

Taxonomic Note

A quantitative taxonomic review of *Fusichonetes* and *Tethyochonetes* (Chonetidina, Brachiopoda)

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Abstract.—Two middle Permian (Capitanian) to Early Triassic (Griesbachian) rugosochonetidae brachiopod genera, *Fusichonetes* Liao in Zhao et al., 1981 and *Tethyochonetes* Chen et al., 2000, have been regarded as two distinct taxa and used as such for a wide range of discussions including biostratigraphy, paleoecology, paleobiogeography, and the Permian-Triassic boundary mass extinction. However, the supposed morphological distinctions between the two taxa are subtle at best and appear to represent two end members of a continuum of morphological variations. In this study, we applied a range of quantitative and analytical procedures (bivariate plots, Kolmogorov-Smirnov test, categorical principle component analysis, and cladistic analysis) to a dataset of 15 quantified morphological variables, integrating both key external and internal characters, measured from 141 specimens of all well-known *Fusichonetes* and *Tethyochonetes* in order to test whether or not these two genera could be distinguished in view of the chosen characters. The results indicate that these two genera are morphologically indistinguishable and that the species classification previously applied to these two genera appears to represent polyphyletic groupings within the genus *Fusichonetes*. Consequently, *Tethyochonetes* is concluded to be a junior synonym of *Fusichonetes*. The diagnosis and key characteristics of *Fusichonetes* are clarified and refined based on a new suite of well-preserved specimens from the Permian–Triassic Xinmin section in South China.

Introduction

Fusichonetes Liao in Zhao et al., 1981 and *Tethyochonetes* Chen et al., 2000 both belong to the Rugosochonetidae, the most species-rich family among chonetidine brachiopods (Racheboeuf, 2000). As a genus, *Fusichonetes* was first mentioned in Liao (1979), without description. Later, Liao in Zhao et al. (1981) formally proposed and defined this genus, with *Plicochonetes nayongensis* Liao, 1980a from the Changhsingian strata at the Zhongling section, Nayong, Guizhou, South China as the type species (Fig. 1). *Tethyochonetes* was proposed by Chen et al. (2000) with *Waagenites soochowensis quadrata* Zhan, 1979 from the Late Permian of Lianxian, Guangdong, South China as the type species (Fig. 1).

Since *Fusichonetes* was proposed, only two species have been recorded, *F. nayongensis* (type species) and *F. pygmaea* (Liao, 1980a), both designated to this genus originally by Liao (1981), and both restricted to Lopingian (late Permian) and Griesbachian (earliest Triassic) strata in South China (Fig. 2.3). In contrast, at least 14 species of *Tethyochonetes* have been recognized (online supporting data: Appendix 1), most of which had been assigned to either *Chonetes* Fischer von Waldheim, 1830 or *Waagenites* Paeckelmann, 1930 in the old literature.

The collective stratigraphical range of these 14 *Tethyochonetes* species is from the Capitanian (middle Permian) to Griesbachian (Early Triassic), while their paleogeographic ranges spread across the Paleo-Tethys and Neo-Tethys (Fig. 2.3). Notably, both genera apparently survived the Permian-Triassic boundary mass extinction (PTBME), accounting for 11.8% of the Permian brachiopod genera that persisted into the Griesbachian before their final extinction at the Griesbachian-Dienerian boundary (Liao, 1980b; Yang et al., 1987; Chen et al., 2005; Clapham et al., 2013). As such, these two taxa, especially *Tethyochonetes*, have attracted much attention in recent years, especially in connection to their extinction, paleobiogeographical distribution, and body-size change patterns (Chen et al., 2009; He et al., 2010; Wu et al., 2016; Zhang et al., 2016).

However, despite their close connection to the PTBME and potential significance for a better understanding of this major bio-crisis, the identity of these two genera and their mutual relationship have been problematic and never properly been investigated. Significantly, the problem arose because when Liao in Zhao et al. (1981) proposed *Fusichonetes*, he appears to have based the definition of his new genus primarily on a combination of external characteristics, including a very transverse outline, acute cardinal extremities, and coarse and angular

