

Gondolelloid multielement conodont apparatus (*Nicoraella*) from the Middle Triassic of Yunnan Province, southwestern China

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ABSTRACT

The morphology and position of elements in the apparatus are keys to resolving the taxonomy, homology, evolutionary relationships, structure, function and feeding patterns among conodont taxa. Fused clusters preserving natural associations between elements provide direct information on element morphology, the positions of elements within the apparatus, and even their original three-dimensional arrangement. Here, we report 41 fused conodont clusters from Member II of the Guanling Formation in Luoping County, Yunnan Province, southwestern China, which provide a basis for inferring the multielement composition of the apparatus of the early Middle Triassic *Nicoraella*. The apparatus is composed of 15 elements (a single S_0 element, two pairs of S_{1-4} , M and P_{1-2} elements) like other apparatuses in Gondolellidae, i.e. the genera *Novispathodus* and *Neogondolella*. These Luoping Biota clusters are significant because (a) they permit a positional homology-based comparison of multielement *Novispathodus* with form genera such as *Cypridodella* (S_1), *Enantiognathus* (S_2), and *Hindeodella* (S_3 and S_4), (b) they facilitate a review of apparatus composition within superfamily Gondolelloidea, (c) they provide direct insight into apparatus architecture currently interpreted largely in light of distantly related Carboniferous polygnathacean ozarkodinins, and (d) these clusters, along with collections of discrete conodont elements, provide a model for inferring the multielement composition of closely related species known only from discrete element collections.

1. Introduction

Conodonts are a group of extinct jawless vertebrates known almost exclusively from their microscopic tooth-like skeletal elements, which can be recovered readily from marine carbonates ranging in age from upper Cambrian to the latest Triassic. Conodont elements occur in a range of morphologies, forming the basis of their original taxonomy. However, the discovery of articulated assemblages of elements of different morphologies, representing the remains of single individuals (Schmidt, 1934; Scott, 1934), demonstrated the need for a multielement taxonomy that forms

the basis of the modern homology-based taxonomy and systematics of conodonts. Indeed, these articulated assemblages, which occur on the surface of bedding planes, or as clusters of elements fused together by diagenetic minerals, provide direct evidence of element morphology within homologous positions in the multielement apparatus. Through comparative morphology, the multielement composition of species known only from discrete element collections can be reconstructed, using articulated assemblages as a template. This approach fails, however, when element morphology diverges significantly from those species known from articulated assemblages.

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Notwithstanding the hundreds of conodont natural assemblages and fused clusters that have been reported, they are relatively scarce in China (Zhang and Zhang, 1986; Lai, 1995). Till now, only three clusters preserving their 3D structure have been reported from the Guanling Formation of Yunnan Province, southwestern China (Huang et al., 2010), and 24 fused clusters were noted from the Luolou Formation in Guangxi, south China (Goudemand et al., 2011, 2012). More recently, seven fused clusters of *Hindeodus* were described from the bottom of the Feixianguan Formation in the Shangshi section in Sichuan Province (Zhang et al., 2017). Outside China, other Triassic conodont clusters include materials from the Olenekian (Spathian) Taho Formation of Japan (Koike, 2004), the Induan Mino Terrane, Gifu Prefecture and the Olenekian Oritate, Kumamoto Prefecture of Japan (Agematsu et al., 2008, 2014, 2017), the Ladinian of Slovenia (Ramovš, 1977, 1978; Kolar-Jurkovšek et al., 2018), the Ladinian Grenzbitumenzone of Monte San Giorgio, Switzerland (Rieber, 1980), and the Ladinian of Trento (Mietto, 1982) and Sardinia in Italy (Bagnoli et al., 1985). The Monte San Giorgio clusters include examples of *Neogondolella* natural assemblages, which provided the basis for a gondolelloid multielement apparatus template (Orchard and Rieber, 1999; Goudemand et al., 2011). A series of 15-element reconstructions have been proposed for Triassic conodont species based on discrete element collections, using the gondolelloid template (Orchard, 2005), and the biggest difference between the apparatuses was the morphology of elements occupying the P position. Regarding *Nicoraella*, a number of conodont researchers reconstructed its apparatus based on discrete elements from collections that were constrained to single sedimentary horizons (Kozur, 1989; Kozur and Mock, 1991; Kolar-Jurkovšek et al., 2005; Sun et al., 2009; Kolar-Jurkovšek and Jurkovšek, 2010), and their views are summarised in Table 1. These multielement reconstructions are readily testable based on the suite of fused clusters described here.

The Luoping conodont clusters were first reported by Huang et al. (2010), with only four specimens discovered, but later many discrete elements were systematically described in Huang et al. (2011). In both cases, elements in the S₂ position of the clusters were interpreted as S₁ elements due to lack of complete clusters or natural assemblages, following previous studies where cypridodellan elements within the gondolelloidean apparatus were placed in the S₂ (Sb₂) position (Orchard and Rieber, 1999; Koike, 2004; Orchard, 2005; Sun et al., 2009; Ishida and Hirsch, 2011). Only after some incomplete fused conodont clusters of *Novispathodus* were discovered at the Early Triassic (Spathian) Tsoteng section of Tiandong District, Guangxi, China (Goudemand et al., 2011, 2012), were cypridodellan elements recognized to occupy S₁ rather than S₂ (Sb₂) positions, but the incomplete nature of the clusters renders this conclusion moot. Here we report some exceptionally preserved conodont clusters from the Dawazi and Shangshikan sections in Luoping County, Yunnan Province, southwestern China (Fig. 1), including three specimens that preserve all of the S and M elements in the apparatus (Fig. 5B, D, F), and one cluster that includes all elements of the apparatus (viz. P, M and S elements) (Fig. 4); all of these clusters were collected along with abundant discrete elements (Huang et al., 2009, 2011). These materials provide a firm basis for reviewing the multielement composition of the *Nicoraella* apparatus, as well as testing established hypotheses for a generalized gondolelloid apparatus template. The Luoping fused clusters reveal a skeletal arrangement in the Superfamily Gondolelloidea that is very similar to previous reconstructions of the early Triassic *Novispathodus* (Goudemand et al., 2011, 2012), but displays some differences from other gondolelloids, e.g. *Neogondolella* (Orchard and Rieber, 1999; Orchard, 2005).

Table 1
Summary of previous Triassic conodont apparatuses in superfamily Gondolelloidea.

