

Quantitative insights into the community shifts of bivalves following the end-Permian mass extinction: New evidences from Guizhou, southwestern China



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ABSTRACT

The Early Triassic provides crucial insights into the initial biotic recovery following the end-Permian mass extinction, the most severe biotic catastrophe during the Phanerozoic. This study presents the newly compiled bivalve data from the Lower Triassic of the Liuzhi and Bozhou sections. Based on multiple quantitative methods, five distinct ecological associations are recognized. The bivalve associations exhibit high level of spatial homogeneity with temporally equivalent bivalve faunas in taxonomic composition. The rapid diversification of cosmopolitan genus *Clariaia* contributes to the significantly higher species diversity observed in *Clariaia*-dominated associations. Despite the taxonomic changes, the trophic structure is not substantially altered, indicating the high resilience of bivalves to the complex abiotic and biotic conditions with strong capacity of niche filling. The high faunal homogeneity with contemporary communities and relatively simple trophic structure of the post-extinction bivalve associations identified herein are indicative of limited biotic recovery of level-bottom community in the studied sections.

1. Introduction

The end-Permian mass extinction (EPME) witnessed the most severe biodiversity loss in the Phanerozoic with extinction of more than 81 % of marine species (Raup, 1979; Stanley, 2016) and a critical ecological restructuring of marine ecosystems (Sepkoski, 1981; McGhee et al., 2013; Muscente et al., 2018). Taxonomic groups with different niches exhibited variations in the timing and patterns of extinction and recovery (Chen and Benton, 2012; He et al., 2025). Nektonic organisms, e.g., ammonoids (Brayard et al., 2009; Dai and Song, 2020) and conodonts (Orchard, 2007), showed relatively rapid recovery, whereas the benthic communities did not fully rebound until the Middle Triassic (Foster and Sebe, 2017; Song et al., 2018; Guo et al., 2020, 2022; Kelley et al., 2023). The protracted biotic recovery is attributed to the persistent or fluctuating harsh environmental conditions (Hallam, 1991; Sun et al., 2012; Wei et al., 2015; Foster et al., 2018; Saito et al., 2023) and diminished intensity of biotic interactions, such as reduced interspecific competition (Hautmann et al., 2015).

Bivalves, as crucial representatives of the post-extinction level-bottom community, experienced slight to moderate impacts from the EPME in terms of functional diversity and taxonomic diversity (Li, 1995; Wang et al., 2024). Extensive studies on Permian-Triassic bivalves have been conducted on various aspects, e.g., systematics (Gao et al., 2009; Hautmann et al., 2011; Pan et al., 2014; Foster et al., 2019), biostratigraphy (Chen et al., 1979; Chen, 1983; Yin, 1985a; McRoberts, 2010), body size changes (Metcalfe et al., 2011; Foster et al., 2020; Huang et al., 2023), extinction and recovery patterns (Li, 1995; Posenato, 2008a; Huang et al., 2015; Tu et al., 2016; Song et al., 2019). Quantitative paleoecological studies have also been undertaken to some extent in regions such as the western United States and Italy (Hautmann et al., 2013; Hautmann et al., 2015; Foster et al., 2017; Prinotto and Posenato, 2023). South China records exceptionally well-developed Lower Triassic sedimentary successions with abundant bivalve fossils yielded (Yang et al., 1987). However, quantitative studies on the post-extinction bivalve community of South China remain surprisingly limited (Song et al., 2019; Zhao et al., 2022). Newly compiled bivalve data from the

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Liužhi and Bozhou sections in Guizhou are analyzed in this study to provide quantitative insights into taxonomic and ecological changes of bivalve faunas following the EPME.

2. Geological setting and age

The samples investigated in this study were collected from the Bozhou and Liužhi sections in Guizhou Province, South China (Fig. 1A). The Bozhou section is located at about 30 km southwest of Zunyi city (Fig. 1B). The Liužhi section is situated at approximately 15 km southwest of Liužhi county (Fig. 1C). The distance between the two sections is approximately 190 km. During the earliest Triassic, the studied sections are positioned within the transitional zone between shallow-water clastic and carbonate facies, with the uppermost Permian and Lower Triassic successions well exposed.

The succession of the Bozhou section comprises the upper part of the Changhsing Formation (uppermost Permian) and Yelang Formation (Lower Triassic) (Fig. 2). The Changhsing Formation mainly consists of limestone and bioclastic limestone. Abundant brachiopods are yielded from the succession. The brachiopod community is characterized by the dominance of *Fusichonetes*, *Acosarina*, and *Spinomarginifera* (Wu et al., 2021). The conodont zones ranging from *Clarkina changxingensis* to *Hindeodus praeparvus* indicate the Changhsingian (latest Permian) age (Chen et al., 2022). The FAD of *Hindeodus parvus* suggests that the Permian–Triassic boundary should be assigned to the bed 7 (Chen et al.,

2022). The Yelang Formation conformably overlies the Changhsing Formation. The formation can be further subdivided into three distinct members from the basal to the top: the Shabaowan member, consisting of yellowish-green, thin- to medium-bedded mudstone, sandstone, and siltstone; the Yulongshan member, composed of grey, thin- to thick-bedded limestone; and the Juijitan member, characterized by purple-red, thin- to medium-bedded mudstone, sandstone, and siltstone. Fossiliferous beds are commonly found in the Yelang Formation, particularly within the Shabaowan member. The invertebrate fauna exhibits typical paleoecological characteristics of the Early Triassic, such as the proliferation of *Claraia* and *Lingularia*. More precisely, the Early Triassic age, ranging from Griesbachian substage to the early Smithian substages, can be determined based on the conodont and bivalve zones (Chen et al., 2022; this study).

The Liužhi section spans successive strata composed of the upper part of Wangjiazhai Formation (uppermost Permian) and the lower part of Yelang Formation (Lower Triassic) (Fig. 3). The exposed Wangjiazhai Formation at the Liužhi section exhibits a distinct lithological and faunal transition, indicative of a shift from shallow-water carbonate facies to shallow-water clastic facies. The lower part of this formation predominantly consists of siliceous limestone and yields abundant brachiopods characterized by *Peltichia*, *Spinomarginifera*, *Acosarina*, *Oldhamina*, and *Araxathyris*. The brachiopod fauna resembles those documented from carbonate facies in its taxonomic composition and morphological characteristics (Liao, 1980; Wu et al., 2019). In contrast, the upper part

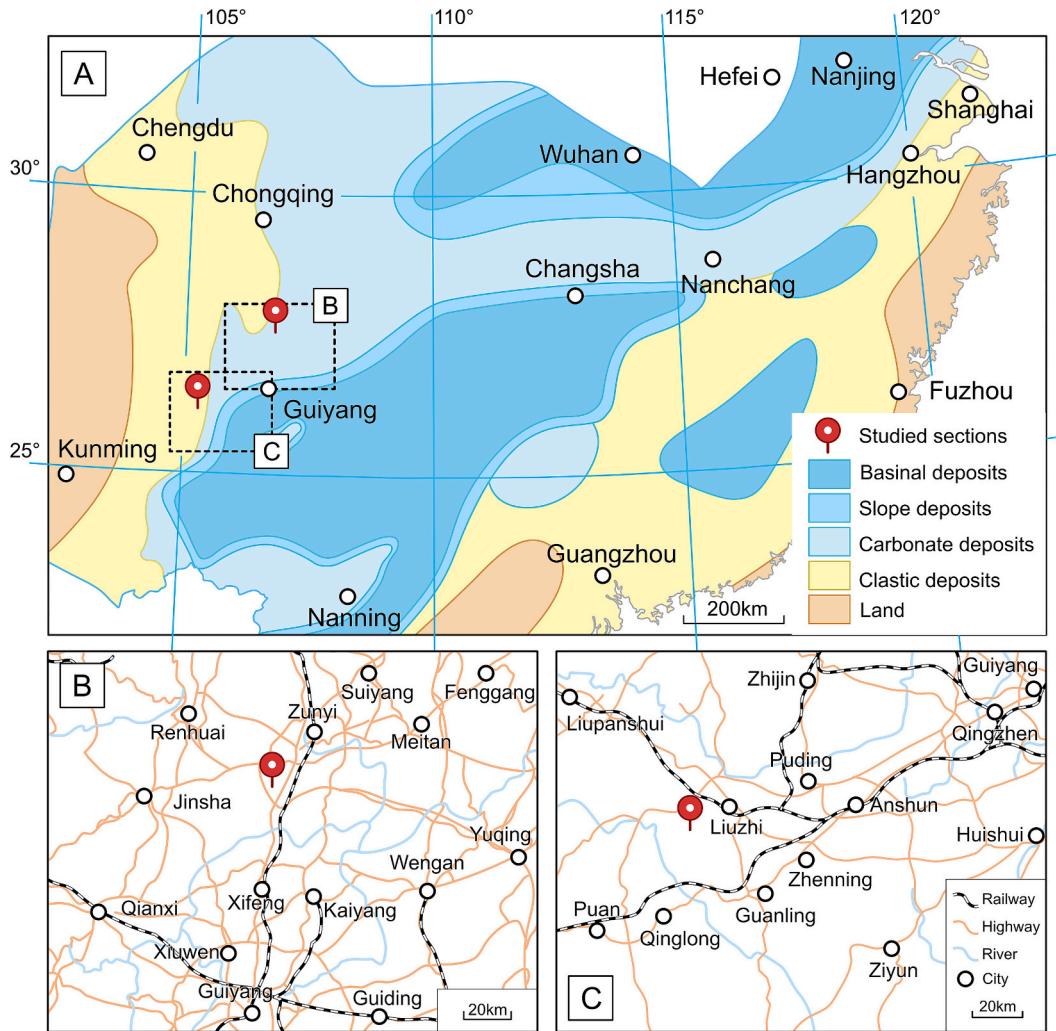


Fig. 1. A. Paleogeography of South China during the Induan (Early Triassic), with the base map modified from Feng et al. (1997). B, C. Locations of Bozhou and Liužhi sections, respectively.

