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**Recovery brachiopod associations from the lower Silurian of
South China and their paleoecological implications**

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Complete List of Authors:	HUANG, Bing; Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Zhan, Renbin; Nanjing Institute of Geology and Palaeontology Wang, Guangxu; Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences
Keyword:	Recovery, brachiopod, South China, paleoecology, Network Analysis

1 Recovery brachiopod associations from the lower Silurian of South China and their
2 paleoecological implications

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4 HUANG Bing, ZHAN Renbin and WANG Guangxu

5

6 Affiliation and address for all authors: State Key Laboratory of Palaeobiology and
7 Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of
8 Sciences, 39 East Beijing Road, Nanjing 210008, China.

9

10 Corresponding author: Bing HUANG (e-mail: bhuang@nigpas.ac.cn; Tel:
11 +862583282189).

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Abstract: A recovery brachiopod fauna occurs in the lower Niuchang Formation (upper Rhuddanian–lower Aeronian, Llandovery) of the Xinglongchang section, Meitan County, northern Guizhou Province, South China. Nine collections were made at the section, all of which are dominated by brachiopods, and three associations are recognized here and their paleoecology is discussed. Paleoenvironmental analysis shows a shallowing upward trend for the lower Niuchang Formation although a global transgression was happening at that time. The balance between the global transgression and the regional Qianzhong Uplift guaranteed a stable environment for the formation of the Niuchang Formation and the recovery of brachiopods in South China after the end-Ordovician mass extinction. In addition to the traditional methods of PCA and CA, a relatively new technique to paleontology, “Network Analysis” (NA), is applied successfully in this study. It is suggested that Network Analysis could be used as one of the supporting methods in investigating brachiopod paleoecology.

Keywords: Recovery, brachiopod, South China, paleoecology, Network Analysis.

Introduction

Following the end-Ordovician mass extinction, the interval of the latest Ordovician to the earliest Silurian was marked by a widespread transgression (Sheehan 1973, 2001; Brenchley et al. 1994, 2003; Harper and Rong 1995). The earliest Silurian brachiopod fauna has been documented from a number of regions (see Cocks and Rong 2008; Rong and Cocks 2014 for review). However, with rare

35 exceptions (e.g. Rong et al. 2013), the precise age of most of those assemblages is not
36 sure. Recently, we reported a *Dicoelosia* (Brachiopoda) species in the benthic shelly
37 assemblages of the lower Niuchang Formation of South China (Huang et al. 2013).
38 Constrained by graptolite data, the associated shelly fauna was assigned to the late
39 Rhuddanian (early Llandovery), which belongs to the recovery interval after the
40 end-Ordovician mass extinction.

41 From the rocks immediately above the *Dicoelosia* horizon but still in the lower
42 Niuchang Formation (Huang et al. 2013), more collections have been made
43 intensively. Here, we will analyze the taxonomic composition of the brachiopod fauna
44 from the entire section, and conduct a paleoecological analysis, including
45 differentiating brachiopod-dominated associations and discussing their paleoecology.
46 Under the general background of global transgression, the environmental settings of
47 the brachiopod fauna from the Niuchang Formation will be investigated taking the
48 regional tectonic activity into account.

49 A method relatively new to paleoecological study, Network Analysis (NA), is
50 applied for the first time together with Principal Component Analysis (PCA) and
51 Cluster Analysis (CA). Concerning the advantages and disadvantages of PCA and CA,
52 we suggest that the traditional numerical methods like PCA and CA should be
53 complemented by NA in deriving the most comprehensive paleoecological
54 information.

55

56 **Material**

57 The material was collected from the lower Niuchang Formation at
58 Xinglongchang section, 1 km southeast of Xinglong Village, southeast of Meitan
59 County Town, northern Guizhou, South China (GPS: 27°42'24.6"N, 107°33'02.0"E)
60 (Fig. 1). Sedimentologically the Niuchang Formation belongs to the nearshore,
61 shallower-water, clastic facies (Rong and Zhan 2004). The rocks of this formation are
62 characterized by brownish-yellow silty mudstone or grey mudstone that includes
63 several fossil groups, such as brachiopods, trilobites, and a few bryozoans and
64 graptolites.