The components of Conodont apparatus	Triassic						
	Lower		Middle				Upper
	<i>Hindeodus parvus</i> apparatus, Hashikadani Fm., lower Induan, Japan, Agematsu et al., 2017	<i>Novispathodus</i> apparatus, Luolou Fm., lower Spathian, Guangxi, Goudemand et al., 2011, 2012	<i>Nicoraella</i> apparatus, Upper Member of Guanling Fm., Anisian, Guizhou Panxian, Sun et al., 2009	Luoping <i>Nicoraella</i> apparatus element, Member II, Guanling Fm., Anisian, Yunan Luoping, this paper	<i>Neogondolella mombergensis</i> , lower Ladinian, Monte San Giorgio, Rieber, 1980, Orchard and Rieber, 1999, Orchard, 2005	<i>Pseudofurnishius murcianus</i> , Ladinian, Central Slovenia, NW Jugoslavia, Ramovš, 1977, 1978	<i>Nicoraella ? budaensis</i> , Middle Carnian, Kozur, 1989, Kozur and Mock, 1991, Kolar-Jurkovšek et al., 2005, Kolar-Jurkovšek and Jurkovšek, 2010
Preserved status	Nature assemblage on bedding plane	Part of clusters	discrete elements of the collections	15 elements clusters	Nature assemblage on bedding plane	Part of clusters	discrete elements of the collections
P ₁	carminate to angulate	segminate neospathodiform	segminate neospathodiform (Pa)	carminate or angulate (<i>Nicoraella kockeli</i>)	segminiplanate neogondoleliform (<i>Neogondolella mombergensis</i>) (Pa)	<i>Pseudofurnishius murcianus</i> (Pa)	segminate neospathodiform (Pa)
P ₂	carminate	angulate ozarkodiniform	Cornudina-like ozarkodiniform (Pb)	carminate or segminate (<i>Xaniognathus</i> sp.)	angulate (Xaniognathiform) (Pb)	pollognathiform (Pb)	? Angulate modified ozarkodiniform (Pb)
S ₀	alate hibbardelliform	alate hibbardelliform	alate hibbardelliform	alate hibbardelliform (Sa)	alate (hibbardelliform) (Sa)	hibbardelliform (Sa)	alate hibbardelliform (Sa)
S ₁	digyrate	digyrate cypridodelliform	breviform digyrate (<i>Enantiognathus latus</i>) (Sb ₁)	breviform digyrate (<i>Cypridodella</i> cf. <i>delicatula</i>)	breviform digyrate (enantiognathiform) (Sb ₁)	prioniodiform (Sb ₁)	breviform digyrate enantiognathiform (Sb ₁)
S ₂	digyrate	breviform digyrate enantiognathiform	dolabrate cypridodelliform (Sb ₂)	breviform digyrate (<i>Enantiognathus latus</i>)	dolabrate or similar grodeliform or cypridodelliform (Sb ₂)	enantiognathiform (Sb ₂)	dolabrate cypridodelliform (Sb ₂)
S ₃	bipennate	bipennate hindeodelliform	bipennate hindeodelliform (Sc ₁)	bipennate (<i>Hindeodella bogschi</i>)	resembles tetriopedate cf. hindeodelliform; bipennate with anterior process) (Sc ₁)	hindeodelliform (Sc ₁)	bipennate hindeodelliform (Sc ₁)
S ₄	bipennate	bipennate hindeodelliform	bipennate cf. hindeodelliform (Sc ₂)	bipennate (<i>Hindeodella bogschi</i>)	bipennate cf. hindeodelliform (Sc ₂)	hindeodelliform (Sc ₂)	?
M	Breviform digyrate	breviform digyrate cypridodelliform	digyrate prioniodiniform (M)	breviform digyrate (<i>Cypridodella</i> cf. <i>conflexa</i>)	breviform digyrate cypridodelliform (M)	prioniodiform (M)	digyrate ? Prioniodiniform (M)

Previous Triassic apparatus reconstructions in superfamily Gondolelloidea, element composition in each position of the apparatus as shown in the original diagnosis without any modification, and comparison with the new apparatus of *Nicoraella*, based on well-preserved clusters, presented in this paper.



Fig. 1. Location map of the Shangshikan and Dawazi sections in Luoping, eastern Yunnan, southwestern China, with indication of location in Luoping County (top right) and in China as a whole (top left).

2. Geological setting

All studied conodont clusters come from the lower fossil unit of the Luoping Biota in the Dawazi and Shangshikan sections of the Guanling Formation (member II) (Huang et al., 2009), Luoping County, Yunnan Province, southwestern China. The Guanling Formation is exposed widely over eastern Yunnan and western Guizhou provinces, in the southwestern part of the Yangtze Platform between the Nanpanjiang Basin and the Yangtze Platform (Enos et al., 2006; Hu et al., 2011). It can be subdivided into two members, of which Member I is about 333 m thick, and consists mainly of mudstones and argillaceous dolomites with a volcanic ash bed (green pisolite) at the base. Member II is about 580 m thick, and is composed of nodular limestones, silty limestones, micritic limestones, and bands of dolomite (Zhang et al., 2009). The Guanling Formation has attracted attention because of the discovery of the Luoping Biota in Member II, a rich and diverse assemblage of exceptionally preserved marine invertebrates and vertebrates, including marine reptiles, fishes, and lightly sclerotized arthropods, associated with bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, foraminifers, ostracods, limulids, conodonts and trace fossils (Hu et al., 2011, 2017; Wen et al., 2012, 2013; Feldmann et al., 2012, 2017; Huang et al., 2013; Luo et al., 2017a, 2017b; Liu et al., 2017). As such, the Luoping Biota has been interpreted to record the rebuilding of shallow marine ecosystems following the end-Permian mass extinction, some 10 Myr earlier than previously anticipated (Zhang et al., 2008; Hu et al., 2011; Benton et al., 2013; Liu et al., 2014). The presence of the index conodont *Nicoraella kockeli* dates the Luoping Biota as Middle Triassic (Pelsonian substage of the Anisian) in age (Huang et al., 2009; Zhang et al., 2009).

3. Materials and methods

The conodont clusters in the Shangshikan and Dawazi sections are preserved in two ways. First, there are accumulations of disarticulated conodont elements (Fig. 2) that may represent faecal residues or stomach remains of animals that preyed upon conodonts (Hao et al., 2015; Ji et al., 2017), or just disarticulated accumulations washed together by ocean-floor currents. Second, are articulated clusters (Figs. 3–7) with elements arranged in recurrent associations reflecting their original relative arrangement in the living organism, fused together by diagenetic mineral crusts; these preserve evidence of the composition and

architecture of the feeding apparatus of *Nicoraella*. All figured specimens are housed in the Chengdu Center of China Geological Survey, China, and their collection numbers are shown in Table 2.

The fused conodont clusters and discrete elements were collected from 5 m thick sections of thinly-bedded bituminous limestone of the Luoping Biota; some specimens illustrated here in Fig. 3B, G, I, Fig. 5G, and Fig. 6J were briefly reported in previous works (Huang et al., 2009, 2010, 2011). In total, 202 samples, each of them weighing about 3 kg, were collected bed by bed in the Shangshikan and Dawazi sections. Samples were crushed into small pieces (2–6 cm in diameter) and dissolved in 10% acetic acid. The insoluble residues were washed through a sieve (160 grids per cm²) in tap water to remove the acid, and subsequently dried. The dry residues were density-separated using heavy liquid (2.8 g/ml; Jiang et al., 2004) and manually picked under a binocular stereomicroscope. Using this method, 41 conodont clusters were recovered from 24 samples. The specimen in Fig. 4 was scanned using SRXTM at the X02DA TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute (Villigen, Switzerland), and the remaining specimens were photographed using scanning electron microscopy (Quanta 200) at the State Key Laboratory Geological Processes and Mineral Resources, China University of Geosciences, Wuhan, China.

In order to interpret the multielement taxonomy, nomenclature follows the anatomical notation of S_n - P_n (S_{0-4} , M, and P_{1-2}) following Purnell et al. (2000). We also used the traditional notation (Pa, Pb, M, Sa, Sb, Sc) (Clark et al., 1981) in comparing element morphologies.

4. Results

Not all clusters preserve the complete complement of elements due to taphonomic processes, but one cluster seems to preserve the expected complement of 15 elements (4P, 2M, 9S) (Fig. 4). The P, S and M elements of the cluster are compressed together, and they are slightly dislocated in sinistral view. We identify four P elements within the cluster based on their morphologies, bilateral pairing, and separation from the ramiform S and M elements; the P_1 element pair is most distant from the ramiform S elements and the P_2 element pair is intermediate. Indeed, within the cluster, the P_2 elements overlap with the S-M elements, and the P_1 elements through only marginal overlap with the P_2 elements and the broken posterior process of the dextral M element which overlaps all of the P elements. A single S_0 element is located

