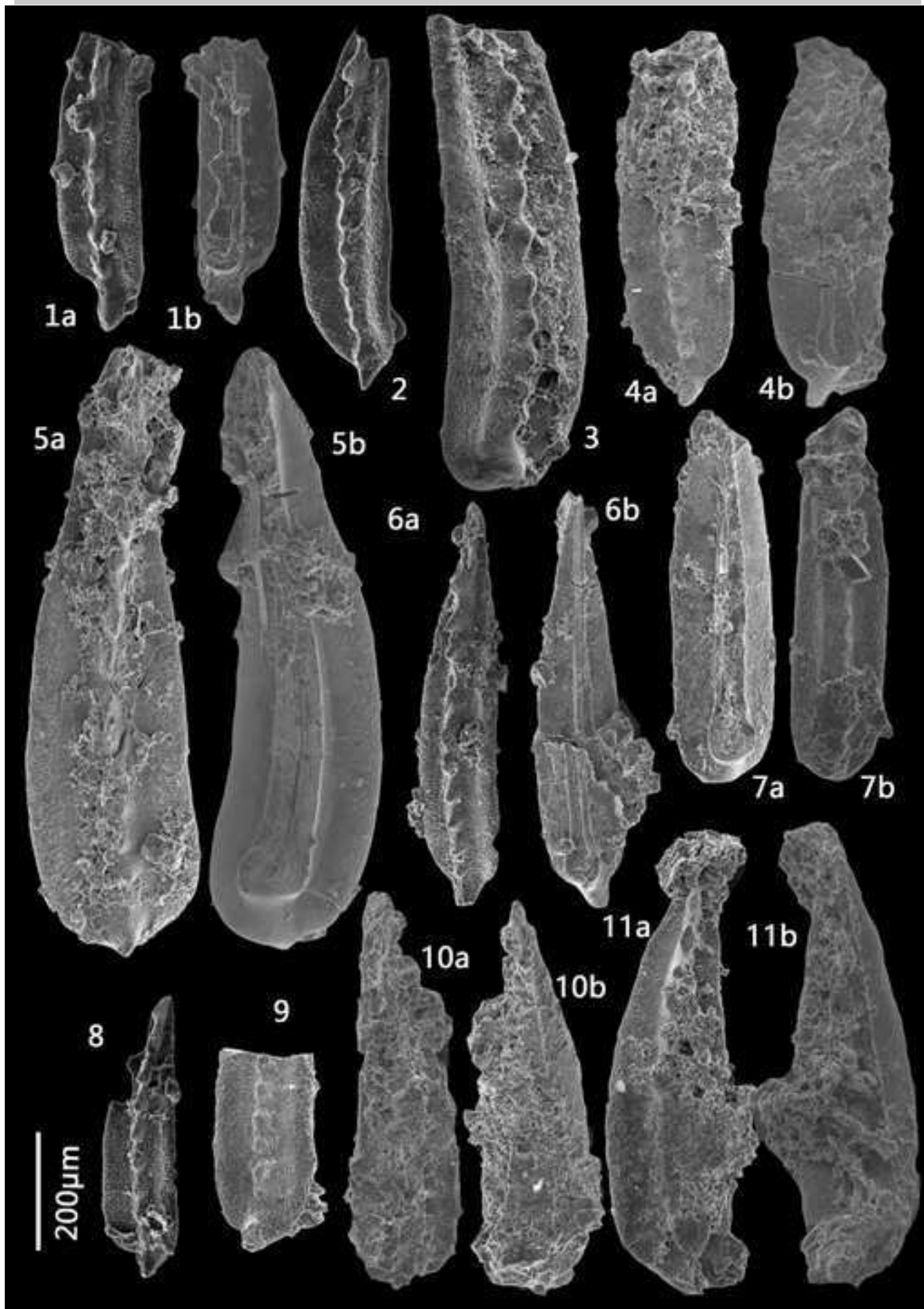


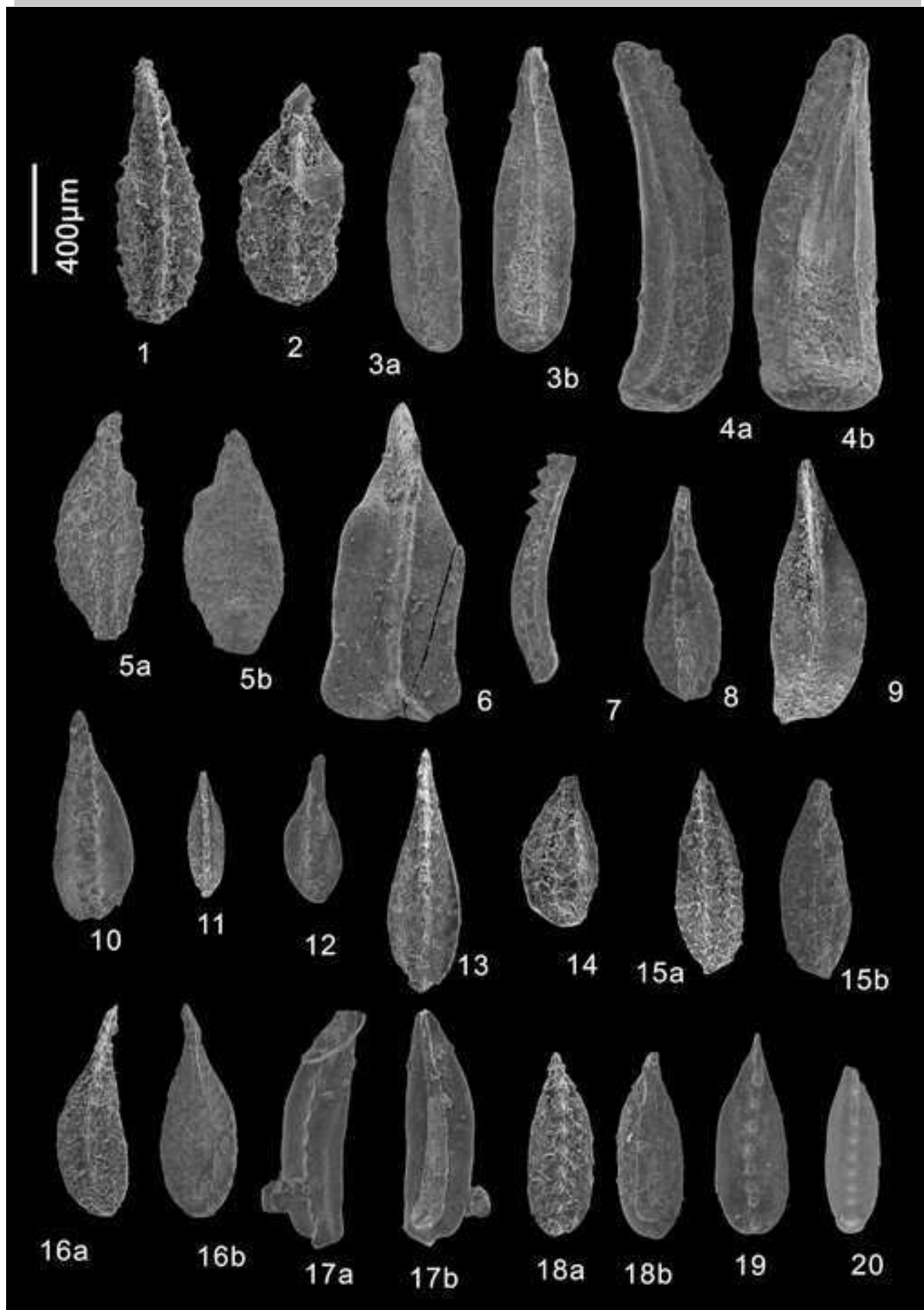