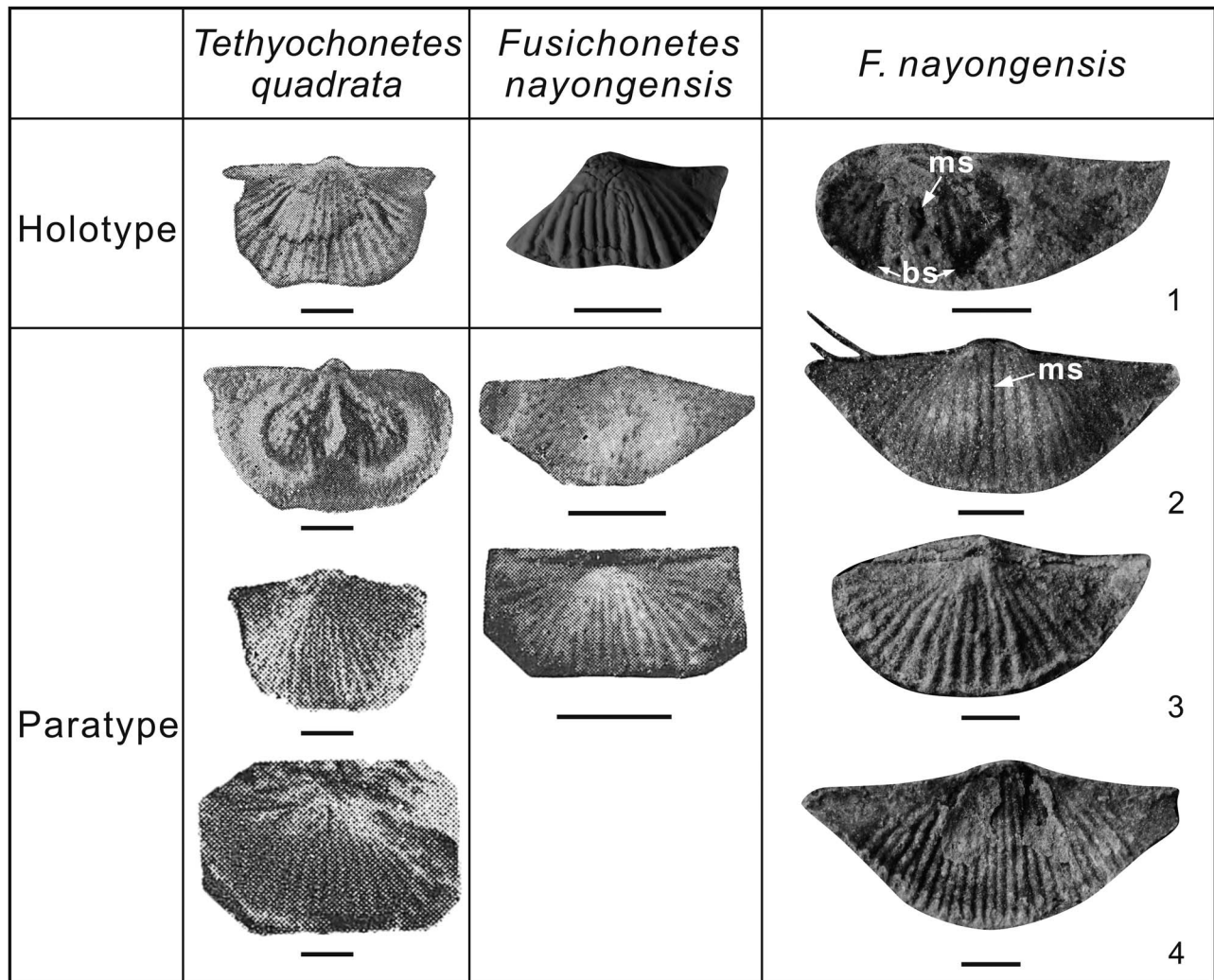


Figure 1. Type species of *Tethyochonetes* Chen et al., 2000 and *Fusichonetes* Liao, 1981. *Tethyochonetes quadrata* (Zhan, 1979), copied from Zhan (1979, pl. 4, figs. 16–19), original designation as *Waagenites soochowensis quadrata*, and *Fusichonetes nayongensis* (Liao, 1980a) copied from Liao (1980a, pl. 4, figs. 7–9) and from Xinmin section: (1) dorsal valve internal mold, CUG26123, bs: brachial scar, ms: median septum; (2) ventral valve internal mold, CUG25824; (3) dorsal valve external mold, CUG25224; (4) ventral valve external mold, CUG25524. All scale bars = 2 mm.

costellae with deep interspaces. Although no internal features were illustrated by Liao in Zhao et al. (1981), he did indicate that the dorsal interior of *Fusichonetes* possessed a cardinal process that is bilobate internally and quadrilobate externally. Interestingly, however, of the two *Fusichonetes* species recognized by Liao, only the type species, *F. nayongensis*, most consistently demonstrates the external morphological features that Liao used to define *Fusichonetes*. The second species, *Fusichonetes pygmaea* (see Liao, 1979, fig. 14; 1980a, pl. 4, figs. 4–6; 1980b, pl. 1, figs. 5, 6; 1981, pl. 8, figs. 7, 8), is in fact characterized by a subquadrate outline, cardinal extremity with an angle $\sim 75\text{--}90^\circ$, and coarse costellae with a few bifurcations.

When Chen et al. (2000) proposed *Tethyochonetes*, based on *Waagenites soochowensis quadrata* Zhan, they emphasized both external features as well as internal characteristics. Among the external features, Chen et al. (2000) considered the complexity of costellae (i.e. whether costellae are simple and undivided, or increase by bifurcation), the shell width/length ratio and the cross-section shape of the interspace between costellae

as the main characteristics to distinguish the two genera, supplemented by differences in internal structures. In comparing *Tethyochonetes* with *Fusichonetes*, Chen et al. (2000) noted that the former had a ventral median septum, an internally bilobate and externally trilobate cardinal process, a dorsal median septum, and lateral septa and brachial scars. But, it should be pointed out that most of these features that supposedly are diagnostic of *Tethyochonetes* were unknown in *Fusichonetes* when it was first formally proposed by Liao in Zhao et al. (1981) as he only had limited amount of internal material to study (this is evident from the fact that he figured no internal shell characteristics, nor mentioned any internal features, except for a brief comment on the cardinal process). Furthermore, even though Chen et al. (2000) mentioned that *Tethyochonetes* possessed a cardinal process that is bilobate internally and trilobate externally, they did not illustrate the trilobate aspect. But, when examining the illustrations of a well-preserved dorsal interior of *Tethyochonetes cheni* figured by Zhang et al. (2013, fig. 9J), we found that it clearly has an internally bilobate and externally quadrilobate cardinal process, which is the same as what Liao in

