



Qiu, X., Xu, Y., Chen, Z. Q., Benton, M. J., Wen, W., Huang, Y., & Wu, S. (2019). The Early Triassic Jurong fish fauna, South China: Age, anatomy, taphonomy, and global correlation. *Global and Planetary Change*, 180, 33-50. <https://doi.org/10.1016/j.gloplacha.2019.05.012>

Peer reviewed version

License (if available):
CC BY-NC-ND

Link to published version (if available):
[10.1016/j.gloplacha.2019.05.012](https://doi.org/10.1016/j.gloplacha.2019.05.012)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the accepted author manuscript (AAM). The final published version (version of record) is available online via Elsevier at <https://doi.org/10.1016/j.gloplacha.2019.05.012> . Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: <http://www.bristol.ac.uk/pure/user-guides/explore-bristol-research/ebr-terms/>

Accepted Manuscript

The Early Triassic Jurong fish fauna, South China: Age, anatomy, taphonomy, and global correlation

Xincheng Qiu, Yaling Xu, Zhong-Qiang Chen, Michael J. Benton, Wen Wen, Yuangeng Huang



PII: S0921-8181(18)30719-7
DOI: <https://doi.org/10.1016/j.gloplacha.2019.05.012>
Reference: GLOBAL 2972
To appear in: *Global and Planetary Change*
Received date: 26 December 2018
Revised date: 20 May 2019
Accepted date: 29 May 2019

Please cite this article as: X. Qiu, Y. Xu, Z.-Q. Chen, et al., The Early Triassic Jurong fish fauna, South China: Age, anatomy, taphonomy, and global correlation, *Global and Planetary Change*, <https://doi.org/10.1016/j.gloplacha.2019.05.012>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

The Early Triassic Jurong fish fauna, South China: age, anatomy, taphonomy, and global correlation

Xincheng Qiu^a, Yaling Xu^a, Zhong-Qiang Chen^{a,*} zhong.qiang.chen@cug.edu.cn,
Michael J. Benton^b, Wen Wen^c, Yuangeng Huang^a

^aState Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan), Wuhan 430074, China;

^bSchool of Earth Sciences, University of Bristol, BS8 1 QU, UK;

^cChengdu Center of China Geological Survey, Chengdu 610081, China

*Corresponding author.

Abstract

As the higher trophic guilds in marine food chains, top predators such as larger fishes and reptiles are important indicators that a marine ecosystem has recovered following a crisis. Early Triassic marine fishes and reptiles therefore are key proxies in reconstructing the ecosystem recovery process after the end-Permian mass extinction. In South China, the Early Triassic Jurong fish fauna is the earliest marine vertebrate assemblage in the recovery period. It is constrained as mid-late Smithian in age based on both conodont biostratigraphy and carbon isotopic correlations. The Jurong fishes are all preserved in calcareous nodules embedded in black shale of the Lower Triassic Lower Qinglong Formation, and the fauna comprises at least three genera of Paraseminotidae and Perleididae. The phosphatic fish bodies often show exceptionally preserved interior structures, including network structures of possible organ walls and cartilages. Microanalysis reveals the well-preserved micro-structures (i.e. collagen layers) of teleost scales and fish fins. Abundant small pyrite framboids, 2–5 μm in diameter, are detected from the nodules and fish body surfaces, indicating a calm, euxinic burial environment. Coccoid-like microspheroids are also very abundant in the host rocks and near the fish fossil surfaces, implying that microbes may have participated in the burial process of the fishes. Taphonomic analysis uncovers the four-step formation process of the fish nodules. (1) Fishes lived in the oxic seawater in the upper ocean, and (2) their bodies sank to the anoxic seabed after death, with the body surface being wrapped by bacteria. (3) Microbial biofilms sealed body surfaces to prevent or delay the decay of the fleshy body. The decomposition of the body cavity and interior organs produced some CO_2 and H_2S gases. The former formed bicarbonate ions in seawater and attracted calcium ions to facilitate the precipitation of calcium carbonate, while the H_2S combined with iron ions in seawater to form pyrite framboids. (4) The fish nodule gradually grew by precipitation of calcium carbonate in layers and embedding with pyrite framboids, and later the fish fossil nodule was compacted during diagenesis. Global faunal correlations indicate that the Jurong fishes are closely related to the Early Triassic fish faunas from Chaohu, Anhui Province and Madagascar.

Keywords: Lower Triassic, fish nodule, redox condition, ecosystem, taphonomy

ACCEPTED MANUSCRIPT

1. Introduction

After the devastating biocrisis at the end of the Permian (e.g. Erwin, 2006), marine ecosystems experienced a much more prolonged recovery process than in the aftermath of any other mass extinction (Chen and Benton, 2012). Marine vertebrates (i.e. fishes, reptiles) often represent the higher trophic guilds in food chains, and their presence in the Early Triassic therefore is crucial in reconstructing the ecosystem recovery process (Benton et al., 2013). Lower Triassic marine successions yield a few fish faunas worldwide, such as Chaohu (Tong et al., 2006) and Jurong (Qian et al., 1997; Liu et al., 2002) in South China, India (Romano et al., 2016b), Madagascar (Beltan, 1996; Falconnet and Andriamihajia, 2012), Spitsbergen (Weitschat, 2008; Romano and Brinkmann, 2010), Greenland (Mutter, 2005; Kogan, 2011), British Columbia in Western Canada (Mutter and Neuman, 2008a, b; Neuman and Therrien, 2015), and Idaho in the USA (Romano et al., 2012). Interestingly, all these Early Triassic fish fossils are preserved in calcareous nodules embedded in black shales/mudstones. The diversity dynamics and body size evolution of Permian–Triassic Osteichthyes (bony fishes) have been studied by Romano et al. (2016a). Although these Lower Triassic fish faunas have been taxonomically documented (Qian et al., 1997; Liu et al., 2002; Mutter, 2005, Mutter and Neuman, 2008a), there are very few studies (but see Beltan, 1996; Zhou et al., 2015) concerning their anatomy and taphonomy.

In South China, a moderate fish fauna has been documented from the Lower Qinglong Formation in the Qingshan section of Jurong City, southern Jiangsu Province, South China (Qian et al., 1997; Liu et al., 2002; Jin et al., 2003; Jin, 2006; Tong et al., 2006; Fig. 1). Six fish species have been identified in the Jurong fish fauna, namely *Plesioperleidus jiangsuensis* Qian (in Qian et al., 1997), *Suius brevis* Liu (in Liu et al., 2002), *Stensionotus dongchangensis* Liu (in Liu et al., 2002), *Qingshania cercida* Liu (in Liu et al., 2002), *Jurongia fusiformis* Liu (in Liu et al., 2002), and *Lepidontes jurongensis* Qian (in Qian et al., 1997). Of these, *P. jiangsuensis* is assigned to the Perleididae, and the other five species to the

Parasemionotidae (Tong et al., 2006). However, insufficient anatomical information prevents precise identification of these Early Triassic fishes to generic or even familial level (Lombardo, 2001; Zuo et al., 2013; Marramà et al., 2017). Accordingly, it is essential to update knowledge of the Jurong fish fauna.

There have been disputes over dating. The upper Lower Qinglong Formation was dated as Dienerian based on conodont and bivalve faunas in southern Jiangsu Province (Wang, 1991), and this age assignment was followed by Sun et al. (2012). However, the Jurong fish fauna closely resembles the Helongshan Formation fishes of the adjacent Chaohu section in Anhui Province in terms of faunal composition and lithology of the fish-bearing strata (Chen et al., 2011; Li, 2009). Abundant conodonts date the Helongshan Formation as late Smithian in the Chaohu section (Zhao et al., 2007). Accordingly, Benton et al. (2013) re-assigned the Jurong fishes to a late Smithian age. Nevertheless, no conodonts have been extracted directly from the Qingshan section of the Jurong area, and the age of the Jurong fish fauna remains uncertain.

Here we document new fish materials extracted from the Qingshan section of the Jurong area, which are investigated alongside a diverse new data set including new conodont biostratigraphy, pyrite framboid analysis, carbon isotopes values, anatomy, and taphonomy, that reveals (1) the age of the Jurong fish fauna, (2) taxonomic notes and faunal correlations, (3) anatomy of fishes, and (4) taphonomy and formation process of the fish nodules.