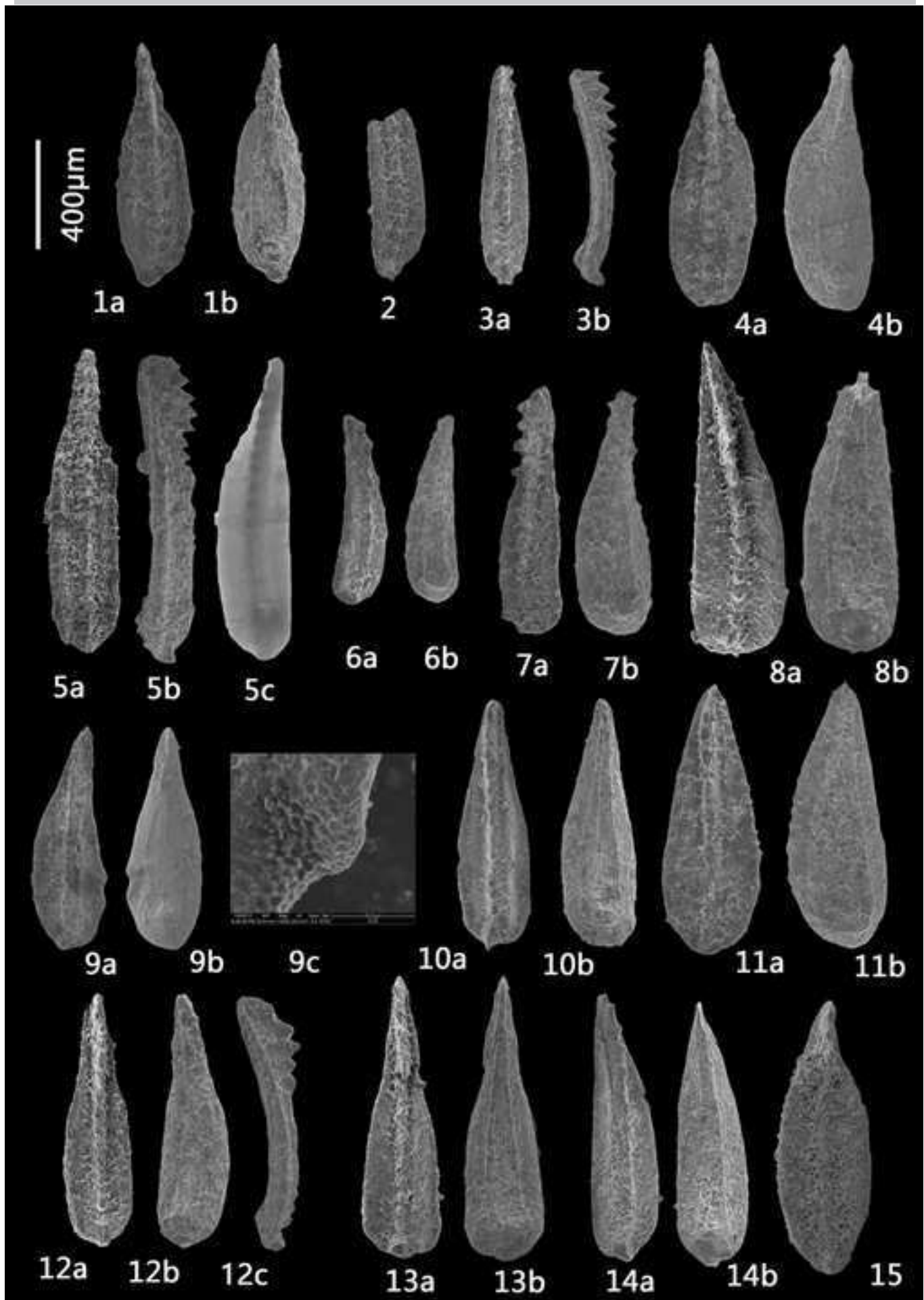


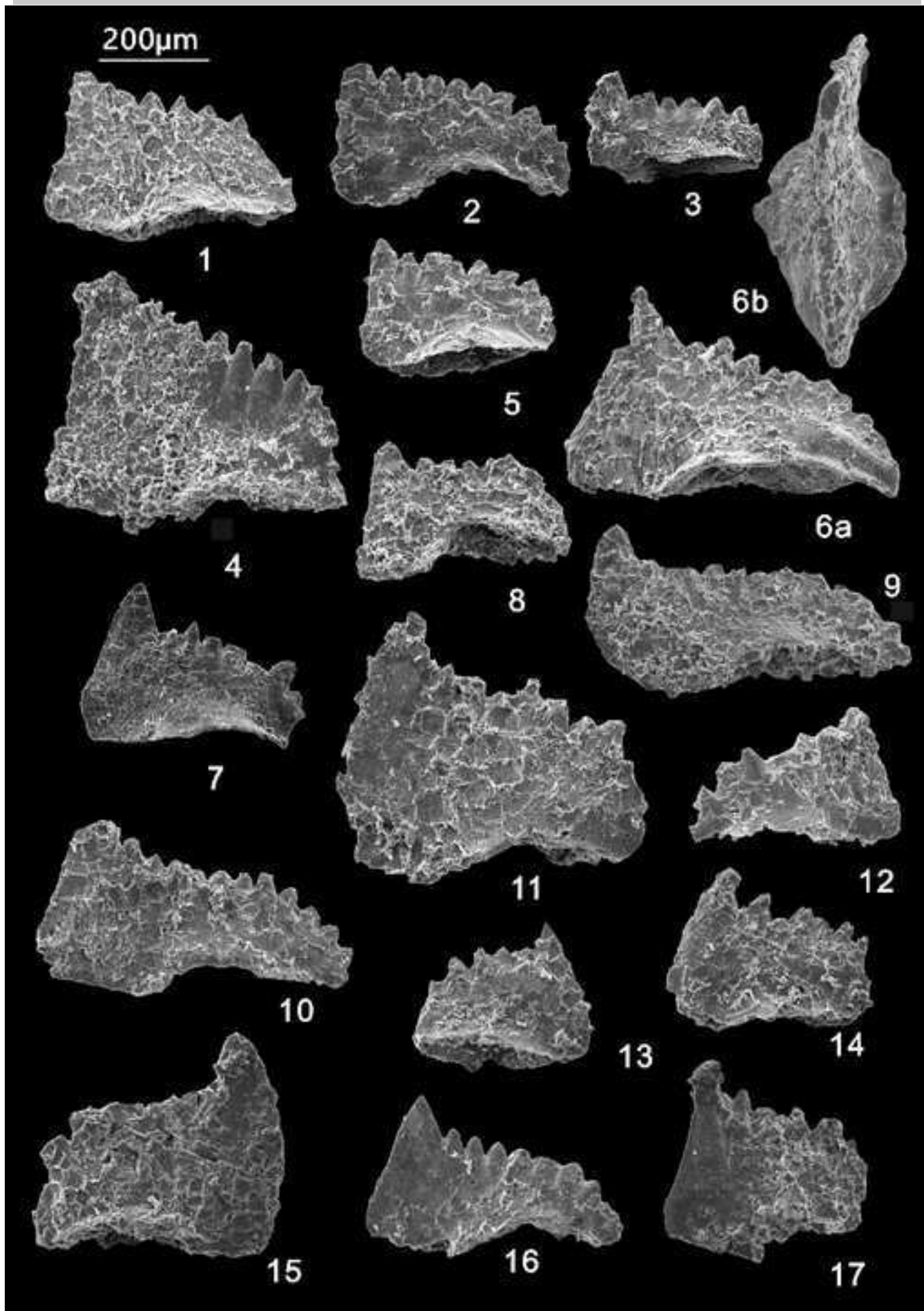


