PROCEEDINGS OF THE ROYAL SOCIETY **B** | **BIOLOGICAL SCIENCES**

A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates

Guang-Hui Xu, Li-Jun Zhao, Ke-Qin Gao and Fei-Xiang Wu

Supplementary data	"Data Supplement" http://rspb.royalsocietypublishing.org/content/suppl/2012/10/24/rspb.2012.2261.DC1.html
References	**This article cites 33 articles, 4 of which can be accessed free** http://rspb.royalsocietypublishing.org/content/early/2012/10/24/rspb.2012.2261.full.html#ref-list-1
P<P	Published online 31 October 2012 in advance of the print journal.
Subject collections	Articles on similar topics can be found in the following collections palaeontology (111 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Proc. R. Soc. B* go to: **http://rspb.royalsocietypublishing.org/subscriptions**

Research

Author for correspondence:
Ke-Qin Gao
e-mail: kqgao@pku.edu.cn

Royal Society Publishing
Informing the science of the future

A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates

Guang-Hui Xu[1], Li-Jun Zhao[2], Ke-Qin Gao[3] and Fei-Xiang Wu[1]

[1]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, People's Republic of China
[2]Zhejiang Museum of Natural History, Hangzhou 310014, People's Republic of China
[3]School of Earth and Space Sciences, Peking University, Beijing 100871, People's Republic of China

Flying fishes are extraordinary aquatic vertebrates capable of gliding great distances over water by exploiting their enlarged pectoral fins and asymmetrical caudal fin. Some 50 species of extant flying fishes are classified in the Exocoetidae (Neopterygii: Teleostei), which have a fossil record no older than the Eocene. The Thoracopteridae is the only pre-Cenozoic group of non-teleosts that shows an array of features associated with the capability of over-water gliding. Until recently, however, the fossil record of the Thoracopteridae has been limited to the Upper Triassic of Austria and Italy. Here, we report the discovery of exceptionally well-preserved fossils of a new thoracopterid flying fish from the Middle Triassic of China, which represents the earliest evidence of an over-water gliding strategy in vertebrates. The results of a phylogenetic analysis resolve the Thoracopteridae as a stem-group of the Neopterygii that is more crown-ward than the Peltopleuriformes, yet more basal than the Luganoiiformes. As the first record of the Thoracopteride in Asia, this new discovery extends the geographical distribution of this group from the western to eastern rim of the Palaeotethys Ocean, providing new evidence to support the Triassic biological exchanges between Europe and southern China. Additionally, the Middle Triassic date of the new thoracopterid supports the hypothesis that the re-establishment of marine ecosystems after end-Permian mass extinction is more rapid than previously thought.

1. Introduction

The end-Permian mass extinction devastated the marine ecosystem (causing 90–95% of marine species to become extinct), with restructuring of communities in the Triassic [1]. By the Middle Triassic, several groups of aquatic reptiles occupied the top trophic levels of the marine ecosystems [2], and the Neopterygii ('new fins'), the largest group of Actinopterygii (ray-finned fishes), exhibited a high morphological diversity, probably adapted for different ecological niches [3,4]. The Thoracopteridae [5–10], a primitive neopterygian group that was confined to the Triassic marine ecosystem of the Palaeotethys Ocean, first evolved the remarkable strategy of over-water gliding. The modern analogue of the Thoracopteridae is represented by the Exocoetidae, tropical to subtropical teleosts that possess a fossil record no older than the Eocene [11–13]. Exocoetids show successful gliding capabilities over water; they can glide over total distances of as much as 400 m in 30 s by a successive sequence of taxiing and flight, with a maximum flight speed of approximately $10–20 \, m \, s^{-1}$ [12–14]. Based on behavioural studies and molecular-based phylogeny of the Exocoetidae, Kutschera [15,16] suggested that the evolution of the exocoetid flying fishes was driven by attacks of aquatic predators such as dolphins. Studies of extant exocoetid flying fishes [12–16] potentially provide a