2. Geological and stratigraphic setting

The Qingshan section (Fig. 2A) is located in Jurong City, southern Jiangsu Province, which was situated on the north-eastern margin of the Yangtze Platform during the Early Triassic (Feng et al., 1997; Fig. 1). The fish-bearing successions are assigned to the lower–middle part of the Lower Qinglong Formation, which is subdivided into three members. The lower member is dominated by medium-bedded argillaceous limestone and mudstone. The middle member (Beds 7 to 15) consists

mainly of thin layers of argillaceous limestone, calcareous mudstone, and black shale with calcareous nodules (Fig. 2B–D) and abundant horizontal bedding. The upper member comprises argillaceous limestone and vermicular limestone (Fig. 3).

Fish fossils are preserved in calcareous nodules embedded in black shales and mudstones of the middle member of the Lower Qinglong Formation in the Qingshan section (Figs. 2B–C, 3). Ammonoids and trace fossils are also abundant in the Lower Qinglong Formation in the study section. Most ammonoids are represented by external moulds, which prevent precise identification. Trace fossils are composed mainly of horizontal, simple and non-branched worm tubes of *Planolites* and a few *Palaeophycus* burrows (Chen et al., 2011; Feng et al., 2017).

3. Materials and methods

All analyzed samples were collected from the Lower Qinglong Formation in the Qingshan section, including 25 conodont samples, 53 carbon isotopes samples, 38 pyrite framboid samples, and over 80 fish nodules.

3.1. Conodont specimen process and extraction

Twenty-five conodont samples were collected within a sampling interval of 10–50 cm in the Qingshan section. Acetic acid at 10 % concentration was used for sample dissolution, and individual conodont specimens were picked under the microscope after they were extracted (Zhao et al., 2013). The conodonts were identified and photographed using a Scanning electron microscope (SEM, Hitachi SU8010) at the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan).

3.2. Fish specimen preparation

Fish fossils were studied in terms of identification and anatomy. We chose

complete fish fossils from the tubercular plane of the long axis of the carbonate nodules (Supplementary materials, Fig. S1, Plane OAC) for identification. Cross sections of nodules (Supplementary materials, Fig. S1, Plane OBC) were also polished to observe fossils, microorganisms, and fish internal structures under the microscope. The SEM was also used to observe the surface micro-structures and internal anatomy of the fish fossils at higher accuracy. According to observations of thin sections and SEM images, we inferred the processes of burial and formation of the nodules, combined with the existing mechanisms of biological nucleation.

3.3 Thin section, SEM, and pyrite framboid analysis

Some samples were ground into thin sections and observed under the polarized light microscope to study petrology and to measure the grain size of the pyrite framboids, which can indicate redox conditions (Wilkin et al., 1996; Bond and Wignall, 2010; Chen et al., 2015; Huang et al., 2017, 2019a). Thirty-eight pyrite framboid samples were observed under SEM using the back-scattering mode (BSE) for pyrite framboid analysis, following the methods of Huang et al. (2017). Measurement accuracy is higher than 0.1 μm when measuring directly on the SEM screen. When a pyrite framboid is transected through its margins, instead of its centre, this analysis results in a value smaller than its true diameter, but calculations show that the difference does not exceed 10% (Wilkin et al., 1996). If the sample is strongly weathered, pyrite framboids therefore are also oxidized to some extent, and may be replaced by iron oxides. The oxidized grains of framboids may involve a theoretical molar volume loss ranging from 13.0% to 38.1% (Wilkin and Barnes, 1997). Statistical study of the oxidized pyrite framboids from weathered samples of the Permian–Triassic boundary beds in the Kashmir area, northern India reveals that the weathered framboids are only oxidized in the outer parts, and the mean size of oxidized pyrite framboids is 2.17% less than unaltered pyrite framboids, resulting in a bias even less than the measurement error (<10%; Wilkin et al., 1996; Huang et al., 2019a). Accordingly, some oxidized pyrite framboids from the weathered samples are

also suitable for identifying redox conditions (Huang et al., 2019a).

3.4. Carbon isotopes

Carbon isotope stratigraphy is often used for Lower Triassic stratigraphic correlations across the South China (Tong et al., 2007). A total of 53 carbon isotopes samples were collected in the Qingshan section, avoiding calcite veins and outcrops with high degrees of weathering. All samples were tested by Thermo-Fisher MAT-251 at the State Key Laboratory of Geological Process and Mineral Resources, China University of Geosciences (Wuhan) with the 200-mesh powder. For the analysis we adopted the national standard sample (GBW04416: $\delta^{13}\text{C PDB} = (1.6 \pm 0.03) \text{‰}$, $\delta^{18}\text{O PDB} = (-8.29 \pm 0.15) \text{‰}$), and the standard deviations of the measured values of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ were less than 0.1‰.

4. Results

4.1. Conodont biostratigraphy

In total, 83 well-preserved conodont specimens were extracted from 25 samples in the Lower Qinglong Formation of the Qingshan section, and nine species including one indeterminate species belonging to seven genera of conodonts were identified (Figs. 4–5), including *Cratognathodus kochi*, *Cypridodella* cf. *subsymmeirica*, *Ellisonia gradate*, *Neospathodus dieneri*, *Ns.* sp., *Novispathodus radialis*, *Nv. pingdingshanensis*, *Scythogondolella lachymiformis*, and *Sc. milleri* (Fig. 3). Of these, *Ns. dieneri*, *Nv. pingdingshanensis*, and *Sc. milleri* are biostratigraphically important elements.

4.2. Taxonomic notes and fish anatomical features

4.2.1. Taxonomic notes and fish faunal compositions

Of the previously reported fish taxa from the Lower Qinglong Formation, the most disputed taxonomic assignment is *Plesioperleidus jiangsuensis* (Qian et al., 1977; Liu et al., 2002; Jin et al., 2003; Jin, 2006; Tong et al., 2006). Similar specimens were named as two new species, *Perleidus jiangsuensis* Qian (in Qian et al., 1997) and *Perleidus piveteaui* Liu (in Liu et al., 2002). Later, Jin et al. (2003) argued that these two species are synonymous, and erected a new genus, *Zhangina* Jin et al., 2003, to accommodate them, with the single species *Zhangina jiangsuensis* (Qian, 1997). In contrast, Tong et al. (2006) re-assigned Qian's species to another genus, *Plesioperleidus*, based on study of similar materials from uppermost Smithian strata (lower Olenekian) of the neighbouring Chaohu area, Anhui Province, South China. In South China, Early Triassic "*Perleidus*" was first ascribed to *Peia*, and then to *Plesioperleidus* (Jin et al., 2003; Jin, 2006; Tong et al., 2006). None of these anatomical analyses of *Plesioperleidus* mentioned details of the caudal fin. However, Lombardo (2001) has clearly shown that the absence of epaxial rays prevents any taxa from being ascribed either to the Perleididae or Perleidiformes (Sun et al., 2013). In addition, these two Early Triassic species, *Perleidus madagascariensis* and *P. piveteaui*, are also comparable with one another, and they have been considered as a single species, *madagascariensis*, which is better assigned to *Teffichthys* than to *Perleidus* since they lack epaxial rays (Marramà et al., 2017). Besides, *Teffichthys* does not belong to either the Perleididae or Perleidiformes (Marramà et al., 2017).

The illustrated specimen BGEG JR 08101 (Fig. 6A) is an incompletely preserved fish with fusiform body, lacking skull roof, snout, preoperculum, circumorbital series, most of the jaw, and the caudal fin. The operculum is slightly smaller than the suboperculum. The interoperculum is absent. At least four branchiostegal rays occur. The second specimen BGEG JR 08105 (Fig. 6B) has a relatively complete mandible. The maxilla has a narrow anterior region bearing strong and conical teeth. The posterior region is expanded. According to the shape of mandible, operculum, and suboperculum, it is proper to ascribe these two specimens to *Plesioperleidus jiangsuensis* (Qian). The specimen BGEG JR 08101 (Fig. 6A) has about 40 scale rows. The dorsal fin is displaced behind the mid-length of the body, inserting at the

level of the 21st vertical scale row. The anal fin originates at the 18th scale row. Lepidotrichia of all fins have long proximal bases, segmented and bifurcated distally. The anterior flank scales are deeper than wide, becoming rhomboidal on the caudal peduncle. The surface of scales is smooth and not serrated on their posterior margins. Based on the fin system and squamation, *Plesioperleidus* is more like *Teffichthys* than *Chaohuperleidus*. Although the caudal fin is not preserved in our specimen, *Plesioperleidus* has a hemi-heterocercal caudal fin like *Teffichthys* from a previous description (Jin et al., 2003). Thus, we suggest that *Plesioperleidus* cannot be ascribed to the Perleididae any longer. The only perleidid fish from the Early Triassic in South China is *Chaohuperleidus primus* from the upper Nanlinghu Formation (Spathian) of the Chaohu section, Anhui Province (Sun et al., 2013).