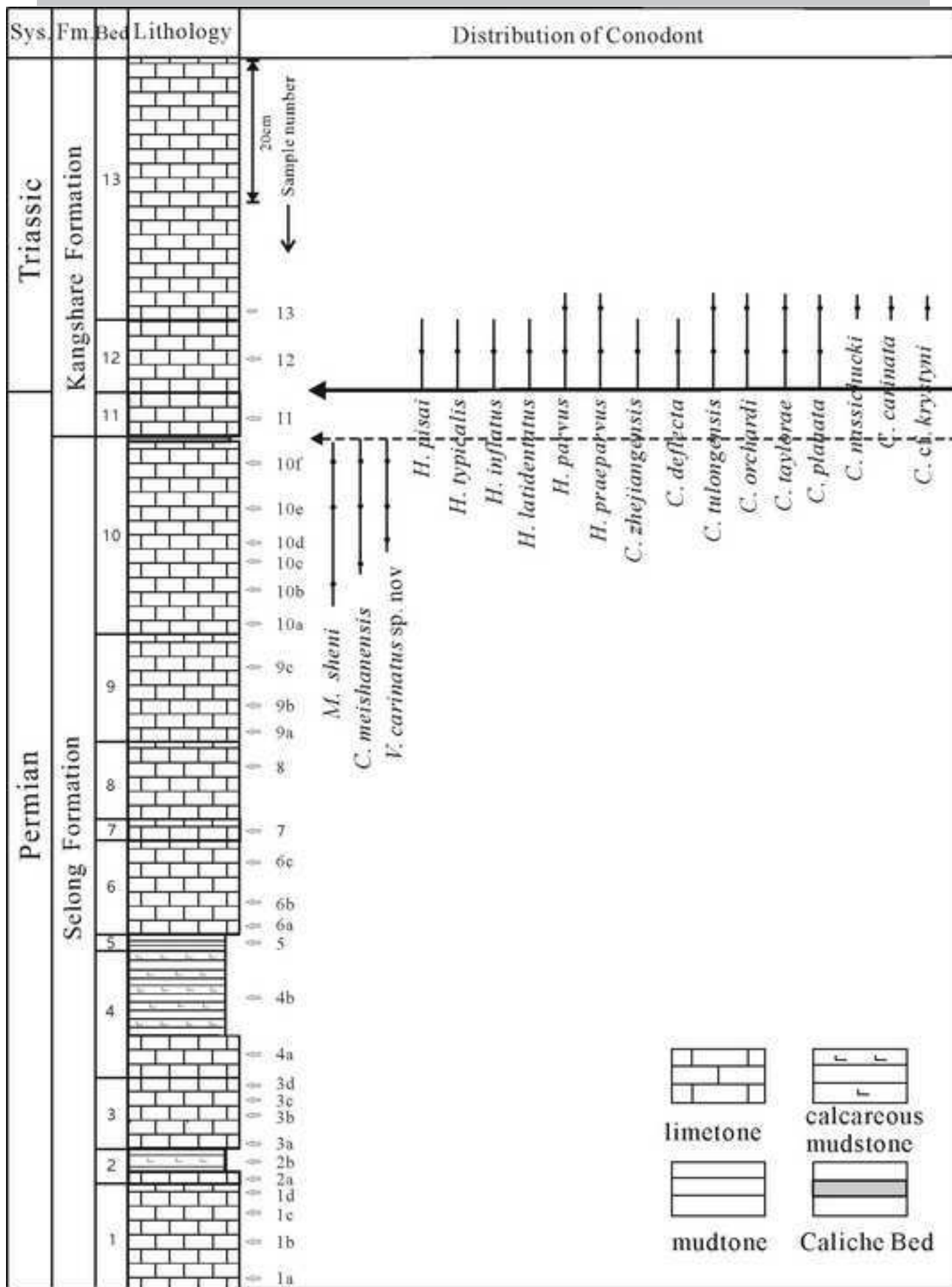


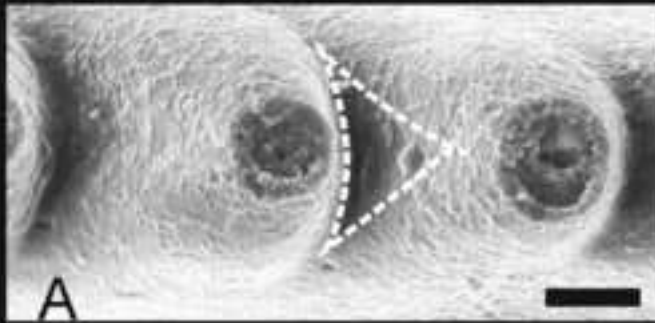




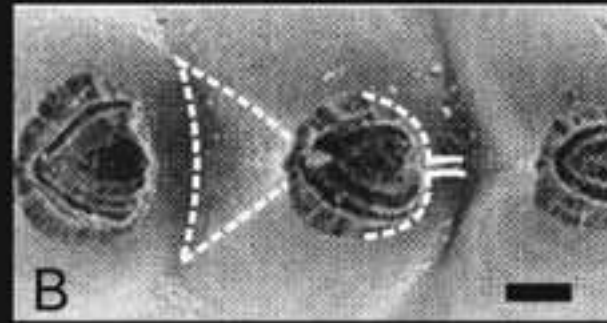