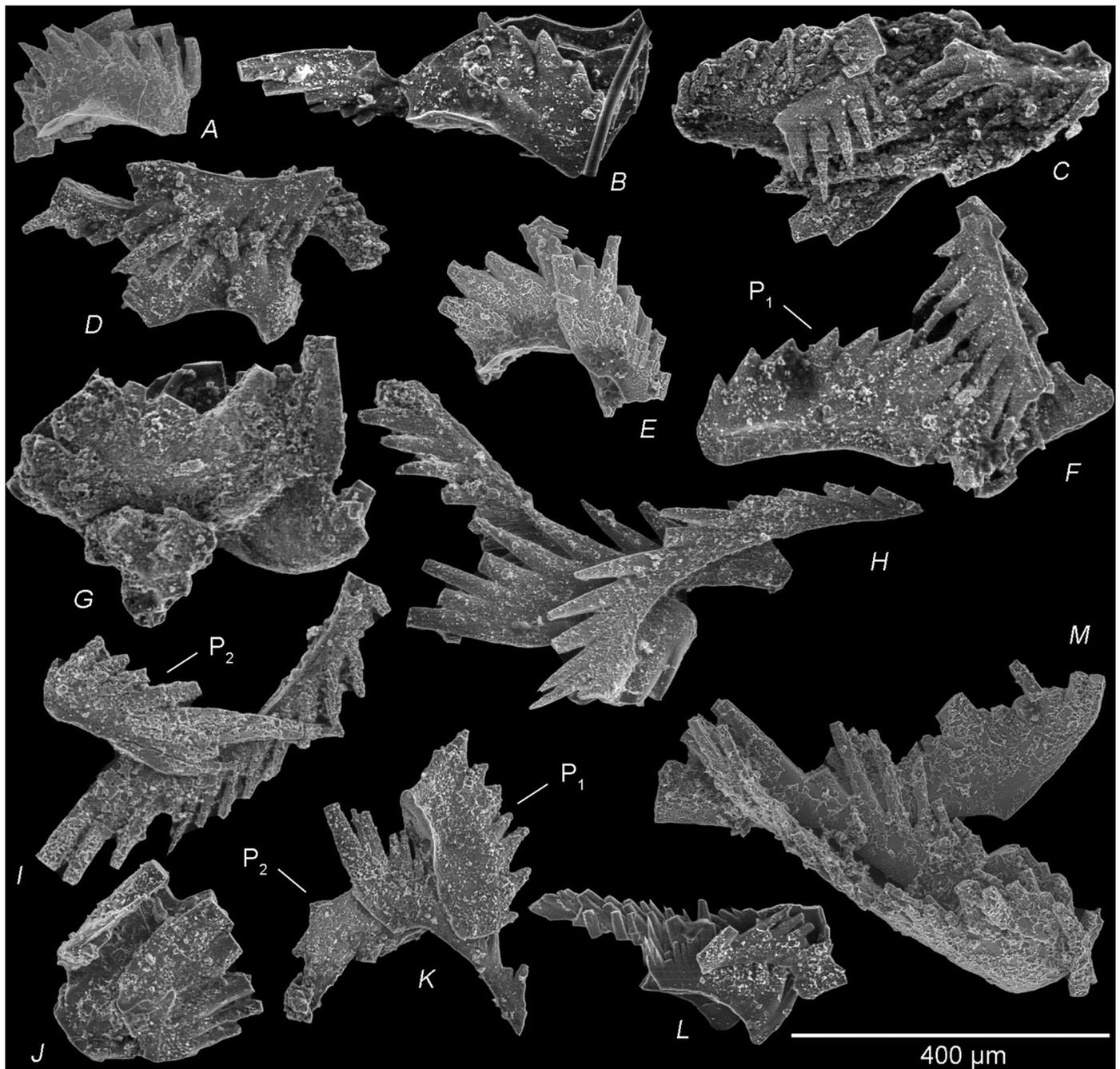


Fig. 2. Disarticulated conodont accumulation from the Dawazi and Shangshikan sections. These conodont elements are from bed (–17) (A), bed 12 (B–D, L), bed 20 (F–G), bed 25 (E, H–I, K), and bed 35 (J) in the Dawazi section respectively, and Fig. M is from bed 10 of the Shangshikan section. These have been interpreted as accumulations in faecal residues of predators or post-mortem accumulations by current winnowing. Although they do not have the full characters of apparatus architecture, they also provide valuable clues on apparatus architecture, of the P and S elements occur together in Figs. B, F, I and K.

innermost within the cluster, and five pairs of S_{1-4} and M elements occur in a disrupted nested arrangement. The S_1 elements are embraced by inner lateral processes of the S_2 elements, and their cusps are aligned parallel with the anterior-posterior processes of the S_{3-4} elements.

Other clusters preserve subsets of the apparatus, such as disarticulated cluster aggregations, individual pairs of associated P_1 and P_2 elements, and articulated S-M combinations. Of the disarticulated clusters, four clusters fuse a P_1 element and S elements (Fig. 2A, B, E, F), one cluster preserves a P_2 element and an S_1 element together (Fig. 2I), one cluster associates a P_1 , P_2 and an S_1 element (Fig. 2K), and the rest are ramiform element clusters. Clusters of P elements pairs preserve their natural articulation (e.g. Fig. 3), with their denticles opposed and

the lateral faces of their processes adpressed; there are eight clusters of P_1 pairs and one P_2 element pair (Fig. 3H). Eighteen articulated S-M combinations preserve the original biological relative arrangement of elements (Figs. 5–7), of which four to ten or eleven elements are preserved in different clusters. Seven clusters preserve S_0 elements intercalated in the innermost part of the cluster (Figs. 5A–D, F, 6K and 7O), one could be clearly identified in the cluster in Fig. 5F, which is wholly exposed because all anterior processes of the S_{2-4} elements are broken. S_{1-4} elements can be identified directly based on positional homology from the dextral and sinistral sides of the clusters (Figs. 5B–D, F, H, 6I–M and 7O, R) or from an axial or abaxial perspective (Fig. 5G), S_3 and S_4 elements exhibit similar morphology and bracket the position of