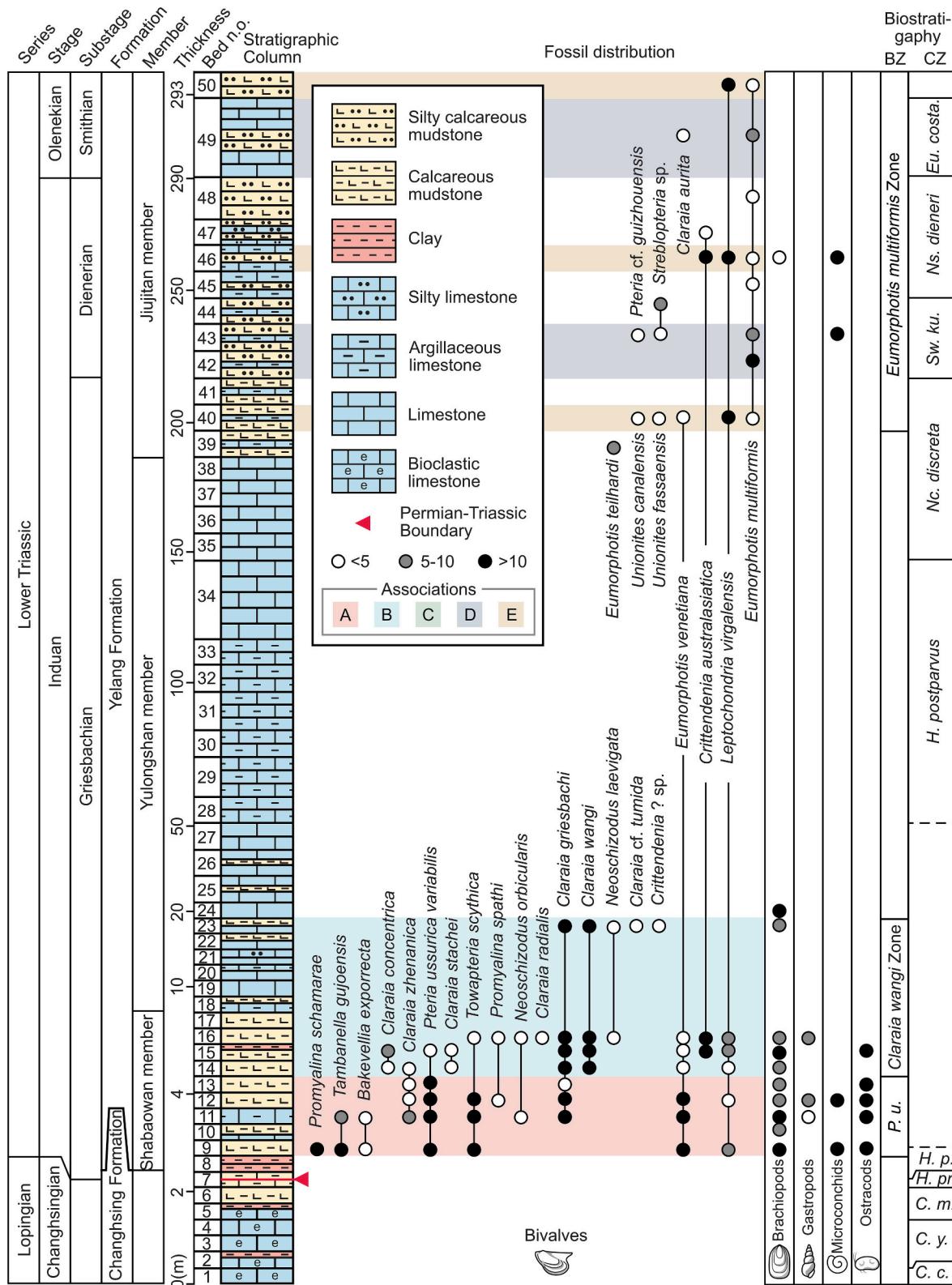


Fig. 2. Lithostratigraphy and fossil distributions of the Bozhou section, showing bivalve associations and biostratigraphic zones. Brachiopod distribution data are partially derived from Wu et al. (2021), and conodont zones follow Chen et al. (2022). Associations A–E correspond to the paleoecological associations identified through cluster analysis: *Pteria ussurica variabilis* association, *Claraia griesbachi*-*Claraia wangii* association, *Claraia aurita* association, *Eumorphotis multiformis* association, and *Leptochondria virgalensis* association, respectively. Abbreviations: BZ, bivalve zones; CZ, Conodont zones; P. u., *Pteria ussurica variabilis*; C. c., *Clarkina changxingensis*; C. y., *Clarkina yini*; C. m., *Clarkina meishanensis*; H. pr., *Hindeodus praeparvus*; H. p., *Hindeodus parvus*; H. postparvus, *Hindeodus postparvus*; Nc. discreta, *Neoclarkina discreta*; Sw. ku., *Sweetospathodus kummeli*; Ns. dieneri, *Neospathodus dieneri*; Eu. costatus, *Eurygnathodus costatus*.

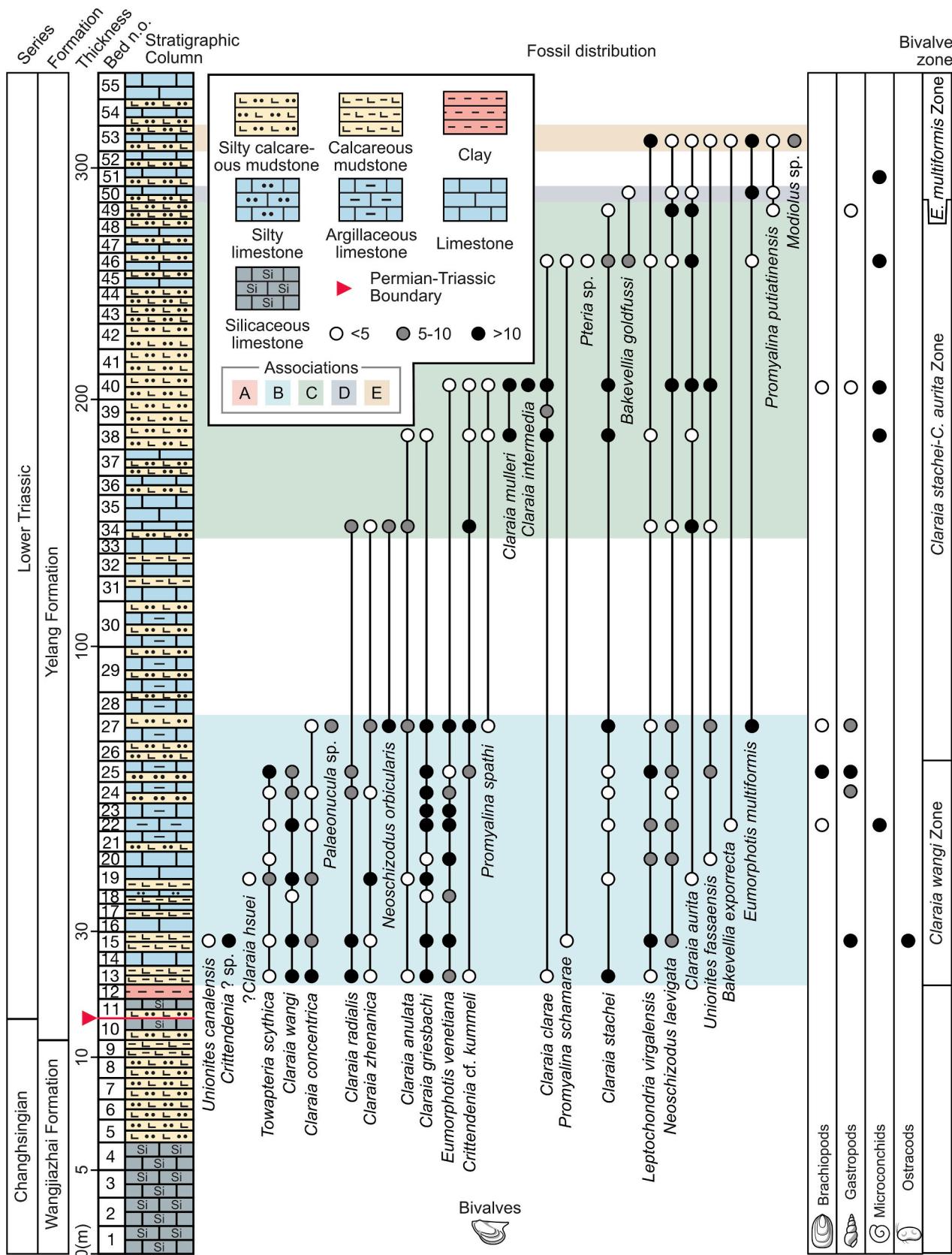


Fig. 3. Lithostratigraphy and fossil distributions of the Liuwei section, showing bivalve associations and biostratigraphy zones. Abbreviations for associations A–E are consistent with Fig. 2.

of this formation is composed of silty and calcareous mudstone. The brachiopods recorded are comparable to those from shallow-water clastic facies in the dominance of *Fusichonetes* and *Neochonetes* (Zhang et al., 2017; Wu et al., 2019). The Yelang Formation conformably overlies the Longtan Formation. Lithologically, the formation is characterized by calcareous and silty mudstone with intercalations of limestone and argillaceous limestone. The Permian-Triassic boundary is tentatively placed at the bed 11 (equivalent to the bed 8 in Wu et al., 2019) based on the lithological correlations with the nearby Zhongzhai section (Zhang et al., 2014; Chen et al., 2022) and the bivalve zones identified herein.

