Multielement Neogondolella (Conodonta, upper Permian - middle Triassic)

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ABSTRACT – Neogondolella is reconstructed as a multielement conodont genus bearing eight kinds of elements, seven of which are paired, making a total of fifteen elements in all. The Pb element is seminiplanate, the Pb angulate, Sb is alate, Sb1 is breviform digyrate, Sb2 is dolobrate, Sc1 resembles teretipedate, Sc2 is bipennate, and M is breviform digyrate. The Sb and Sc elements commonly occur as separate anterior and posterior parts. This reconstruction is based on abundant collections of disjunct elements and is supported by natural assemblages of Neogondolella from Switzerland. The apparatus remained essentially the same from the Upper Permian through the Middle Triassic, with relatively minor changes in the morphology of some elements regarded as of specific rank. The apparatus of Neogondolella differs from that of other Triassic taxa which are nevertheless united in bearing enantiognathiform Sb1 elements, on which basis they are classed as members of the superfamily Gondolellacea. Apart from the Sb elements, the morphology and apparatus plan of gondolellaceans generally correspond to that of the Ozarkodinida. Within the family Gondolellidae, Gondolella and Neogondolella can be distinguished on multielement grounds.


INTRODUCTION

Triassic conodont apparatuses are relatively poorly known in spite of having been amongst the first to be interpreted in multielement terms (Huckriede, 1958). This is due primarily to the extreme rarity of Triassic natural assemblage templates, but both morphological convergence and process fragility have rendered statistical reconstructions difficult. In this paper, the apparatus of the common and long-ranging conodont Neogondolella is reconstructed. This is accomplished using collections of well preserved and low diversity discrete elements from Permian and Triassic strata of North America and Eurasia. These collections facilitate an understanding of the gross morphology of the frequently broken ramiform elements, which in turn leads to insights into how they were configured in the collapsed apparatuses that are now preserved as Neogondolella natural assemblages in the Middle Triassic of Switzerland (Rieber, 1980; Orchard & Rieber, in prep.).

A common view of Triassic conodonts is that most taxa are closely related variations on a prioniodinide root stock that diverged in the Late Carboniferous as two families, the Gondolellidae and the Ellisionidae (Sweet, 1988, fig. 5.28). The common and stratigraphically useful Triassic elements are almost entirely assigned to the former family, which includes both seximembrate and unimembrate apparatuses according to Sweet (1988, p. 87). Other researchers hold the view that the apparatuses of all gondolellids are multielement, at least during infancy, and essentially the same in composition (e.g. Kozur, 1989a; Hirsch, 1994a). In this paper, Neogondolella and other gondolellids are excluded from the Prioniodinida primarily because their apparatus does not feature a digyrate Pb element but rather an angular element like the ozarkodinides. It is also recognized that there are several different apparatus types represented amongst the taxa presently combined within the Gondolellidae.

A diverse generic nomenclature of gondolellid conodonts has developed based on the morphological features and supposed phyletic relationships of the Pa platform elements. The proposed Neogondolella multielement apparatus, although relatively conservative and long-ranging, differs from that of many other Triassic conodonts and facilitates new ideas on phyletic relationships. Multielement reconstructions support a revised classification, and strengthen biochronological schemes.
The earliest descriptions of Triassic Neogondolella-bearing faunas, at that time referred to Gondolella, were from the Middle Triassic Muschelkalk of Germany (Tatge, 1956). Later, Bender & Stoppel (1965) introduced the name Neogondolella with N. mombergensis Tatge as the type species (Text-fig. 1). Concurrent with her description of N. mombergensis, Tatge (1956) also described the pectiniform element Ozarkodina (=Nicoraella) kockeli and many new ramiform elements, several of them incompletely preserved, as single element- or form-species. These ramiform elements were parts of both the Neogondolella and Nicoraella apparatuses. The Tatge form-species (Text-fig.2) that are regarded as parts of the Neogondolella apparatus are listed below: most of these came from the same stratum and locality. The proposed notation is shown in brackets, with proximal and distal referring to relative position of element parts with respect to the cusp.