good comparative basis for understanding the Thoracopteridae. Thoracopterid flying fishes were previously only represented by material from the Upper Triassic of Austria and Italy [5–10]. This limited fossil evidence hampers understanding of the temporal and spatial distribution of the Thoracopteridae. Furthermore, incomplete preservation of previous material prevents detailed description of several phylogenetically significant characters of this group, and, as a result, the phylogenetic relationships of the Thoracopteridae are unclear [7–9]. Here, we report a new thoracopterid based on the fossils found from the Zhuganpo Member of the Falang Formation, exposed in Xingyi, Guizhou Province, southwest China. These fossils are exceptionally well preserved in grey mudstone, permitting a description of much of thoracopterid morphology. For the first time in the Thoracopteridae, we can observe the ventral braincase (figure 1a). These new morphological data are incorporated into a cladistics analysis to determine the relationships of the Thoracopteridae within the Neopterygii. Also from the same fossil locality and horizon are abundant marine reptiles, including pachypleurosaurs, ichthyosaurs, nothosaurs, thalattosaurs and placodonts [17], and several other fishes [18], documenting an early fauna of marine reptiles and neopterygian fishes in the Triassic Yangtze Sea (a part of the eastern Palaeotethys Ocean) in southern China.

2. Systematic palaeontology

Actinopterygii [19]
   Neopterygii [20]
   Thoracopteridae [21]
   Potanichthys xingyiensis gen. et sp. nov.

(a) Etymology

The generic name is from *potanos* (Greek), meaning 'winged, flying', and *ichthys* (Greek), meaning 'fish'. The species epithet refers to Xingyi city, near the fossil site.

(b) Holotype

A nearly complete skeleton in the collection of the Zhejiang Museum of Natural History, Hangzhou, China (ZMNH M1692).

(c) Paratype

A nearly complete skeleton in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP V17744).

(d) Type locality and horizon

Xiemi, Wusha, Xingyi, Guizhou Province, China; lower part of the Zhuganpo Member, Falang Formation, Middle Triassic (Ladinian) [17,18,22].

(e) Diagnosis

Distinguished from other members of the family by possession of enlarged skull roughly one-third of standard length, two supraorbitals, two suborbital bones and reduction in body scales to only four vertical rows in caudal region.

3. Morphological observation

The holotype (figure 1a) and the paratype (figure 1b) represent a new thoracopterid flying fish that has a total length of 153 mm. The new fish displays aerodynamic characteristics in having a 'four-winged' body plan: a pair of greatly enlarged pectoral fins as 'primary wings' and a pair of pelvic fins as 'auxiliary wings'. The caudal fin is highly asymmetrical and deeply forked, with the ventral lobe noticeably stronger than the dorsal lobe. Swift movement of such a caudal fin could generate the power to launch the fish for over-water gliding. The general morphology of *Potanichthys* is restored in figure 2.

(a) Skull and mandible

The skull is proportionally large (approx. one-third of standard length), with a flat and laterally expanded roof formed by paired trapezoidal frontals and enlarged dermopterotics. The median rostral is broad and subcircular, contacting the nasals laterally and the frontals posteriorly. As in other thoracopterids, the anterior border of the orbit is formed by the deep, enlarged antorbital, without contribution from the nasal. The premaxillae are fused into a single element, a derived feature shared with the Italian *Thoracopterus* species [10], but different from the paired condition in the type species of *Thoracopterus* [7] and most other actinopterygians. The fused premaxillae bear a row of 10 conical teeth.

Two supraorbital bones are present between the nasal and dermosphenotic, including an elongated anterior and a subcircular posterior bone. In comparison, the type species of *Thoracopterus* possesses a single, elongated supraorbital bone, whereas *Gigantopterus* has three narrow supraorbital bones [7]. The condition is unknown for the two species of *Thoracopterus* from Italy [10]. The infraorbital bones include a rod-like lachrymal and a slightly wider jugal. In addition, two large suborbital bones (a trapezoidal upper bone and a triangular lower one) are present in the cheek region.