3. Materials and methods

The field work was carried out during the summers of 2022 and 2023. Macrofossils were systematically collected at the Liuzhi and Bozhou sections. All samples were collected from beds without evidence of obvious reworking such as size-sorting, pronounced gradation or extensive abrasion of fossils. Each bed was sampled as consistently as possible to minimize the sampling bias. A standardized sampling protocol, with 15 replicates of approximately $0.5 \times 0.5 \times 0.3 \text{ m}^3$ volume,

was applied to each bed. When quantifying the abundance, specimens with articulated valves were treated as single individuals. Isolated molds and unarticulated valves without counterparts were also counted as independent individuals. Specimens with poor preservation or uncertainty in recognizing counterparts were excluded from the quantification. In this study, a total of 7386 bivalve individuals from 36 samples were comprehensively quantified and taxonomically identified as 37 species belonging to 14 genera. Representative specimens of the identified taxa are presented in Fig. 4.

Besides the taxonomic identification, ecological categorization was implemented to each taxon inferred from the external morphology and previous studies (Stanley, 1972; Ros-Franch et al., 2014). The ecological categories take three aspects into account, i.e., tiering, mobility, and feeding source. The detailed ecological categorization for each taxon can be obtained from the supplementary material.

Multiple quantitative methods were conducted to investigate the community shifts after the EPME. Paleoecological associations were recognized with Q-mode cluster analysis based on the taxonomic abundance data from each bed. Beds with less than ten individuals were excluded here. The raw abundance matrix was logarithmic transformed for data standardization as suggested by Anderson et al. (2006). Then

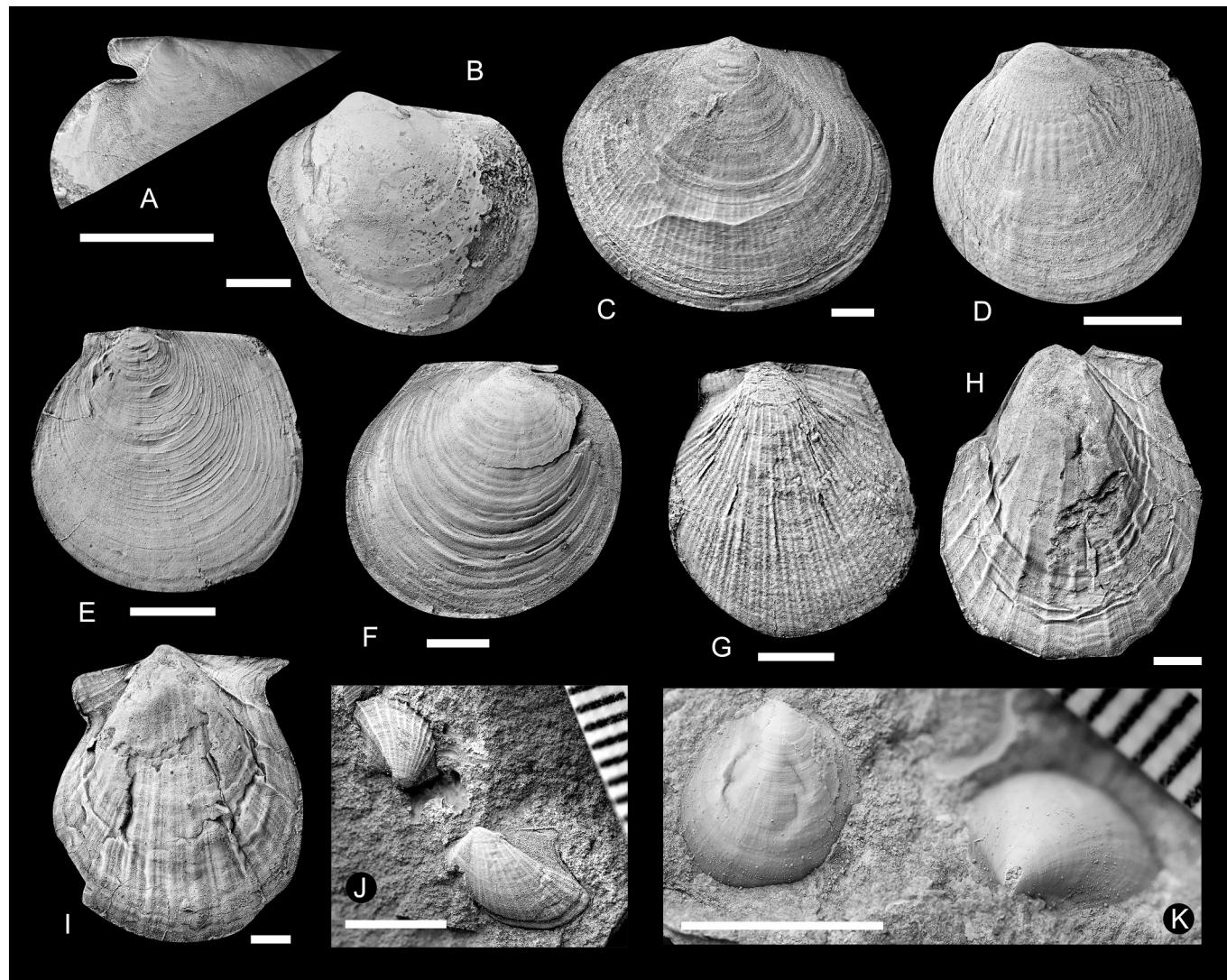


Fig. 4. Bivalve fossils from the Liuzhi and Bozhou sections. **A, B.** *Claraia griesbachi*: A, external mold of right valve, LZ-154762; B, left valve, LZ-154728. **C.** *Claraia stachei*, left valve, LZ-404690. **D.** *Claraia radialis*, left valve, LZ-154719. **E.** *Claraia wangi*, left valve, LZ-154749. **F.** *Claraia aurita*, right valve, LZ-464716. **G.** *Eumorphotis venetiana*, left valve, LZ-124738. **H, I.** *Eumorphotis multiformis*, left valves, LZ-534675 and LZ-534683, respectively. **J.** *Towapteria scythica*, left valves, LZ-254816 and LZ-254817. **K.** *Crittendenia australasiatica*, left valves, LZ-464840 and LZ-464841 (dorsal view). All scale bars represent 5 mm.

the dataset was clustered using UPGMA (unweighted pair group method with arithmetic mean) method with Horn-Morisita dissimilarity index (Wolda, 1981). Non-metric multidimensional scaling (NMDS) ordination was performed to visualize the compositional dissimilarities among associations in low dimensional space. The statistical significance of differences among associations was tested with permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using the same dissimilarity matrix (Anderson, 2007). The diversity characteristics of the associations were assessed based on three metrics, including species richness, Gini-Simpson index (Simpson, 1949), and Shannon entropy (Shannon and Weaver, 1949). Gini-Simpson index and Shannon entropy were transformed to effective numbers of species for unified and intuitive interpretation (Jost, 2006), and herein termed as Gini-Simpson effective diversity (SimED) and Shannon effective diversity (ShED), respectively (cf. Foster et al., 2018). Since the empirical richness was highly dependent on sample size and sampling effort, rarefaction and extrapolation methods based on Hill numbers were applied to compare diversities across associations with different sample

sizes (Chao et al., 2014). Detailed algorithms and methods for estimating corresponding diversity index with rarefaction and extrapolation can be accessed with original literatures (Good, 1953; Chao, 1984, 1987; Chao et al., 2013, 2014).

To explore the co-occurrence patterns of species within and between samples, co-occurrence network analysis was implemented with the presence-absence dataset. Spearman's rank correlation coefficients were calculated to build the network. In this study, co-occurrence relationship between two species was considered as robust and ecologically meaningful when the absolute value of coefficient exceeds 0.4 and shows statistical significance (P -value <0.05) (see details in Steinhauser et al., 2008).

All specimens are housed in the School of Earth Science and Resources, China University of Geosciences (Beijing), China. The paleo-ecological analyses were conducted with vegan (version 2.6, Oksanen et al., 2022) and iNEXT (version 3.0, Hsieh et al., 2016) packages under R (version 4.4.1, R Core Team, 2024). Co-occurrence network is visualized with Gephi (version 0.10.1, Bastian et al., 2009). The R codes used