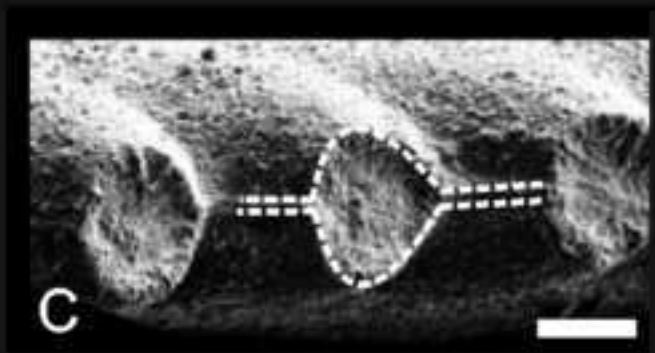




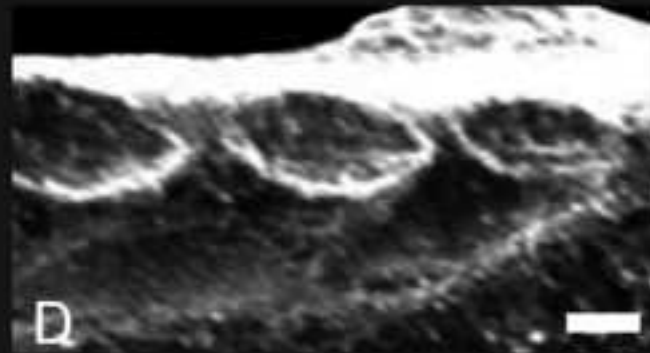
