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

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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\(_1\)–S\(_4\), M and P\(_1\)–P\(_2\) elements) like other apparatuses in Gondolellidae, i.e. the genera *Novispathodus* and *Neogondolella*. These Luoping Biotia 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 ozarkodinids, 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.

**ARTICLE INFO**

Keywords: Fused cluster Multielement taxonomy 15-element apparatus Anisian Guanling Formation Luoping Biotia

**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\(_1\)–S\(_4\), M and P\(_1\)–P\(_2\) elements) like other apparatuses in Gondolellidae, i.e. the genera *Novispathodus* and *Neogondolella*. These Luoping Biotia 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 ozarkodinids, 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.

https://doi.org/10.1016/j.palaeo.2018.07.015

Received 9 January 2018; Received in revised form 15 July 2018; Accepted 15 July 2018
Available online 20 July 2018
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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 Oleneikian (Spitian) Taho Formation of Japan (Koike, 2004), the Induan Mino Terrane, Gifu Prefecture and the Oleneikian Oritate, Kumamoto Prefecture of Japan (Agenatsu et al., 2008, 2014, 2017), the Ladinian of Slovenia (Ramović, 1977, 1978; Kolar-Jurkovšek et al., 2018), the Ladinian Grenzbizumenzone 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 a 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 cypridodellian 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 (Spitian) Tsoteng section of Tiandong District, Guangxi, China (Goudemand et al., 2011, 2012), were cypridodellian 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.

<table>
<thead>
<tr>
<th>The components of Conodont apparatus</th>
<th>Triassic</th>
<th>Upper</th>
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<td>Lower</td>
<td>Middle</td>
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<tr>
<td>Novispathodus apparatus, Luolou Fm.</td>
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<tr>
<td>lower Spatian, Guanling, Goudemand</td>
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<td>et al., 2011, 2012</td>
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<tr>
<td>Nicoraella apparatus, Upper Member</td>
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<tr>
<td>of Guanling Fm., Anisian,</td>
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<td>Guizhou Panxian, Sun et al, 2009</td>
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<tr>
<td>Luoping Nicoraella apparatus element,</td>
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<tr>
<td>Member II, Guanting Fm., Anisian,</td>
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<td>Anisian, Yunan, Luoping, this paper</td>
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<tr>
<td>Neogondolella hornbergensis, lower</td>
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<td>Ladinian, Monte San Giorgio, Rieber,</td>
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<td>1980, Orchard and Rieber, 1999,</td>
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<td>Orchard, 2005</td>
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<tr>
<td>Pseudofurnishius murcianus, Ladinian,</td>
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<td>Central Slovenia, NW Yugoslavia,</td>
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<td>Ramović, 1977, 1978</td>
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<tr>
<th>Preserved status</th>
<th>Nature assemblage on bedding plane</th>
<th>Part of clusters</th>
<th>discrete elements of the collections</th>
<th>15 elements clusters</th>
<th>Nature assemblage on bedding plane</th>
<th>Part of clusters</th>
<th>discrete elements of the collections</th>
</tr>
</thead>
<tbody>
<tr>
<td>P_1</td>
<td>carinate to angulate</td>
<td>segmentate</td>
<td>segminate neospathodiform (Pa)</td>
<td>carinate or angulate (Nicoraella kockeli)</td>
<td>segminate neospathodiform</td>
<td>Neogondolella hornbergensis (Pa)</td>
<td>Pseudofurnishius murcianus (Pa)</td>
</tr>
<tr>
<td>P_2</td>
<td>carinate</td>
<td>angulate</td>
<td>ozarakodiform (Pb)</td>
<td>carinate or segmentate (Kaniognathus sp.)</td>
<td>angulate (Kaniognathus sp)</td>
<td>Pollognathiform (Pb)</td>
<td>? Angulate modified ozarakodiform (Pb)</td>
</tr>
<tr>
<td>S_1</td>
<td>alate hibbardiform</td>
<td>alate hibbardiform</td>
<td>alate hibbardiform (Sa)</td>
<td>alate (hibbardiform) (Sa)</td>
<td>hibbardiform (Sa)</td>
<td>hibbardiform (Sa)</td>
<td>alate hibbardiform (Sa)</td>
</tr>
<tr>
<td>S_2</td>
<td>digerate</td>
<td>digerate</td>
<td>cypridodiform (Sb)</td>
<td>breviform digrate (Enantiongnathus latus)</td>
<td>breviform digrate (Cypridodella cf. delictula)</td>
<td>Pseudofurnishius murcianus (Sb)</td>
<td>breviform digrate (enantiongnathiform) (Sb)</td>
</tr>
<tr>
<td>S_3</td>
<td>digerate</td>
<td>breviform</td>
<td>digrate enantiongnathiform (Sb)</td>
<td>breviform digrate (Enantiongnathus latus)</td>
<td>breviform digrate (enantiongnathiform) (Sb)</td>
<td>Pseudofurnishius murcianus (Sb)</td>
<td>breviform digrate (enantiongnathiform) (Sb)</td>
</tr>
<tr>
<td>S_4</td>
<td>breviform</td>
<td>breviform</td>
<td>digrate enantiongnathiform (Sb)</td>
<td>breviform digrate (Enantiongnathus latus)</td>
<td>breviform digrate (enantiongnathiform) (Sb)</td>
<td>Pseudofurnishius murcianus (Sb)</td>
<td>breviform digrate (enantiongnathiform) (Sb)</td>
</tr>
<tr>
<td>M</td>
<td>breviform</td>
<td>breviform</td>
<td>digrate enantiongnathiform (M)</td>
<td>breviform digrate (Cypridodella cf. conflexa)</td>
<td>breviform digrate (Cypridodella cf. conflexa)</td>
<td>Pseudofurnishius murcianus (M)</td>
<td>breviform digrate (enantiongnathiform) (M)</td>
</tr>
</tbody>
</table>