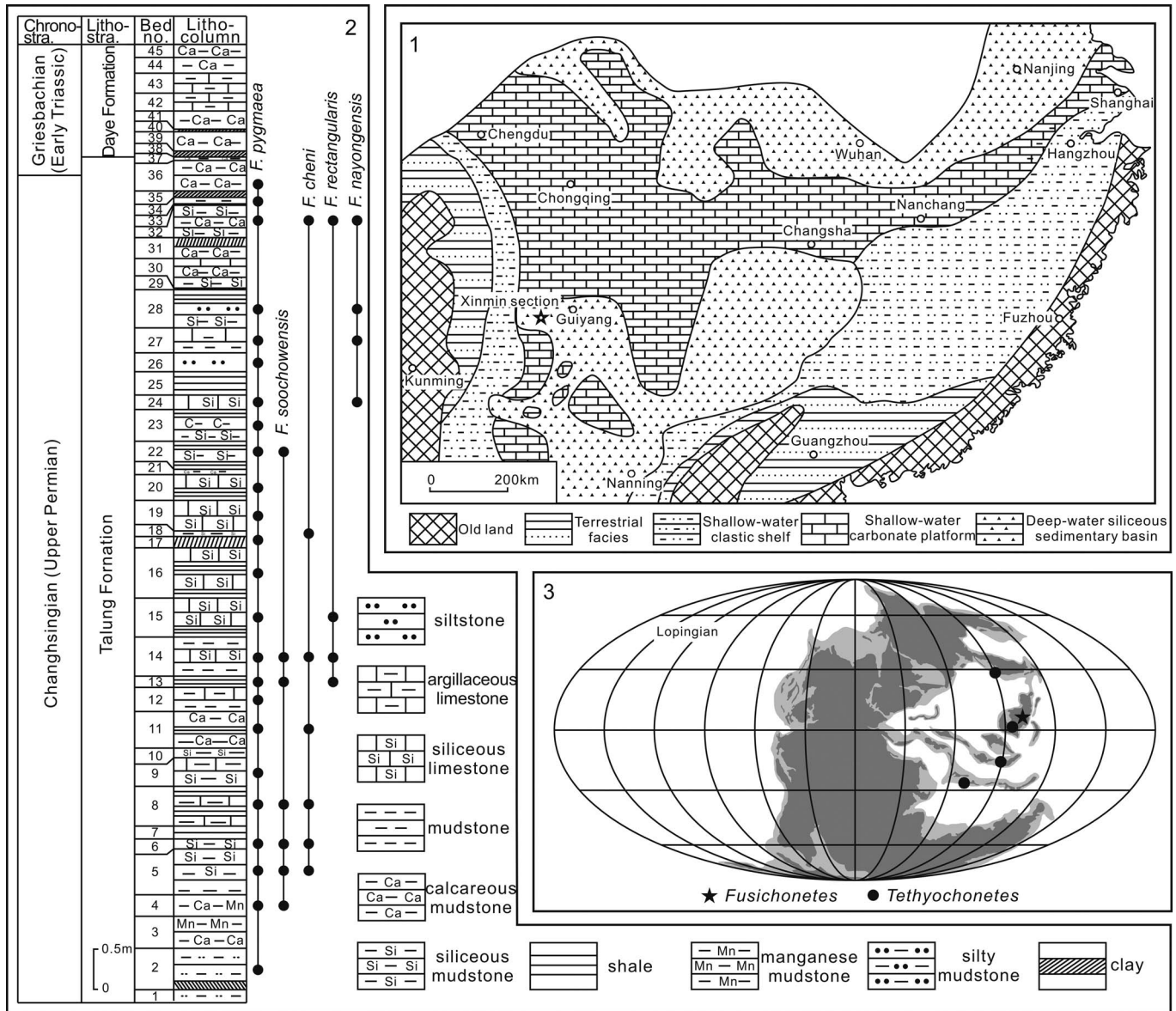


Figure 2. (1) Paleogeographical map of South China during the Permian–Triassic transition (from Feng et al., 1997; Yin et al., 2014), also showing the location of the Xinmin section (marked by a star). (2) Stratigraphical column of the Xinmin section, showing the lithology of the Talung Formation and the lower part of Daye Formation, as well as the stratigraphic distribution of *Fusichonetes*, as revised here (including species that would have been assigned to *Tethyochonetes* prior to this study). (3) Global paleogeographical distribution of *Fusichonetes* and *Tethyochonetes* according to previous literature (basal map after Blakey, 2008).

Zhao et al. (1981) had described for the dorsal interior of *Fusichonetes*.

As for the supposed significance of a ventral median septum, brachial scars, and a dorsal median septum in distinguishing *Tethyochonetes* from *Fusichonetes*, they are equally dubious. This is because from the specimens we have recently collected from the Xinmin section in South China, the ventral interior of *Fusichonetes* possesses a median septum, and its dorsal interior has well-developed brachial scars and a median septum (Fig. 1). Although until now no lateral septa are known from *Fusichonetes*, this does not necessarily mean it was originally absent in this genus, because even in some species of *Tethyochonetes* (e.g., Zhang et al., 2013, fig. 5O; He et al., 2014, fig. 4K, N) where lateral septa are supposed to exist, they are in fact absent, and presumably not preserved. With these observations, it suggests

that the two genera not only resemble each other strongly in external morphology, they also share very similar internal structures.

Recently, we collected 1150 well-preserved rugosochonetid specimens from a stratigraphic section in South China that straddles the Permian–Triassic boundary (Fig. 2.2, also see below for more details about the section). Our initial inspection of these specimens suggested that this collection, from a single section, seemed to represent a continuum of morphological variations from *Fusichonetes* (as one end member) to *Tethyochonetes* (at the other end), and that it was not possible to distinguish them with great confidence. The inability to separate them was due to the fact that there are specimens in the collection that clearly represent transitional forms between typical *Fusichonetes* characterized by a transversely quadrate outline to typical *Tethyochonetes* characterized by a

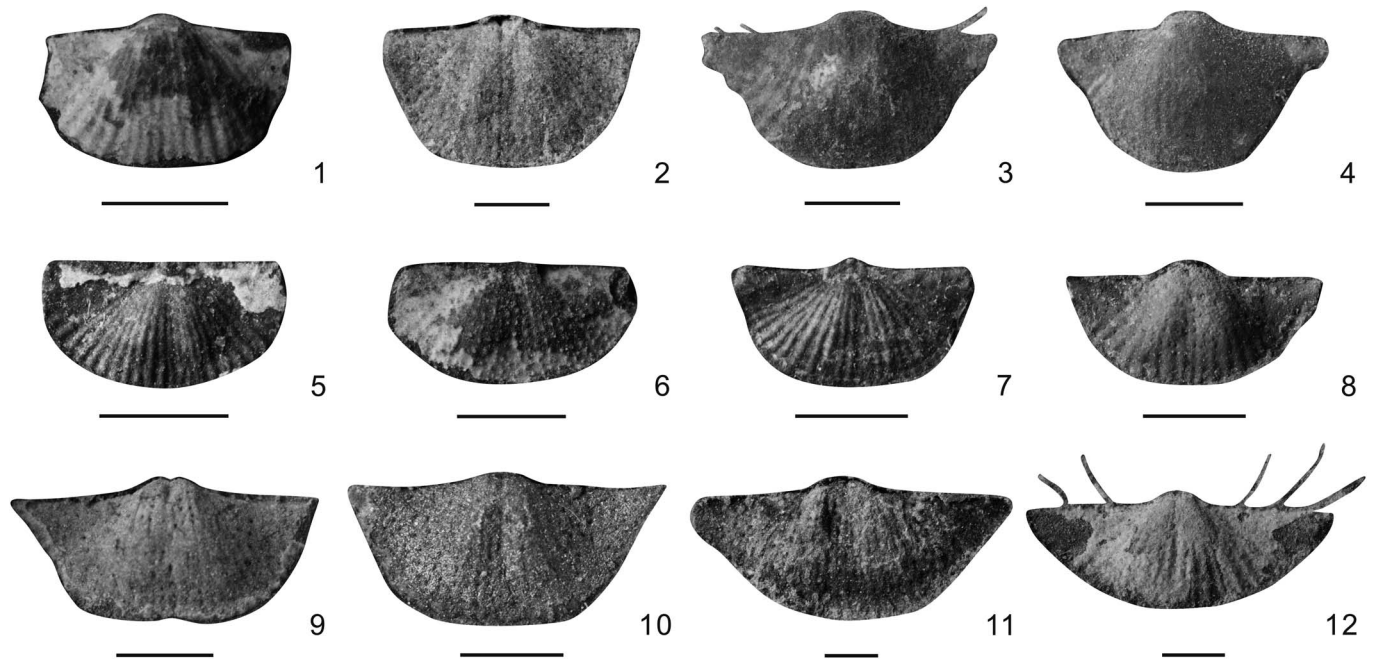


Figure 3. A range of *Fusichonetes* specimens from the Xinmin section showing a continuum of external morphological variation from a typical quadrate-shaped individual (1) to a more transform-shaped individual (12): (1, 2) *Fusichonetes pygmaea*, ventral valve exterior, CUG20309; ventral valve internal mold, CUG23702; (3, 4) *Fusichonetes cheni*, ventral valve exteriors, CUG22202, CUG23801; (5, 6) *Fusichonetes rectangularis*, dorsal valve external mold, CUG20011; dorsal valve interior, CUG21009; (7, 8) *Fusichonetes chaoi*, dorsal valve external mold, CUG19104; ventral valve internal mold, CUG21228; (9, 10) *Fusichonetes soochowensis*, ventral valve internal molds, CUG24110, CUG23910; (11, 12) *Fusichonetes nayongensis*, ventral valve internal mold, CUG25424; ventral valve exterior, CUG24924. All scale bars = 2 mm.

more quadrate outline (Fig. 3). On this basis, we hypothesized that the entire collection, in all probability, should only be assigned to one genus, not two. If this hypothesis is correct, we further propose that the two genera be synonymized with *Fusichonetes* taking priority because it was proposed before *Tethyochonetes*.