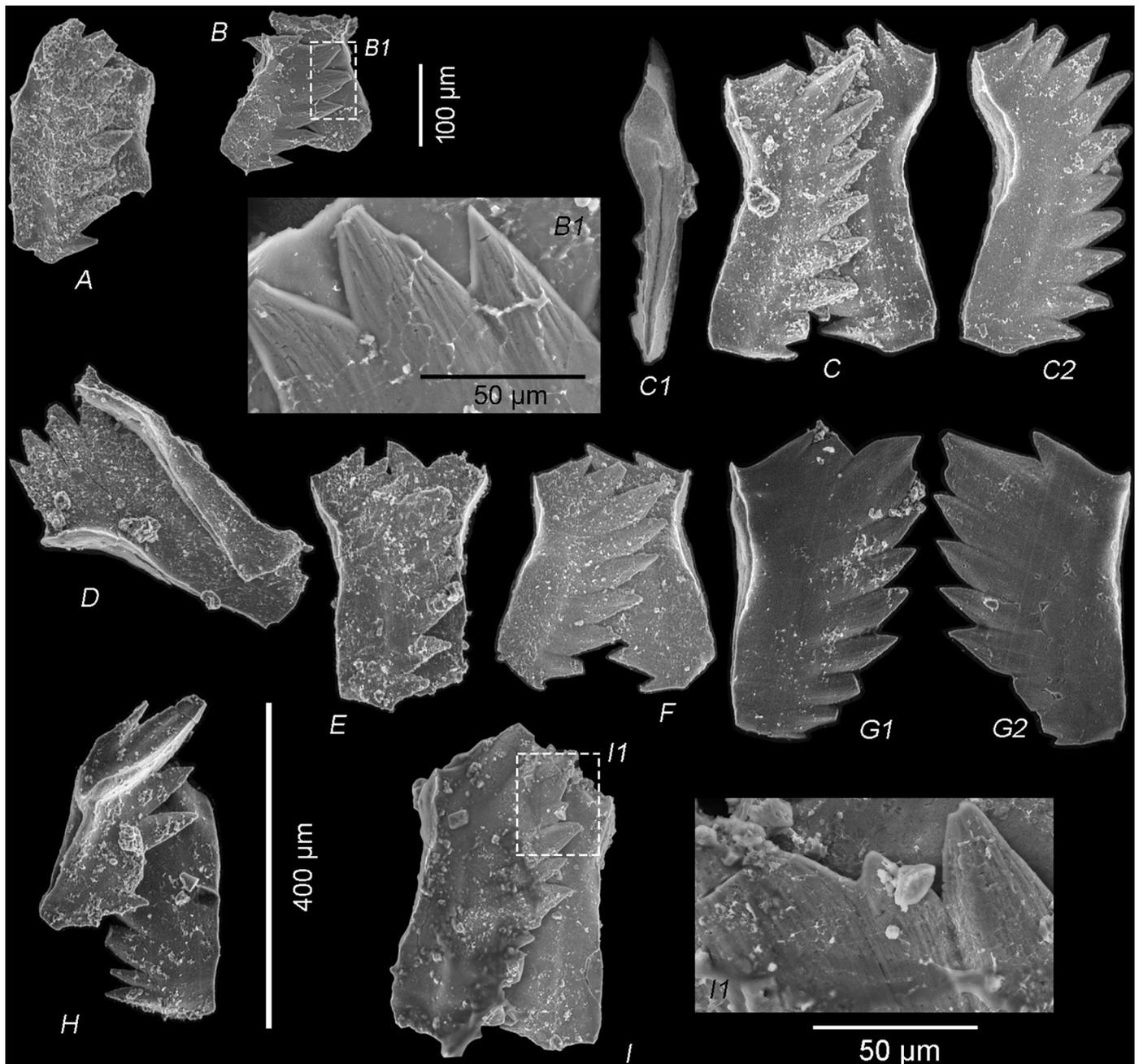


Fig. 3. Articulated conodont clusters of P_1 and P_2 elements from the Dawazi section and Shangshikan section, as SEM photographs. P_1 elements (A–G) and P_2 elements (H) clusters from the Dawazi section are from bed 3 (A), bed 19 (B), bed 25 (C), bed 35 (D), bed 36 (E–F), and bed 42 (G–H) respectively, and Fig. (I) (P_1 elements) from bed 32 in the Shangshikan section; figure (B₁) and (I₁) shows microwear on the distal denticles.

the S_2 elements; S_1 elements are embraced abaxially by the inner lateral processes of the S_2 elements (Fig. 5G). M elements lie at the most outer parts of the clusters, overlap the S_4 elements, but at a discordant angle of about 60 degrees (Figs. 5D, F, 6I–J, L and 7R).

These clusters preserve consistent and repeated patterns of juxtaposition, discriminating them as natural assemblages and allowing us to infer element position based on their topological relationships and morphology.

5. Systematic palaeontology

Phylum Chordata [Haeckel, 1874](#).

Subphylum Vertebrata-Craniata [Linnaeus, 1758](#).

Class Conodonta [Eichenberg, 1930](#).

Division Prioniodontida [Dzik, 1976](#).

Order Ozarkodinida [Dzik, 1976](#).

Suborder Ozarkodinina [Dzik, 1976](#).

Superfamily Gondolelloidea ([Lindström, 1970](#)).

Family Gondolellidea [Lindström, 1970](#).

Genus *Nicoraella* [Kozur, 1980](#).

5.1. Type species and holotype

Ozarkodina kockeli [Tatge, 1956](#), p. 137, pl. 5, Figs. 13 and 14.

Nicoraella kockeli ([Tatge, 1956](#)).

Multielement:

2009 *Nicoraella kockeli* Sun et al., p. 230, Fig. 2F–K; p. 231, Fig. 2B–L, p. 232, Fig. 4

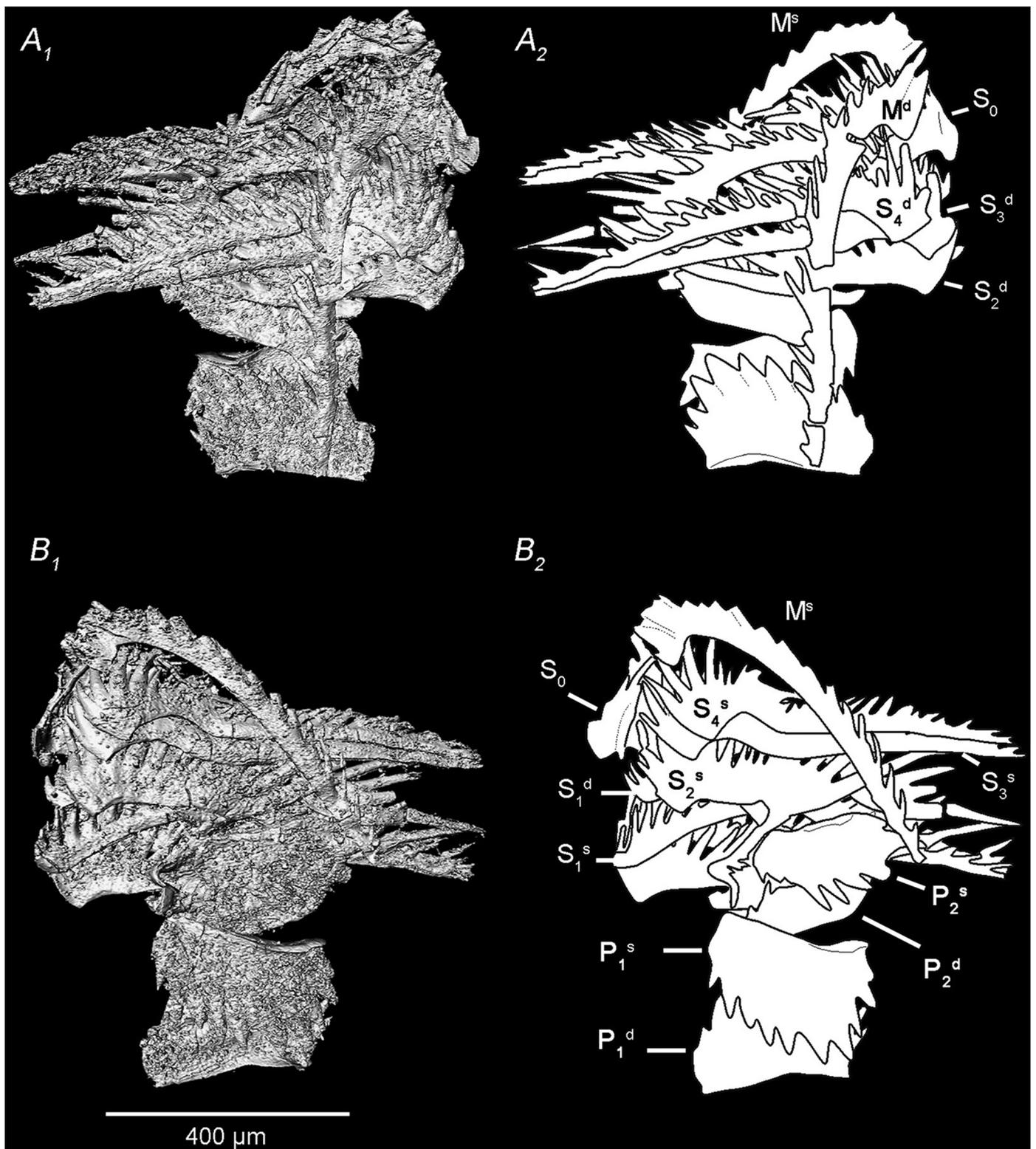


Fig. 4. Articulated conodont cluster from the bed 18 in Dawazi section, in which all elements were fused together as shown in line photographs, A: dextral side, B: sinistral side. It presents the complete elements of the *Nicoraella* apparatus, which containing 15 elements (seven paired P₁₋₂, S-M elements and one unpaired S₀ element).

5.2. Materials

Forty-one clusters from the fossil layers of the Luoping Biota, Yunnan Province, southwestern China. Each component of the apparatus is illustrated in Fig. 8.

5.3. Original diagnosis and type species

Blade-shaped carminate P₁ element possesses a pronounced sub-terminal main cusp with one or two small denticles in succession, partly fused denticles of variable height (Tatge, 1956, p. 137).