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.
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 pisolith) 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-Permain 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). Indeed, within the cluster, the P1 elements pair is most distant from the ramiform S and M elements; the P2 element pair is intermediate. In order to interpret the multielement taxonomy, nomenclature follows the anatomical notation of \( S_0 \)–\( P_n \) (\( S_0 \), M, and \( P_1 \)) 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...
innermost within the cluster, and five pairs of S1–4 and M elements occur in a disrupted nested arrangement. The S1 elements are embraced by inner lateral processes of the S2 elements, and their cusps are aligned parallel with the anterior-posterior processes of the S3–4 elements.

Other clusters preserve subsets of the apparatus, such as disarticulated cluster aggregations, individual pairs of associated P1 and P2 elements, and articulated S-M combinations. Of the disarticulated clusters, four clusters fuse a P1 element and S elements (Fig. 2A, B, E, F), one cluster preserves a P2 element and an S1 element together (Fig. 2I), one cluster associates a P1, P2 and an S1 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 P1 pairs and one P2 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 S0 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 S3–4 elements are broken. S1–4 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), S3 and S4 elements exhibit similar morphology and bracket the position of

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.
the S2 elements; S1 elements are embraced abaxially by the inner lateral processes of the S2 elements (Fig. 5G). M elements lie at the most outer parts of the clusters, overlap the S4 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 juxta-position, 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.

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

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Fig. 3. Articulated conodont clusters of P1 and P2 elements from the Dawazi section and Shangshikan section, as SEM photographs. P1 elements (A–G) and P2 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) (P1 elements) from bed 32 in the Shangshikan section; figure (B1) and (I1) shows microwear on the distal denticles.
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. 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–P₂, S-M elements and one unpaired S₀ element).
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 elements), pair of S1 (cypridoellidian elements), pair of S2 (enantioellidian elements), S3–4 (hindeoellidian elements), and M (cypridoellidian elements).

Fig. 5.
Articulated conodont clusters from the Dawazi section, as SEM photographs (a) and interpretive drawings (b). Conodont clusters are from bed 25 (J–L), bed 27 (K), and bed 34 (M) respectively. They have the same pattern of the juxtaposition in the clusters of J–M, single example of S0 (hibbardellan elements), pairs of S1 (cypridodellan elements), pairs of S2 (enantiognathiform elements), S3–4 (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 $S_0$ (hibbardellan elements), pairs of $S_1$ (cypridodellan elements), $S_2$ (enantiognathiform elements), $S_{3,4}$ (hindeodellan elements) and $M$ (cypridodellan elements).
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 (hibbardenellae) S0, breviform digyrate (cypridoddellae) S1, breviform digyrate (enantiognathiform) S2, bipennate (hindeodellan) S3 and S4, breviform digyrate (cypridoddellae) M, carminate (nicoraellae) P1, and carminate to segminate (xaniognathiform) P2. 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 cypridoddellae elements as Sb1, respectively, which usually equates to S1–2 positional homologies, respectively. Here we demonstrate that the positional homologies are reversed. The long process of the S0–4 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 (S5, 1M, 2P) whose morphological description and positions in the apparatus are as follows:

S0 (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 hibbardenellae elements occupied an S0 position in the apparatus of Nicoraella (Figs. 4, 5A–D, F and 6K).