Text-fig. 2 - Neogondolella mombergensis (Tatge, 1956). Sketch diagrams of the discrete elements and part-elements named by Tatge and their interpretation as whole element components of the Neogondolella apparatus.
Gondolella mombergensis (Pa)
Ozarkodina tortilis (Pb)
Lonchodina multieri (M, proximal)
Roundya magnidentata (Sa, proximal)
"Angulodus" prioniodelloides (Sa, distal)
Prioniodella decrescens (SB1, distal)
Apatognathus longidentatus (SB1, proximal)
Prioniodella inquisis (SB1, proximal)
"Metalonchodina mediorbis" (SB2, proximal)
Metalonchodina digitoformis (M or SB2, proximal)
"Prioniodina laticentata" (Sc, proximal)
"Prioniodina ctenoides" (Sc, distal)
Metalonchodina cf. bidentata (Gunnel) (SC2, proximal)
Gen. et sp. indet. C (Sc1, proximal)
Gen. et sp. indet. B (Sc1, proximal)

### Previous Multielement Reconstructions

Huckriede (1958, p. 164) listed eight of Tatge's elements (shown above with asterisks) under the "conodonten-"Satz" of Neogondolella navicula, and thereby introduced the notion of a multielement Triassic conodont species. His "apparatus" consisted of the following (with current notation):

Gondolella navicula Huckriede, 1958 (Pa)
Ozarkodina tortilis Tatge, 1956 (Pb)
Lonchodina multieri Tatge, 1956 (M)
Roundya magnidentata Tatge, 1956 (Sa, proximal)
Prioniodella prioniodelloides (Tatge, 1956) (Sa, distal)
Prioniodella decrescens Tatge, 1956 (SB1, part)
Metalonchodina mediorbis Tatge, 1956 (SB2)
Lonchodina latidentata (Tatge, 1956) (Sc, proximal)
Prioniodella clausis Tatge, 1956 (Sc, distal)
Hindeodella triassica Muller, 1956 (Sc)
Apatognathus zieglerteie Diebel, 1956 (SB1)

The platform (Pa) element of Huckriede's species-group, Neogondolella (=Norigondolella) navicula, is now known to be restricted to the Late Triassic (Norian) and has a somewhat different apparatus to that of Middle Triassic N. mombergensis. Hence, Tatge's form-species should not be regarded as parts of N. navicula. Similarly, "Hindeodella triassica", originally described by Muller (1956) from the Smithian of Nevada, and "Apatognathus zieglerteie", originally described by Diebel (1956) in association with Ladinian Budurovignatius mungoensis, are parts of other apparatuses. Neither element is regarded as part of any Neogondolella apparatus.

Huckriede (1958) also illustrated examples of two of Tatge's species, Lonchodina latidentata (op. cit., pl. 10, fig. 32; pl. 11, fig. 42, 47) and Prioniodella decrescens (op. cit., pl. 14, figs. 37, 38), that had bifurcate processes. Neither of Tatge's types showed such morphology, so, in making these and other assignments, Huckriede pointed to the incomplete nature of many of Tatge's elements, a recurrent problem in Triassic multielement taxonomy. This problem was also noted by Kozur & Mostler (1972) who illustrated many Triassic ramiform form-species. These authors recognized that Prioniodella (Angulodus?) prioniodelloides was the posterior process of Hibbardella (Roundya) magnidentata, although they did not discuss the implications of this interpretation (see below). The fragmented nature of many ramiform elements also led Kozur & Mostler (1972) to group together dissimilar elements, such as those they referred to Hindeodella (Metaprioniodus) suecica: their concept embraced both the Sc1 and Sc2 of this paper plus contiguous Sc elements like the holotype of H. suecica, which is not part of a Neogondolella species.