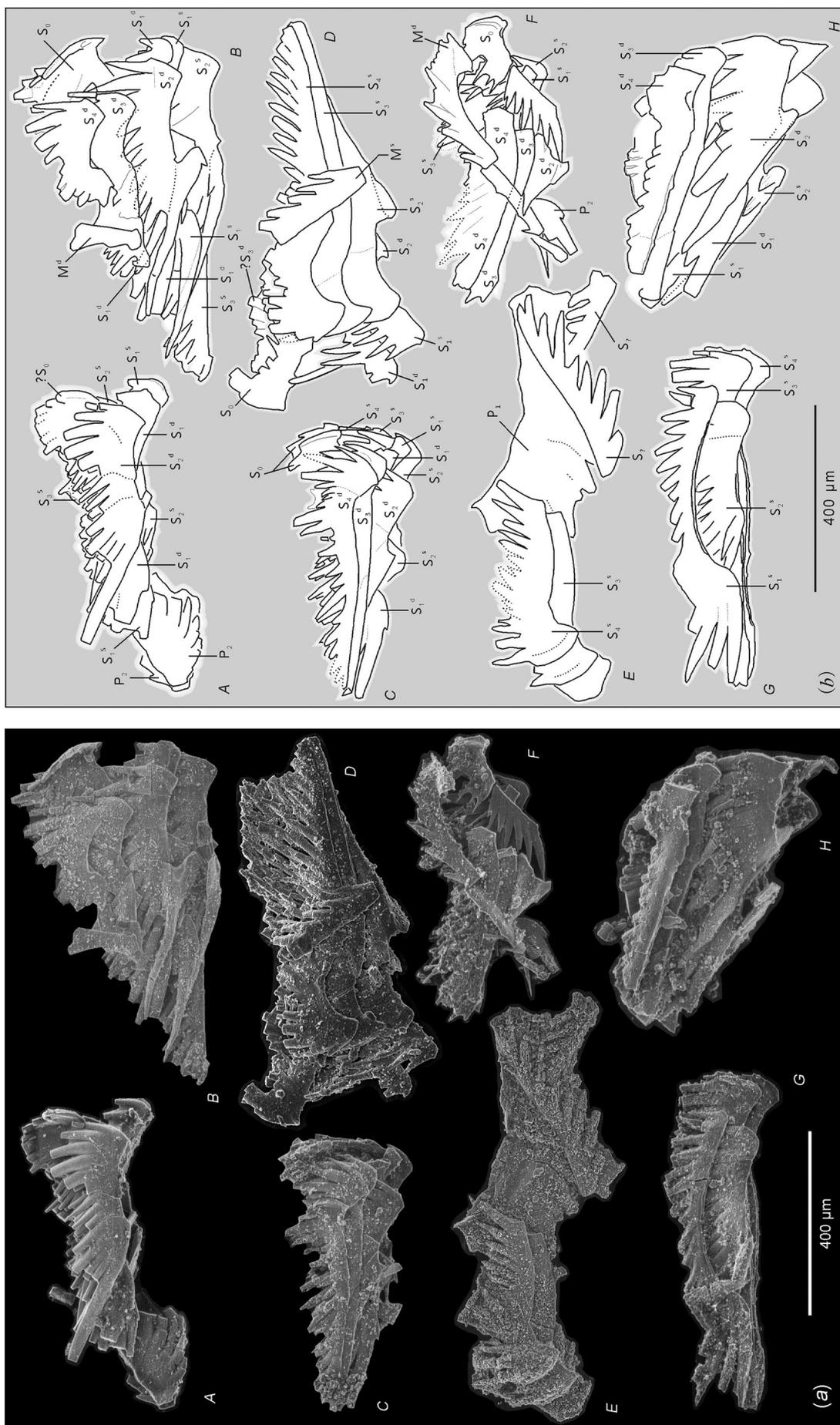


Fig. 5. Articulated conodont clusters from the Dawazi section, as SEM photographs (a) and interpretive drawings (b). Clusters are from bed (-17) (A), bed 12 (B-E), bed 18 (F-G), and bed 23 (H) respectively. Their elements stack in the same relative order in clusters A-H. Single example of S₀ (hibbardellan element), S₂ (enantiognathiform element), S₃₋₄ (hindeodellan elements) and M (cypridodellan elements).

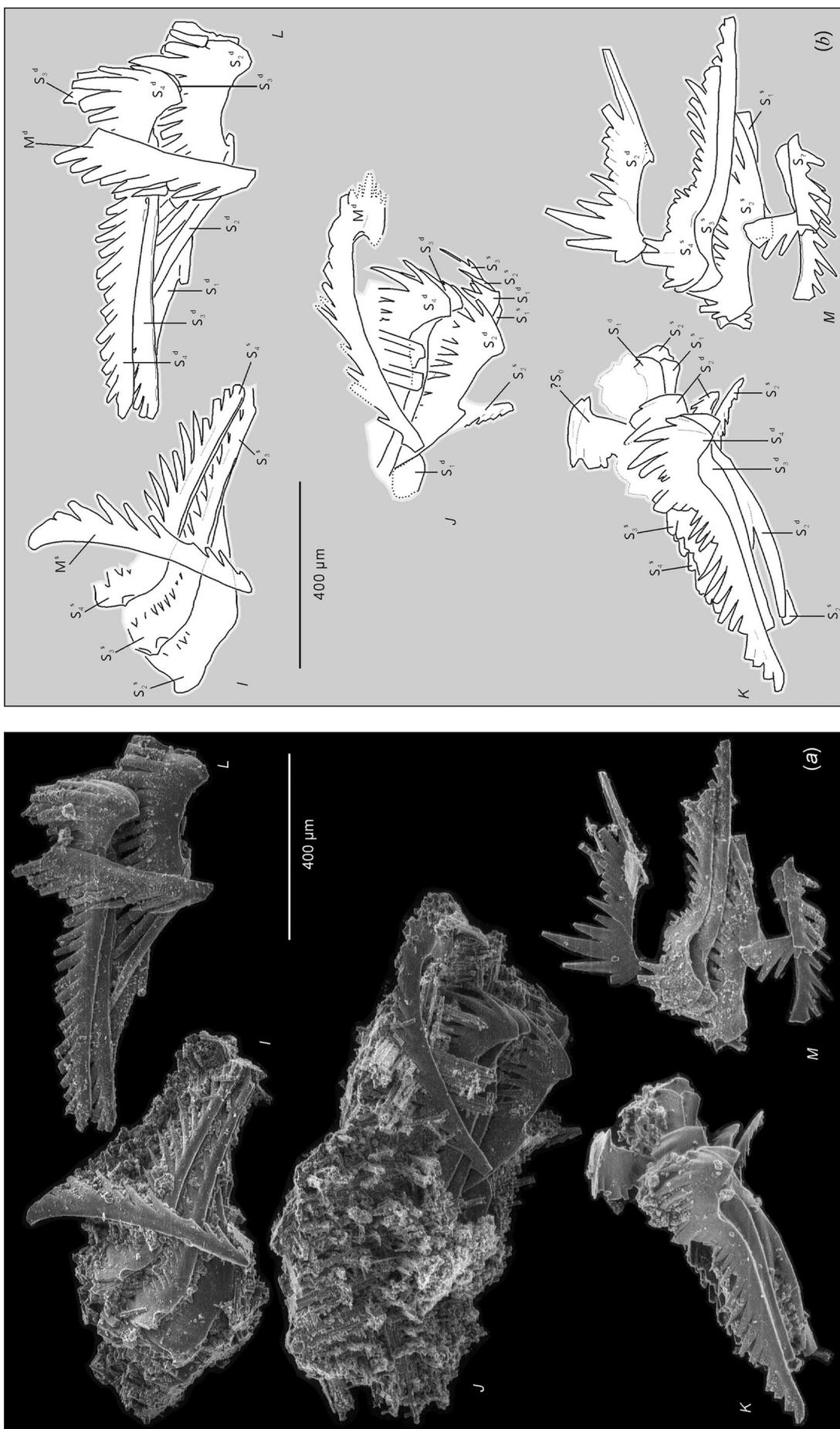


Fig. 6. Articulated conodont clusters from the Dawazi section, as SEM photographs (a) and interpretive drawings (b). Conodont clusters are from bed 25 (I–J), bed 27 (K), and bed 34 (L–M) respectively. They have the same pattern of the juxtaposition in the clusters of I–M. Single example of S₀ (hibbardellan elements), S₂ (enantiognathiform elements), S_{3–4} (hindeodellan elements) and M (cypridodellan elements).