Thus, the purpose of this paper is to test this hypothesis by applying several quantitative and analytical procedures (bivariate plots, Kolmogorov-Smirnov test, categorical principle component analysis, and cladistic analysis) to a dataset of quantified morphological variables comprising both external and internal characters from all well-known *Fusichonetes* and *Tethyochonetes* species plus newly collected specimens from the Xinmin section.

Materials and methods

In this study, 330 well-preserved specimens belonging to 13 *Tethyochonetes* species and two *Fusichonetes* species were selected from the literature, as well as from our own fieldwork at the Xinmin section. The 130 specimens measured from literature were selected from those only with adequate description and photographic illustrations. The remaining 200 specimens were systematically collected from the Talung Formation of the Xinmin section, which was located in the northern margin of a deep-water basin in South China during the Permian–Triassic transition (Fig. 2.1). All specimens figured in this paper from the Xinmin section are stored in the Faculty of Earth Sciences, China University of Geosciences (Wuhan), China, with prefixes CUG.

At this section, the Permian–Triassic boundary is defined by the first occurrence of the typical basal Triassic conodont species

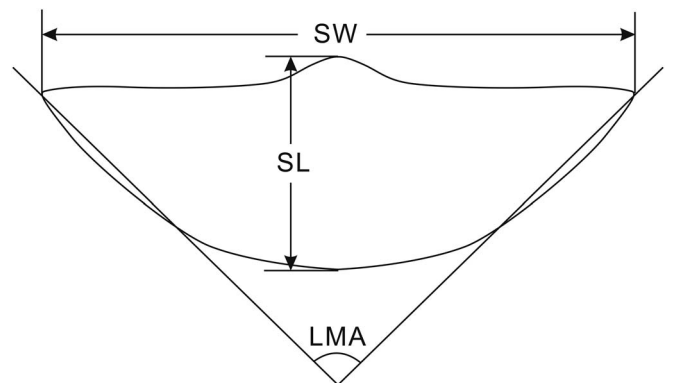


Figure 4. Biometric measurements of external shell morphology used for this study. The full explanation of abbreviated morphological variables is given in Table 1.

Hindeodus parvus (Kozur and Pjatakova, 1976) in the middle of Bed 36 (Zhang et al., 2014), within the uppermost part of the Talung Formation. The Talung Formation is dominated by siliceous mudstone, siliceous limestone, and shale, intercalated with siltstone and calcareous mudstone, suggesting an outer-shelf to deep-basin paleoenvironment (Feng et al., 1997). Apart from brachiopods including the rugosochonetidines studied here, the Talung Formation also contains abundant ammonoids, bivalves, and radiolarians, as well as plant fragments.

For each studied specimen, six numerical variables and nine categorical variables were recorded (Fig. 4; Table 1). Some variables have been adopted from previous studies using similar morphometric and phylogenetic approaches for brachiopod taxonomy (e.g., Shi and Waterhouse, 1991; Bauer and Stigall,

Table 1. Numerical and categorical variables measured in *Fusichonetes* and *Tethyochonetes* (see Figure 4 for illustration of the chosen variables in a hypothetical rugosoconetid shell).

Code No.	Variables	Abbreviation	Unit	Score		
				0	1	2
Numerical	1	Costellae amount	CA	-		
	2	Density of papillae in marginal area	DP	/mm ²		
	3	Lateral margin angle	LMA	°		
	4	Shell length	SL	mm		
	5	Shell width	SW	mm		
	6	Width/length ratio	WLR	-		
Categorical	7	Costellae complexity	CC	Simple pointed	Slightly bifurcated	Moderately bifurcated
	8	Cardinal extremity	CE	Flat	Acutangular	Obtuse
	9	Ear convexity	EC	Smooth	Slightly inflated	
	10	Ear ornamentation	EO	Small	Slightly costellate	
	11	Ear size	ES	Absent/weak	Medium	Large
	12	Sulcus development	SD	Well demarcated	Moderately developed	Distinctly developed
	13	Transition of ear to visceral area	TEV		Not well demarcated from visceral region	
	14	Umbonal region width	URW	Moderate	Broad	
	15	Valve convexity	VC	Flat	Moderately developed	Strongly

2016). Others, mainly those concerning the complexity of costellae and ears, represent morphological characters widely regarded as important for distinguishing conetid genera and species (Brunton et al., 2000; Chen et al., 2000; Shen and Archbold, 2002). The quantitative values for all variables were collected from either complete ventral valves or complete dorsal valves. For body-size measurements (length, width) taken from the literature, they were measured from the published actual fossil illustrations with a digital caliper from the Foxit Reader to the nearest 0.1 mm. According to Krause et al. (2007), size estimates of brachiopod fossil shells from photographed images correlate well with their real sizes and can therefore be used for studies of body size variations. For specimens from the Xinmin section, the width and length were measured from the actual specimens with a vernier caliper to the nearest 0.1 mm.

Four different approaches were applied to the dataset, in order to test and visually demonstrate whether species of *Fusichonetes* and *Tethyochonetes* could be distinguished with rigor. First, we used simple bivariate plots and linear regression models to analyze and visually depict the relationships between certain pairs of key morphological variables (e.g., shell length versus width, density of costellae versus shell outline, shell shape [outline] versus shell length) (see online supporting data: Appendix 2).

Second, the Kolmogorov-Smirnov test was used to analyze differences in shell size and width/length ratio between the two previously recognized genera; this was carried out using the software PAST (Hammer et al., 2001). In this analysis, brachiopod shell size was approximated with the geometric mean of length and width, following Jablonski (1996).