Kozur (1974, 1976) identified the multielement components of Neogondolella, and indeed gondolellids in general, as comprising six form-species. These were (again, with current notation):

<table>
<thead>
<tr>
<th>Species</th>
<th>Platform (Pa)</th>
<th>Ozarkodina tortilis (Pb)</th>
<th>Lonchodina multieri (M)</th>
<th>Roundya magnidentata (Sa)</th>
<th>Prioniodella prioniodelloides (SB1)</th>
<th>Prioniodella decrescens (SB2)</th>
<th>Metalonchodina mediorbis (Sc)</th>
<th>Lonchodina latidentata (Sc)</th>
<th>Hindeodella triassica (Sc)</th>
<th>Apatognathus zieglerteie (SB1)</th>
</tr>
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</table>

Later, Kozur (1989b) used revised genera-based descriptive terms for the apparatus elements of gondolellids but did not provide an explicit notion of homology. Whereas Kozur was clear on his view of the platform (Pa) and ozarkodiniform (Pb) couplet, his cypridodelliform (=prioniodiform) element apparently included both the M and SB2 elements (in the sense of this paper), whilst the Sc elements were regarded as contiguous hindeodelliform elements. This generalized notion of a 6-element gondolellid apparatus has generally persisted in the literature.

### A New Octomembrate Model

Although the interpretation of Neogondolella proposed herein rests on the study of a large number of Permian and Triassic collections, it is those from the Middle Triassic that are particularly important because that is the age of the type species of the genus. Fortunately, the natural assemblages of Neogondolella from Switzerland are also Middle Triassic in age. Hence, the latter can be compared directly to both the North American reconstructions and the type collections of Neogondolella mombergensis from Germany. Disjunct Neogondolella collections from North America include species that are broadly coeval with N. mombergensis. All of these collections contain ramiform elements that compare closely with Tatge's specimens and the same apparatus is clearly represented. This is contrary to the opinion of Budurov & Sudar (1989) who introduced the new genus Pridaeella for "Tethyan-Pacific" platform gondolellids of this age.

The constituent elements of Neogondolella are described fully in the taxonomic part of this paper. For purposes of the following discussion, the diagrammatic
seven symmetrical pairs, former and posterior parts of the Sc (and Sa) elements have been regarded as contiguous.

representation of the new 8-element model in Text-fig. 3 (and Pl. 1) suffices. Of the eight different elements in collections of disjunct elements of Neogondolella, seven of them are sinistral and dextral mirror-image pairs, which makes a total of 15 elements. The ramiform basket of elements are assigned a notation that conforms with that utilized by Purnell & Donoghue (1997, 1998), which reflects relative proximity of the elements to the apparatus midline or axis. Hence the symmetrical and medial Sa element is bordered on both sides by a sequence of Sb1, Sb2, Sc1, and Sc2 elements. The other elements - Pa, Pb, and M - lie outside the former series in relative positions identical to that seen in the ozarkodinides (Purnell & Donoghue, op. cit.), the order in which Neogondolella is included here.

The assignment of particular conodont elements of Neogondolella to a locational notation differs from most previous interpretations, which are compared in Tab. 1. The natural assemblages show convincingly that the enantiognathiform element occupied an Sb1 position. They also show that a grodelliform or similar element occupied an Sb2 position. Interpretations of elements assigned to both the Sa and Sc positions also differ radically from earlier ones. Each of these elements appears to have consisted, at least through most later growth stages, of disjunct (or barely joined) proximal (biologically antero-ventral) and distal (postero-dorsal) parts (Pls. 2, 3). The elements have not been recovered as contiguous elements (except possibly as very small growth stages) although functionally the parts must have been more or less aligned in the apparatus, as shown by the natural assemblages. Were this not the case, the Neogondolella apparatus would consist of 20 elements, and a rather incongruent notation would be required.

### Table 2 - Comparison of the locational notation applied to elements comprising Neogondolella Assemblage 1 (Rieber, 1980; Column A) by von Bitter & Merrill (1998; Column B) and the present authors (Orchard & Rieber, in prep.; Column C).

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
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<tbody>
<tr>
<td>1</td>
<td>Pa</td>
<td>Pa</td>
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<td>2</td>
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<td>10</td>
<td>Sc</td>
<td>Sb1 or Sb2</td>
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<td>Sb1</td>
<td>Sc</td>
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<tr>
<td>17</td>
<td>Sc</td>
<td>Sc</td>
</tr>
<tr>
<td>18</td>
<td>Sc</td>
<td>Sa</td>
</tr>
</tbody>
</table>