Parasemionotid fish fossils were first found in the Lower Triassic marine strata of Madagascar and Greenland (Ketchum and Barrett, 2004). The Jurong specimen BGEG JR 08201 (Fig. 6C) is relatively small with a standard length of 130 mm. The operculum is larger than the suboperculum. The latter is low and shaped as a long parallelogram. The interoperculum exists. The preoperculum is large and upright. The skull roof, snout, circumorbital series, and most of the jaws are not well preserved. The cleithrum is relatively small, while the supracleithrum and postcleithrum are relatively large. About 30 transversal scale rows are counted. These materials can be confidently assigned to the genus *Suius*, although the species remains uncertain.

Specimens BGEG JR 08401 (Fig. 6E) and BGEG JR 08501 (Fig. 6F) have a shuttle-like outline. The operculum is larger than the suboperculum. The suboperculum is relatively broad. The interoperculum is large and triangular in outline. The preoperculum is upright and fusiform, not oval in shape. The lower jaw is well preserved. The coronoid process, angular and surangular can be clearly observed. The cleithrum is arched with an enlarged ventral branch; two postcleithra are pronounced, and of these, the dorsal one is clearly longer than the ventral. About 40 transversal scale rows. The number of radials is equal to that of fin rays in the median fin. All characteristics observed suggest *Qingshania* sp.

In addition, specimen BGEG JR 08301 (Fig. 6D) has no diagnostic features, and

it is tentatively referred to ?*Stensionotus* sp. Both *Zhangina cylindrica* (Qian et al., 1997) and *Peia jurongensis* were reportedly present in this section (Li, 2009), but we did not find similar specimens in the present collection.

To sum up, the Jurong fish fossils can be confidently assigned to at least three species in three genera, *Plesioperleidus*, *Suius*, and *Qingshania*. The taxonomic assignment of other taxa is rather tentative.

4.2.2. Anatomy of fishes

Previous anatomical studies of fishes have focused on observation of the head and tail features (Weitschat, 2008; Gardiner and Schaeffer, 2010), such as the size and thickness of the sacral bone slices, the depth of the orbital bones, connections with the nasal bone, and the shape of the caudal fin, which are the main characteristics for identifying the species (Liu et al., 2002; Tong et al., 2006; Tintori, 2014). In this paper, we observe the structure of the surface and interior of the fish to understand their anatomy. Some coelacanth and the neopterygian *Marcopoloichthys* in the Anisian Luoping fauna generally retain only the skeletal parts (Wen, 2011; Wen et al., 2013). In contrast, the Jurong fish fossils retain the complete structure of the body because they are preserved in carbonate nodules.

Fish nodules were cut along the cross section (Fig. 7A), and the boundary between the fish body and the surrounding rock can be distinguished by the naked eye because the grey-white colour (Fig. 7B) of the fish body is significantly different from that of the surrounding rock. The fish body is usually surrounded by a circle of scales (Fig. 7C). The scales are yellowish brown to dark brown, ~0.3 mm thick, and they bear concentric laminae (Fig. 7E–F). Modern ichthyological studies have shown that the concentric laminae in teleost scales record the growth cycle of the fish (Shen, 2011). By comparison with such modern examples, the inner ring pattern of the scale (Fig. 7F) is loose and the outer concentric laminae are closely packed, indicating that the fish may have been only one year old when it died (Edgar, 1951; Horká et al., 2010).

Under the SEM, the scale surfaces are covered with a dense honeycomb structure

(Fig. 8B, D). Individual honeycomb holes are polygonal or elliptical, with a diameter of ~200 nm, and are connected to each other in an orderly manner. This is very similar to the surface structure of modern teleost fish scales observed by Nicolas et al. (1997) who interpreted this as an orderly superposition of collagen fibres to form a collagen layer on the surface, in which the veins of the collagen layer are microtubules and actin filaments, and the protein fills between the veins (Nicolas et al., 1997).

Energy spectrum analysis shows that the main components of the honeycomb structure of the scales (Fig. 8C–D) are P, Ca and O, indicating calcium phosphate. Perhaps during the burial process, the protein decomposes to form a cavity, and the microtubules are phosphatised. The choroidal structure of the collagen layer forms a cellular pore structure.

The cavity of the fish body is filled with calcite, which is greyish white, and a distinct calcite crystal can also be observed occasionally (Fig. 9E). Irregularly shaped network structures are common in areas with thick fish bodies (Figs. 7D, 9B–C), which are brownish yellow, appearing alone or symmetrically. Currently, it is impossible to determine if these network-like structures are internal organs or organ walls and cartilages of the fish body. More detailed anatomical detail is needed in future to clarify this. These structures, however, are probably derived from the bones of the fish because energy spectrum analysis also shows a composition of calcium phosphate, and they are non-perishable or had a slow rate of decay.

In addition, abundant fossils of ostracods and microgastropods are also scattered in the surrounding rock around the fish (Fig. 10). These gastropods are very small, between 0.3 to 3 mm in width (Fig. 10A, F). Ostracods are 0.2–1 mm wide (Fig. 10G, I), and the body comprises two symmetrical lobes, or a single embossed impression (Fig. 10I).

4.3. Carbon isotopes

Carbon isotope values in the Qingshan section range from -2‰ to 7‰ (Fig. 3), and the excursion overall shows a slow shift from negative to positive. Carbon isotope

values are relatively stable and maintained a constant value of about -1‰ from the upper part of Bed 1 to the top of Bed 6. The signal becomes slowly positive from the bottom of Bed 7 to mid-Bed 8 below the occurrence of fish nodules and reaches a peak value (1.39‰) at ~10 cm below the fish nodules. Subsequently, it becomes slowly negative, by mid-Bed 9 reaching close to 0‰. From mid-Bed 9 to mid-Bed 14, the carbon signal shows a gradual positive bias, with values remaining around 1‰ from the bottom of Bed 10 to the bottom of Bed 13. Carbon isotope values rose rapidly to more than 5‰ from the top of Bed 13 to the top of Bed 17 and reached up to 6.32‰ at the top of Bed 17, then fell back to 3‰ at the top of Bed 20.

The $\delta^{13}\text{C}$ excursion of the Qingshan section is comparable with the Early Triassic carbon isotope curve of the adjacent Chaohu section (Tong et al., 2007). In general, the carbon isotope excursions of the two sections have a certain contrast significance, and there is no significant global negative shift in the upper Smithian of the Qingshan section, corresponding to Chaohu (Liang et al., 2011; Sun et al., 2012). Moreover, a distribution diagram of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the Qingshan section shows no correlation. The relatively low coefficient ($r = 0.13$) indicates that the carbon isotope values were not affected by diagenesis (Supplementary materials, Fig. S2).

4.4. Pyrite framboid analysis

A total of 29 samples from Beds 6–16 in the Qingshan section were used to calculate the particle size distribution of pyrite framboids, and eight samples do not yield pyrite framboids (Fig. 3). A large amount of small-sized pyrite framboids was found in Beds 7–16 (Fig. 3), in which samples JR-15 and JR-17 are in the fish nodules. Pyrite framboids are preserved completely and clearly, generally appearing alone and clustered in some samples. The variations and frequency distributions of framboid sizes in the study samples are shown in Figure 3 and Supplementary materials (Fig. S3).

The total number of pyrite framboids used for statistical analysis is more than

2000, and at least 100 grains are counted for each sample. The statistical results show that the minimum particle size of pyrite framboids of each sample from Bed 7–14 is very small, only 2 μm or less; the mean of particle size is 3–5 μm , and the range of maximum particle sizes is between 6–10 μm (Fig. 3).

5. Discussion

5.1. Age of the Jurong fish fauna

The conodont species *Neospathodus dieneri* from Beds 3 and 6 (Fig. 3) is a zonal species of the Dienerian (substage) of the Induan (Zhao et al., 2007, 2008, 2013; Lyu et al., 2018, 2019). This species was first discovered in Lower Triassic strata of Pakistan (Sweet, 1970), and it is also reported in Tibet, Guizhou, and Anhui in China (Zhao et al., 2005, 2007), and Kashmir and Spiti in India (Bhatt, 1999). However, this species may extend into the Smithian substage (Zhao et al., 2007).

Another key element *Novispathodus pingdingshanensis* from Bed 16 (Fig. 3) is the zonal species of the earliest conodont zone of the Spathian substage. This zone was established in Chaohu, South China by Zhao et al. (2005, 2007). The lower limit of this zone is marked by the first occurrence (FO) of this zonal species, while the upper limit is defined by the FO of *Triassospathodus homeri* (Zhao et al., 2005, 2007, 2013; Orchard et al., 2008; Liang et al., 2011, 2016; Lyu et al., 2018, 2019). Thus, the FO of *Nv. pingdingshanensis* indicates that the age of Bed 16 is early Spathian.