The maxilla is anteriorly elongated for its orbital portion and posteriorly expanded for the cheek portion, bearing about 20 conical teeth along the oral margin. The opercular series includes a deep preopercle, a large and tall opercle, and a much smaller subopercle. The preopercle has a narrow vertical bar, and a slender anterior maxillary process that ventrally contacts the expanded cheek portion of the maxilla. Ventral to the subopercle, two branchiostegal rays are exposed on the right aspect of the paratype, although the total number is unknown owing to preservation.

The azygous parasphenoid is elongate and covered with densely arranged, conical teeth along the palatal margin of the bone. The basioccipital, which anteriorly contacts the parasphenoid, is slightly longer than wide, with a pair of foramina for the occipital artery penetrating the ventral surface. The paired palatoquadrates are triangular and large, and are covered with dense, blunt teeth. Dorsally, the hyomandibula has a thickened head for articulation with the neurocranium, and postventrally possesses a strong process for articulation with the opercle. Four pairs of ceratobranchials are ossified as slender and rod-like bones. The hypohyal is a small, subcircular bone, with a foramen for the hyoidean artery.

No distinct sutures between the dentary, angular and other elements of the lower jaw can be discerned.
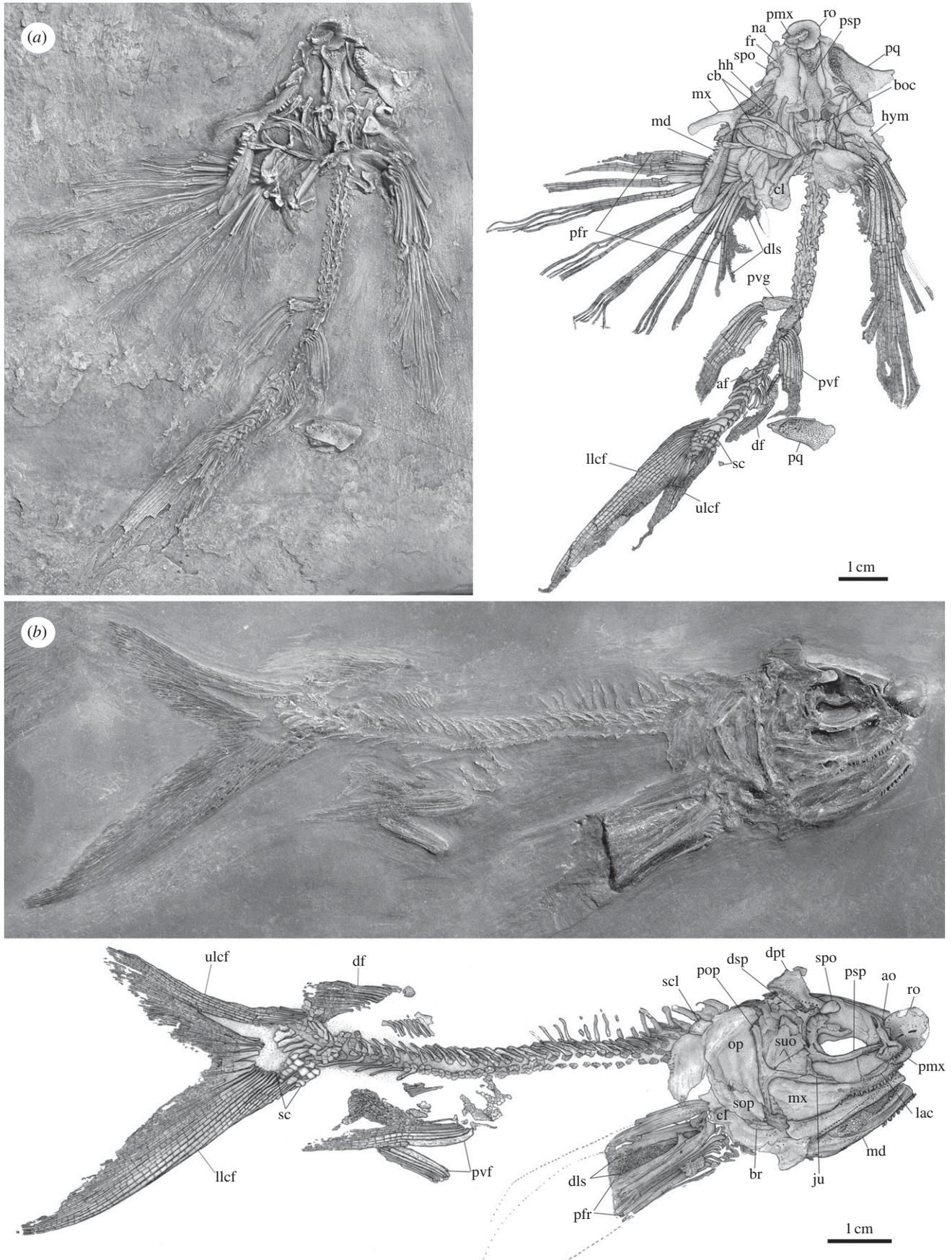
Figure 1. *Potanichthys xingyiensis* gen. et sp. nov. (*a*) Holotype, ZMNH M1692; (*b*) paratype, IVPP V17744. af, anal fin; ao, antorbital; boc, basioccipital; br, branchiostegal ray; cb, ceratobranchials; cl, cleithrum; df, dorsal fin; dls, dense lepidotrichial segments; dpt, dermopterotic; dsp, dermosphenotic; fr, frontal; hh, hypohyal; hym, hyomandibular; ju, jugal; lac, lachrymal; llcf, lower lobe of caudal fin; md, mandible; mx, maxilla; na, nasal; op, opercle; pfr, pectoral fin rays; pmx, premaxilla; pop, preopercle; pq, palatoquadrate; psp, parasphenoid; pvf, pelvic fin; pvg, pelvic girdle; ro, rostral; sc, scales; scl, supracleithrum; sop, subopercle; spo, supraorbital; suo, suborbital; ulcf, upper lobe of caudal fin.