### Text-fig. 3 - Neogondolella mombergenis (Tate, 1956). Sketch diagrams of the components of the apparatus.

### Natural Assemblages

Although some Triassic gondolellids have been regarded as platform-only, unimembrate apparatuses, the natural assemblages of Neogondolella in Middle Triassic bituminous shales ("Grenzbittenzonen") on Monte San Giorgio in Switzerland (Rieber, 1980; Orchard & Rieber, in prep.) leave no doubt about the multi-element nature of these particular Middle Triassic species. Two Neogondolella species appear to be represented within the currently available material, the more common being younger examples of the N. constricta group (Pl. 4). The conodont assemblages, although broken by intense compression of the shale layers, are otherwise undisturbed and the present
EXPLANATION OF PLATE 1

Figs. 1-11 - Neogondolella sp. Reconstructed multielement apparatus based on Middle Anisian material from Nevada. Mostly sample HB-105, except figs. 2, 11=HB-165, and fig. 6=HB-111 (see locality registry). All x80. Mostly inner views of 1=GSC 101780, dPa (upper); 2=GSC 101781, sPb; 3=GSC 101782, dM (image reversed); 4=GSC 101783, dSb1; 5=GSC 101784, dSb2; 6=GSC 101785, Sc distal; 7=GSC 101786, sSc2 proximal (image reversed); 8=GSC 101787, dSc1 proximal; 9, 10=GSC 101788, Sa proximal (posterior, antero-lateral); 11=GSC 101789, Sa distal.
disposition of the elements clearly reflects the original but collapsed apparatus structure.

Rieber (1980) employed descriptive generic terms to identify elements within the original published assemblage (hereafter Assemblage 1). He recognized at least six or seven element types, and a minimum of 18 elements in all. This included pairs of platforms, ozarkodiniform, hindeodelliforms, enantiognathi-forms, prioniodiniforms, and prioniodiniforms, as well as undetermined element types and unassigned fragments. No elemental notation or architectural interpretation was attempted on the single specimen but certain anomalous features of the assemblage were noted. For example, the two pairs of hindeodelliforms lacked convincing anterior processes, and in one case the denticulation of an apparent hindeodelliform pointed in the opposite direction to all the other element denticles.

The new interpretation of Assemblage 1 differs from that presented recently by von Bitter & Merrill (1998) as shown in Tab. 2. The most conspicuous difference concerns the identity of the Sb and Sc elements. The elements regarded here as the anterior parts of Sc elements were interpreted as a pair of complete Sb1 elements by von Bitter & Merrill (1998, fig.15) because they lay adjacent to the medial Sa element. This relative position appears true at the anterior end of the apparatus but that is because the true Sb1 elements (the enantiognathiform pair) lie to the posterior of the Sa-Sc anterior ramiform basket (Text-fig. 4). The enantiognathiform pair were referred to the Sb2 position by von Bitter & Merrill (1998). In fact the cusps of both the Sb1 and Sb2 elements lie further to the posterior (and more dorsally) than those of the Sc and Sa elements, which is perhaps a unique feature of the gondolellaceans.

Applying the numbers originally used by Rieber (1980, fig. 1), element fragments 13, 14, 16-18 are here interpreted as anterior parts of the 'hindeo-delliform' Sc elements (5-8). Bar fragments 34 and 35 are here interpreted as the inner lateral process of the dextral Sb1 element which has been flipped back-to-front (explaining the anomaly noted by Rieber, 1980), possibly aided by the collapse of the 'overlying' distal part of the medial Sa element. The equivalent process on the opposed Sb1 element is thought to be represented by fragment 26, which was interpreted as a Sc element by von Bitter & Merrill (1998). New illustrations and detailed analysis of Assemblage 1 are provided by Orchard & Rieber (in prep.).
EXPLANATION OF PLATE 2

Figs. 1-11 - *Neogondolella* Sc1 and Sc2 elements showing details of the process terminations. Note either minimal breakage, indicating narrow process attachment (Figs. 2, 5, 10), or apparently unbroken terminus suggesting functional detachment (Figs. 7, 9). Complete specimens views are x80. Various localities (see locality registry). Inner views of 1, 2 (x320)=GSC 101786, dSc2 proximal (sample HB-105); 3=GSC 101810, dSc2, juvenile with relatively long and contiguous posterior process (sample FH-44); 4, 5 (x300)=GSC 101787, dSc1 proximal (sample HB-105); 6, 7 (x300)=GSC 101807, dSc2 proximal (sample D-12); 8, 9 (x600)=GSC 101811, Sc distal (sample WAP-A6); 10 (x600), 11=GSC 101812, Sc distal (sample HB-185).
SUPRAGENERIC CLASSIFICATION