Third, owing to the fact that our dataset is comprised of a mixture of both numerical and categorical variables (see online supporting data: Appendix 3), we performed a categorical principle component analysis (CATPCA) to conduct a multivariate analysis of the dataset. This procedure simultaneously analyzes numerical and categorical variables while reducing the dimensionality of the original data. CATPCA has been used for similar taxonomic studies (Domínguez-Rodrigo et al., 2009; Claerhout et al., 2016). The CATPCA was performed with the software SPSS Statistics 22 (SPSS Inc. Chicago, IL, USA). To maintain the category order in the quantifications on theoretical grounds,

categorical variables were discretized and optimally scaled by ordinal transformation. Since we are interested only in the relations between variables and objects, or between objects, rather than the relationships between the variables, numerical variables were scaled by numeric transformation. The discretization method selected was symmetrical normalization, given that our aim was to examine the differences or similarities between the objects.

Finally, we employed cladistics to investigate the phylogenetic relationship of the 15 species that have hitherto been assigned to the two genera. For this analytical procedure, *Neochonetes* (*Huangichonetes*) *substrophomenoides* (Waagen, 1884) and *N.* (*Sommeriella*) *strophomenoides* (Huang, 1932) were selected as outgroups. The cladistic analysis was conducted in TNT (Goloboff et al., 2008), treating continuous characters (numerical variables) ‘as such’ (Goloboff et al., 2006). For each species, the total range of measured morphometric values was adopted in order to show data information on specimen level. All measured values were transformed by log ($x+1$) for standardization (Kitching et al., 1998) (online supporting data: Appendix 4).

Results

The bivariate plots of width versus length and the number of costellae versus width/length ratio of the two genera are shown in Figure 5 and Figure 6, respectively. Figure 5 suggests that the two genera have very similar shell size variation trends through ontogeny. Figure 6, on the other hand, shows two interesting features. First, taking the dataset for both genera as a whole, the number of costellae appears quite stable and changes little with the variation of the shell outline, expressed by the width/length ratio. Second, based on this plot, the data points representing *Fusichonetes* cannot be well separated from those of *Tethyochonetes*, although *F. nanyongensis*, the type species of this genus, appears to stand out quite clearly from the rest of the plot. Also of note from Figure 6 is that although *F. nanyongensis* is more transverse than *Tethyochonetes*, they have a similar number of costellae.

To test whether the visual differences observed in Figures 5 and 6 are of any statistical significance, we applied the Kolmogorov-Smirnov test. The result suggests, while there is no

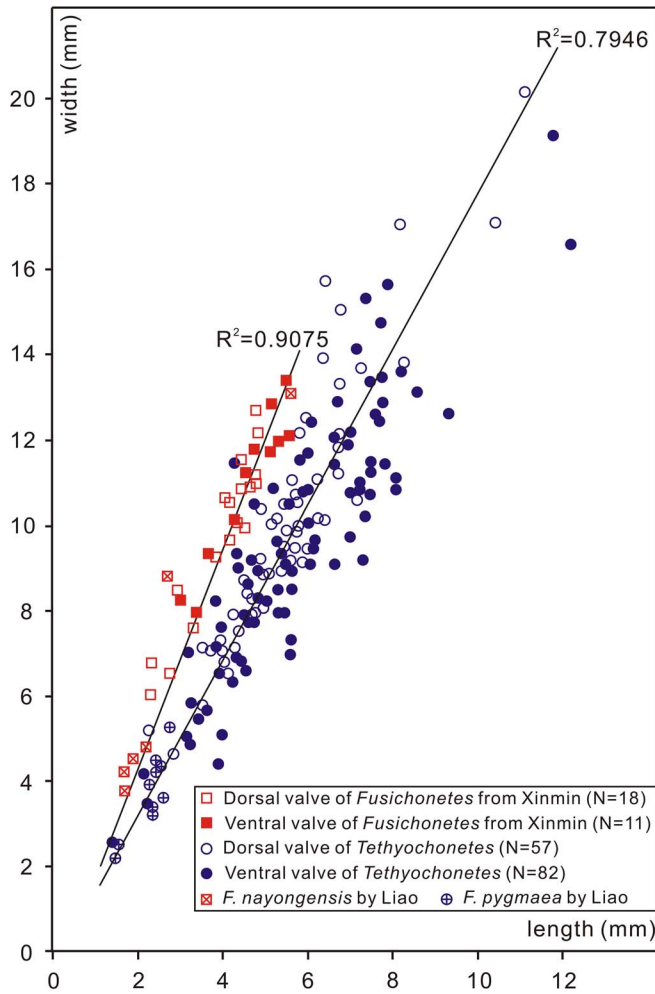


Figure 5. Graph of shell length to width of previously recognized *Tethyochonetes* and *Fusichonetes* species, plus some *Fusichonetes nayongensis* specimens from the Xinmin section.

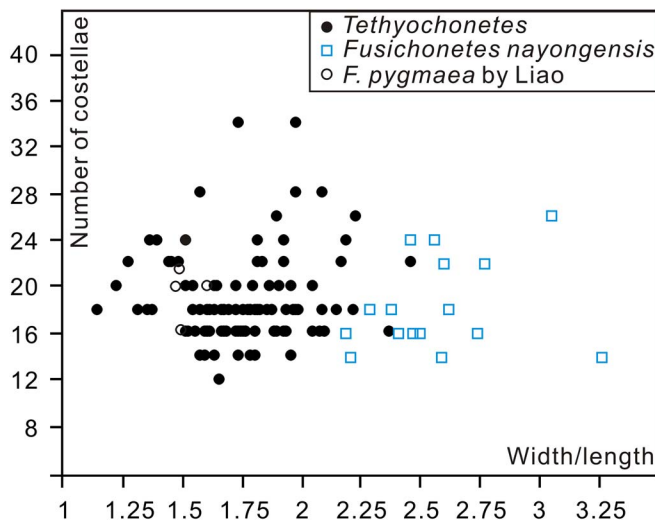


Figure 6. Graph showing the relationship between the total number of costellae and the shape (here measured by the width/length ratio) of *Tethyochonetes* and *Fusichonetes* shells (data points are comprised of measurements from literature and some *Fusichonetes nayongensis* specimens from the Xinmin section).