Two species of *Scythogondolella*, namely *Sc. lachymiformis* and *Sc. milleri* (Fig. 3) were found in mid-Bed 9. *Sc. milleri* belongs to the last international conodont zone in the Smithian (Sweet, 1970). This species was reported in Tibet in China, the Arctic region in Canada, and the Russian Far East in the upper Smithian (Müller, 1956; Kozur and Mostler, 1976; Wang, 1991; Orchard, 2007, 2008). The occurrence of *Sc. milleri* in Bed 9 indicates that the age of this bed is late Smithian.

The Dienerian–Smithian boundary could not be determined, as the boundary-marking species *Novispathodus waageni* (Zhao et al., 2007, 2013; Lyu et al.,

2018) was not found in the Qingshan section. The strata below Bed 6 therefore are early-middle Smithian or older in age. Comparison of carbon isotope excursions suggests that the negative shift below Bed 6 may correspond to the negative excursion in the lower part of the Helongshan Formation in the Chaohu section (Fig. 3), implying that strata below Bed 6 may be early-middle Smithian in age.

In total, the age of Bed 8 containing fish nodules may be mid-late Smithian, and not younger than the latest Smithian. The Chaohu fishes came from the top of the Helongshan Formation, which is constrained as late Smithian to early Spathian in age (Zhao et al., 2007). Thus, the age of the Jurong fish fauna may be slightly older than that of the Helongshan Formation fishes in the adjacent Chaohu section.

5.2. Redox interpretation

The plot of Mean (M) vs Standard Deviation (SD) of pyrite framboid sizes is used to interpret redox conditions (Wignall and Newton, 1998; Bond and Wignall, 2010). The boundary between the euxinic and dysoxic states is determined based on the formula $M = -3.3 \cdot SD + 14$ (Fig. 11; Tian et al., 2014; Huang et al., 2017, 2019a).

The M-SD plot diagram of pyrite framboids shows that all samples are in an euxinic environment (Fig. 11). The underlying water was in an euxinic state when sediments from Beds 7–14 were deposited, according to the M-SD model (Bond and Wignall, 2010) (Fig. 3). The fish-bearing strata (Bed 8) therefore were deposited in anoxic environments. Few or no pyrite framboids were found in Beds 6, 15–16, suggesting that the seawater was no longer in an anoxic state or even in a dysoxic to oxic state during these two intervals (Bond and Wignall, 2010).

5.3. Taphonomy of fish fauna

The Jurong fish fossils are preserved intact with neatly arranged scales, and no broken fins or scales around the fish, indicating that they were buried in situ. Complete ostracods and gastropods, together with the fish, are also preserved in the

nodules.

The above pyrite framboid analyses of JR-15 and JR-17 samples indicate that the fish nodules (Bed 8) were formed in a calm and euxinic environment, as suggested by Beltan (1996). Interestingly, pyrite framboids were detected in the rock surrounding the fish body and fish body surfaces, but not within the fish body cavity (Fig. 12E–F). The same phenomenon also occurs in the contact between the ostracods or gastropods and the surrounding rocks (Fig. 12C–D), in which pyrite framboids appear in the form of aggregates (Fig. 12D). The pyrite framboids therefore were presumably formed during the formation process of the fish nodules.

In addition, a large number of microspheres that might represent coccoid-like spheroids were seen in thin sections around the fish fossils (Fig. 13); these feature a round shape with a coarse-grained calcite nucleus inside a coating layer of dark micrite (Fig. 13). Coccoid-like microspheres are very common in Lower Triassic microbialites in South China, and they have usually been interpreted as products of microbial activity in which possible sulfur-reducing bacteria were active (Ezaki et al., 2008; Yang et al., 2011; Chen et al., 2014, 2019; Luo et al., 2014, 2016; Fang et al., 2017; Wu et al., 2017; Huang et al., 2019b). The presence of many suspected spheroidal microalgae and pyrite framboids indicates that sulfur-reducing bacteria may have participated in the process of formation of the fish nodules.

A biogenic origin has been reported as an important factor in the formation of carbonate nodules (Weeks, 1953; Berner, 1969). The dead organism decomposes in an anoxic environment, and can cause the local environment to become alkaline, resulting in the rapid deposition of carbonate from the calcium-rich seawater, forming a nodule around the organism (Weeks, 1953). Sulfur-reducing bacteria are the main decomposers in anoxic environments (Berner, 1969), and they can improve the mineralisation of biological remains, which is beneficial to the preservation of organisms in anoxic sediments (Briggs, 2003).

In Jurong, most fishes are neopterygians covered by hard bony scales (Wen, 2011), and the relatively heavy bony scales helped the dead body to sink to the seabed, instead of floating in the water layer, soon after their death. Then the dead body

attracted abundant bacteria to gather on the surface, forming a dense protective film which protects the fleshy part of the fish from decomposition, following the 'death mask' hypothesis (Gehling, 1999). This can keep the fish body in a closed, anoxic environment, avoiding extensive decay and rupture of the body by marine turbulence. The fish body therefore can be completely preserved (Bienkowska, 2004).

The slow decomposition of the fish body and flesh could produce some CO_2 , which then could form bicarbonate ions in the seawater. The bicarbonate ions could also easily form calcium carbonate precipitates with calcium ions in an alkaline environment and adhere to the surface of the fish. Moreover, the decomposition of the body cavity and decay of some organs and the surrounding bacteria also produced a small amount of H_2S , which can combine with iron ions in seawater to form pyrite framboids in anoxic water (Briggs, 2003). The nodules gradually grow as the calcium carbonate is wrapped layer by layer, with some pyrite framboids being wrapped in.

In conclusion, a vast array of microbes and possible sulfur-reducing bacteria worked together in an anoxic water environment to accelerate the formation of the fish fossil nodules in Jurong. A four-step taphonomic process for the Jurong fish nodule is recognized (Fig. 14):

Step A: Fish lived in oxygen-rich water in the upper ocean.

Step B: Fish quickly settled to the anoxic seabed after death, and the body surface was quickly wrapped by bacteria.

Step C: Thin microbial biofilms sealed in the body surface to prevent the fleshy part of the fish from decaying or delaying its decay. Decomposition of the body cavity and some organs produced some CO_2 and H_2S . The former then formed bicarbonate ions in the seawater and combined with calcium ions to form calcium carbonate precipitates, and the H_2S combined with iron ions in seawater to form pyrite framboids.

Step D: The fish nodules gradually grew by precipitation of calcium carbonate in layers, embedding with some pyrite framboids, and further calcium carbonate layers were precipitated, and later the fish fossil nodules were compacted during diagenesis.

5.4. Global correlations of the Jurong fishes

In South China, Early Triassic fish fossils have been reported from many areas. For example, *Sinocoelacanthus fengshanensis* was first to be reported from the Lower Triassic of Fengshan, Guanxi Province (Liu et al., 1964). Su et al. (1981, 1983) also reported *Perleidus yangtzensis* from Hexian, Anhui Province and *Plesioperleidus dayeensis* from the 4th Member of the Daye Formation in Huangshi City, Hubei Province. Abundant fish fossils have also been described from the Lower Triassic Helongshan Formation of the Chaohu area, Anhui Province (Tong et al., 2006; Tintori, 2014), including the perleidiforms *Perleidus yangtzensis*, *Plesioperleidus dayeensis*, *Plesioperleidus jiangsuensis*, and *Jurongia fusiformis*, as well as the parasemionotiforms *Suius brevis* and *Qingshania cercida* (Tong et al., 2006). The Helongshan Formation fishes are the most abundant and diverse among the Early Triassic fish faunas of South China (Benton et al., 2013). When compared with the Helongshan Formation fishes, the Jurong fauna shares four species, *Plesioperleidus jiangsuensis*, *Jurongia fusiformis*, *Suius brevis* and *Qingshania cercida*, and thus appears highly similar with the former in terms of faunal compositions.