V. australis



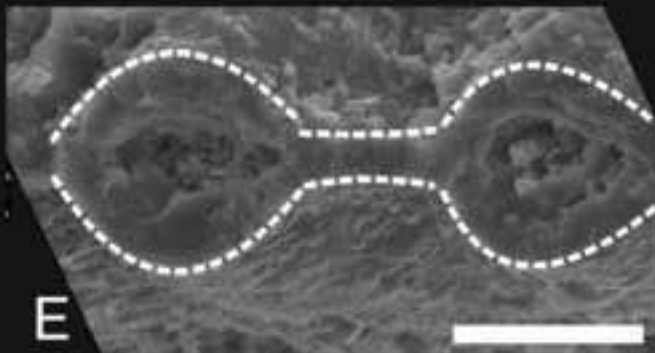
V. shindyensis



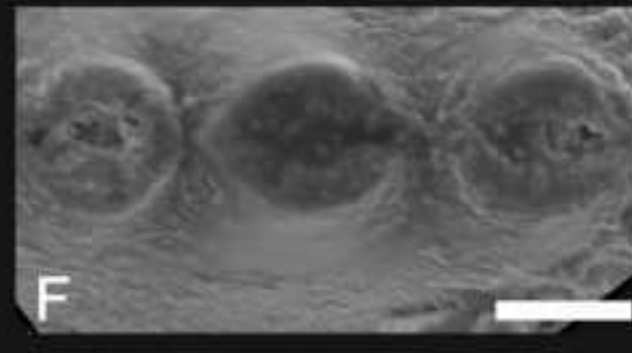
V. nicolli



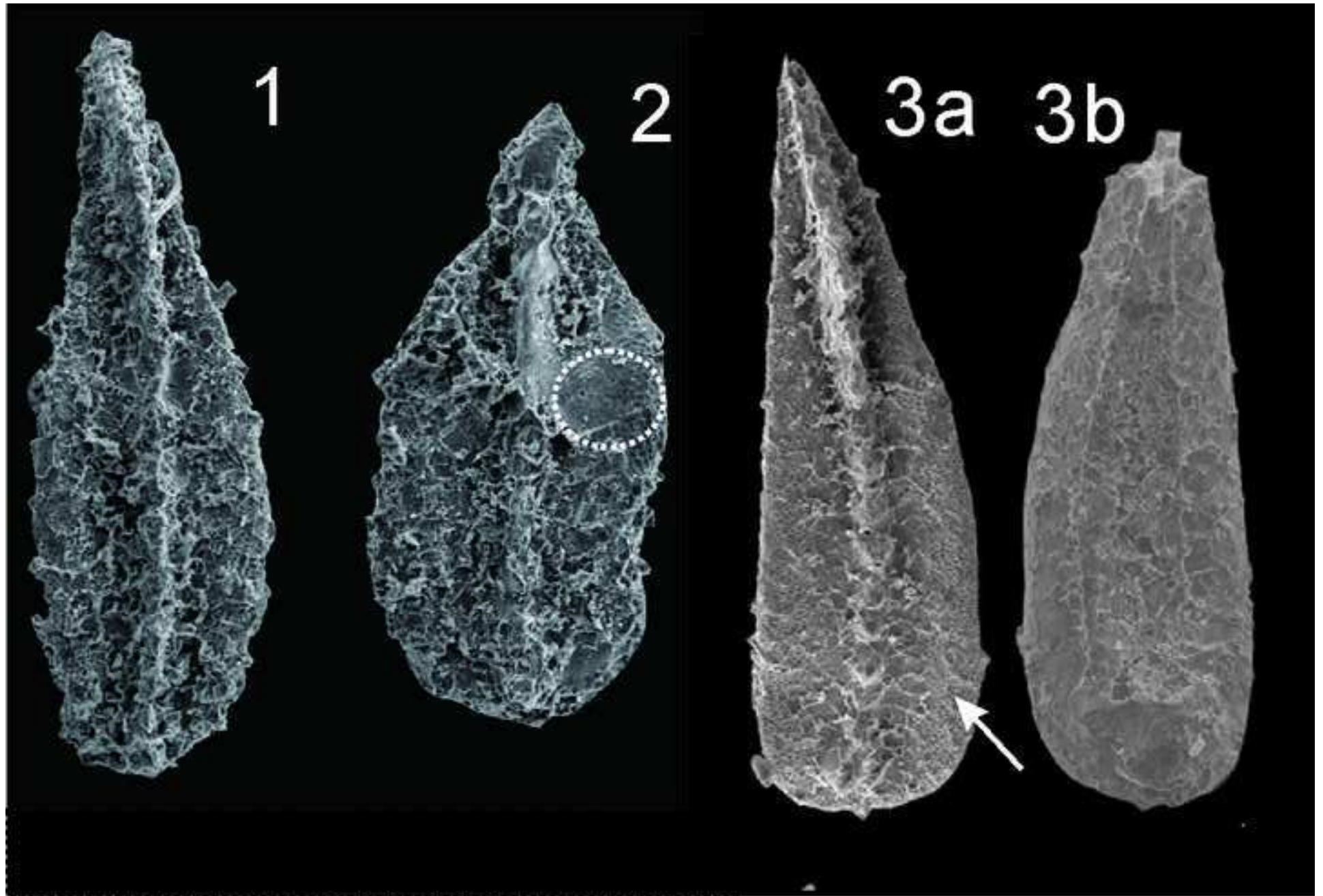
V. sp. X