65 For the age of the brachiopod fauna, the lower part of the section (AGI 521–522)
66 is suggested of the late Rhuddanian age (Huang et al. 2013). AGI 524 is about 1 m
67 above AGI 522, and there is no lithological change from AGI 522 to AGI 532 (Fig. 2).
68 Thus, the age of the brachiopods at this entire section may be proposed as late
69 Rhuddanian to the earliest Aeronian, early Silurian.

70 A preliminary study on the brachiopods (from 9 collections: AGI 521–522,
71 524–527 and 530–532) indicates the presence of 6 major groups of brachiopods,
72 including orthids, strophomenids, rhynchonellids, atrypids, athyridids, and spiriferids,
73 represented by 14 genera, amongst which *Eostropheodonta*, *Katastrophomena*,
74 *Levenea*, *Dicoelosia*, *Thulatrypa* and *Eospirifer* are abundant, and *Aegiria*, *Leptellina*
75 (*Merciella*), *Fardenia*, *Chrustenopora*?, *Epitomyonia*, *Zygospiraella*, *Eospirigerina*
76 and *Whitfieldella* are less common. Orthids and strophomenids are predominant in
77 both abundance and generic diversity. The fossiliferous beds of the Xinglongchang
78 section can be roughly divided into three parts. The brachiopods of the lower part

79 have already been published (Huang et al. 2013), and the representative species
80 occurring in the upper part of the section are shown in Figure 3.

81 After identifying specimens bed by bed, we compile a range chart for the
82 brachiopod genera from the lower Niuchang Formation (Fig. 2). From the diagram, a
83 trend of diversity decrease and a variation of brachiopod composition can be
84 recognized. Here, we will analyze the binary data of taxonomic composition (see
85 Table A1) for the nine collections.

86

87 **Methods**

88 To investigate the paleoecology of the brachiopods from the lower Niuchang
89 Formation at the Xinglongchang section, differentiating brachiopod-dominated
90 associations is a key step. Traditionally, statistical methods, such as PCA and CA are
91 used (e.g. Rong and Zhan 2006) to recognize associations or even communities, and
92 which will also be adopted in our study using the software PAST (version 3.01,
93 Hammer et al. 2001). However, information obtained from these methods has some
94 limitation.

95 A new method, called “Network Analysis” (NA), can provide a network diagram,
96 by which more information about the structure of the dataset is shown. The study of
97 network systems has a long history, but it has experienced a particular surge of
98 interest in the past decade (Newman 2006), mainly due to the fact that many systems
99 of scientific interest can be represented as networks—sets of nodes or vertices joined
100 in pairs by lines or edges. Recently, NA has often been used in biogeographic studies

101 (e.g. Sidor et al. 2013). For biogeographic studies, NA can provide detailed insight
102 into the underlying structure of the biogeographic assemblages, and the network
103 diagrams visualize the similarities and differences between faunas at various localities
104 (Vilhena and Antonelli 2015). Similarly, the network diagram can visualize the
105 connection between different collections within a certain area (or region), through
106 which some unique associations or even communities could be differentiated. Here,
107 for the first time, we apply this method to paleoecological study, in order to visualize
108 the relationships among different brachiopod associations. Instead of species-locality
109 data used in biogeographic studies, a genus-collection dataset is produced for this
110 study. The connectivity between two collection nodes is established through the taxa
111 they share, which are inherently a bipartite network. Therefore the bipartite network
112 method incorporates both collection data and the presence-absence information of
113 different taxa, and aims to minimize information loss.