Lower Triassic marine successions yield a few fish faunas worldwide, including South China, India, Madagascar, Spitsbergen, Greenland, and Western Canada (Beltan, 1996; Qian et al., 1997; Liu et al., 2002; Jin et al., 2003; Ketchum and Barrett, 2004; Mutter, 2005; Jin, 2006; Tong et al., 2006; Weitschat, 2008; Mutter and Neuman, 2008b; Romano and Brinkmann, 2010; Falconnet and Andriamihajia, 2012; Romano et al., 2012; Scheyer et al., 2014; Romano et al., 2016), and their detailed faunal compositions are listed in Table 1. Of these, the Madagascar fish fauna is the most abundant and diverse, with more than 35 species belonging to the Actinopterygii and Sarcopterygii (Table 1). The Madagascar fauna is characterized by the presence of abundant *Perleidus*, *Parasemionotus*, and *Coelacanthus*. The Triassic fish faunas of South China have a certain affinity with the Madagascar fauna. The species of *Parasemionotus* from Jurong and Chaohu are different from that in Madagascar, but they are similar morphologically (Liu et al., 2002). *Perleidus piveteaui*, re-assigned to

Plesioperleidus jiangsuensis (Jin et al., 2003; Tong et al., 2006), was also identified by Liu et al. (2002) from Jurong. In addition, *Perleidus* from Fengshan, Guangxi, Hexian, Ahhui, and Madagascar all have similar specific characteristics (Liu, 1964; Su, 1981; Su et al., 1983). *Saurichthys* from the Upper Qinglong Formation of Longtan in Nanjing is a common component of the Early Triassic fish faunas of Madagascar, Spitzbergen, and Europe (Beltan, 1996; Romano et al., 2016). The Jurong fish fauna therefore is closely related to that of northern Madagascar. Moreover, *Saurichthys* and other fossil fishes belonging to *Coelacanthus* have been reported in North America (Romano et al., 2012). The North American Early Triassic fishes therefore also share some similarities with the Jurong fauna, although faunas there are not diverse.

6. Conclusions

Our work leads to four important conclusions:

- 1) Conodont biostratigraphy and carbon isotopic correlations indicate that the Jurong fish Bed 8 is likely mid-late Smithian in age, and not younger than end-Smithian.
- 2) Critical review of the Jurong fish fauna identifies three species in three genera, namely *Plesioperleidus*, *Suius*, and *Qingshania*, belonging to Perleididae and Parasemionotidae, and the taxonomic assignment of other taxa remains uncertain. Anatomical study of the fishes shows micro-structures of scales and fins, and well-preserved bones and internal cartilage structures within the body cavity.
- 3) Many coccoid-like microspheres of suspected sulfur-reducing bacteria and abundant tiny pyrite framboids are recognized from the calcareous fish nodules, with pyrite framboids scattered on the fish fossil surfaces and surrounding rocks within the nodule.
- 4) A four-step taphonomic process of the fish nodules is recognised. (1) The fishes presumably lived in oxic seawater in the upper ocean, and (2) the body sank quickly to the anoxic seabed and was wrapped by microbes, which

- prevented the body and flesh from decaying, enabling preservation of the complete fish body. (3) Decomposition of the fish body and organs produced some CO₂ and H₂S. The former then formed bicarbonate ions in the seawater and combined with calcium ions to form calcium carbonate precipitates, while the H₂S combined with iron ions in seawater to form pyrite framboids. (4) The fish nodules gradually grew by precipitation of calcium carbonate in layers, embedded with some pyrite framboids, and later the fish fossil nodules were compacted during diagenesis.
- 5) The Jurong fishes share high similarity to the Helongshan Formation fish fauna from the adjacent Chaohu area, South China and are also comparable with the Early Triassic fish fauna from Madagascar.

Acknowledgments

Constructive editing and comments from Dr Marret-Davies and an anonymous reviewer are appreciated. This study was supported by the National Key R & D Program of China (2017YFC0603103), four NSFC grants (41661134047, 41673011, 41772007, 41821001), a Hubei Provincial Natural Science Foundation grant (2017CFA019), and the NERC-BETR programme grant NE/P013724/. It is a contribution to IGCP Project 630.

References

- Beltan, L., 1968. La faune ichthyologique de l'Eotrias du NW de Madagascar: le neurocrâne. Centre National de la Recherche Scientifique, Paris, 135 pp.
- Beltan, L., 1980. Sur la présence d'un poisson volant, *Icarealcyon malagasium* n. gn. sp. dans l'Eotrias malagache. 26th International Geological Congress, Paris (Section 1–5), 155.
- Beltan, L., 1984. A propos d'un poisson volant biplan de l'Eotrias du NW de Madagascar: *Icarealcyon malagasium* Beltan. Annales de la Société Géologique du Nord 103, 75–82.
- Beltan, L., 1996. Overview of systematics, paleobiology, and paleoecology of Triassic fishes of northwestern Madagascar. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes: Systematics and Paleoecology, Gustave Fisher Verlag, Stuttgart, p. 479–500.
- Benton, M.J., Zhang, Q.Y., Hu, S.X., Chen, Z.Q., Wen, W., Liu, J., Tong, J.N., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Science Reviews 125, 199–243.
- Berner, R.A., 1969. Chemical changes affecting dissolved calcium during the bacterial decomposition of fish and clams in sea water. Marine Geology 7, 253–274.
- Bhatt, D.K.J.V., 1999. Conodont biostratigraphy of the Lower Triassic in Spiti Himalaya, India. Journal of the Geological Society of India 54, 153–168.
- Bienkowska, M., 2004. Taphonomy of ichthyofauna from an Oligocene sequence (Tylawa Limestones horizon) of the outer Carpathians, Poland. Geological Quarterly 48, 81–92.
- Bond, D.P.G., Wignall, P.B., 2010. Pyrite framboid study of marine Permian–Triassic boundary sections: A complex anoxic event and its relationship to contemporaneous mass extinction. Geological Society of America Bulletin 122, 1265–1279.
- Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft

- bodied fossils. *Annual Review of Earth and Planetary Sciences* 31, 275–301.
- Chen, Z.Q., Benton, M.J., 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* 5, 375–383.
- Chen, Z.Q., Tong, J.N., Fraiser, M.L., 2011. Trace fossil evidence for restoration of marine ecosystems following the end-Permian mass extinction in the Lower Yangtze region, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299, 449–474.
- Chen, Z.Q., Wang, Y.B., Kershaw, S., Luo, M., Yang, H., Zhao, L.S., Fang, Y.H., Chen, J.B., Li, Yang, Zhang, L., 2014. Early Triassic stromatolites in a siliciclastic nearshore setting in northern Perth Basin, Western Australia: geobiologic features and implications for post-extinction microbial proliferation. *Global and Planetary Change* 121, 89–100.
- Chen, Z.Q., Yang, H., Luo, M., Benton, M.J., Kaiho, K., Zhao, L.S., Huang, Y.G., Zhang, K.X., Fang, Y.H., Jiang, H.S., Qiu, H., Li, Y., Tu, C.Y., Shi, L., Zhang, L., Feng, X., Chen, L., 2015. Complete biotic and sedimentary records of the Permian–Triassic transition from Meishan section, South China: Ecologically assessing mass extinction and its aftermath. *Earth-Science Review* 149, 67–107.
- Chen, Z.Q., Tu, C.Y., Pei, Y., Ogg, J., Fang, Y.H., Wu, S.Q., Feng, X.Q., Huang, Y.G., Guo, Z., Yang, H., 2019. Biosedimentological features of major microbe-metazoan transitions (MMTs) from Precambrian to Cenozoic. *Earth-Science Reviews* 189, 21–50.
- Edgar L.A.J., 1951. An impression method for preparing fish scales for age and growth analysis. *The Progressive Fish-Culturist* 13, 11–16.
- Erwin, D.H., 2006. *How Life on Earth Nearly Ended 250 Million Years Ago*. Princeton University Press, Princeton (306 pp.).
- Ezaki, Y., Liu, J., Nagano, T., Adachi, N., 2008. Geobiological aspects of the earliest Triassic microbialites along the southern periphery of the tropical Yangtze Platform: initiation and cessation of a microbial regime. *Palaios* 23, 356–369.
- Falconnet, J., Andriamihajia, M.L., 2012. First procolophonid (Reptilia, Parareptilia) from Lower Triassic of Madagascar. *Comptes Rendus Palevol* 11, 357–369.