V. carinatus sp. nov.



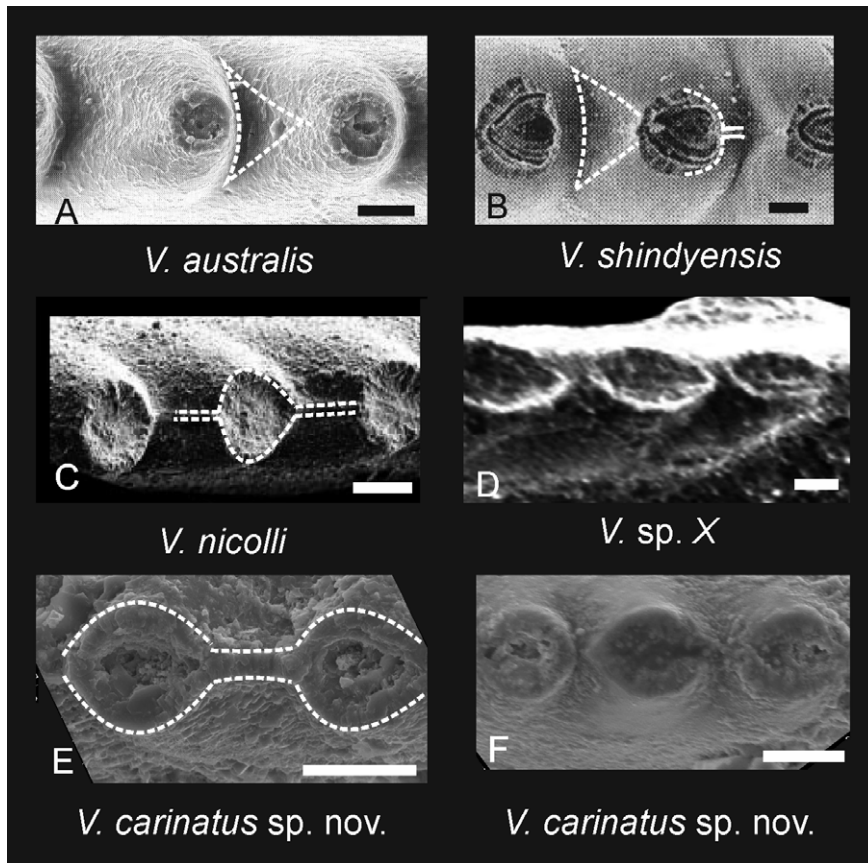
V. carinatus sp. nov.