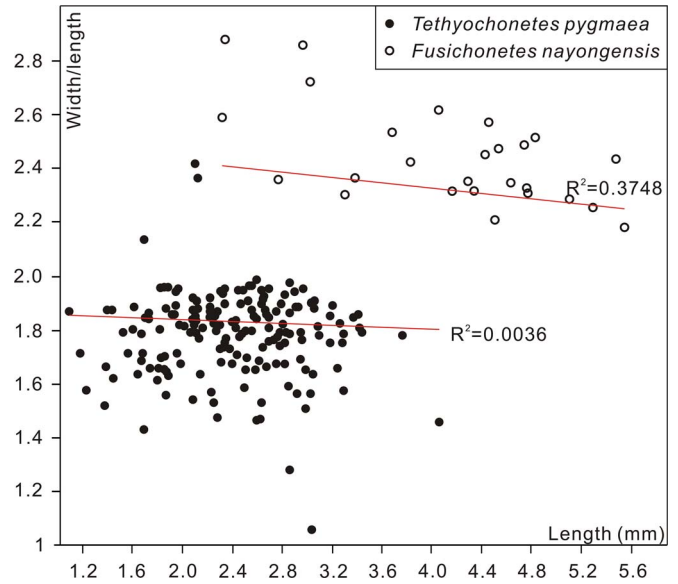


Figure 7. Linear regression of shell width/length ratio to length of *Tethyochonetes pygmaea* from bed 9, and *Fusichonetes nayongensis* from bed 24 of the Talung Formation in the Xinmin section.

significant difference in shell size among the 15 species that have previously been assigned to the two genera (Fig. 5; $D=0.2849$, $p=0.0796$), the difference in the width/length ratio between the two genera is statistically significant (Fig. 6; $D=0.7765$, $p<0.001$), suggesting a possibility of distinguishing the two genera based on their shell outline or shape.

To further investigate whether shell outline varies consistently with shell size, we used a subset of our dataset with specimens collected from discrete beds of the Xinmin section. This sub-dataset contains the measurements of shell length and width from 174 specimens representing what would be considered as *T. pygmaea* using traditional qualitative taxonomy from bed 9, and 26 specimens representing *F. nayongensis* from bed 24. As shown in Figure 7, there is no significant linear correlation between the width/length ratio and length of the shell for either of them, suggesting that the shell shape or outline, approximated by the width/length ratio, is a rather stable feature because it changes little with shell size. This would translate to mean that the shell shape does not fluctuate much with ontogeny and, therefore, could be used as a reliable parameter for the comparison of other morphological features.

The result from CATPCA is summarized in Figure 8, with the 15 species previously assigned to the two genera arranged in a biplot defined by the first two principle components (PC). PC 1 explains 25.3% of the total variance while PC 2 accounts for 16.7%. In the biplot, the 15 variables (see Table 1 for abbreviations) are projected as vectors whose lengths vary according to their variance accounted for (i.e., the longer the variable line in the plot, the larger the variance it accounts for). It is evident from the figure that the positive side of PC 1 holds *F. nayongensis*, *T. soochowensis*, and part of *T. quadrata*, *T. chaoi*, *T. guizhouensis*, *T. wongiana*, and *T. cheni*. These specimens are represented by having a significantly larger lateral margin angle (LMA) coupled with a large umbonal region width (URW). Next to this, specimens of *F. nayongensis* and *T. soochowensis*, located on the negative side of PC 2 in the

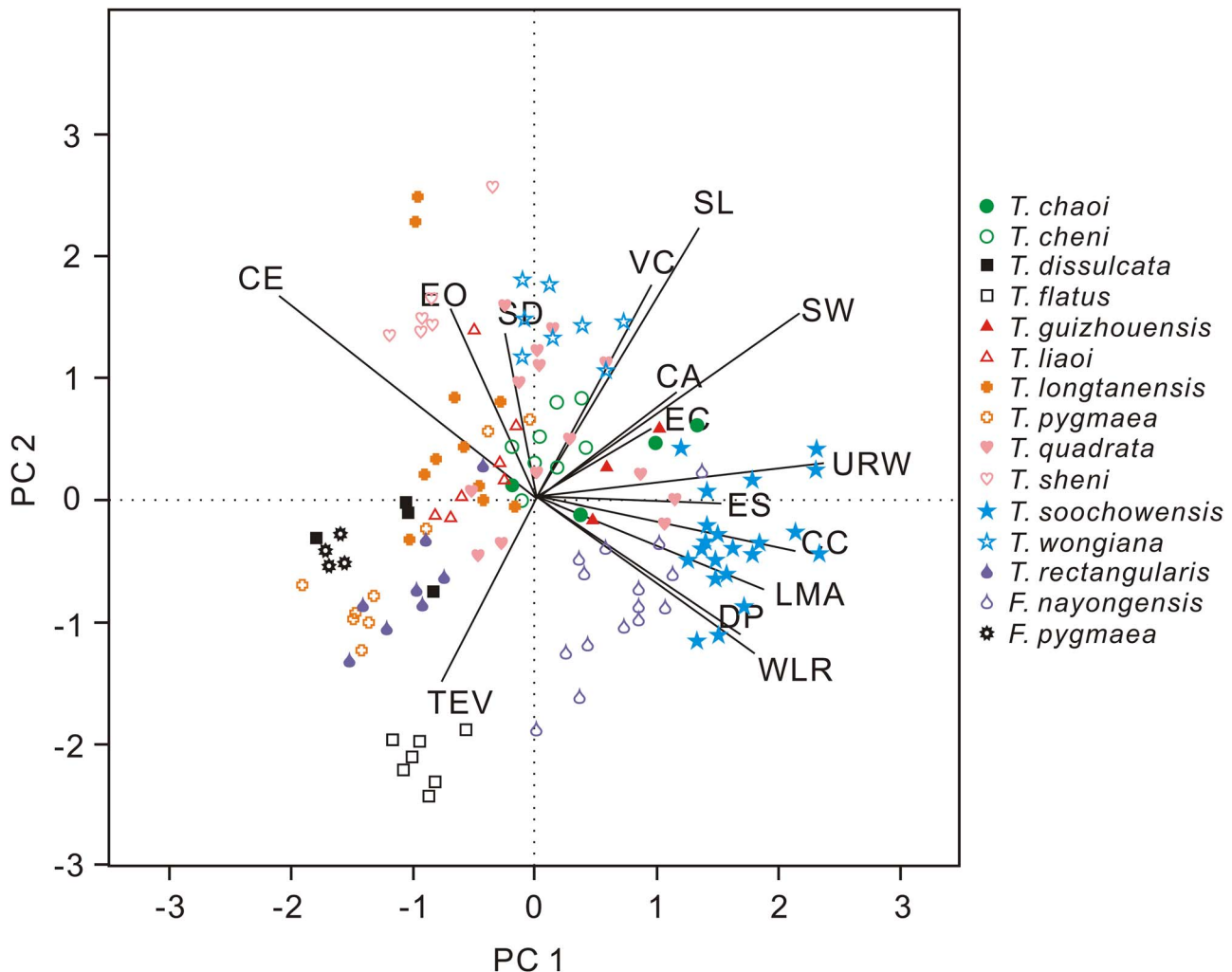


Figure 8. Result of categorical principle component analysis (CATPCA) plotted on the first two principle axes (PC 1 and PC 2). The black lines represent vectors of the analyzed 15 variables comprised of six numerical variables (CA, DP, LMA, LWR, SL, SW) and nine categorical variables. See Table 1 for explanation of abbreviations. Dashed lines divide the biplot into four quadrants according to PC 1 and PC 2.

biplot (Fig. 8), are drawn together because they both have a high width/length ratio (WLR). Specimens of *F. pygmaea* are located on the negative side of both PC 1 and PC 2, and possess ears that are not well demarcated from the visceral region. *Fusichonetes pygmaea* and most *T. pygmaea* are both restricted to the left side of the plot and, in particular, cluster closely together in the lower left quadrant of the plot. This is because both species have ears that are not well demarcated from visceral area (TEV). Overall, CATPCA, as shown in Figure 8, suggests that data points for *F. nayongensis* and *F. pygmaea* are well merged with those of *Tethyochonetes* and, hence, the two genera cannot be well separated based on the multivariate analysis of both external and internal morphological characteristics.