As in other members of this family, these elements proba- bly have firmly fused into a strong mandible. The mandible is slightly deeper posteriorly than anteriorly,

and laterally ornamented by small tubercles. Sixteen conical teeth are present along the oral margin of the mandible in the holotype.
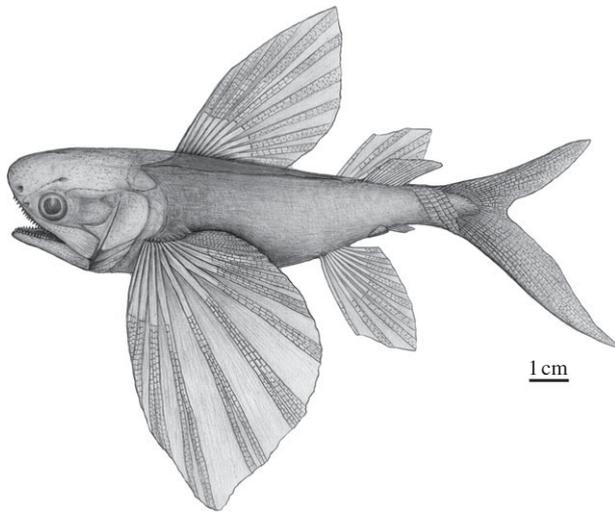
Figure 2. Reconstruction of the phenotype of *Potanichthys xingyiensis* gen. et sp. nov.

(b) Postcranium

A small supracleithrum and a large, curved cleithrum can be identified in the pectoral girdle of the paratype, and a single deep pelvic plate in the pelvic girdle of the holotype. The axial skeleton shows no ossification of centra and ribs, but includes a series of dorsal and ventral arcual elements in the trunk, and median supraneurals in the abdominal region. The posteroventral arcual elements at the base of the caudal fin are enlarged, providing a strong support for the lower caudal lobe.