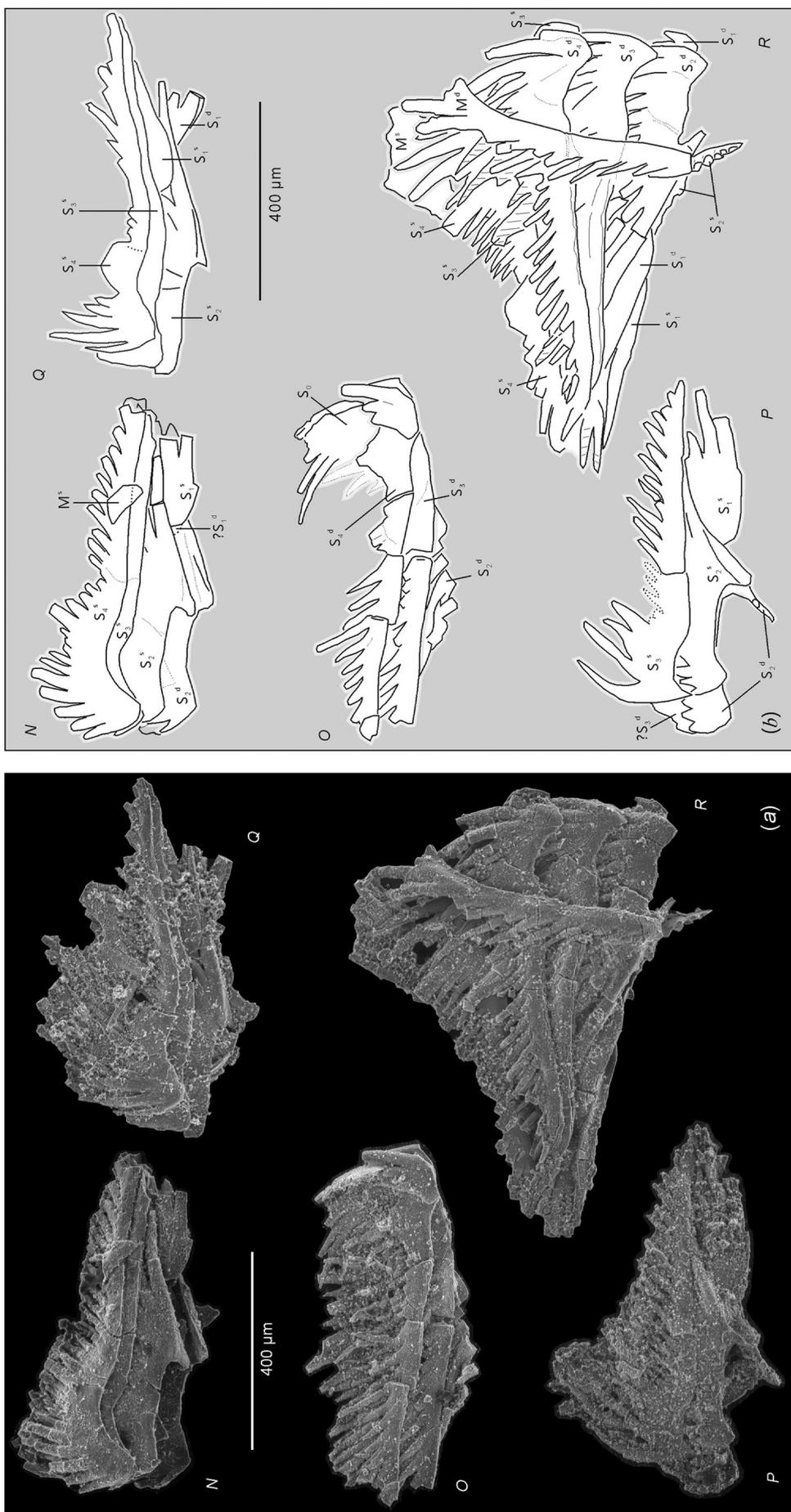


Fig. 7. Articulated conodont clusters from the Dawazi section and Shangshikan sections, as SEM photographs (a) and interpretive drawings (b). Conodont clusters from the Dawazi section are from bed 35 (N) and bed 37 (O–P), and Figs. (Q) and (R) from bed 27 and bed 32 respectively in the Shangshikan section. (N–P) and (Q–R) share patterns of juxtaposition, and comprise a single of S_0 (hibbardellian elements), pairs of S_1 (cypridodellian element), S_2 (enantiognathiform elements), S_{3-4} (hindeodellian elements) and M (cypridodellian elements).

Table 2
Collection numbers of the conodont clusters in the paper.

Text-Figures	Numbers in the figure	Sections	Original bed numbers	Catalog numbers
Fig. 2	A	Dawazi	–17	pm028-(–17)-wy1-C1
	B	Dawazi	12	pm028-12-wy1-C1
	C	Dawazi	12	pm028-12-wy1-C2
	D	Dawazi	12	pm028-12-wy1-C3
	E	Dawazi	25	pm028-25-wy1-C3
	F	Dawazi	20	pm028-20-wy1-C1
	G	Dawazi	20	pm028-20-wy1-C2
	H	Dawazi	25	pm028-25-wy1-C4
	I	Dawazi	25	pm028-25-wy1-C5
	J	Dawazi	35	pm028-35-wy1-C1
	K	Dawazi	25	pm028-25-wy1-C6
	L	Dawazi	12	pm028-12-wy1-C4
	M	Shangshikan	10	pm032-10-wy1-C1
Fig. 3	A	Dawazi	3	pm028-3-wy1-C1
	B	Dawazi	19	pm028-19-wy1-C1
	C	Dawazi	25	pm028-25-wy1-C7
	D	Dawazi	35	pm028-35-wy1-C2
	E	Dawazi	36	pm028-36-wy1-C1
	F	Dawazi	36	pm028-36-wy1-C2
	G	Dawazi	42	pm028-42-wy1-C1
	H	Dawazi	42	pm028-42-wy1-C2
	I	Dawazi	32	pm028-32-wy1-C1
Fig. 4	A–B	Dawazi	18	pm028-18-wy1-C1
Fig. 5	A	Dawazi	–17	pm028-(–17)-wy1-C2
	B	Dawazi	12	pm028-12-wy1-C5
	C	Dawazi	12	pm028-12-wy1-C6
	D	Dawazi	12	pm028-12-wy1-C7
	E	Dawazi	12	pm028-12-wy1-C8
	F	Dawazi	18	pm028-18-wy1-C2
	G	Dawazi	18	pm028-18-wy1-C3
	H	Dawazi	23	pm028-23-wy1-C1
Fig. 6	I	Dawazi	25	pm028-25-wy1-C8
	J	Dawazi	25	pm028-25-wy1-C9
	K	Dawazi	27	pm028-27-wy1-C1
	L	Dawazi	34	pm028-34-wy1-C1
	M	Dawazi	34	pm028-34-wy1-C2
Fig. 7	N	Dawazi	35	pm028-35-wy1-C3
	O	Dawazi	37	pm028-37-wy1-C1
	P	Dawazi	37	pm028-37-wy1-C2
	Q	Shangshikan	27	pm032-27-wy1-C1
	R	Shangshikan	32	pm032-32-wy1-C1

5.4. Multielement diagnosis

Interpreting the articulated cluster, and combining 40 conodont fused clusters and rich assemblages of discrete elements from the Luoping Biota, a 15-element apparatus is reconstructed, consisting of seven morphological types of elements (Fig. 8): alate (hibbardellan) S_0 , breviform digyrate (cypridodellan) S_1 , breviform digyrate (enantiognathiform) S_2 , bipennate (hindeodellan) S_3 and S_4 , breviform digyrate (cypridodellan) M, carminate (nicoraellan) P_1 , and carminate to segminate (xaniognathiform) P_2 . Previous researchers have arrived at a similar multielement reconstruction based on discrete element assemblages (Kozur and Mock, 1991; Kozur, 1989; Kolar-Jurkovšek et al., 2005; Sun et al., 2009; Kolar-Jurkovšek and Jurkovšek, 2010), with the exception that they have usually interpreted the enantiognathiform and cypridodellan elements as S_{1-2} , respectively, which usually equates to S_{1-2} positional homologies, respectively. Here we demonstrate that the positional homologies are reversed. The long process of the S_{2-4} elements are aligned in a subparallel arrangement within the clusters (Figs. 4–7).