114 The advantages of using NA compared to such traditional methods as PCA and
115 CA can be summarized as: 1) PCA and CA cannot detect the relationship between two
116 collections which apparently do not share common taxa. Compared with direct
117 connection between two data columns always measured by the similarity index (e.g.
118 CA), NA can use the data of collection-taxon, and takes into account the indirect
119 connections between collections (see Vilhena and Antonelli 2015, fig. 1 for detail). 2)
120 It is difficult to investigate the connection between collection and taxa via the results
121 from CA or PCA, whereas the network diagram from NA can show how a collection
122 links to others via their common taxa. 3) Last but not least, the network method also

calculates the connectivity, clustering and range size of data, and detects the community structure of the fauna investigated (Fortunato 2010). Through various functions NA could provide, more information from the data can be revealed by NA than the traditional methods. The advantages of this new method will be shown in the results of the study. However, the disadvantages of this method are also apparent, such as the connectivity between two indirectly linked nodes should be treated as an underlying relation rather than a real connection. Without other information, misinterpretation of the connections between different collections could cause an imprecise or even incorrect conclusion.

There are several free software for performing network analysis. Gephi (v0.8.2; www.gephi.org) is used in this study to visualize the bipartite genus-collection networks. The following visualization settings were used: Force Atlas 2, number of threads 2, edge weight influence 1.0, scaling 10.0, gravity 1.0, tolerance 0.1, and approximation 1.2. Average Degree of the network was calculated and out degree was used to detect the size and gray scale of the collection nodes.

Brachiopod associations and their environmental settings

Based on binary data of the collections (see Appendix), PCA was performed firstly and three brachiopod-dominated associations were recognized (Fig. 4A). In order to investigate the relationship between collections in detail, we conducted CA (cluster analysis) using four similarity indices: Jaccard, Dice, Ochiai and Raup-Crick. Considering the consistency of the results derived from these indices, the dendrogram

145 from Raup-Crick is shown here (Fig. 4B). By the bipartite network analysis, the
146 diagram generated by the software Gephi (Fig. 5) supports the results from PCA and
147 CA.

148 Some phenomena from the bipartite network diagram could be observed. 1)
149 Three associations can be recognized, which are similar to the results of PCA and CA.
150 2) The taxonomic information of each collection is shown. 3) The connection among
151 collections based on their common taxa is displayed. 4) The diversity of each
152 collection is visualized by the size and gray scale of the collection nodes through the
153 “out degree”, which is represented by the number of edges of each node. Almost all
154 information the study needs from the binary data (Appendix) could be visualized by
155 the NA.

156 From the three methods above, three associations based mainly on faunal
157 composition were clearly recognized: the *Dicoelosia*–*Zygospiraella* association, the
158 *Eostropheodonta*–*Levenea* association and the *Thulatrypa*–*Eospirifer* association,
159 which are described as follows:

160 1) The *Dicoelosia*–*Zygospiraella* association (AGI 521–522)

161 This association is represented by two collections with 196 specimens at AGI 521
162 and AGI 522. Ten genera occur in this association, representing the highest diversity
163 in the section. *Dicoelosia cathaysiensis* accounts for 41.8% of the total and
164 *Zygospiraella* (25.0%) is the second-most abundant. Other invertebrates associated
165 include abundant crinoids, a few bryozoans, trilobites, and rare graptolites.

166 The population of *Dicoelosia cathaysiensis* was assigned to a BA3 environment
167 with several lines of evidences (Huang et al. 2013). After careful consideration for the

168 *Dicoelosia*–*Zygospiraella* association, especially some deep water indicators, such as
169 *Epitomyonia*, *Aegiria*, the bathymetry of the collections AGI 521–522 can now be
170 refined to lower BA3 to BA4.

171 2) The *Eostropheodonta*–*Levenea* association (AGI 524–527, AGI 530)

172 This association includes 5 samples with only 59 specimens in total, mainly due
173 to its low brachiopod diversity leading to a relatively small collection made in the
174 field respectively. However, rarefaction analysis for these collections shows that the
175 sampling is sufficient. Faunal composition of this association is quite different from
176 the older *Dicoelosia*–*Zygospiraella* association. *Eostropheodonta* (50.8%) is the most
177 common genus followed by *Levenea* (33.9%). Graptolites are not found in this
178 association, but other kinds of shelly fossils, such as trilobites, crinoids and bryozoans
179 are present.