Previous classifications of *Neogondolella* have varied considerably. Lindstrom (1970) referred the genus to the Gondolellidae, the single constituent family within the superfamily Gondolellacea. This superfamily was retained by the Treatise authors (Clark et al., 1981) who distinguished within it two additional families, the Ellissonidae and the Xaniognathidae. *Neogondolella* was separated from *Gondolella* and placed in the Xaniognathidae. Neither Lindstrom (1970) nor Clark et al. (1981) provided a diagnosis for members of the Gondolellacea, other than to note that the normally multielement apparatus may have been reduced to a unimembrate one in some genera, as was thought to be the case with *Neogondolella*.

Dzik (1976) included the Gondolellidae in a new suborder, the Ozarkodinina. Again, the specific features of the family Gondolellidae were not discussed, but the salient features of the ozarkodinid apparatus were listed (op. cit., p. 398). These features are essentially those of the superfamilies Polygnathacea sensu the Treatise, which Sweet (1988) later subsumed in the Ozarkodinida. In contrast to Dzik, Sweet (1988) included *Neogondolella* and other xaniognathids (recombined with *Gondolella* in the family Gondolellidae) into a new order, the Prioniodinida, an amalgam of the superfamilies Gondolellacea and Hibbardellacea of the Treatise. The Prioniodinida included multielement genera with "highly distinctive extensiform diglyrate elements in the two P positions", and morphologically intergradational elements with generally discrete, peg-like denticles. The gondolellids were regarded as evolving from prioniodinides, like *Idioprioniodus*, in the Late Carboniferous (Sweet, 1988, fig. 5.28). Central to this idea was the interpretation of the enantiognathiform elements as occupants of the Pb position. The natural assemblages from Switzerland show this is not the case.

Dzik (1991, p. 315) maintained both the family Gondolellidae and the superfamily Gondolellacea as part of the order Ozarkodinida. Hirsch (1994b), followed Dzik's suprageneric classification of *Neogondolella*, but in addition he erected two new superfamilies, the Neogondolellinae and Gladigondolellinae. The former, encompassing all Triassic taxa with pectiniform platform elements other than Gladigondolella, was regarded as possessing a generalized apparatus plan curiously combining both ozarkodinide and prioniodinide attributes.

Although they did not regard the enantiognathiform element as the Pb element of *Gondolella*, von Bitter & Merrill (1998, p. 128) nevertheless retained *Gondolella* and its derivatives in the Prioniodinida. This was based on the denticle of the S and M elements and their interpretation of its ancestry in the *Idioprioniodus-Embyognathus* lineage. Triassic gondolellids display a variety of denticles types and this criterion cannot be used to characterize them as prioniodinide. Both the Carboniferous roots of the gondolellids, and the nature of prioniodinide apparatus remain enigmatic. Although the multielement apparatus of *Gondolella* as shown by von Bitter & Merrill (1998) is not the same as that of *Neogondolella* as interpreted here, both are clearly gondolellids.

*Neogondolella* is here regarded as an Ozarkodinide. Within that order, it shows similar complexity to Devonian *Palmatolepis*, as noted by Dzik (1991). Apart from the predominant 'anterior' growth of the platform, the presence of an enantiognathiform Sb1 element serves to distinguish the Gondolellacea. Furthermore, the Gondolellacea are characterized by the gondola-shaped Pa elements. Subfamilial subdivision is unwarranted at this time.

SYSTEMATIC PALEONTOLOGY

Class **Conodonti** Sweet, 1988
Order **Ozarkodinida** Dzik, 1976
Superfamily **Gondolellacea** Lindstrom, 1970
Family **Gondolellidae** Lindstrom, 1970.

Genus **Neogondolella** Bender & Stoppel, 1965

1965 *Neogondolella* Bender & Stoppel, p. 343.

Type species - *Neogondolella mombergensis* Tatge 1956 (see text-fig. 1, this paper).