System	Stage	Selong, South Tibet			Guryul Ravine, Kashmir				Salt Range, Pakistan			Manang, Nepal		
		Fm.	Lith. U	fauna	Fm.	Member	Bed	fauna	Fm.	Member	fauna	Fm.	Member	fauna
Triassic	Griesbachian	Kangshare Fm.	Ophiceras Bed	<i>Ophiceras tibeticum</i>	Khunamuh Fm.	E3		<i>Ophiceras tibeticum</i>	Mianwali Fm.	Kathiwali	<i>Ophiceras tibeticum</i>	Pangjang Fm.		<i>Ophiceras tibeticum</i>
			Otoceras Bed	<i>I. isarcica</i> <i>Otocera woodwardi</i> <i>H. parvus</i> <i>Otocera latilobatum</i>		E2	52	<i>H. parvus</i> <i>Otocera woodwardi</i>			<i>H. parvus</i>		Pengba	<i>Otocera woodwardi</i>
Permian	Changshingian	Selong Fm.	Waagenites Bed	<i>C. meishanensis</i> <i>C. taylorae</i> <i>Lunucammia sp.</i> <i>Spiriferus rajah</i> <i>M. sheni</i>	Zewan Fm.	E1	48-51	<i>V. carinatus</i> <i>Schizodus</i>	Chhidru Fm.	Khisor	<i>C. meishanensis</i>	Marsyangdi Fm.	Kcho-Gungsang	<i>C. taylorae</i>
			Caliche Bed	<i>Spiriferus rajah</i> <i>M. sheni</i>			47				<i>Vjalovognathus</i>			<i>Vjalovognathus</i> <i>Schizodus</i>
		Coral Bed	<i>V. carinatus</i>	D		46	<i>V. carinatus</i> <i>Schizodus</i>	Ganjaroh	<i>Vjalovognathus</i>	Senja Fm.	Pija-Ngawal	<i>Spiriferus rajah</i>		
			<i>V. carinatus</i>			45	<i>Lunucammia spp.</i> <i>Vjalovognathus</i>		<i>Vjalovognathus</i>		Popa	<i>Schizodus</i>		
		<i>Retimarginifera xizangensis</i>			44	Late Changshingian Carbon excursion								

— Extinction level
 — Sequence conformity

Graphical abstract



Highlights

- A cool-temperature tolerant conodont, *Vjalovognathus* has been found in Changshingian strata from Selong section, South Tibet.
- The youngest *Vjalovognathus*, *V. carinatus* sp. nov. has been described.
- A possible Permian *Vjalovognathus* evolutionary trend proposed: in ascending order this is, *V. australis* (late Sakmarian-early Artinskian), *V. shindyensis* (early Kungurian), *V. nicolli* (late Kugurian-Early Roadian) and ultimately *V. carinatus* sp. nov. (Changshingian).
- Numerous Permian specimens (e.g. *M. phosphoriensis*; *M. omanensis*-*J. granti*-*C. postbitteri*-*C. hongshuiensis*) appeared in the *Otoceras latilobatum* Bed.