180 This association is thought to have lived in a shallower environment owing to
181 several lines of evidences. The sharply decreased brachiopod generic diversity (from
182 10 to 5) could be one of the clues. The lithology in which the brachiopods occur also
183 suggests shallow water habitats, and a turbulent environment evidenced by the
184 disarticulation of the brachiopod valves. Deeper water indicators, such as *Dicoelosia*
185 and *Epitomyonia*, disappeared from the collection AGI 524, indicating a shallow
186 environment corresponding to upper BA3 to BA2 for the *Eostropheodonta*–*Levenea*
187 association.

188 3) The *Thulatrypa*–*Eospirifer* association (AGI 531–532)

189 The *Thulatrypa*–*Eospirifer* association is the most interesting one among all
190 collections. *Thulatrypa* is a newly erected genus (Huang et al. 2016), and several

191 similar and contemporary assemblages are found in other areas of South China. The
192 diversity of the association further decreases compared with its underlying
193 associations, and only 4 brachiopod genera are identified within 151 specimens. The
194 major components of the associations are totally different from the other two
195 associations. *Thulatrypa* (68.2%) becomes the most abundant genus with proportion
196 significantly higher than the others, and *Eospirifer* (18.5%) takes the second position.

197 Compared with the associations preceding it, i.e. the *Eostropheodonta–Levenea*
198 association and the *Dicoelosia–Zygospiraella* association, the *Thulatrypa–Eospirifer*
199 association is closer to the *Eostropheodonta–Levenea* association, mainly according
200 to their low diversity, similar lithology, and absence of deeper water indicators, which
201 suggest a similar shallow water environment for the *Thulatrypa–Eospirifer*
202 association.

203

204 **Paleoecological implications**

205 From the basal to the upper part of the Xinglongchang section, a shallowing
206 upward trend is indicated. The brachiopod associations recognized in this paper are of
207 late Rhuddanian to the earliest Aeronian age when a global transgression was
208 occurring. The shallowing upward trend indicated by these associations in South
209 China apparently conflicted with the global trend. Our study area was
210 paleogeographically located in the northern marginal belt of the Qianzhong (central
211 Guizhou) Old Land, southern Upper Yangtze Region. Although the beginning of the
212 Silurian was marked by a significant and rapid eustatic sea level rise, the Qianzhong
213 Uplift remained active during the Llandovery as a result of the Kwangsian orogeny, a

214 regional tectonic movement corresponding to the Caledonian orogeny in Europe and
215 the Taconic orogeny in North America (e.g. Rong et al. 2011). The global sea level
216 drop caused by the Late Ordovician glaciation together with the Qianzhong Uplift
217 near the end of Ordovician truncated the youngest Ordovician rocks in northern
218 Guizhou, South China. Consequently, a near shore shelly fauna inhabited this area in
219 the southern marginal area of the Upper Yangtze epicontinental sea during the early
220 Llandovery transgression. Xinglongchang was located very close to the
221 paleoshoreline, indicating a relatively shallow water environment.

222 The balance between the global transgression and the Qianzhong Uplift
223 guaranteed a stable regional environment for the development of the
224 brachiopod-dominated associations. The Qianzhong Uplift might play a more
225 important role during the recovery interval after the end-Ordovician mass extinction,
226 causing a shallowing upward trend recorded at this section. This provided a shallow
227 water benthic regime that favored the recovery of brachiopods in South China.

228

229 **Conclusion**

230 The beginning of the Silurian was marked by a significant and rapid eustatic sea
231 level rise, which induced an anoxic event in many regions of the world; however,
232 shelly biotas of this interval have been discovered in a number of regions. In this
233 study, we report a recovery brachiopod fauna from the lower Niuchang Formation
234 (upper Rhuddanian–lower Aeronian, Llandovery) at the Xinglongchang section,
235 Meitan County, northern Guizhou Province, South China. Nine collections with
236 mainly brachiopod fossils are analyzed using different numerical methods, and three
237 brachiopod-dominated associations are recognized. On the basis of paleoecological

analyses for these associations, a shallowing upward trend was deduced for the study area and the southern part of South China. Under the background of eustatic transgression, such environmental setting might be related with the regional tectonic activity, i.e. the Kwangsi orogeny. In particular, the Qianzhong Uplift was progressing during Rhuddanian to early Aeronian, which guaranteed a shallow water “refugium” in the study area after the biotic crisis.