**Diagnosis** - *Neogondolella* boric an octomembrate apparatus consisting of a total of 15 elements (7 pairs plus symmetrical Sα): Pa is segmental (neogondolelliform), Pb is angulate (xaniognathiform), Sα is alate (hibbardelliform), Sβ1 is breviform diglyrate (enantiognathiform), Sβ2 is dolarate or similar (gondolelliform, cypridolelliform), Sγ1 resembles tertiopodate (cf. hindeodelliform with bifurcate anterior process), Sγ2 is bipennate (cf. hindeodelliform), and

**EXPLANATION OF PLATE 3**

Figs. 1-9  *Neogondolella* elements. Distal parts of Sα elements from Nevada and China showing unbroken process terminations. Complete specimens views are x80. 1, 2 (x400)=GSC 101813, sample HB-165; 3, 4 (x380)=GSC 101814, sample D-6; 5, 6, 7 (x250)=GSC 101800, sample HB-519; 8 (x100), 9=GSC 101789, sample HB-165.
M is breviform digyrate (cypridodelliform). The Sa and Sc elements commonly occur as disjointed anterior and posterior parts.

Description – Pa element: segmented plane with variably upturned, generally unornamented platform ledges developed along part or all the length of the central blade-carina-cusp axis, which is variably elevated and fused. The lower side features a variably developed double pit located near the posterior end of a zone of recessive lamellae that outline a narrow to broad, mediolaterally grooved keel.

Pb element: angular with a long anterior process and a shorter, lower, and variably inturned posterior process bearing denticles that are often smaller.

M element: breviform digyrate (cypridodelliform) element; with two markedly unequal processes, one long and gently arched and a second short and anteriorly flexed. The long, strongly differentiated cusp is inclined perpendicularly to the plane of the processes. The shorter process bears up to 6 small denticles.

Sa element: alate with two down-arched lateral processes that meet at the large medial cusp or a denticle immediately to its anterior to form a right-angle with the posterior process. The latter is short in all available specimens, bearing a maximum of 8 small denticles. As interpreted here, the contiguous posterior process is supplemented by a large 'detached' distal process (the element Angulodus? prioniodelloides Targ sensu formos). This element has denticles that increase in size towards the posterior one third of the process and then decrease in size beyond, where the process is often strongly down turned. The element is commonly sinuous in upper view, particularly in its central part (Plate 3).

Sb1 element: strongly bent, digyrate with one relatively strongly developed 'deep' anterior process and a weakly developed 'thin' and arcuate lateral process that at first is directed toward the anterior and then is laterally flexed distally. The large, high cusp stands at the junction of the two dissimilar but equally long processes and projects posteriorly. The larger process has denticles that form a high convex crest distally, become smaller towards process mid-length (where the element completely breaks), and then become larger towards the cusp. The smaller process is somewhat sinuous, very thin, and fragile; it is rarely preserved intact, commonly breaking close to its junction with the cusp where its orientation changes.

Sb2 element: dolobrate or similar (typically gondelliform) with one long anterior process that bears regular denticulation that may be higher distally. The longest denticle of the element is the apical cusp, which projects posteriorly and has a convex posterior edge. The basal margin of the element is commonly evenly curved but in some species there is a small secondary process bearing a few small denticles. Such elements are gradational to the M element.

Sc1 element: 'tertiopedate' with a bifid anterior process, and a commonly disconnected posterior process. It differs from the Sc2 element only in possessing a bifurcate anterior process: the third "process" is developed on the outer side of the more strongly inturned anterior process about mid-way along its length; the two anterior-most branches that result are subequal in size but are asymmetrically arranged, unlike in the tertiopedate Sa element.

Sc2 element: bipennate and commonly occurring in two parts. The proximal part includes two processes: a down-arched and inwardly turned anterior process, and a short posterior process. The cusp is the largest of the denticles, and is followed anteriorly by several smaller and then higher denticles which form a convex crest declining in size progressively toward the distal end of the process. The preserved posterior process bears up to 6 relatively small denticles on a short bar that is broken or narrowly terminated. A second, distal part of the Sc elements is a long and narrow, regularly denticulate posterior bar that is often broken into smaller fragments.