The pectoral fins are greatly enlarged, representing approximately 42.5 per cent of the total body length. Each pectoral fin consists of 11 principal fin rays that have a sturdy basal shaft, but segmented distal extensions. All but the first fin ray are distally branched, providing a large surface support of the pectoral fin. In addition, dense lepidotrichial segments (the 'sensenförmig' of Abel [5] or 'voile falciforme' of Lehman [8]) are present between the innermost principal fin ray and the body wall, further enlarging the surface area for gliding. This feature is unique to the Thoracopteridae. The pelvic fins extend to approximately 20 per cent of the total body length, and show the biplane gliding design of the body observed in other thoracopterids [7–9].

The triangular dorsal fin is positioned far posteriorly, close to the caudal peduncle. It has nine to 10 fin rays, preceded by a single basal fulcrum and four ridge scales. The endoskeletal support of the dorsal fin includes radials of roughly the same number to that of the dorsal fin rays, a derived condition of the Neopterygii, with the exception of *Australosomus* and other basal neopterygians. The greatly reduced anal fin has three short fin rays, preceded by a pair of enlarged scales. The endoskeletal support of the anal fin is lost, as in other members of this family. The deeply forked, asymmetrical caudal fin has a total of 34 fin rays, evenly distributed between the dorsal and ventral lobes. There are two basal fulcra in the lower lobe and one in the upper lobe. Fringing fulcra are absent in all fins, as in other thoracopterids [7–9].

Differing from the type genus *Thoracopterus*, which has a fully scale-covered body, *Potanichthys* shows great reduction in body scales, with only four vertical rows of rhomboic scales at the base of the caudal fin. *Gigantopterus* shows further reduction in body scales, having only a single vertical row of scales in the caudal region. By contrast, the two thoracopterids from Italy [10], although assigned to *Thoracopterus*, are

characterized by the total loss of body scales. The scale reduction in thoracopterid evolution could provide the advantage of manoeuvrability and energy efficiency for gliding.

4. Discussion

(a) Phylogenetic analysis

The phylogenetic affinity of the Thoracopteridae within the Neopterygii is controversial. This family has been placed in the Luganoiiformes or Perleidiformes [7–9]. Here, we present a phylogenetic analysis to assess the relationships of this group, based on a dataset composed of 83 characters coded across all thoracopterids, two living flying fishes and 11 other neopterygians. The Early Triassic *Australosomus*, which is often reconstructed as a basal neopterygian [21,23–26], was selected as the out-group. The characters were adopted from previous studies of basal actinopterygians [21,23–31]. Parsimony analysis was conducted using the branch-and-bound algorithm of PAUP v. 4.0b10 [32], with all characters equally weighted and treated as unordered. The analysis resulted in three most parsimonious trees, the strict consensus of which is shown in figure 3.

The results of our phylogenetic analysis are consistent with Gardiner & Schaeffer [21], placing the orders Perleidiformes, Peltopleuriformes and Luganoiiformes as stem neopterygians. However, our analysis fails to support the Thoracopteridae as a subgroup of either the Luganoiiformes (contra [7]) or Perleidiformes (contra [8,9]). Rather, the Thoracopteridae are resolved as a stem-group of the Neopterygii that is more crown-ward than the Peltopleuriformes, but more basal than the Luganoiiformes. The Thoracopteridae possess a suite of unambiguous synapomorphies of the clade Perleidiformes plus more crown-ward neopterygians, including dorsal and anal fin rays only distally segmented, dorsal and anal fin rays equal to endoskeletal radials in number, and nearly vertical suspensorium. The Thoracopteridae lie above the Peltopleuriformes, and consist of the sister-group of the clade Luganoiiformes plus crown-group Neopterygii; the sister-group relationships between them are supported by one derived character state (i.e. nasal not contributing to anterior border of orbit). However, they lack unambiguous synapomorphies of the Luganoiiformes plus crown-group Neopterygii, including maxilla free from the preopercle, possession of prominent coronoid process in the lower jaw, and hinge position of jaws near or well anterior to posterior border of orbit.