The cladistic analysis resulted in three most parsimonious trees with 29.2 TL (CI: 0.543, RI: 0.602). Their strict consensus tree (Fig. 9) demonstrates a monophyletic group including the *F. nayongensis*-*T. chaoi*-*T. wongiana*-*T. cheni* clade, and three species (*T. soochowensis*, *T. quadrata*, and *T. guizhouensis*) as sister taxa. This tight grouping, consisting of a clade and three sister taxa, is also supported by the biplot mentioned above in that all these species are located on the positive side of PC 1,

grouped together by having larger values of LMA (3) and URW (14) (Fig. 8). Notably, in Figure 9, *F. pygmaea* is shown to group together with *T. pygmaea* and *T. liaoi* as sister taxa, rather than with its supposed co-generic species *F. nayongensis*. Furthermore, in accord with the cladistic analysis, *F. pygmaea* and *F. nayongensis* appear to represent a polyphyletic group (Fig. 9).

Discussion

In view of the preceding descriptions and interpretations derived from the four different analytical procedures applied to the same dataset, it is clear that: (1) *F. pygmaea* and *F. nayongensis*, originally recognized as two distinct species within the same genus by Liao (1979, 1980b, 1981), in fact have considerably disparate morphological features and thus cannot be treated as forming a closely related coherent group; and (2) when the currently known species of both *Fusichonetes* and *Tethyochonetes* are analyzed together based on a common set of both external and internal morphological features, regardless of the analytical method used, they cannot be separated as two

distinct genera with consistency and rigor. Instead, as particularly demonstrated by the cladistic analysis (Fig. 9), they appear to constitute a highly coherent monophyletic clade evolved from *Neochonetes*. Consequently, we conclude that *Tethyochonetes* should be considered as a junior synonym of *Fusichonetes* and, as such, be suppressed as an invalid genus name.

Following from this, it is necessary to provide an updated and refined diagnosis for *Fusichonetes*. In part, this is essential because the original genus diagnosis given by Liao contained little information about the internal features. On the other hand,

merging *Tethyochonetes* with *Fusichonetes* by suppressing the former means that all previously recognized *Tethyochonetes* species need to be transferred to *Fusichonetes*, thus substantially increasing the species composition of this genus. Another strong reason for updating and expanding the genus diagnosis of *Fusichonetes* is due to the availability of a large number of exceptionally well-preserved materials from the Xinmin section, including both dorsal and ventral interiors that show important internal features unknown to previous studies.

Emended genus diagnosis for *Fusichonetes*.—Small to medium in size, 1.47–11.77 mm long and 2.22–20.14 mm wide (online supporting data: Appendix 5); transversely rectangular to reverse trapezoidal in outline, width/length ratio 1.13–3.26, and lateral margin angle 14°–101° (online supporting data: Appendix 5); concavoconvex to almost planoconvex in lateral profile; ears normally smooth, flattened or slightly swollen; external surface ornamented by simple costellae, occasionally with micro-ornament of tubes; sulcus and fold variable. Ventral interior with median septum; dorsal interior with median septum, lateral septa (possibly) and brachial scars, cardinal process quadrilobate; internal surface of both valves with radially distributed papillae.

Distinguishing *Fusichonetes* from similar chonetid genera.—As defined, *Fusichonetes* bears some similarities with several other rugosochonetid genera (Fig. 10). The genus is similar to *Quinquenella* Waterhouse, 1975, because both have a subquadrate outline, a moderately concavoconvex profile, and similar ventral interior, but differ in the latter having concentric stria, a long accessory septa in the dorsal interior, and lacking costellae. *Rugaria* Cooper and Grant, 1969 can be easily distinguished from

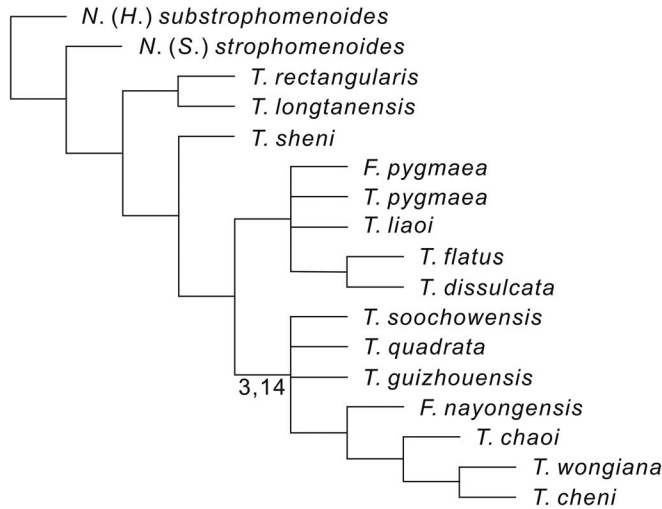


Figure 9. A strict consensus tree of three most parsimonious trees (TL: 29.2; CI: 0.543; RI: 0.602). Code number 3 represents variable LMA (lateral margin angle), 14 represents variable URW (umbonal region width).