5.5. Multielement descriptions

The 15-element apparatus of *Nicoraella* is composed of seven different element types (5S, 1M, 2P) whose morphological description and positions in the apparatus are as follows:

S_0 (Sa) element: Alate, with two short denticulate and symmetrical disposed processes and a longer posterior process, which are slightly recurved along its aboral margin. This character is shown in the best-known Carboniferous conodont apparatus *Idiognathodus* (Purnell and Donoghue, 1997). Also, many reconstructions of the apparatus based on discrete elements (Kozur, 1989; Kolar-Jurkovšek et al., 2005; Sun et al., 2009; Kolar-Jurkovšek and Jurkovšek, 2010) or parts of fused clusters (Goudemand et al., 2012) follow this rule. Based on their symmetrical morphology and position within the apparatus, sandwiched by dextral and sinistral S elements, we infer that the alate hibbardellan elements occupied an S_0 position in the apparatus of *Nicoraella* (Figs. 4, 5A–D, F and 6K).

S_1 (S_{b1}) elements: Breviform digyrate cypridodellan morphology, an erect cusp with a long downwardly recurved outer lateral process and an inner lateral process that may be adenticulate or include a small number of denticles. Their location, immediately abaxial of the S_0 element evidences their S_1 positional homology (Figs. 4, 5A–D, F, G). By inference, positional homologies can be established in clusters of *Novispathodus* (Goudemand et al., 2011, 2012). Previously, many researchers interpreted these morphotypes as S_2 (S_{b2}) elements in the superfamily Gondolelloidea (Orchard and Rieber, 1999; Koike, 2004; Orchard, 2005; Sun et al., 2009). Here we identify ‘*Cypridodella cf. delicatula*’ elements as having occupied an S_1 position.

S_2 (S_{b2}) element: Breviform digyrate elements with a denticulate or adenticulate adaxial inner lateral process and a long denticulate abaxial inner lateral process. Strictly, we have not yet been able to determine the position of the primary cusp in these elements. The cusp is either at the rostral end of the element (making it bipennate) or else, the cusp is the largest denticle at the caudal end of the element (making it breviform digyrate). Identification of the position of the tip of the primary basal cavity will reconcile these alternative interpretations. For the moment, we assume that the largest denticle is the cusp. These ‘enantiognathiform’ elements are recognized as having occupied an S_2 position based on their location abaxial of the elements occupying the S_1 position. Discrete elements of the form taxonomy genus ‘*Enantiognathus*’ were discriminated previously as S_{b1} and, therefore, might be considered to have occupied an S_1 position (Orchard and Rieber, 1999; Koike, 2004; Orchard, 2005; Sun et al., 2009). Here we demonstrate that these ‘*Enantiognathus latus*’ element morphotypes occupied an S_2 position (Figs. 4, 5A–D, F–H, 6I–M and 7N, P, R).

S_3 , S_4 (S_{c1} , c_2) element: Bipennate with a short recurved anterior process and a long posterior process. The S_3 and S_4 elements are almost identical but show some subtle difference. These include the form taxonomy morphotypes ‘*Hindeodella bogschi*’ (Figs. 4, 5B–H, 6I–M and 7N–R), which has a sitar-like profile in lateral view, with nearly straight posterior processes, and the anterior processes laterally bowed inward and downward beginning at the cusp, and all denticles deflected inward; and ‘*Neohindeodella triassica*’ (Fig. 2M). The ‘*H. bogschi*’ morphotype elements are much more abundant ‘*N. triassica*’, of which just one example was found in the clusters; the same imbalance occurred among the discrete elements (Huang et al., 2011).

M elements: Breviform digyrate with a long downwardly recurved outer lateral process, a short, straight inner lateral process, and a prominent cusp. These ‘cypridodellan’ elements have traditionally been identified as M elements (Purnell and Donoghue, 1997; Koike, 2004; Koike et al., 2004; Orchard, 2005). Here, their positional homology can be established based on the location flanking abaxially the elements occupying the S_4 position (Figs. 4, 5B, D, F, 6I, L, J and 7R). These conform to the ‘*Cypridodella cf. conflexa*’ morphotype in single element taxonomy. The difference between M and S_1 elements lies in the orientation of the cusp relative to the lateral processes: in M elements the

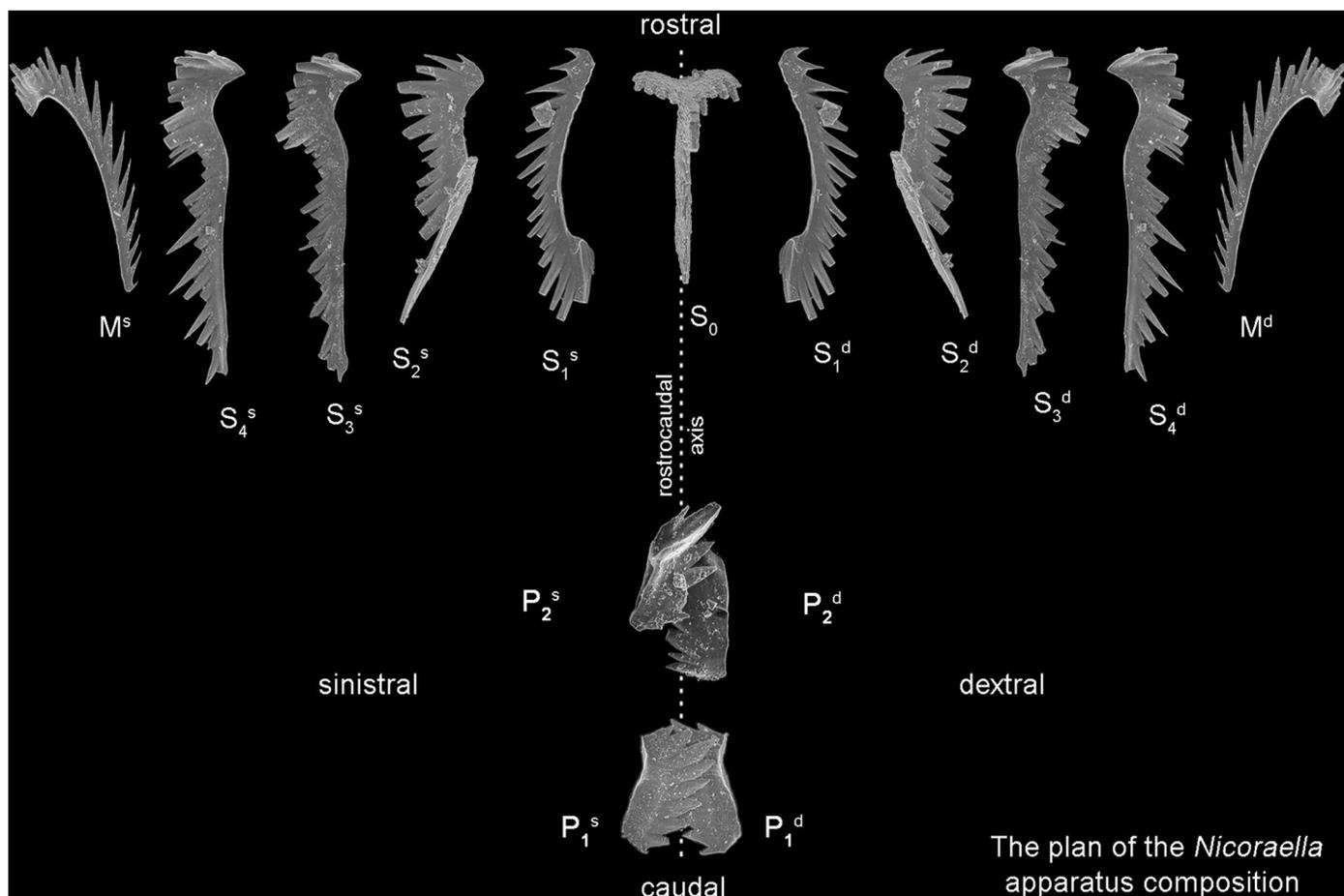


Fig. 8. Map of the relative positions of elements with the topological scheme of notation of the *Nicoraella* apparatus. In the medial position, the S_0 element is a hibbardellan element, at the sinistral and dextral of the S_0 element, the S_1 , S_2 , S_{3-4} and M elements flank successively, and they are *Cypridodella* cf. *delicatula*, *Enantiognathus* *latus*, *Hindeodella* *bogschi* and *Cypridodella* cf. *conflexa* respectively.

lateral processes are true lateral processes and the cusp is curved in a plane that is perpendicular to the plane defined by the two lateral processes, whereas in S_1 elements the cusp is often twisted in such a way that it ends up being oriented along the largest process (outside lateral process).