The Thoracopteridae have evolved an unusual combination of morphological features associated with gliding. Like the extant Exocoetidae, the Thoracopteridae have a pair of laterally expanded frontals, wing-like pectoral fins and an asymmetrical caudal fin with lower caudal lobe noticeably larger than upper lobe. They have pelvic fins enlarged as 'auxiliary wings', a derived feature shared with 'biplane-type' exocoetids (e.g. *Cypselurus*), but differing from 'monoplane-type' exocoetids (e.g. *Exocoetus*). It is noteworthy that most thoracopterids (except *Thoracopterus*) have reduction or complete loss of body scales, a feature that is otherwise independently evolved in few other ray-finned fishes (e.g. *Birgeria*), and which is unknown among extant exocoetids. Furthermore, the Thoracopteridae possess several synapomorphies that are unique among the Neopterygii, including dense lepidotrichial segments present between innermost principal
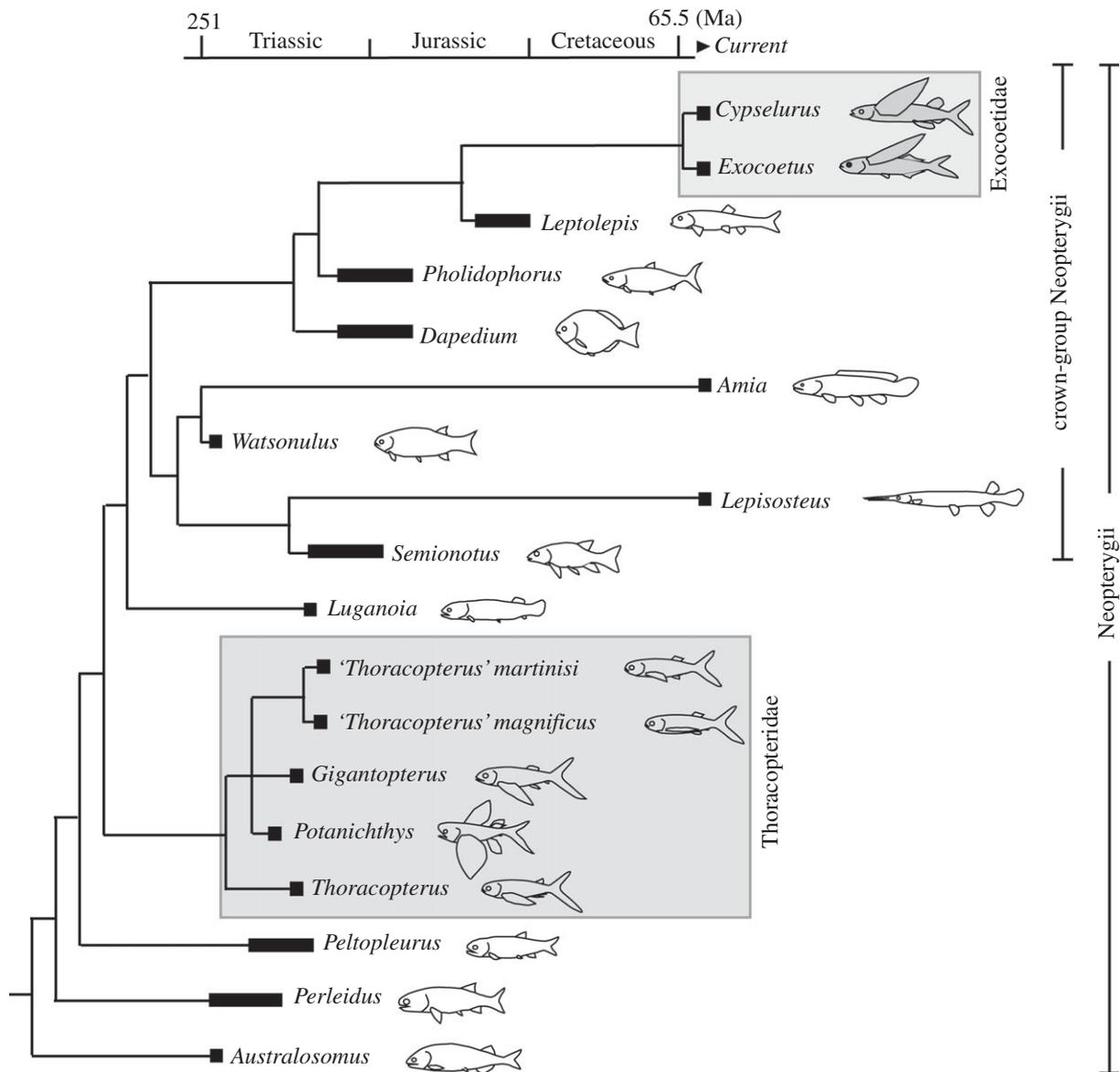
Figure 3. Time-calibrated strict consensus of the three most parsimonious trees (TL = 131 steps, CI = 0.6336, RI = 0.7913, RC = 0.5014), illustrating the phylogenetic relationships of the Thoracoperidae within the Neopterygii. For character description and coding of the characters for the sampled taxa, see the electronic supplementary material.