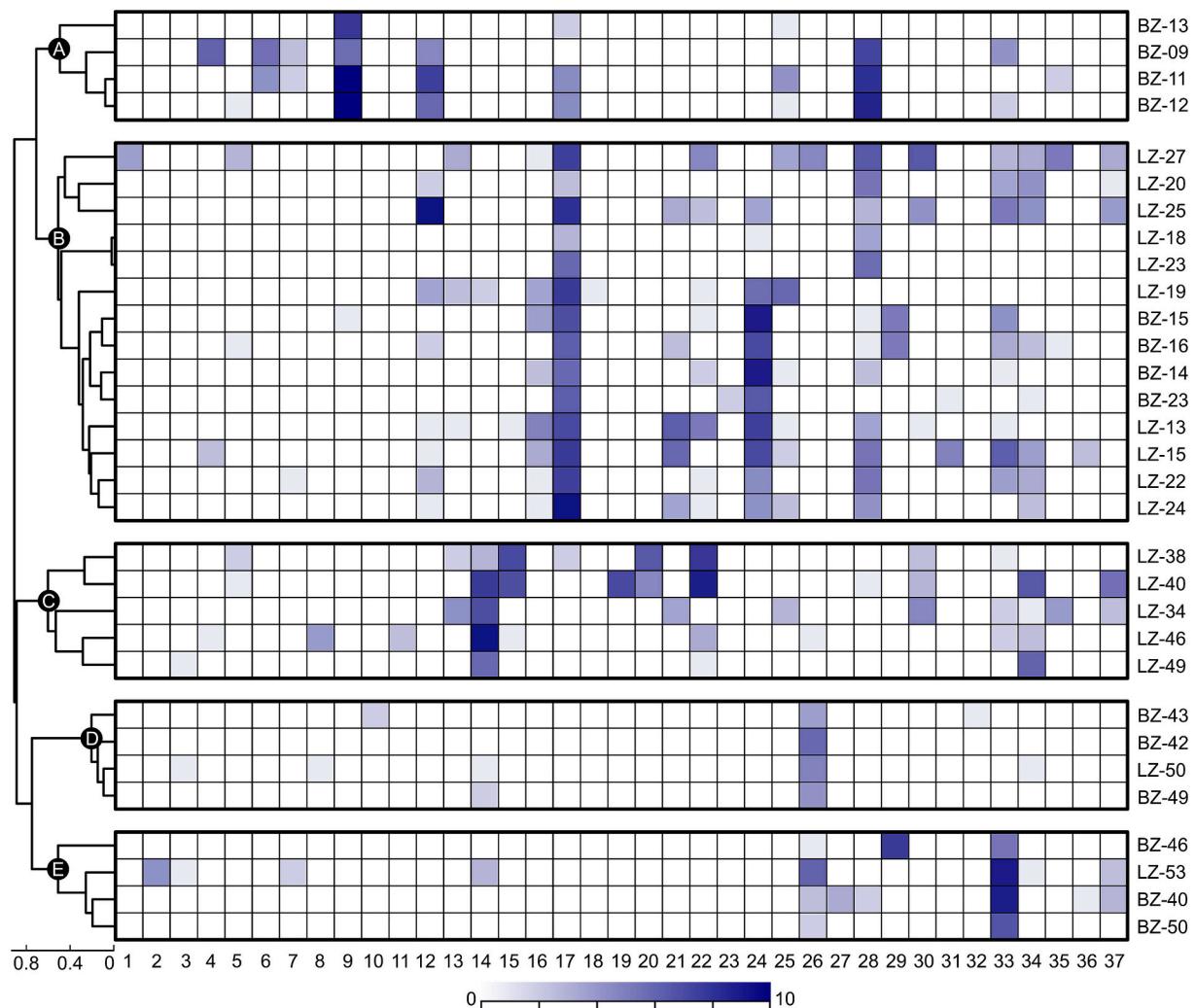


Fig. 5. Q-Mode (samples) cluster analysis using the unweighted paired group algorithm and Horn-Morisita dissimilarity index. The heatmap represents log-transformed abundance data for each sample, with color intensity corresponding to relative magnitude. Samples are labeled with the prefixes BZ (Bozhou section) and LZ (Liuwei section). Abbreviations for species: 1, *Palaeomucula* sp.; 2, *Modiolus* sp.; 3, *Promyalina putiatinensis*; 4, *Promyalina schamarae*; 5, *Promyalina spathi*; 6, *Tambanella gujoensis*; 7, *Bakevelliya exporrecta*; 8, *Bakevelliya goldfussi*; 9, *Pteria ussurica variabilis*; 10, *Pteria cf. guizhouensis*; 11, *Pteria* sp.; 12, *Towapteria scythica*; 13, *Claraia anulata*; 14, *Claraia aurita*; 15, *Claraia clarae*; 16, *Claraia concentrica*; 17, *Claraia griesbachi*; 18, ?*Claraia hsuei*; 19, *Claraia intermedia*; 20, *Claraia mulleri*; 21, *Claraia radialis*; 22, *Claraia stachei*; 23, *Claraia cf. tumida*; 24, *Claraia wangi*; 25, *Claraia zhenanica*; 26, *Eumorphotis multifloris*; 27, *Eumorphotis teilhardi*; 28, *Eumorphotis venetiana*; 29, *Crittendenia australasiatica*; 30, *Crittendenia cf. kummeli*; 31, *Crittendenia?* sp.; 32, *Streblopteria* sp.; 33, *Leptochondria virgalensis*; 34, *Neoschizodus laevigata*; 35, *Neoschizodus orbicularis*; 36, *Unionites canalensis*; 37, *Unionites fassaensis*. Abbreviations for associations A–E (nodes on the cluster) are consistent with Fig. 2.

in this study have been uploaded to a public GitHub repository: <https://github.com/tingluyang/Paleoecology/tree/main/T1CommunityShiGuizhou>.

4. Results

4.1. Paleoecological associations

Based on Q-mode cluster analysis, five associations have been identified and are labeled with the abbreviated codes A–E (Fig. 5). The NMDS ordination, with a stress value of 0.135, suggests a fair representation of the data (Clarke, 1993) and supports the clustering results (Fig. 6). Additionally, the PERMANOVA test ($F = 18.94$, $R^2 = 0.74$, $p < 0.01$) indicates that the compositional differences between associations are both substantial and statistically significant. The details of each association are described below.

Pteria ussurica variabilis association is recorded in the Bozhou section. The rarefaction curve suggests the association is sufficiently sampled (Fig. 7D). The trophic nucleus includes *Pteria ussurica variabilis* and *Eumorphotis venetiana* (Fig. 7A). The association is characterized by the relatively high proportion of endobenthic suspension feeders, e.g., *Towapteria* and *Promyalina*, in both diversity (Figs. 7B, C) and abundance (Fig. 8). The diversity of the association is relatively low in richness but slightly higher than *Eumorphotis multiformis* association and *Leptochondria virgalensis* association in Shannon and Gini-Simpson effective diversities (Figs. 9, 10). Trophic guild diversity is 3, including epibenthic, endobenthic and infaunal suspension feeders (Figs. 7B, C). The association is limited to the lowermost of the Yelang Formation with the age of earliest Triassic (Fig. 2).

Claraia griesbachi-C. wangi association comprises samples from both

Bozhou and Liuzhi sections. *Claraia griesbachi*, *C. wangi*, *Towapteria scythica*, and *Eumorphotis venetiana* constitute the trophic nucleus (Fig. 7A). *Leptochondria virgalensis*, *C. radialis* and *Crittendenia cf. kummeli* are also commonly recorded. The association is well sampled as suggested by the rarefaction curve (Fig. 7D) and represented by the highest diversity among all the recognized associations (Figs. 9, 10). Furthermore, the association yields the highest trophic guild diversity with the presence of infaunal detritivore (Figs. 7, 8), though it is dominated by the epibenthic suspension feeders as other associations. The common presence of *C. wangi*, an index fossil of Lower Triassic, suggests that the age of the association is restricted to the *Claraia wangi* Zone (Figs. 2, 3).

Claraia aurita association is recorded in the Liuzhi section. The association is characterized by the dominance of genus *Claraia*. The trophic nucleus includes *Claraia aurita*, *C. stachei*, *C. clarae*, and *Neoschizodus laevigata*. The species *C. intermedia* and *C. mulleri* are also commonly observed (Fig. 7A). With the species diversification of *Claraia*, the association is dominated by the epibenthic suspension feeders and exhibits a relatively high diversity in species level (Figs. 7C, 9, 10). In addition, infaunal suspension feeders, primarily *Neoschizodus* and *Unionites*, contribute a relatively high proportion to the guild composition (Fig. 8). The age of the association is restricted to the Induan, probably the late Griesbachian, according to the corresponding *Claraia stachei-C. aurita* Zone (Fig. 3; Tong et al., 2019).

Eumorphotis multiformis association is represented by samples from both Bozhou and Liuzhi sections. The trophic nucleus is formed by *Eumorphotis multiformis*. Other species are quite rare (Fig. 7A). The rarefaction curve indicates that the current sampling coverage might be inefficient to directly extract convincing ecological metrics (Fig. 7D). Nevertheless, the diversity index estimated by rarefaction and

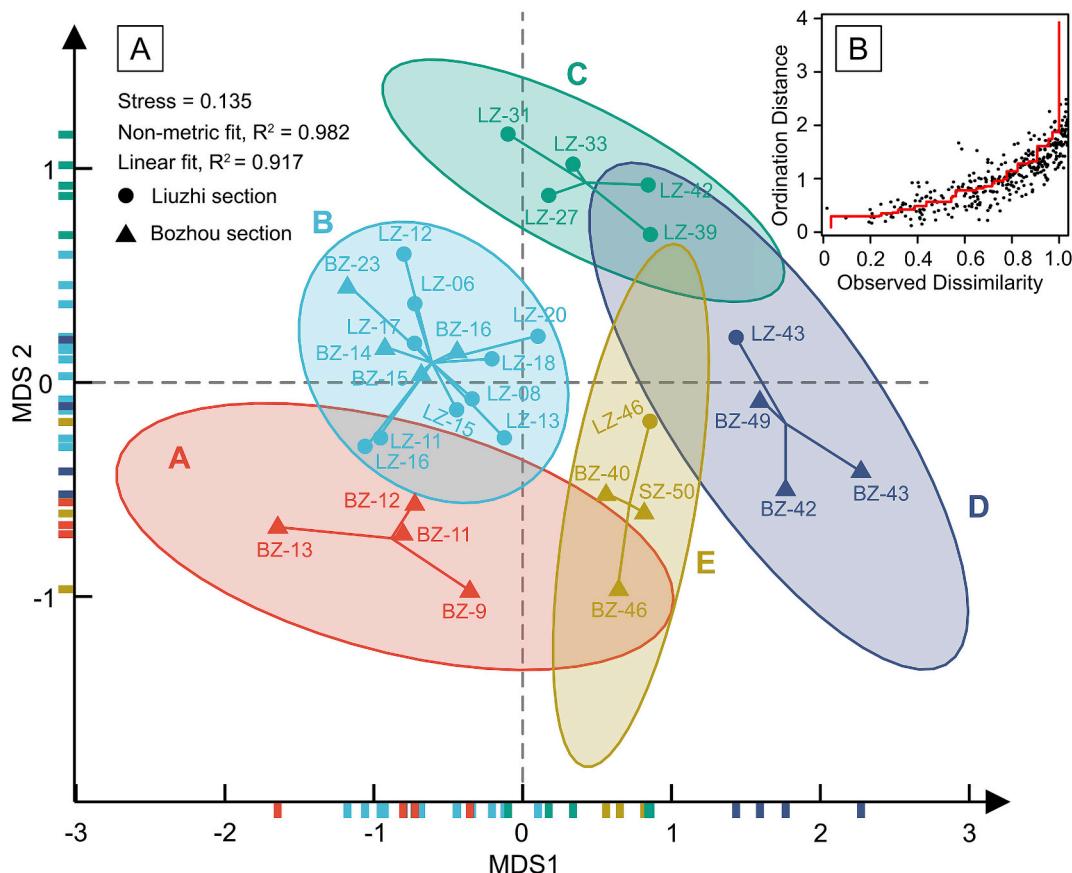


Fig. 6. NMDS ordination showing the distribution of samples from Bozhou and Liuzhi sections based on log-transformed abundance data (A) and the corresponding Shepard stress plot (B). Colored ellipses labeled A–E represent 95 % confidence intervals for paleoecological associations. Abbreviations of associations A–E are consistent with Fig. 2.