- Fang, Y.H., Chen, Z.Q., Kershaw, S., Yang, H., Luo, M., 2017. Permian–Triassic boundary microbialites at Zuodeng section, Guangxi Province, South China: Geobiology and palaeoceanographic implications. *Global and Planetary Change* 152, 115–128.
- Feng, X.Q., Chen, Z.Q., Woods, A., Fang, Y.H., 2017. A Smithian (Early Triassic) ichnoassemblage from Lichuan, Hubei Province, South China: implications for biotic recovery for biotic recovery after the latest Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 496, 123–141.
- Feng, Z., Yang, Y., Jin, Z., 1997. Lithofacies paleogeography of Permian of South China. China University of Petroleum Press, Beijing, 82 pp. (In Chinese)
- Gardiner, B., Schaeffer, B., Masserie, J., 2010. A review of the lower actinopterygian phylogeny. *Zoological Journal of the Linnean Society* 144, 511–525.
- Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. *Palaios* 14, 40–57.
- Grande, L., Bemis, W.E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. *Society of Vertebrate Paleontology Memoir* 4, 1–690.
- Horká, P., Ibbotson, A., Jones, J.I., Cove, R.J., Scott, L.J., 2010. Validation of scale-age determination in European grayling *Thymallus thymallus* using tag-recapture analysis. *Journal of Fish Biology* 77, 153–161.
- Huang, Y.G., Chen, Z.Q., Wignall, P.B., Zhao, L.S., 2017. Latest Permian to Middle Triassic redox condition variations in ramp settings, South China: Pyrite framboid evidence. *Geological Society of America Bulletin* 129, 229–243.
- Huang, Y.G., Chen, Z.Q., Algeo, T.J., Zhao, L.S., Baud, A., Bhat, G.M., Zhang, L., Guo, Z., 2019a. Two-stage marine anoxia and biotic response during the Permian–Triassic transition in Kashmir, northern India: pyrite framboid evidence. *Global and Planetary Change* 172, 124–139
- Huang, Y.G., Chen, Z.Q., Wignall, P.B., Grasby, S.E., Zhao, L.S., Wang, X.D., Kaiho, K., 2019b. Biotic responses to volatile volcanism and environmental stresses over the Guadalupian–Lopingian (Permian) transition. *Geology* 47, 175–178.
- Jin,

- F., Wang, N.Z., Cai, Z.Q., 2003. A revision of the perleidid fishes from the Lower Yangtze region of south China-Second report on the fish sequence study near the Permian-Triassic boundary in south China. *Vertebrata Palasiatica* 41, 181–190. (In Chinese with English abstract)
- Jin, F., 2006. An overview of Triassic fishes from China. *Vertebrata Palasiatica* 44, 28–42.
- Ketchum, H.F., Barrett, P.M., 2004. New reptile material from the Lower Triassic of Madagascar: implications for the Permian–Triassic extinction event. *Canadian Journal of Earth Science* 41, 1–8.
- Kogan I., 2011. Remains of *Saurichthys* (Pisces, Actinopterygii) from the Early Triassic Wordie Creek Formation of East Greenland. *Bulletin of the Geological Society of Denmark* 59, 93–100.
- Kozur, H., Mostler, H., 1976. Neue Conodonten aus dem Jungpaläozoikum und der Trias. *Geologisch-Paläontologische Mitteilungen Innsbruck* 636, 1–40.
- Lehman, J.P., 1952. Etude complémentaire des poissons de l'Eotrias de Madagascar. *Kungliga Svenska Vetenskapsakademiens Handlingar, Fjärde Serien* 2, 1–201.
- Lehman, J.P., Chateau, C., Laurain, M., Nauche, M., 1959. Paléontologie de Madagascar. XXVIII. –Les poissons de la Sakamena moyenne. *Annales de Paléontologie* 45, 177–219.
- Li, M.S., Ogg, J.G., Zhang, Y., Huang, C., Hinnov, L., Chen, Z.Q., Zou, Z.Y., 2016. Astronomical-cycle scaling of the end-Permian extinction and the Early Triassic Epoch of South China and Germany. *Earth and Planetary Science Letters* 441, 10–25.
- Li, Q.G., 2009. A new parasemionotid-like fish from the Lower Triassic of Jurong, Jiangsu Province, south China. *Palaeontology* 52, 369–384.
- Liang, D., Tong, J.N., Zhao, L.S., 2011. Lower Triassic Smithian–Spathian Boundary at West Pingdingshan Section in Chaohu, Anhui Province. *Science China Earth Sciences* 41, 149–157. (In Chinese with English abstract)
- Liang, L., Tong, J., Song, H.J., Song, T., Tian, L., Song, H.Y., Qiu, H., 2016. Lower–Middle Triassic conodont biostratigraphy of the Mingtang section,

- Nanpanjiang Basin, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 459, 381–393.
- Liu, G., Feng, H., Wang, J., Wu, T., Zhai, Z., 2002. Early Triassic fishes from Jurong, Jiangsu. *Acta Palaeontologica Sinica* 41, 27–52. (In Chinese with English abstract)
- Liu, X., 1964. *Coelacanthus* from Early Triassic marine facies in Fengshan, Guangxi. *Vertebrata Palasiatica* 8, 115–116. (In Chinese)
- Lombardo, C., 2011. Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): anatomical descriptions and nomenclatural problems. *Rivista Italiana di Paleontologia e Stratigrafia* 107, 345–369.
- Luo, M., Chen, Z.Q., Shi, G.R., Fang, Y., Song, H., Jia, Z., Huang, Y., Yang, H., 2016. Upper Lower Triassic stromatolite from Anhui, South China: Geobiologic features and paleoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 452, 40–54.
- Luo, M., Chen, Z.Q., Zhao, L.S., Kershaw, S., Huang, J., Wu, L., Yang, H., Fang, Y., Huang, Y., Zhang, Q., Hu, S., Zhou, C., Wen, W., Jia, Z., 2014. Early Middle Triassic stromatolites from the Luoping area, Yunnan Province, Southwest China: geobiologic features and environmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 412, 124–140.
- Lyu, Z.Y., Orchard M.J., Chen, Z.Q., Zhao, L.S., Zhang, L., Zhang, X.M., 2018. A taxonomic re-assessment of the *Novispathodus waageni* group and its role in defining the base of the Olenekian (Lower Triassic). *Journal of Earth Science* 29, 824–836.
- Lyu, Z.Y., Orchard, M.J., Chen, Z.Q., Wang, X.D., Zhao, L.S., Han, C., 2019. Uppermost Permian to Lower Triassic conodont successions from the Enshi area, western Hubei Province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 519, 49–64.
- Marramà, G., Lombardo, C., Tintori, A., Carnevale, G., 2017. Re-description of ‘*Perleidus*’ (Osteichthyes, Actinopterygii) from the Early Triassic of northwestern Madagascar. *Rivista Italiana di Paleontologia e Stratigrafia* 123,

219–242.

Müller, K.J., 1956. Triassic conodonts from Nevada. *Journal of Paleontology* 30, 818–830.

Mutter, R.J., 2005. Re-assessment of the genus *Helmolepis* Stensiö 1932 (Actinopterygii: Platysiagidae) and evolution of platysiagids in the Early–Middle Triassic. *Eclogae Geologicae Helvetiae* 98, 271–280.

Mutter, R.J., Neuman, A.G., 2008a. Jaws and dentition in an Early Triassic, 3-dimensionally preserved eugeneodontid skull (Chondrichthyes). *Acta Geologica Polonica* 58, 223–227.

Mutter, R.J., Neuman, A.G., 2008b. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of Western Canada. In: Cavin, L., Longbottom, A., Richter, M. (Eds.), *Fishes and the Break-up of Pangaea*. Geological Society, London, Special Publications 295, 9–41.

Nielsen, E., 1936. Some few preliminary remarks on Triassic fishes from East Greenland. *Meddelelser om Grønland* 112, 1–55.

Nicolas, G., Gaill, F., Zylberberg, L., 1997. In situ localization of two fibrillar collagens in two compact connective tissues by immunoelectron microscopy after cryotechnical processing. *Journal of Histochemistry & Cytochemistry* 45, 119–128.

Neuman, A.G., Therrien, F., 2015. Fishes from the Lower Triassic portion of the Sulphur Mountain Formation in Alberta, Canada: geological context and taxonomic composition 1. *Canadian Journal of Earth Sciences* 52, 557–568.

Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252, 93–117.

Orchard, M.J., 2008. Lower Triassic conodonts from the Canadian Arctic, their intercalibration with ammonoid-based stages and a comparison with other North American Olenekian faunas. *Polar Research* 27, 393–412.

Owen, R., 1861. *Palaeontology or a Systematic Summary of Extinct Animals and Their Geological Relations*. Edinburgh: A & C Black.