characteristic genus	shape	lateral profile	costellae	sulcus	papillae	ventral interior		dorsal interior			age	type species
						median septum	vascular trunks	median septum	accessory septa	lateral septa		
<i>Fusichonetes</i> Liao in Zhao et al., 1981	subquadrate	moderately concavoconvex	simply costellate	shallow	moderate	short	absent	short	?	?	Wuchiapingian –Griesbachian	
<i>Tethyochonetes</i> Chen et al., 2000	subquadrate	moderately concavoconvex	simply costellate	deep– absent	moderate	short	absent	short –long	absent	short	Capitanian– Griesbachian	
<i>Quinquenella</i> Waterhouse, 1975	subquadrate	moderately concavoconvex	absent	weak– absent	moderate	long	absent	short	long	short	Permian	
<i>Rugaria</i> Cooper and Grant, 1969	subquadrate	strongly concavoconvex	costate	weak– absent	coarse	?	absent	short	absent	absent	Permian	
<i>Prorugaria</i> Waterhouse, 1982	subquadrate	moderately concavoconvex	costate	moderate	coarse	?	absent	short	long	short	lower Carboniferous	
<i>Neochonetes</i> Muir-wood, 1962	subquadrate– semicircular	moderately concavoconvex	costellate	deep– absent	fine in marginal area	short	strong	short –long	absent	short	Carboniferous –Griesbachian	
<i>Pygmochonetes</i> Jin and Hu, 1978	semicircular	strongly concavoconvex	costellate	absent	moderate	long	absent	short	long	absent	Kugurian– Changhsingian	
<i>Linshuichonetes</i> Campi and Shi, 2002	subquadrate– semicircular	moderately concavoconvex	simply costellate	weak– absent	moderate	long	absent	absent	absent	absent	Artinskian	
<i>Waagenites</i> Paeckelmann, 1930	quadrate	strongly concavoconvex	costate	deep	coarse	long	strong	long	absent	short	Carboniferous –Permian	
<i>Waterhouseiella</i> Archbold, 1983	subquadrate	strongly concavoconvex	costellate	weak– absent	moderate	long	variably developed	long	absent	short	Permian	

Figure 10. Comparison of *Fusichonetes* and *Tethyochonetes* with selected other morphologically similar chonetid genera. Gray blocks show the distinctive characteristics dividing genera from each other. Question marks indicate information that was not provided by the original authors when the genera were proposed. Holotype specimens of all genera are from the original references (Cooper and Cooper, 1969; Waterhouse, 1975; Jin and Hu, 1978; Zhan, 1979; Liao, 1980a; Waterhouse, 1982; Campi and Shi, 2002), except for *Neochonetes* from Racheboeuf (2000) and holotype specimens of *Waagenites* and *Waterhouseiella* separately from Waagen (1884) and Waterhouse and Piyasin (1970). Scale bars = 5 mm.

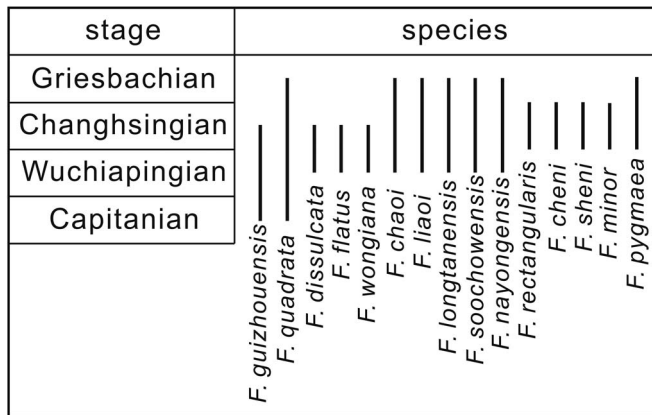


Figure 11. Stratigraphic ranges of all *Fusichonetes* species as recognized in this paper, including species that had previously been assigned to *Tethyochonetes*.

Fusichonetes by having a strongly concavoconvex profile and much coarser papillae and costae, although *Rugaria* also has a subquadrate outline and short dorsal median septum. *Prorugaria* Waterhouse, 1982, a Mississippian genus, is similar to *Fusichonetes* in having a subquadrate outline, but can be distinguished from the latter in having coarser papillae and costae and long accessory septa in the dorsal interior. *Neochonetes* Muir-Wood, 1962 differs from *Fusichonetes* in having a larger size, denser and bifurcate costellae, and papillae increasing in number and decreasing in size towards margin (Wu et al., 2016). *Pygmochonetes* Jin and Hu, 1978 could be easily distinguished from *Fusichonetes* by having a semicircular outline, being strongly concavoconvex, and lacking a sulcus and long accessory septa in the dorsal interior. *Linshuichonetes* Campi and Shi, 2002 differs from present genus in lacking any median, accessory or lateral septa. *Waagenites* Paeckelmann, 1930 differs from *Fusichonetes* by its much coarser costae, a more highly convex ventral valve and very incurved umbo. *Waterhousiella* Archbold, 1983 is similar to the present genus in its simple costellae, but differs in having a more convex ventral valve and vascular trunks developed in the ventral interior.

Implications for survival of brachiopods in the aftermath of the PTBME.—A final point that is worth mentioning is the implication of this study in relation to the survival of brachiopods in the aftermath of the PTBME. According to some previous studies on the Permian–Triassic brachiopods (Yang et al., 1987; Shen and Shi, 1996; Chen et al., 2005; Shen et al., 2006; Clapham et al., 2013; Ke et al., 2016), there are 17 Changhsingian brachiopod genera that survived into the aftermath of the PTBME, but did not play a role in the post-extinction recovery. After merging the two genera, the revised number of surviving Permian brachiopod genera is now 16, including *Fusichonetes*, as revised and its species expanded here. Following this revision, the expanded *Fusichonetes* includes a total of 15 species at present time, comprised of 13 species transferred from *Tethyochonetes* and two original *Fusichonetes* species. Among the 15 species, two originated from the Capitanian (late Guadalupian), eight from the Wuchiapingian (early Lopingian) and five originated from the Changhsingian (late Lopingian), seven of which survived the PTBME until their final disappearance at the early Griesbachian (Chen et al., 2005)

(Fig. 11). Paleogeographically, these species were all restricted to the shallow- to moderately deep-marine environments of the Paleo-Tethys and Neo-Tethys region (Wu et al., 2016).

Conclusions

Four different approaches (bivariate plots, Kolmogorov-Smirnov test, categorical principle component analysis, and cladistic analysis) were employed to analyze a dataset composed of 15 species belonging to *Fusichonetes* and *Tethyochonetes* by 15 variables. The variables chosen are a mixture of both numerical and categorical characters and include important external and internal morphological features. Except for the Kolmogorov-Smirnov test demonstrating the possibility of separating the two genera in terms of shell outline approximated by the shell width/length ratio, all other analytical procedures suggest that species of the two genera cannot be separated as two distinct taxa with consistency and statistical rigor. Consequently, we conclude that: (1) *Tethyochonetes* and *Fusichonetes* be merged, and (2) *Fusichonetes* be maintained as a valid genus in recognition of its chronological priority over *Tethyochonetes*, while the latter be suppressed as an invalid genus. With this revision and the merger of the two genera, the diagnosis of *Fusichonetes* is updated and refined, in part based on observations of new well-preserved material from South China. Additionally, the number of brachiopod genera that survived the Permian–Triassic boundary mass extinction is revised from 17 to 16.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vb051>

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