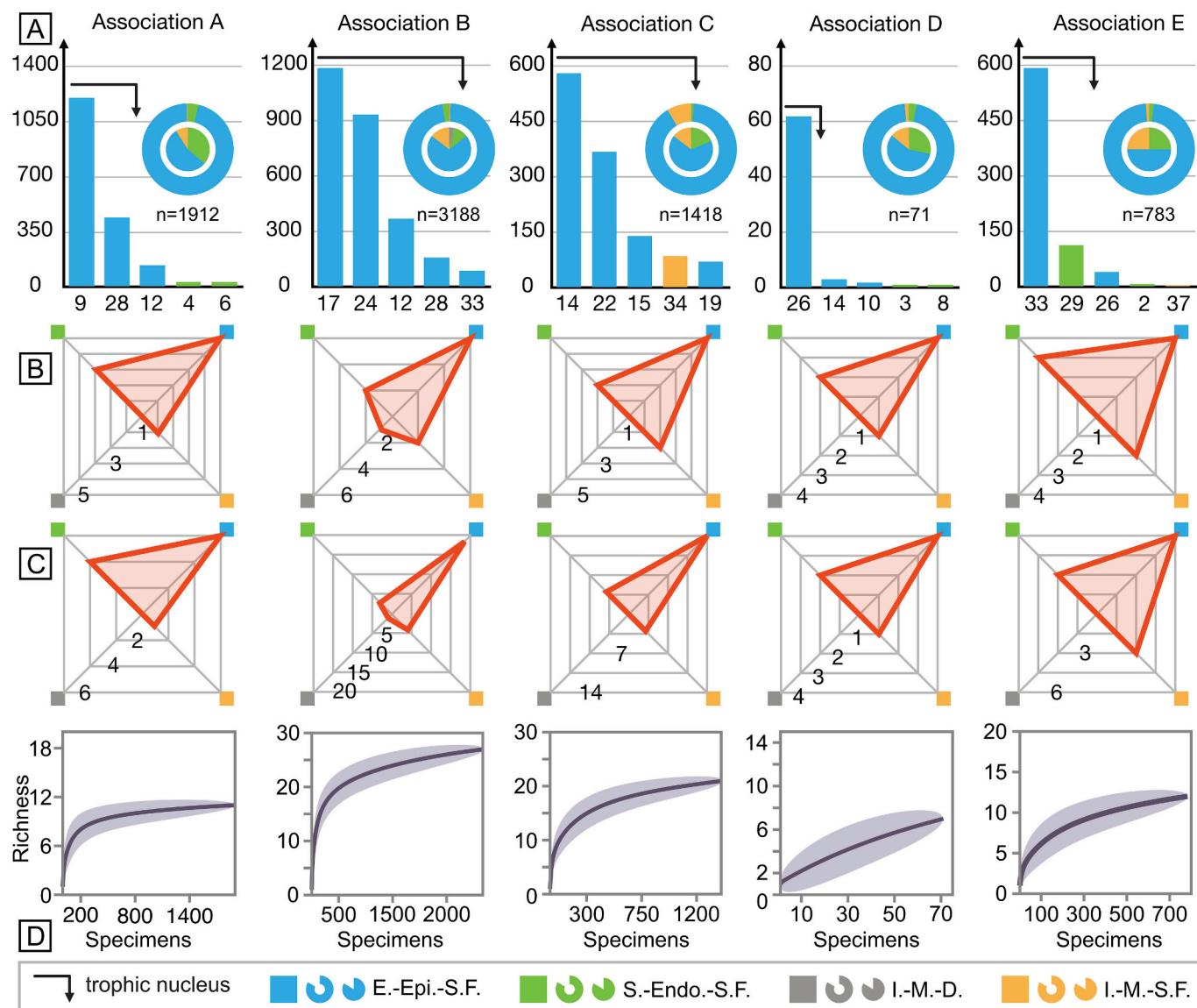


Fig. 7. Taxonomic composition and trophic structure of each association. A. Histogram, pie chart and ring chart illustrating the taxonomic composition with frequencies (only the five taxa with the highest abundance are shown here), guild-species diversity and absolute abundances of guilds, respectively. B. Radar charts showing genus-level richness within each ecological category for each association. C. Radar charts showing species-level richness within each ecological category for each association. D. Rarefaction curves for each association. Abbreviations of ecological modes: E.-Epi.-S.F. = epibyssate suspension feeders; S.-Endo.-S.F. = semi-infaunal endobysate suspension feeders; I.-M.-D. = infaunal mobile detritus feeders; I.-M.-S.F. = infaunal mobile suspension feeders. Abbreviations of associations A–E are consistent with Fig. 2.

extrapolation methods are indicative of a relatively low diversity in Shannon and Gini-Simpson effective diversities (Fig. 10). The absolute abundance of guilds suggests that epibyssate suspension feeders clearly dominate the association. Although endobysate and infaunal suspension feeders are rarely recorded, their presence indicates that the diversity of guilds is not significantly lower compared to other associations. The age of the association ranges from the Dienerian to the earliest Smithian based on the zonation of conodonts and bivalves (Figs. 2, 3).

Leptochondria virgalensis association is recorded in upper part of Yelang Formation of the Bozhou and Liužhi sections. The trophic nucleus is formed by *Leptochondria virgalensis* and *Crittendenia australasiatica*. Other species are rare. Among them, *Eumorphotis multiformis* and *Modiolus* sp. are the only species with an absolute abundance exceeding ten (Fig. 7A). The diversity of the association is relatively low (Figs. 9, 10). The rarefaction curve indicates that the sampling effort is sufficient (Fig. 7D). That is, further sampling is unlikely to significantly

increase species richness. The abundance of guilds shows that epibyssate suspension feeders dominate the association as observed in other associations. Endobysate and infaunal suspension feeders are also recorded in the association (Fig. 8). The age of the association is the same as that of *Eumorphotis multiformis* association.

4.2. Co-occurrence analysis

The co-occurrence network identifies *Claraia* as a key taxon based on its centrality within the network (Fig. 11, nodes 13–25). This suggests that the presence of *Claraia* and/or its interactions with other species play a crucial role in shaping the community structure during the earliest Triassic. Most epibyssate suspension feeders, represented by *Claraia griesbachi*, *C. wangii*, and *C. mulleri*, are interconnected through dense positive correlations, suggesting a shared ecological preference. Negative correlations are observed in the nodes involving *C. aurita* and *Eumorphotis multiformis*, which are trophic nuclei of corresponding

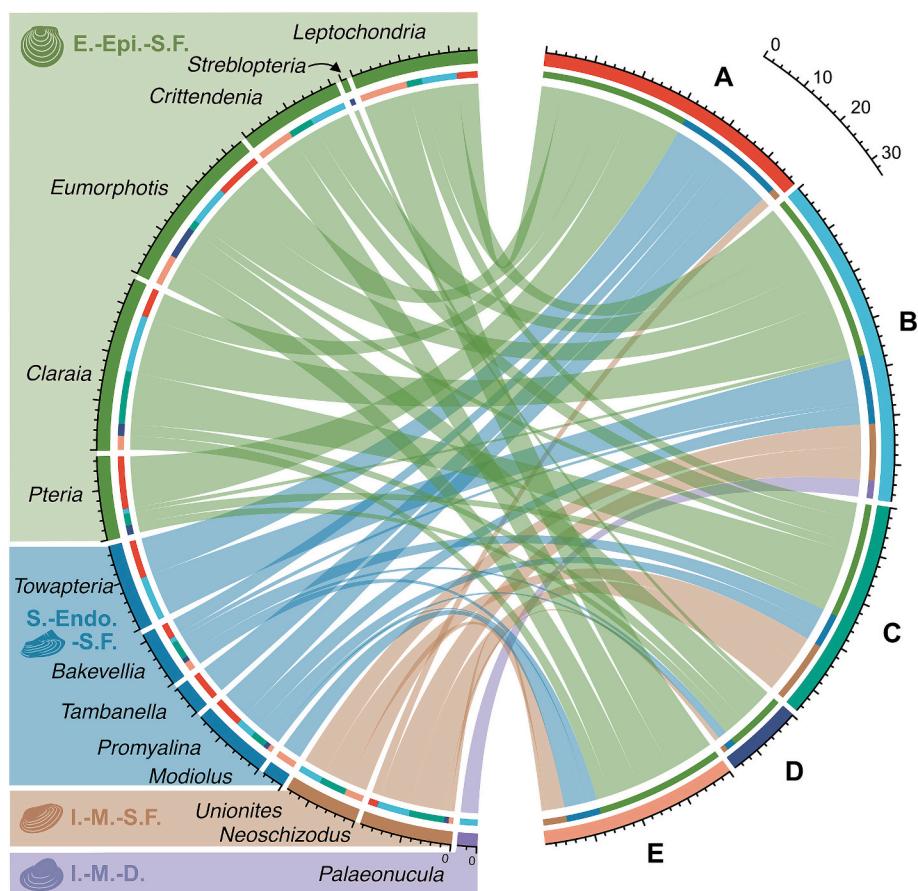


Fig. 8. Chord diagram illustrating the contribution of each genus, grouped by ecological categories, to the paleoecological associations. Associations A–E correspond to those identified by cluster analysis, with the abbreviations defined in Fig. 2. The raw abundance data were log-transformed to enhance the visibility of rare species.