- Patterson, C., 1973. Interrelationships of holosteans. In: Greenwood, P.H., Miles, R.S., Patterson, C. (Eds.), *Interrelationships of Fishes*. London: Academic Press, pp. 233–305.
- Patterson, C., 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London B* 269, 275–579.
- Qian, M.P., Zhu, S.P., Zhao, F.M., Zhou, X.D., Su, R., Gu, G.H., Zhai, Z.H., 1997. Discovery of Early Triassic fish fossils and its significances in Jurong, Jiangsu Province. *Jiangsu Geology* 21, 65–71. (In Chinese with English abstract)
- Romano, C., Brinkmann, W., 2010. A new specimen of the hybodont shark *Palaeobates polaris* with three-dimensionally preserved Meckel's cartilage from the Smithian (Early Triassic) of Spitsbergen. *Journal of Vertebrate Paleontology* 30, 1673–1683.
- Romano, C., Kogan, I., Jenks, J., Brinkmann, W., 2012. *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. *Bulletin of Geosciences* 87, 543–570.
- Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H., Kriwet, J., 2016a. Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews* 91, 106–147.
- Romano, C., Ware, D., Brühwiler, T., Bucher, H., Brinkmann, W., 2016b. Marine Early Triassic Osteichthyes from Spiti, Indian Himalayas. *Swiss Journal of Palaeontology*, 135, 275–294.
- Scheyer, T.M., Romano, C., Jenks, J., Bucher, H., 2014. Early Triassic marine biotic recovery: the predators' perspective. *PloS One* 9, 1–20.
- Shen, W., 2011. Overview of research on fish scales. *Jiangsu Agricultural Sciences* 39, 307–310. (In Chinese)
- Stensiö, E., 1932. Triassic fishes from East Greenland 1–2. *Meddelelser om Grønland* 83, 1–305.
- Su, D.Z., 1981. A new species of *Perleidus* from Anhui. *Vertebrata Palasiatica* 4,

- 108–122. (In Chinese with English abstract)
- Su, D.Z., Li, Z.C., 1983. A new Triassic perleiid fish from Hubei, China. *Vertebrata Palasiatica* 21, 9–16. (In Chinese with English abstract)
- Sun, Y.D., Michael, M.J., Wignall, P.B., Yan, C., Chen, Y., Jiang, H., Wang, L., Lai, X., 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338, 366–370.
- Sun, Z., Tintori, A., Jiang, D., Motani, R., 2013. A new Perleididae from the Spathian (Olenekian, Early Triassic) of Chaohu, Anhui Province, China. *Rivista Italiana di Paleontologia e Stratigrafia* 119, 275–285.
- Sweet, W.C., 1970. Uppermost Permian and Lower Triassic conodonts of the Salt Range and Trans-Indus Ranges, West Pakistan. In: Kummel, B., Teichert, C. (Eds.), *Stratigraphic Boundary Problems: Permian and Triassic of West Pakistan*, Department of Geological Special Publications of University of Kansas, pp. 207–205.
- Tian, L., Tong, J., Algeo, T.J., Song, H., Song, H., Chu, D., Shi, L., Bottjer, D.J., 2014. Reconstruction of Early Triassic ocean redox conditions based on framboidal pyrite from the Nanpanjiang basin, South China. *Palaeogeography Palaeoclimatology Palaeoecology* 412, 68–79.
- Tintori, A., 2014. A new *Saurichthys* (Actinopterygii) from the Spathian (Early Triassic) of Chaohu (Anhui Province, China). *Rivista Italiana di Paleontologia e Stratigrafia* 120, 157–164.
- Tong, J.N., Zhou, X., Erwin, D.H., Zuo, J., Zhao, L. 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. *Journal of Paleontology* 80, 146–161.
- Tong, J.N., Zuo, J.X., Chen, Z.Q., 2007. Early Triassic carbon isotope excursions from South China: Proxies for devastation and restoration of marine ecosystems following the end-Permian mass extinction. *Geology Journal* 42, 371–389.
- Wang, C.Y., 1991. Chinese Triassic conodont biostratigraphy. *Journal of Stratigraphy* 15, 311–314. (In Chinese)
- Weeks, L.G., 1953. Environment and mode of origin and facies relationships of

- carbonate concretions in shales. *Journal of Sedimentary Research* 23, 162-173.
- Weitschat, W., 2008. Intraspecific variation of *Svalbardiceras spitzbergensis* (Frebald) from the Early Triassic (Spathian) of Spitsbergen. *Polar Research* 27, 292-297.
- Wen, W., 2011. Fish fossils and their paleoecological features of Luoping biota, Middle Triassic, Yunnan, South China. Master's thesis. Chengdu University of Technology (Chengdu). (In Chinese with English abstract)
- Wen, W., Zhang, Q.Y., Hu, S.X., Benton, M.J., Zhou, C.Y., Tao, X., Huang, J.Y., Chen, Z.Q., 2013. Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica* 58, 175–193.
- Wignall, P.B., Newton, R., 1998. Pyrite framboid diameter as a measure of oxygen deficiency in ancient mudrocks. *American Journal of Science* 17, 22–36.
- Wilkin, R.T., Barnes, H.L., 1997. Formation processes of framboidal pyrite. *Geochimica et Cosmochimica Acta* 61, 323–339.
- Wilkin, R.T., Barnes, H.L., Brantley, S.L., 1996. The size distribution of framboidal pyrite in modern sediments: An indicator of redox conditions. *Geochimica et Cosmochimica Acta* 60, 3897–3912.
- Wu, S.Q., Chen, Z.Q., Fang, Y.H., Pei, Y., Yang, H., Ogg, J., 2017. A Permian-Triassic boundary microbialite deposit from the eastern Yangtze Platform (Jiangxi Province, South China): Geobiologic features, ecosystem composition and redox conditions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 486, 58–73.
- Yang, H., Chen, Z.Q., Wang, Y.B., Tong, J.N., Song, H.J., Chen, J., 2011. Composition and structure of microbialite ecosystems following the end-Permian mass extinction in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 308, 111–128.
- Zhao, L.S., Chen, Y.L., Chen, Z.Q., Cao, L., 2013. Uppermost Permian to Lower Triassic conodont zonation from Three Gorges area, South China. *Palaios* 28, 523–540.
- Zhao, L.S., Orchard, M.J., Tong, J.N., Sun, Z.M., Zuo, J.X., Zhang, S.X., Yun, A.L.,

2007. Lower Triassic conodont sequence in Chaohu, Anhui Province, China and its global correlation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252, 24–38.
- Zhao, L.S., Tong, J. N., Ochar, M.J., 2005. Lower Triassic conodont zonation of Chaohu area, Anhui Province and their global correlation. *Earth Science-Journal of China University of Geosciences* 30, 623–634. (In Chinese with English abstract)
- Zhao, L.S., Tong, J.N., Zhang, S.X., Sun, Z.M., 2008. An update of conodonts in the Induan-Olenekian boundary strata at West Pingdingshan section, Chaohu, Anhui Province. *Journal of China University of Geosciences* 19, 207–216.
- Zhou, M., Fu, W.L., Zhang, C., Ni, P.G., Ji, C., 2015. Geological significance of the fish-bearing concretions near the Smithian-Spathian boundary, Olenekian, Early Triassic. *Journal of Stratigraphy* 39, 395–402. (In Chinese with English abstract)

Figure and table captions

Fig. 1. A, Location of the Qingshan section of Jurong City, Jiangsu Province, South China. B, Early Triassic Paleogeographic configuration of South China showing that the Jurong area (red star) was situated on the northeastern margin of the Yangtze Platform (base map following Feng et al., 1997)

Fig. 2. A, Field photo showing the exposure of the Qingshan section. B, Thin-bedded argillaceous limestone interbedded with calcareous mudstone and black shale of the middle member. C, Close-up of mudstone layer with fish nodules (yellow arrow). D, Thin layers of calcareous mudstone and argillaceous limestone (Bed 7) of the middle member. E, Thin-bedded calcareous mudstone with alternating reddish and grey/dark layers (Bed 8) of the middle member. F, Microphotograph of argillaceous limestone showing dark, organic-rich laminae (Bed 9) of the middle member.

Fig. 3. Composite lithology, conodont biostratigraphy, carbon isotope excursion and pyrite framboid size variations and redox interpretation throughout the middle Lower Qinglong Formation in the Qingshan section of the Jurong area. Note that fish fossils occur in Bed 8.

Fig. 4. Conodonts from the Lower Qinglong Formation of the Qingshan section. Part 1. Scale bar width = 200 μm , a. lateral view, b. lower view, c. upper view, 1: *Neospathodus dieneri*, BGEG JR 03001. 2: *Neospathodus* sp., BGEG JR 04001. 3–6: *Neospathodus dieneri*, BGEG JR 06001, 06002, 06003, 06004. 7: *Novispathodus radialis*, BGEG JR 16001. 8–10: *Novispathodus pingdingshanensis*, BGEG JR 16002, 16003, 16004. 11: *Cypridodella* cf. *subsymmeirica*, BGEG JR 07001. 12: *Ellisonia gradate*, BGEG JR 09001.