In addition to the traditional numerical methods like PCA and CA, a method relatively new to paleoecology study, “Network Analysis” (NA) is applied in this paper. This method can reveal more detailed information than those traditional methods about the relationship between different collections. But, since some information revealed by NA could be misleading, the results of this method should be used cautiously as one of the supporting evidences in our paleoecological investigation.

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263

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- 326

327 **Figure captions:**

328 Fig. 1. Location map of Xinglongchang section, Meitan County, northern Guizhou,
329 South China, where occurs the brachiopod associations of the recovery interval after
330 the end-Ordovician mass extinction (modified from Huang et al. 2013).

331

332 Fig. 2. Nine collections made in the lower Niuchang Formation (upper Rhuddanian to
333 lowermost Aeronian, Llandovery, lower Silurian) at Xinglongchang section. Range
334 chart showing brachiopod generic composition from AGI 521 to AGI 532.

335

336 Fig. 3. Representative brachiopods from AGI 532 except 1, 7 from AGI 530 and 6
337 from AGI 527. 1–3, 5. *Levenea qianbeiensis* (Rong et al. 1974), ventral (1, 3) and
338 dorsal (2, 5) internal moulds, NIGP 163255–163258. 4, 8, 13. *Thulatrypa orientalis*
339 (Rong et al. 1974), ventral (4, 8) and dorsal (13) internal moulds, NIGP
340 163259–163261. 6, 7. *Eostropheodonta* sp., ventral (6) and dorsal (7) internal moulds,
341 NIGP 163262–163263. 9–12. *Eospirifer* sp., ventral internal moulds (9, 10), dorsal
342 internal mould (11) with its external mould (12), NIGP 163264–163266.

343

344 Fig. 4. The results of Principal Component Analysis (PCA) (A) and Cluster Analysis
345 (CA) (B) for the 9 collections made from the lower Niuchang Formation at
346 Xinglongchang section. Three brachiopod-dominated associations were consistently
347 recognized, with relative water depths proposed shown in the dendrogram (B).

348

349 Fig. 5. The bipartite network diagram of NA supports the results of PCA and CA.

Draft

Fig. 1. Location map of Xinglongchang section, Meitan County, northern Guizhou, South China, where occurs the brachiopod associations of the recovery interval after the end-Ordovician mass extinction (modified from Huang et al. 2013).
76x34mm (300 x 300 DPI)

Fig. 2. Nine collections made in the lower Niuchang Formation (upper Rhuddanian to lowermost Aeronian, Llandovery, lower Silurian) at Xinglongchang section. Range chart showing brachiopod generic composition from AGI 521 to AGI 532.
103x70mm (300 x 300 DPI)

Fig. 3. Representative brachiopods from AGI 532 except 1, 7 from AGI 530 and 6 from AGI 527. 1-3, 5. *Levenea qianbeiensis* (Rong et al., 1974), ventral (1, 3) and dorsal (2, 5) internal moulds, NIGP 163255-163258. 4, 8, 13. *Thulatrypea orientalis* (Rong et al., 1974), ventral (4, 8) and dorsal (13) internal moulds, NIGP 163259-163261. 6, 7. *Eostropheodonta* sp., ventral (6) and dorsal (7) internal moulds, NIGP 163262-163263. 9-12. *Eospirifer* sp., ventral internal moulds (9, 10), dorsal internal mould (11) with its external mould (12), NIGP 163264-163266.
152x136mm (300 x 300 DPI)

Fig. 4. The results of Principal Component Analysis (PCA) (A) and Cluster Analysis (CA) (B) for the 9 collections made from the lower Niuchang Formation at Xinglongchang section. Three brachiopod-dominated associations were consistently recognized, with relative water depths proposed shown in the dendrogram (B).

69x28mm (300 x 300 DPI)

Fig. 5. The bipartite network diagram of NA supports the results of PCA and CA.
89x76mm (300 x 300 DPI)