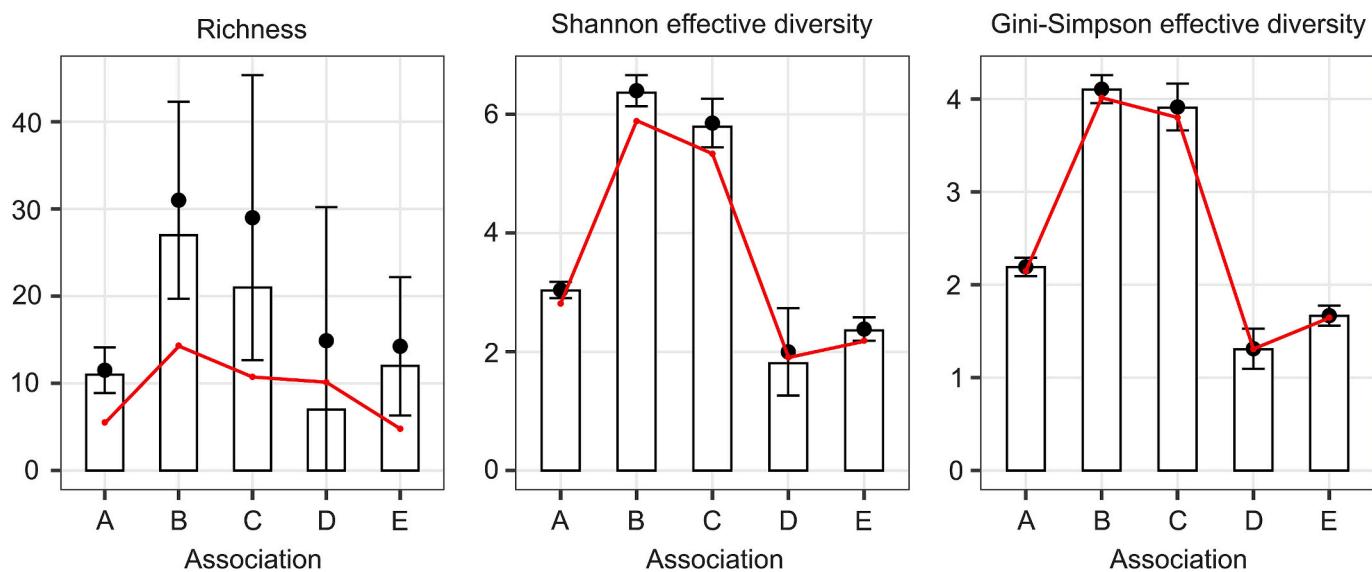


Fig. 9. Richness, Shannon, and Gini-Simpson effective diversity of each paleoecological association. White bars represent diversity metrics calculated using the observed dataset. Black dots and error bars indicate diversity estimates and their corresponding 95 % confidence intervals, calculated using rarefaction and extrapolation methods. Red lines connect diversity metrics under the sample coverage of approximately 0.97. Abbreviations of associations A–E are consistent with Fig. 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

associations. It suggests that the *Claraia aurita* association and *Eumorphotis multiformis* association exhibit distinct co-occurrence patterns compared to other associations. Positive interconnections are also

recorded among endobyssate suspension feeders. Nevertheless, several species, i.e., *Promyalina spathi*, *P. schamareae* and *Bakevella goldfussi*, exhibit frequent co-occurrence with epibyssate suspension feeders

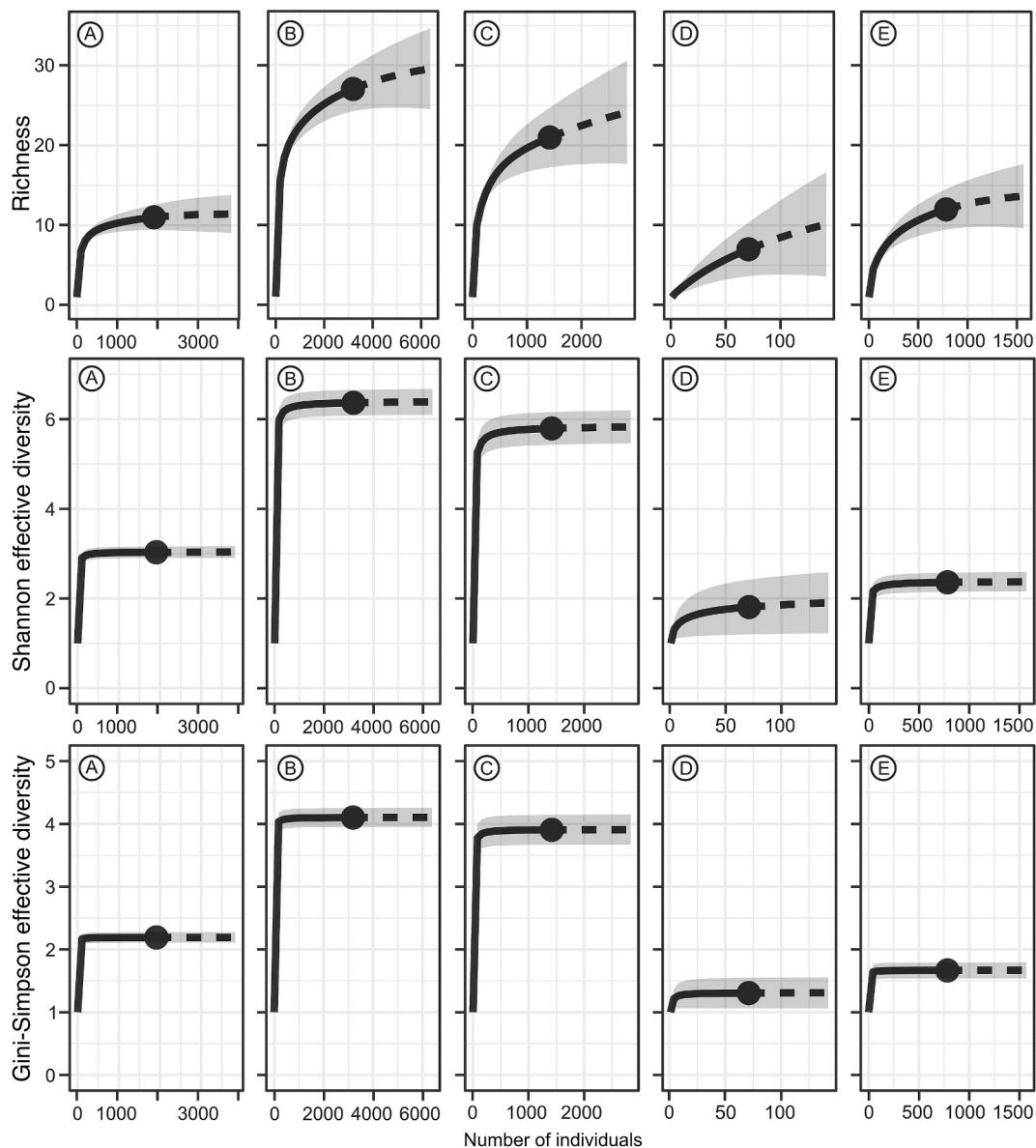


Fig. 10. Estimated species richness, Shannon effective diversity, and Gini-Simpson effective diversity based on rarefaction and extrapolation for each paleoecological association. Associations A–E are defined in Fig. 2.

across different samples. It could be indicative of shared ecological preferences between epibyssate and endobyssate suspension feeders. Notably, the infaunal suspension feeders, *Neoschizodus* and *Unionites*, exhibit relatively weak correlations with other taxa, particularly with endobyssate suspension feeders, which may be attributed to niche differentiation (Fig. 11).

5. Discussion

5.1. Permian–Triassic boundary transitional bivalve association

The post-extinction bivalve faunas of the EPME are characterized by significantly reduced diversity and high level of faunal homogeneity (Nakazawa and Runnegar, 1973). The associations recognized here also exhibit high similarity in taxonomic composition and trophic structure when compared to contemporaneous faunas documented elsewhere. The *Pteria ussurica variabilis* association or comparable ones, characterized by frequent occurrences of *P. ussurica variabilis*, *Towapteria scythica* and *Emorphotis venetiana*, are commonly recorded across various facies

in South China during the immediate aftermath of EPME (Fig. 12), e.g., littoral clastic facies (Song et al., 2019), shallow-water clastic facies (Yang, 2015), and carbonate facies (Shen et al., 1995; Chen, 2004). The stratigraphic duration of the associations is commonly referred to as Permian–Triassic transitional bed (see Yin, 1985b; Tong et al., 2019). Song et al. (2019) termed them as the Permian–Triassic transitional bivalve communities, representing the earliest bivalve faunas after the EPME. The presence of *Pteria cf. ussurica* in the northeastern Russia (Biakov et al., 2018) and the *Towapteria*-bearing beds in Dolomites (Posenato, 2009) might suggest an expanded distribution of similar communities in the Boreal realm and western Tethys during the latest Changhsingian. It should be noted that the stratigraphic ranges of the characteristic taxa mentioned above are not confined to the Permian–Triassic transitional interval. *P. ussurica variabilis*, *T. scythica* are also frequently recorded in the *Claraia wangi* Zone or younger zones, such as the *P. ussurica* association from the eastern Panthalassa margin (Hofmann et al., 2013) and associations with abundant *T. scythica* recorded in the Dolomites (Hofmann et al., 2015).