Comparisons – The apparatus described herein is recognized in many, but not all taxa currently grouped as gondolellids. The multielement configuration of Gondolella has recently been summarized by von Bitter & Merril (1998). Although these authors regarded the Neogondolella natural assemblage as a template for Gondolella, the morphology of several individual elements of Neogondolella as described herein appears to differ sufficiently to distinguish the two genera. For example, the M element of Gondolella has a strongly expanded inner basal cavity and keel; the Sa element has no distal part like that of Neogondolella; there is no bifurcate Sc element; and the similarity between the Pb and Sc elements in Gondolella is not seen in the younger genus. Therefore, Triassic species should no longer be assigned to Gondolella.

The apparatus of Mesogondolella Kozur is not fully described, but it apparently also lacks a bifurcate Sc element. Kozur (1989b, p. 428, pl. 3, figs. 3, 5) noted that the cypridodelliform elements (apparently including both M and Sb2) have a costa along the length of the cusp, as in Gondolella M elements; this feature is also seen in the Sb2 elements of some Neogondolella species. The V-shaped basal configuration of Mesogondolella appears to provide a reliable distinction from Neogondolella.

The apparatus of Middle Permian Jinogondolella is essentially the same as that of Neogondolella, although most of the Pa elements of the former have distinctive platform ornament.

There are no significant differences between the apparatus of Neogondolella and Late Permian-basal Triassic species assigned to Clarkina (Pl. 5). A primary feature cited (Kozur, 1989b, p. 428-9) as diagnostic of Clarkina - the presence of a free blade in the Pa element - is not characteristic of the younger species assigned to
that genus (e.g. Orchard & Krystyn, 1998), but is seen in some species of *Neogondolella*. These two genera have mainly been distinguished on the basis of stratigraphic separation, i.e. *Clarkina* allegedly became extinct in the basal Triassic whereas *Neogondolella* is believed to have evolved from *Neospathodus* in the Middle Triassic (see below). *Neogondolella*-like platform species occurring within the higher Scythian have been referred to other form-genera, namely *Scythogondolella* Kozur, *Kazarella* Budurov & Sudar (=*Pseudogondolella*, =*Chengyuania*), *Chiosella* Kozur, and *Paragondolella* Mosher. The apparatus of these genera await description, an exercise be-
The apparatus of Gladigondolella is quite different from Neogondolella, and the genus should be assigned to a separate family of the Gondolellacea. All elements have markedly discrete denticles, and the Pa, Sb1 and M elements all differ from those of Neogondolella. Revised classification is also required for polyphyletic "Neospathodus"; and Middle-Upper Norian Cypridodella (=Epigondolella partim, Mockina), which contain contiguous and non-bifurcate, bipennate Sc elements and alate Sa elements. Lower Norian Epigondolella, as typified by E. triangularis, has a similar apparatus to Neogondolella but apparently lacks bifurcate Sc2 elements.

The distinction between Neogondolella and other Middle and Late Triassic multielement gondolellids is also in need of resolution. The re-emergence of neogondolelliform-bearing taxa in the Norian may have its roots in species presently assigned to Metapolygnathus (Orchard, 1991a). The genus Norigondolella Kozur has been introduced for these species, which have a Pb element with a distinctive down-arched posterior process, and an M element with a uniquely broad cusp.

Beyond the scope of the present paper. For now, it can be stated that some (including Neospathodus) are different from Neogondolella, whereas others, like Clarkina, are regarded as synonyms.

The explanation of Plate 5

**Fig. 1-11** - *Neogondolella ex gr. subcarinata* Sweet 1973. Reconstructed multielement apparatus based on material from the upper Changshingian (sample D-12) at Meishan, China. All are x80. Mostly inner views of 1=GSC 101801, dPa, (upper); 2=GSC 101802, dPb; 3=GSC 101803, dM; 4=GSC 101804, sSb2; 5=GSC 101805, sSb1; 6, 7=GSC 101806, Sa distal (lateral, upper); 8=GSC 101807, dSc2; 9=GSC 101808, sSc; 10, 11=GSC 101809, Sa (anterior, antero-lateral).
**Remarks** - A particularly distinctive feature of the *Neogondolella* apparatus is the frequent occurrence of Sa and Sc elements in two parts. This phenomenon may be more common in larger specimens, but in the available material there are no completely contiguous elements of any size. This is not the same phenomenon as described by Donoghue (1998) whereby discrete centres of early growth stages coalesce as they enlarge. Rather, the elements may either start as single entities but become disconnected as they grow, or separate parts may have existed from an early growth stage. The process termini of Sc and Sa elements often appear complete (Pls. 2, 3) but this may result from subsequent overgrowth, such as that which occurs when damaged denticles are repaired. Well preserved 'posterior processes' of the Sa elements show no breakage and must have been growing as discrete elements, at least prior to death. The effect of having separate anterior and posterior element parts may have been to impart greater flexibility to the apparatus, and perhaps some advantage to this pelagic genus.