S1 (Sb1) elements: Breviform digyrate cypridoddellae 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 S0 element evidences their S1 positional homology (Figs. 4, 5A–D, F, G). By inference, positional homologies can be established in clusters of No-vispathodus (Goudemand et al., 2011, 2012). Previously, many researchers interpreted these morphotypes as S2 (Sb2) 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 S1 position.

S2 (Sb2) 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 ‘enantiognathiiform’ elements are recognized as having occupied an S2 position based on their location abaxial of the elements occupying the S1 position. Discrete elements of the form taxonomy genus ‘Enantiognathus’ were discriminated previously as Sb3 and, therefore, might be considered to have occupied an S1 position (Orchard and Rieber, 1999; Koike, 2004; Orchard, 2005; Sun et al., 2009). Here we demonstrate that these ‘Enantiognathus latus’ element morphotypes occupied an S2 position (Figs. 4, 5A–D, F–H, 6I–M and 7N, P, R).

S3, S4 (Sc1, c2) element: Bipennate with a short recurved anterior process and a long posterior process. The S3 and S4 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 ‘cypridoddellae’ 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 S4 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 S1 elements lies in the orientation of the cusp relative to the lateral processes: in M elements the...
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 S1 elements the cusp is often twisted in such a way that it ends up being oriented along the largest process (outside lateral process).

**P2 (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).

**P1 (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 S1 and S2 positions, to S2 and S1, respectively, based on the primary positional information provided by the fused clusters (Fig. 4; Goudemand et al., 2012). The reconstructed apparatus is comprised of 15 elements, including a single bilaterally symmetrical element (S0) and seven paired elements (S1–4, M, P1–2). Apparatuses within Superfamily Gondolellioidea exhibit high degrees of similarity in terms of morphology and positions of the S and M elements: S0 elements are traditional alate elements with two antero-lateral processes; M elements are breviform digyrate elements with a very long and a short process; S3–4 elements are usually bipennate but there are exceptions, including the tertiopdate S3 elements in Mullerinae. Breviform digyrate elements (enantioigathiform) were interpreted as characteristic S1 elements, including two lateral processes; and S2 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 S1–2 positions in multielement reconstructions in other species of Gondolellioidea, 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 (Goudemand et al., 2012) and Neogondolella (Orchard and Rieber, 1999; Orchard, 2005). S3 and S4 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 S2 element, and a slightly curving aboral margin to the posterior process of the S0 element.

### 6. Comparison with other gondollellid apparatuses

The reconstructed apparatus of Nicoraella kockeli exhibits great similarity to that of the Early Triassic Novispathodus (Goudemand et al.,
2011, 2012). Earlier researchers added an alate hibbardellan S0 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 Gondolellidae.

Previously, multielement reconstructions of the apparatus of _Nicoraella_ have been based on materials of different species of the genus from the Carnian ‘Railb’ 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_? _badaensis_ from the Late Triassic of Hungary and the Alps is composed of modified hindeolland (metaplanodiodiform), modified prioniodiform (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_(_S_)2, hindeolland _S_(_M_)1–_4_ (_S_(_M_)3–_4_), and the breviform digrate _‘cypridodellan’_ _M_ elements. As shown in Table 1, the morphology of _elements occupying the S–M division is relatively stable among Triassic gondolellids, in that the symmetrical alate hibbardellan element occupies the _S_1 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_3 elements. Many previous researchers have interpreted the _S_(_S_)3 ‘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. As in other _Nicoraella_ from discrete elements and articulated clusters suggests that the apparatus of _Nicoraella_ was a typical 15-element apparatus, including _S-M_ elements (single _S_0, paired _S_1–_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_ and _S_2 positions, respectively (versing previous inferences). This new apparatus represents a new template for the superfamily Gondolellidae, 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.

Acknowledgments

We thank Dr. Chunbo Yan for his enormous help in experiments, and Dr. Mark Purnell for his insightful suggestions. This work was supported by the Chinese Geological Survey projects (Grant Nos. DD20160020 and 1212010612011), the National Natural Science Foundation of China (Grant Nos. 41502013, 41772022, 4161134047, 41572091, 41530104, and 41240016), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No. 133106), and a Sylvester Bradley Award (No. PA-SB201401) from Palaeontological Association (UK). C.M.-P. was partially funded by a Marie Curie FP7-People IEF 2011-299681, and by the Projects GCG14-52662-P and GV/2016/102.

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