The success of *Pteria* and *Towapteria* in post-extinction communities

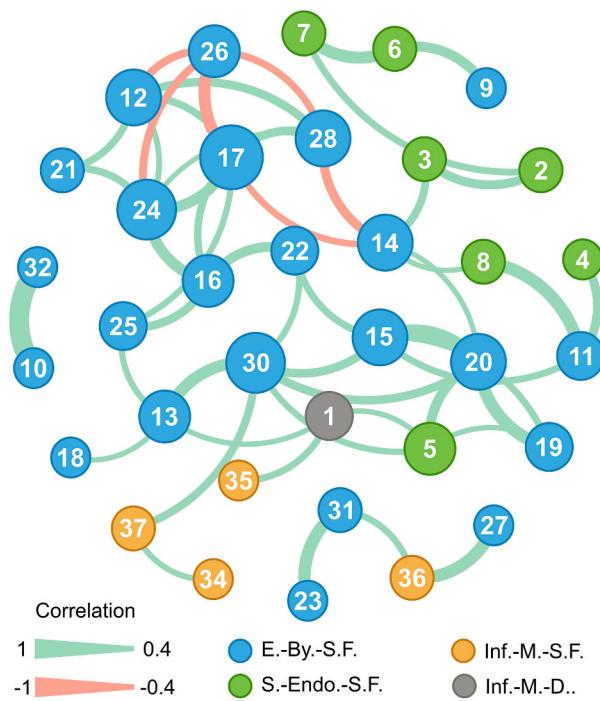


Fig. 11. Co-occurrence network of taxa recorded in the studied sections. Node size is proportional to the degree of connectivity (number of connections). Taxonomic codes within nodes correspond to the abbreviations listed in Fig. 5.

might be attributed to their flexible adaptive capacity for multiple modes of life, which facilitated broad ecological tolerance in harsh and fluctuating environmental conditions (e.g., high temperature and anoxia, Sun et al., 2012; Huang et al., 2017). In this paper, *P. ussurica variabilis* and *T. scythica* are provisionally interpreted as epibyssate suspension feeders following the current consensus (Song et al., 2019). The occurrence of *T. scythica* also shows highly positive correlations with other epibyssate suspension feeders in co-occurrence network ordination (see node 12 in Fig. 11). However, certain morphological features complicate a definitive assignment and might be indicative of adaptations to diverse modes of life. The external morphology of *Towapteria* resembles that of *Costigervillia*, an endobysseate bivalve, while other features, such as the presence of a lobate anterior auricle, suggest an epibyssate mode of life (Ros-Franch et al., 2014, p. 47; see also Priñoto and Posenato, 2023, p. 21). Likewise, extant *Pteria* species are epibyssate suspension feeders, originated from endobysseate ancestors (Stanley, 1972). In contrast to its modern relatives, *Pteria ussurica* has been interpreted as an endobysseate suspension feeder based on morphological affinities with *Bakevillia* (Hofmann et al., 2013, p. 865). Morphological adaptations to facultative ecological niches may have played a crucial role in their survival during the EPME (see Ros and Echevarría, 2011, p. 419).

5.2. The adaptive radiation of *Claraia*

Although bivalve communities dominated by the genus *Claraia* are recorded in many sections during the immediate aftermath of the EPME, e.g., the *Claraia bioni* community in Kashmir (Nakazawa and Kapoor, 1981), *Claraia huzhouica* in southeastern China (Huangzhishan section, Chen, 2004) and *Claraia liuqiaoensis* community in southwestern China (Xinmin section, Yang, 2015), the onset of cosmopolitan homogeneity of post-extinction bivalve fauna is assumed to occur during the *Claraia wangi* Zone (Yin, 1985a, p. 583). The significant increase in bivalve cosmopolitanism during the aftermath of EPME is primarily attributed to the proliferation of disaster taxa exemplified by the genus *Claraia* (Yan et al., 2023). The rapid morphological diversification of *Claraia*

during the earliest Triassic makes it an ecologically and biostratigraphically informative genus with a high level of specific diversity (McRoberts, 2010). Based on the shell ornamentations, Ichikawa (1958) classified the genus *Claraia* into four groups, i.e., *Claraia aurita* Group (shell smooth or with only concentric lines developed), *Claraia clarae* Group (shell with strong commarginal folds or wrinkles developed), *Claraia stachei* Group (radial ornamentations developed), and *Claraia decidens* Group (strongly inflated left shell with absent or weak ornamentations). Species previously assigned to *Claraia decidens* Group have been nominated or revised as *Crittendenia* and *Eobuchia* (see Newell and Boyd, 1995; Wasmer et al., 2012; Komatsu et al., 2013). For the other three groups, Nakazawa (1977) further subdivides each group into two subgroups according to the development or distinctness of the posterior auricle. In this study, we coded them as A for species with distinct posterior auricles and B for those with posterior auricles undeveloped. Accordingly, the *Claraia griesbachi*-*C. wangi* association and *Claraia aurita* association recognized herein are characterized by the dominance of *Claraia aurita* Group A and B, respectively. That is, both associations are dominated by *Claraia* species with smooth shell or ornamented by simple concentric lines. Comparable associations with respect to species abundance composition have been widely reported in South China (Wu, 1985; Zhu et al., 1992; Huang et al., 2018) and northern Italy (Hofmann et al., 2015). It is noteworthy that the proliferation of taxa with relatively simple ornamentation during the aftermath of EPME is also observed in the morphological selectivity of brachiopods and ammonoids (Chen et al., 2015; Dai et al., 2021; Liu et al., 2024). Representatives of *Claraia clarae* Group and *Claraia stachei* Group are also commonly recorded and exhibit even higher level of dominance within some specific stratigraphical intervals, e.g., beds 38 and 40 in the Liuzhi section (Fig. 3). Among these species, *Claraia stachei* is considered as a cosmopolitan species originating from Boreal Realm (Fig. 12; Nakazawa, 1977; Yin, 1981; Fang, 2010). Community dominated by *Claraia stachei* could be distinguished as an independent paleoecological entity in certain sections or regions, e.g., Fujian (Wu, 1985) and Hubei (Zhu et al., 1992; Huang, 2014, p. 24; but see Li et al., 2009) of South China and Tibet (Chen, 1983). Nevertheless, it lacks sufficient quantitative evidence in Guizhou as presented herein (see also Yang et al., 1987; Huang, 2014).

The enhanced mobility and other physiological characteristics are often considered as key factors underlying the rapid proliferation and cosmopolitan distribution of *Claraia* in the post-extinction (Huang et al., 2018), which also promote the diversification of their lifestyles in the Early Triassic (Yin et al., 1994). The circular to subcircular, thin, and flat valves of *Claraia* make it morphologically comparable to other so-called “paper pectens”, such as *Daonella* (Wignall, 1994). These bivalves exhibit advanced adaptations to soft and soupy substrates (snow-shoe strategists, Schatz, 2005). While the precise physiological strategies of paper pectens are debated—with proposed mechanisms including chemosymbiosis (Waller and Stanley, 2015) and enhanced oxygen diffusion through their thin valves (Schatz, 2005)—their consistent occurrence under anoxic to euxinic settings suggests a high tolerance for low oxygen conditions (Huang et al., 2018). Additional and distinct morphological evolution is indicated by changes in the byssal notch of *Claraia*. The reduced size of byssal notch across the Permian–Triassic extinction interval suggests a shift from an obligate to a facultative byssal attachment mode (He et al., 2007).

As for the radiation, it at least includes two different types. One is adaptive radiation which represents significant increase in diversity and different characters for different palaeoecological forms, the other is evolutionary radiation which only has noticeable rise in diversity (Simões et al., 2016; Hernández-Hernández, 2019). Based on these above discussions, *Claraia*, a disaster taxon that thrived after the extinction, should be an example of adaptive radiation during the recovery stage of Early Triassic.