P_2 (Pb) element: Carminate with a long anterior process and short posterior process comprised of few denticles (Figs. 2I, 3H and 4), or segminate ('xaniognathiform') with no posterior process and, consequently, a terminal cusp (Fig. 2K; Huang et al., 2011). These elements are also seen in the Middle Triassic *Nicoraella* apparatus reconstruction on the basis of discrete elements from West Guizhou, South China (Sun et al., 2009).

P_1 (Pa) element: Carminate or angulate with a longer anterior process and shorter posterior comprised of just one or a few small denticles; cusp broader than the surrounding denticles but not much longer (Fig. 3). These are 'nicoraellan' elements (*Nicoraella kockeli*) (Figs. 2B, F, K, 3D, F, I and 4).

5.6. Remarks

Elements morphologies were described fully in previous investigations of *Nicoraella* (Sun et al., 2009; Huang et al., 2011). The most significant difference in our multielement reconstruction is the switch in homology of the elements previously considered to occupy S_1 and S_2 positions, to S_2 and S_1 , respectively, based on the primary positional information provided by the fused clusters (Fig. 4; Goude mand et al., 2012). The reconstructed apparatus is comprised of 15 elements, including a single bilaterally symmetrical element (S_0) and seven paired

elements (S_{1-4} , M, P_{1-2}). Apparatuses within Superfamily Gondolelloidea exhibit high degrees of similarity in terms of morphology and positions of the S and M elements: S_0 elements are traditional alate elements with two antero-lateral processes; M elements are breviform digyrate elements with a very long and a short process; S_{3-4} elements are usually bipennate but there are exceptions, including the tertiope-date S_3 elements in Mullerinae. Breviform digyrate elements (enantiognathiform) were interpreted as characteristic S_1 elements, including two lateral processes; and S_2 elements were diagnosed as digyrate with a prominent posterior process and sometimes connecting one, or two or three anterior denticles before the cusp. However, based on the primary positional information preserved in the clusters of *Nicoraella kockeli*, the element morphotypes inferred to have occupied S_{1-2} positions in multielement reconstructions in other species of Gondolelloidea, should be reversed. Without considering the obvious morphological differences in P elements between taxa, S-M elements are more or less differentiated among the genera, such as *Nicoraella*, *Novispathodus* (Goude mand et al., 2012) and *Neogondolella* (Orchard and Rieber, 1999; Orchard, 2005). S_3 and S_4 elements of *Nicoraella* possess a more recurved antero-lateral process (in aboral view) in comparison to *Novispathodus* and *Neogondolella*, with more denticles on the inner lateral process of the S_2 element, and a slightly curving aboral margin to the posterior process of the S_0 element.

6. Comparison with other gondolelloid apparatuses

The reconstructed apparatus of *Nicoraella kockeli* exhibits great similarity to that of the Early Triassic *Novispathodus* (Goude mand et al.,

2011, 2012). Earlier researchers added an alate hibbardellan S_0 element to the apparatus of *Novispathodus* (Goudemand et al., 2011, 2012) on the basis of former reconstructions (Rieber, 1980; Orchard and Rieber, 1999; Orchard, 2005), as well as two blade-shaped elements as the P_{1-2} elements. Their interpretation of the arrangement of S elements in their reconstructions largely withstands scrutiny, albeit with the swapping of positions of the elements previously interpreted as S_1 and S_2 in apparatuses of this type (see above). This is a new character that may be general for the Superfamily Gondolelloidea.

Previously, multielement reconstructions of the apparatus of *Nicoraella* have been based on materials of different species of the genus from the Carnian 'Raibl Beds' of the Karavanke Mountains of Slovenia (Kolar-Jurkovšek et al., 2005; Kolar-Jurkovšek and Jurkovšek, 2010). Another *Nicoraella* apparatus was reconstructed from the upper Member of the Guanling Formation in Panxian, Guizhou, southwestern China, in which the authors also proposed an apparatus with a total of 15 elements (Sun et al., 2009). Kozur and Mock (1991) suggested that the apparatus of *Nicoraella? budaensis* from the Late Triassic of Hungary and the Alps is composed of modified hindeodellan (metaproniodiform), modified prioniodiniform (cypridodellan), enantiognathiform and hibbardellan elements, but the number of S-M elements and their disposition was not confirmed. These authors made overt comparisons with the much better supported *Neogondolella* apparatus (Orchard and Rieber, 1999) and the *Idiognathodus* apparatus model from the Pennsylvanian Modesto Formation (Purnell and Donoghue, 1997; Purnell et al., 2000). Their conclusions agree with ours in terms of the enantiognathiform S_2 (Sb_2), hindeodellan S_{3-4} (Sc_{1-2}), and the breviform digyrate 'cypridodellan' M elements. As shown in Table 1, the morphology of elements occupying the S-M division is relatively stable among Triassic gondolelloids, in that the symmetrical alate hibbardellan element occupies the S_0 position. However, the S_1 position is more problematic. It was interpreted as occupied by enantiognathiform elements in previous research, but revised for the *Novispathodus* apparatus (Goudemand et al., 2011, 2012), in which the 'cypridodellan' elements were interpreted to occupy the S_1 position, and the 'enantiognathiform' elements, as S_2 elements. Many previous researchers have interpreted the (Sb_2) 'cypridodellan' elements as having been located abaxial of the 'enantiognathiform' elements, but we challenge this viewpoint based on primary positional information from the *Nicoraella* (Figs. 4, 5B, D, G, H, 6I–M and 7P, R, S) and *Novispathodus* (Goudemand et al., 2012) fused clusters.

Similar to the proposed standard apparatus of *Idiognathodus* (Purnell and Donoghue, 1997), the apparatus of *Nicoraella kockeli* was composed of 15 elements. The element number is stable and conservative, including two pairs of P elements, as in other ozarkodinid conodont apparatuses through Carboniferous to Triassic, and showing no evidence of loss of the P_2 position after the P-Tr mass extinction (Zhang et al., 2017). The apparatus composition is seen in other reconstructed Triassic apparatuses, such as the Lower Triassic *Neostrachanognathus* and *Hindeodus parvus* from Japan (Agematsu et al., 2008, 2014, 2017), the Lower Triassic *Novispathodus* (Goudemand et al., 2011), and the Ladinian *Neogondolella* apparatus of Monte San Giorgio, Switzerland (Rieber, 1980; Goudemand et al., 2011). They all retain 15 elements in the apparatus, share similar outlines (the symmetrical alate hibbardellan element in the S_0 position) and, especially, they exhibit great similarity of apparatus structure and morphology of positionally homologous elements within the same family, as evidenced by comparisons to *Novispathodus* and *Neogondolella*.

7. Conclusions

Forty-one fused conodont clusters were collected from the Middle Triassic strata of the Shangshikan and Dawazi sections, Luoping, Yunnan, southwestern China. These articulated clusters present reliable evidence to interpret the numbers of elements, their morphologies, and relative positions in the apparatus. Integrating information derived

from discrete elements and articulated clusters suggests that the apparatus of *Nicoraella* was a typical 15-element apparatus, including 11 S-M elements (single S_0 , paired S_1 – S_4 and M elements) and pairs of P_1 and P_2 elements. Based on juxtaposed and overlapping elements in clusters, 'enantiognathiform' and 'cypridodelliform' elements can be demonstrated to have occupied S_2 and S_1 positions, respectively (reversing previous inferences). This new apparatus represents a new template for the superfamily Gondolelloidea, and it will play a significant role in revision of previous multielement reconstructions. However, fusion of different elements in the clusters or enclosure in the matrix makes it difficult to reconstruct the original three-dimensional apparatus architecture using SEM technology; this must be addressed using X-ray microtomography and computed tomography.

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