The relative position of the Sc1 and Sc2 elements is uncertain. Although Orchard (1998) assumed a 'better fit' would have occurred with the bifurcate element on the outer side, new data from the natural assemblages suggest that the anterior end of the teriopedia elements probably occupied a position adjacent to the Sa element (Orchard & Rieber, in prep.).

The position of the Sb1 and Sb2 elements differs from the Sa and Sc elements in that their apical cusps are situated in a more posterior position. Similarly, the inner lateral processes of the Sb1 pair and the posterior process of the Sa element form a third focal point in a relatively ventral position within the apparatus (Orchard & Rieber, in prep.). These multiple focal points represent an atypical condition for ozarkodinid apparatuses, although the apparatus of some Devonian *Pleurolopes* have been similar. As described, the apparatus plan of *Neogondolella* is regarded as typical of gondolellaceans.

The Sa element of *Neogondolella* shows some variation through the range of the genus (Orchard & Rieber, 1996). All late Paleozoic species and most that are Middle Anisian or older have an Sa element in which the two antero-lateral processes meet at the cusp (Pls. 1, 5), whereas in younger species the processes generally meet at a denticle anterior of the cusp (Pl. 4). Both Tatge (1956) and Huckriede (1958) included both variants of Sa element in *Roundia magnidentata*, although Tatge's holotype was of the latter variety. North American collections of *Neogondolella* from the Upper Anisian also contain both varieties of this Sa element. The difference in Sa elements, which formed a basis of the distinction between *Xaniognathus* and *Cypriodella sensu* Sweet (1988), is here regarded as specific variability in mid Triassic species, including *Neogondolella monobergensis*.

**Origins of Neogondolella** - In the case of *Neogondolella sensu stricto*, it has been argued that the origin of its type species, *N. monobergensis*, lies in the basal Middle Triassic *Chiosella timoresensis*, which itself is thought to have evolved from a species presently assigned to *Neopathodus* (Bender, 1970; Kozur, 1989a). Older examples of elements formerly assigned to *Neogondolella* have therefore been referred to separate genera such as *Clarkina*, *Paragondolella* and others noted above. However, typical *Neogondolella* appears prior to *Chiosella*. Furthermore, Spathian *Neopathodus* has a different apparatus to both *Neogondolella* and *Chiosella*. The ancestors of *Neogondolella* are therefore regarded as lying within Permian complex presently assigned to *Neogondolella* and *Jinogondolella*.

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**APPENDIX 1**

**Locality Registry**

- Sample HB-105 = GSC loc. C-176331; Taylor Zone, M. Anisian, Favret Canyon, Nevada
- Sample HB-111 = GSC loc. C-176333; Shoshonemis Zone, M. Anisian, as 105.
- Sample HB-165 = GSC loc. C-176342; as 105.
- Sample HB-185 = GSC loc. C-176343; as 105.
- Sample HB-519 = GSC loc. C-201581; Occidentalis Zone, U. Anisian, Searle Hill, Nevada.
- Sample FH-44 = GSC loc. C-300225; Meekli Zone, U. Anisian, fossil Hill, Nevada.
- Sample FH-50 = GSC loc. C-300229; Occidentalis Zone, as 44.
- Sample D-6 = GSC loc. C-158616; middle Changshingian, Meishan, China.
- Sample D-12 = GSC loc. C-158625; upper Changshingian, Meishan, China.
- Sample WAP-A6 = GSC loc. C-303533; Ladi, Wapiti Lake, B.C.

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