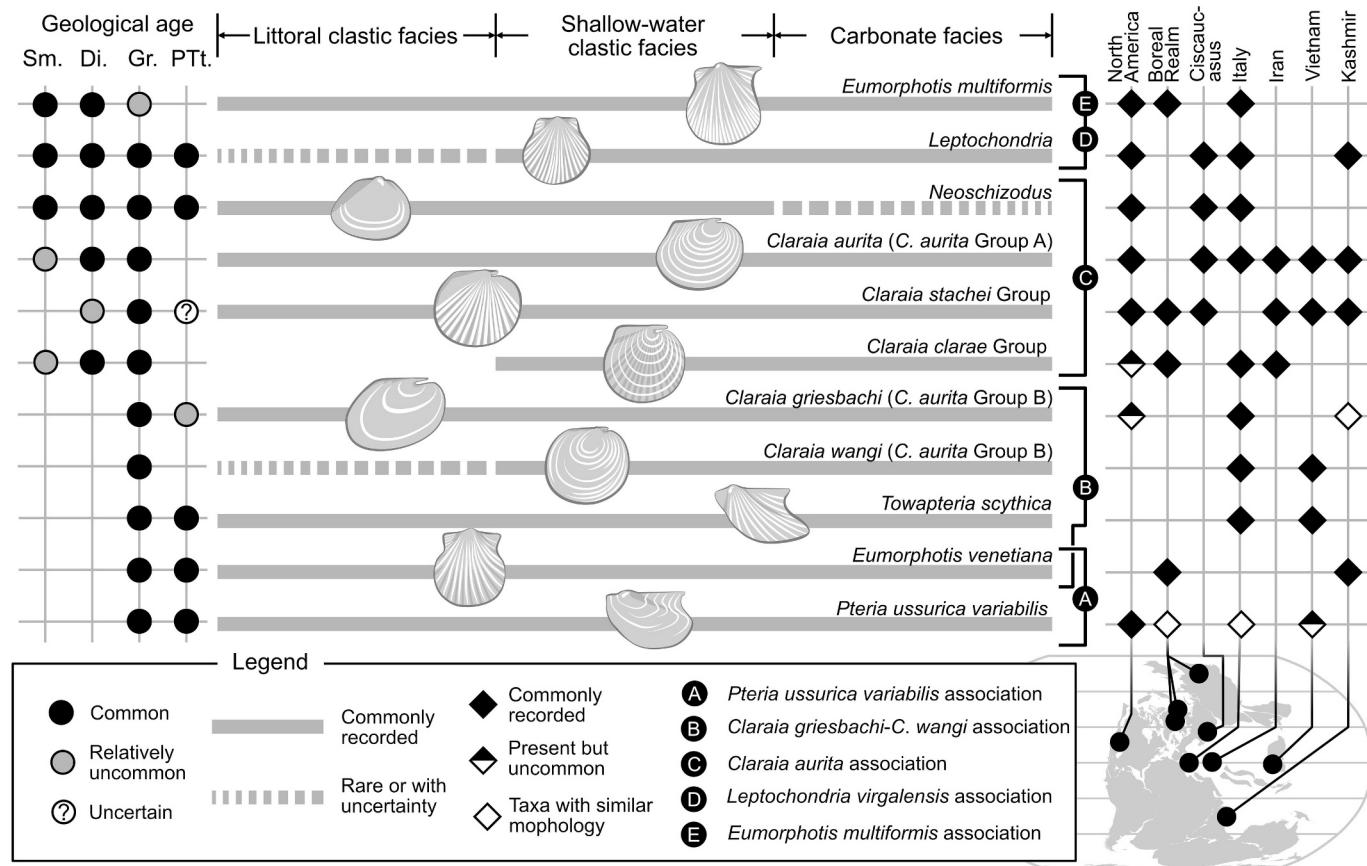


Fig. 12. Taxa representing the trophic nucleus of each association, along with their respective geological age ranges (Yin, 1990; Ros-Franch et al., 2014), occurrences across various sedimentary facies (Chen et al., 1979; Yin, 1985a; Komatsu et al., 2008), and palaeogeographical distributions in North America (Ciriacks, 1963; Hofmann et al., 2013), the Boreal region – including Siberia, East Greenland, and Spitsbergen of Norway (Yin, 1990; Biakov et al., 2018), the Caucasus (Ruban, 2017), Italy (Posenato, 2008b; Hofmann et al., 2015), Iran (Nakazawa, 1977; Taraz et al., 1981), Vietnam (Komatsu et al., 2008), and Kashmir (Nakazawa et al., 1975; Nakazawa and Kapoor, 1981). Abbreviations: Sm., Smithian; Di., Dienerian; Gr., Griesbachian; PTt., Permian–Triassic transitional bed.

5.3. Possible trend of endemicity?

The prevalence of *Claraia* is largely confined to the Induan, particularly the earliest Griesbachian (Yin, 1985a; Petsios and Bottjer, 2016), during which many species of *Claraia* exhibit near-global distributions, such as *Claraia griesbachi*, *C. clarae* and *C. aurita*. This widespread occurrence at the species level makes *Claraia* a highly effective index fossil for biostratigraphic correlation across different regions. In contrast, *Eumorphotis* and *Leptochondria* become more dominant in subsequent intervals, such as the *Eumorphotis multiformis* Zone in the Liuzhi and Bozhou sections. Although both genera maintain cosmopolitan distributions (Fig. 12), the dominant species commonly varies across different associations or paleogeographic regions. For example, the *Eumorphotis ericus* and *Leptochondria occidanea* associations in eastern Panthalassa exhibit distinct species-level composition patterns compared to their counterparts in South China (Hofmann et al., 2014). The shift in faunal homogeneity from the species level to the genus level may reflect the initial breakdown of the globally homogeneous, species-level cosmopolitan faunas that characterized the earliest Triassic, marking the onset of early faunal provincialization. However, this process appears to have been gradual and not yet fully established during this stage. A recent network-based study by Echevarría and Ros-Franch (2024) confirms that a more pronounced and statistically significant increase in bivalve endemicity did not occur until the Middle Triassic.

5.4. Taxa and functional diversity

Growing evidence indicates that the species and functional diversity

of level-bottom communities exhibit an increasing trend during the Griesbachian and a subsequent decline in Dienerian (Foster and Twitchett, 2014; Hofmann et al., 2015, p. 493). The highest diversity levels of Induan benthic communities are commonly recorded in upper Griesbachian (western U.S., Hofmann et al., 2013; northern Italy, Hofmann et al., 2015) or Griesbachian-Dienerian transition (Far East Russian, Shigeta et al., 2009). Nevertheless, post-extinction shelly communities in South China showed highly variable diversity trajectories in different sedimentary settings during the aftermath of the EPME (see Chen et al., 2010, Fig. 5). The variance was interpreted as differential impacts of episodic extinctions across various facies (Chen et al., 2010). In the Liuzhi and Bozhou sections, *Claraia*-dominated associations (middle to late Griesbachian) exhibit significantly higher species diversity compared to other associations (Fig. 9). The diversities also exceed those of temporally equivalent assemblages from neighboring sections of Guizhou province, such as the bivalve fauna recorded in Sidazhai section (five species belonging to two genera; Huang et al., 2018) and the *Pteria ussurica*-*Claraia wangii* assemblage of Zhonghe section (SimED = 1.408; ShED = 1.786; recalculated following Zhao et al., 2022). It should be noted that genus-level richness remains roughly equivalent across the associations in the studied sections (Fig. 7B). The relatively higher species richness observed in *Claraia*-dominated associations is mainly attributed to the morphological diversification and the corresponding rapid speciation rate of *Claraia* during the earliest Triassic (Yang et al., 1987). Nine of the 21 species (43 %) in *Claraia aurita* association belong to the genus *Claraia* (see details in supplementary material). Additionally, the trophic structures of all associations also exhibit similar compositions, predominantly

characterized by epifaunal suspension feeders, though infaunal bivalves are relatively more abundant in *Claraia aurita* association (Figs. 7A, 8). Global occurrences data suggest that bivalves showed high resilience to the EPME via maintaining their ecological niches and reducing the functional redundancy (Wang et al., 2024). It is consistent with the relatively simple and minimally altered trophic structure observed in the studied sections (Figs. 7B, C). The relatively high portion of infaunal bivalves is considered as a potential indicator for relatively advanced recovery state (Hautmann et al., 2011, 2013; Yang et al., 2015). Benthic communities dominated by infaunal bivalves are also commonly observed in Middle to Late Triassic successions, where they exhibit characteristics of more advanced ecological recovery (Friesenbichler et al., 2019). The unexpectedly diverse mollusk fauna in Shanggan section records 11 bivalve species, four of which belong to infaunal suspension feeders (Hautmann et al., 2011). In the Liuzhi and Bozhou sections, guild structures with comparable proportions of infaunal bivalves are only sporadically recorded in specific stratigraphic intervals where *Claraia* shows relatively less importance in abundance and taxonomic composition, e.g., LZ-20, LZ-34 and BZ-40 (Fig. 5). The taxonomic composition of infaunal bivalves is highly monotonous, being primarily composed of *Unionites* and *Neoschizodus*, both of which are commonly recorded across various facies (Fig. 12). Notably, *Unionites* is also commonly documented in the upper Permian succession of the Dolomites, exhibiting certain survival traits such as relatively broad biofacies distribution and high population density (Prinot and Posenato, 2023, p. 55). The restoration of stenotopic hard-bottom dwellers, a hallmark of complete Triassic biotic recovery (Posenato, 2002), is absent from all the associations recognized here. The simple tiering structure observed in the Liuzhi and Bozhou sections suggests that these associations correspond to Recovery Stage 1 of the model proposed by Twitchett (2006), which is characterized by low ecological complexity and limited vertical differentiation. Accordingly, the associations recognized herein, characterized by high levels of dominance and relatively simple and stable trophic structures, show no signal of evident recovery of level-bottom community during the earliest Triassic.

5.5. Implications

Within the Induan Stage (less than one million years after end-Permian mass extinction), five associations were recognized in the Yelang Formation—the *Pteria ussurica variabilis*, *Claraia griesbachii-C. wangi*, *Claraia aurita*, *Eumorphotis multiformis*, and *Leptochondria virgalensis* associations—which are characterized by high dominance and simple tiering structure (Figs. 5, 7, and 8). The frequent alternation of bivalve communities could be attributed to the extremely severe environmental turbulence (e.g., carbon isotope, Payne et al., 2004; temperature, Sun et al., 2012; redox condition, Huang et al., 2017; Zhang et al., 2018) and the high dominance of some specific taxa (Hofmann et al., 2015; Petsios and Bottjer, 2016; Pietsch et al., 2019). In general, the communities with high dominance (Wan et al., 2023; Jiang et al., 2024) and global homogenization (widespread eurytopic taxa and ill-developed biotic province, Dai and Song, 2020; Echevarría and Ros-Franch, 2024) should be the key features of the Early Triassic marine ecosystem, which also delayed the recovery process.

6. Conclusion

Quantitative analysis of bivalve fossils from southwestern China provides insights into the initial stage of biotic recovery following the EPME. Despite substantial changes in taxonomic composition and species diversity across the five distinct bivalve associations, the associations share similar pattern of trophic structure, characterized by the dominance of epifaunal suspension feeders and a low level of functional redundancy of infaunal bivalves. The observed bivalve cosmopolitanism and faunal homogeneity suggest that the biotic recovery of bivalve fauna in studied area remained limited during the earliest Triassic.

CRediT authorship contribution statement

Tinglu Yang: Writing – original draft, Software, Methodology, Formal analysis, Data curation. **Huiting Wu:** Writing – review & editing. **Yang Zhang:** Writing – review & editing, Resources, Conceptualization. **Jingqi Liu:** Investigation, Data curation. **Anfeng Chen:** Investigation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2025.113208>.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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