Fig. 5. Conodonts from the Lower Qinglong Formation of the Qingshan section. Part 2. Scale bar width = 300 μm , a. lateral view, b. lower view, c. upper view, 1, 3: *Scythogondolella lachymiformis*, BGEG JR 09002, 09004. 2: *Neogondolella* sp.,

BGEG JR 09003. 4: *Scythogondolella milleri*, BGEG JR 09005. 5: *Cratognathodus kochi*, BGEG JR 09006.

Fig. 6. Fish fossils from the Lower Qinglong Formation of the Qingshan section, Jurong City, Jiangsu Province, South China. Scale bar width = 1 cm. A–B, *Plesioperleidus jiangsuensis*, BGEG JR 08101, BGEG JR 08105; C, *Suius* sp., BGEG JR 08201; D, ?*Stensionotus* sp., BGEG JR 08301; E, *Qingshania* sp. 1, BGEG JR 08401; F, *Qingshania* sp. 2, BGEG JR 08501.

Fig. 7. Anatomical maps of fish fossils from the Qingshan section. A, Photograph of fish nodule, cut along the red line showing in Figure B; B, Photograph of squashed fish in the cross section of nodule; C, Cross section of fish fossils under the microscope; D, Cross section of internal organ tissue of fish fossil showing in Figure C; E, Cross section of fish scale showing in Figure C; F, Concentric growth lines of fish scale.

Fig. 8. Surface micro-structures of fish fossils from the Qingshan section. A, Photograph of the body of *Qingshania* sp. (BGEG JR 08404) from the Qingshan section; B, Fish scales; C–D, Honeycomb structure on the surface of fish scales; E, Fish fins; F, EDS of fish fins, blue-green fluorescence represents chemical element P; G, Calcium phosphate microcrystals inside the fin; H, Fracture film on the surface of fin.

Fig. 9. The internal structure of fish fossils from the Qingshan section. A, Cross section of fish fossil; B–E, Cross section of internal organ tissue of fish fossil.

Fig. 10. Ostracod and gastropod fossils in surrounding rocks around the fish fossil. A–F, Gastropods; G–H, Ostracods; I, Shells of a gastropod or ostracod.

Fig. 11. Plot diagram of Mean-Standard Deviation (M-SD) of pyrite framboid size in the Qingshan section.

Fig. 12. Evidence for taphonomy of the Jurong fish fossils. A, Ostracods and gastropods in fish nodules; B, Mould of ostracod or gastropod; C, Close-up of the boxed area in Fig. 12B; D, A pyrite framboid in the mould; E, Boundary between a fish fossil and the surrounding rock (yellow dotted line), the left is the surrounding rock, the right is fish scale; F, A pyrite framboid developed at the junction between a fossil fish and the surrounding rock.

Fig. 13. Photomicrographs of thin sections shows coccooid-like microspheres, from the rocks surrounding the fish fossils within the nodule.

Fig. 14. The postulated four-step taphonomic processes of the Jurong fish nodule.

Table 1. Faunal compositions of the global Early Triassic fishes.

Table 1. Faunal compositions of the global Early Triassic fishes.

Stage	Locality	Fishes compositions	References
Early Triassic	South China (China): JuRong, Nanjing, Huangshi, Hexian, Chaohu, Tiandong, Fengshan	<i>Chaohuichthys majiashanensis</i> Coelacanth indet. <i>Hybodus yohi</i> <i>Hybodus zuodengensis</i> <i>Jurongia fusiformis</i> <i>Lepidotes jurongensis</i> <i>Peia jurongensis</i> <i>Plesioperleidus dayeensis</i> <i>Plesioperleidus jiangsuensis</i> <i>Plesioperleidus yangtzensis</i> <i>Polyacrodus tiandongensis</i> <i>Qingshania cercida</i> <i>Saurichthys</i> sp. <i>Sinicoelacanthus fengshanensis</i> <i>Piveteaunotus dongchangensi</i> <i>Suius brevis</i>	This study Liu et al., 1964 Su et al. 1981, 1983 Tong et al., 2006 Benton et al., 2013 Tintori, 2014
	Madagascar	Actinopterygii: <i>Birgeria nielsenii</i> <i>Ambodipia madagascariensis</i> <i>Boreosomus gillioti</i> <i>Pteronisculus cicatrosus</i> <i>Pteronisculus macropterus</i> <i>Pteronisculus broughi</i> <i>Pteronisculus arambourgi</i> <i>Saurichthys stensioei</i> <i>Saurichthys madagascariensis</i> <i>Saurichthys piveteaui</i> <i>Bobasatrania mahavavica</i> <i>Ecrinesomus dixonii</i> <i>Errollichthys mirabilis</i> <i>Perleidus madagascariensis</i> <i>Perleidus piveteaui</i> <i>Australosomus merlei</i> <i>Australosomus longirostris</i> <i>Australosomus altisquamosus</i> <i>Ospia whitei</i> <i>Broughia perleidoidea</i> <i>Watsonulus eugnathoides</i> <i>Parasemionotus besairiei</i> <i>Parasemionotus labordei</i> <i>Stensioenotus intercessus</i>	Lehman, 1952 Lehman et al., 1959 Beltan, 1968; 1980; 1984; 1996 Olsen, 1984 Grande and Bemis, 1998

	<p><i>Jacobulus novus</i> <i>Thomasinotus divisus</i> <i>Lehmanotus markubai</i> <i>Devillersia madagascariensis</i> <i>Piveteaunotus ifasiensis</i> <i>Icarealcyon malagasium</i></p> <p>Sarcopterygii: <i>Whiteia woodwardia</i> <i>Whiteia tuberculata</i> <i>Coelacanthus madagascariensis</i> <i>Coelacanthus evolutus</i> <i>Paraceratodus germaini</i> <i>Beltanodus ambulobensis</i></p>	
Spitsbergen (Norway)	<p><i>Acrodus scaber</i> <i>Acrodus spitzbergensis</i> <i>Acrodus vermiformis</i> <i>Hybodus microdus</i> <i>Hybodus rapax</i> <i>Lissodus angulatus</i> <i>Nemacanthus</i> sp. <i>Palaeobates</i> sp. Edestidae indet. <i>Hybodus microdus</i> <i>Hybodus sasseniensis</i> <i>Hybodus</i> sp. <i>Lissodus angulatus</i> <i>Palaeobates</i> sp.</p>	Romano and Brinkmann, 2010
Greenland	<p><i>Broughia perleididoides</i> <i>Helmolepis</i> sp. <i>Ospia whitei</i> Parasemionotidae indet. <i>Parasemionotus</i> sp. <i>Saurichthys</i> aff. <i>dayi</i> <i>Watsonulus</i> sp.</p>	Stensiö, 1932 Nielsen, 1936 Patterson, 1973; 1975 Mutter, 2005 Kogan, 2011
India	<p>Actinistia indet. Actinopterygii indet. cf. <i>Watsonulus</i> cf. <i>eugnathoides</i> <i>Saurichthys</i> sp.</p>	Romano et al., 2016b
Western Canada: Wapiti Lake,	<p><i>Albertonia</i> sp. <i>Australosomus</i> sp.</p>	Neuman, 2015

	British Columbia, Banff National Park, Alberta	<i>Belemnocerca prolata</i> <i>Birgeria</i> sp. <i>Bobasatrania</i> spp. <i>Boreosomus</i> sp. Caseodontidae indet. <i>Caseodus varidentis</i> <i>Coelacanthus banffensis</i> ?Ctenacanthoidea indet. Eugeneodontida indet. <i>Fadenia</i> sp. <i>Fadenia uroclasmata</i> <i>Helmolepis</i> sp. <i>Homalodontus</i> spp. <i>Listracanthus pectenatus</i> Luganoiiform? cf. <i>Palaeobates</i> sp. Parasemionotidae indet. <i>Paredestus bricircum</i> <i>Perleidiformes</i> sp. ?Polyacrodus sp. ?Pteronisculus sp. <i>Pygopterus</i> sp. <i>Rebellatrix divaricerca</i> <i>Saurichthys</i> spp. <i>Whiteia</i> spp.	
--	--	--	--

Highlights

- The Jurong fishes represent the earliest marine vertebrate fauna in Triassic in China.
- The Jurong fishes resemble the Early Triassic faunas from Chaohu and Madagascar.
- Collagen layers of fish scales, fins, organ walls and cartilages are well-preserved.
- The fish fauna was buried in an euxinic environment indicated by pyrite framboids.
- A four-step taphonomic process is recognized for the formation of the fish nodule.

ACCEPTED MANUSCRIPT