pectoral fin ray and body, loss of parietals and post-temporals, and a greatly reduced anal fin with loss of endoskeletal support.

The results of our analysis identify *Thoracopterus* as the most basal member of the Thoracopteridae. *Potanichthys* and other thoracopterids are more derived than *Thoracopterus*, sharing increased numbers of supraorbital bones and reduction in body scales to only a few vertical rows remaining in caudal region. However, the relationships among *Potanichthys*, *Gigantopterus* and the Italian *Thoracopterus* are unresolved. The sister-group relationships between two Italian *Thoracopterus* species are supported by a complete loss of body scales. Giving this topology, the Italian thoracopterids should probably be removed from *Thoracopterus*.

(b) Over-water gliding strategy

Gliding has evolved many times in animals (see review by Dudley *et al.* [33]). Within the vertebrates, it is principally associated with rainforest tetrapods (e.g. gliding frogs, lizards and mammals), which use this strategy as an energy-efficient means of travelling from tree to tree. However, gliding has evolved only twice among fishes: once in the Triassic

Thoracopteridae, and again in the modern Exocoetidae. In contrast to tetrapod gliders, the gliding of flying fishes is energetically very expensive, and for this reason the hypothesis of gliding in flying fishes as part of an energy-saving strategy for long-distance migration [34] has been rejected [12]. An alternative hypothesis [12,15,16] that the exocoetid flying fishes glide to escape from predators (e.g. dolphin, dolphinfish, tuna and squid) is supported by the observation that flying fishes are a dominant food source in the stomach contents of dolphins [35]. It is unlikely that thoracopterids used gliding as part of an energy-saving strategy for long-distance migration (but see [10]); instead, thoracopterid flying fishes most probably used gliding as an escape strategy from predators—potentially the co-occurring marine reptiles that had body plans convergent with modern marine mammals [2]. These marine reptiles occupied the top trophic levels of Triassic marine ecosystems, feeding on fishes, cephalopods, bivalves and tetrapods [2,17,22]. Other possible thoracopterid predators include large carnivorous fishes, such as *Birgeria* [18], which also occurs in the same units as *Potanichthys* and has a total length of up to 3 m (unpublished material stored in the collection of the Zhejiang Museum of

Natural History). Gliding adaptations in thoracopterid flying fishes represent a remarkable case of convergent evolution of over-water gliding strategy with extant exocoetids.

Previous studies [12,14,15] have demonstrated that exocoetid flying fishes cannot flap their 'wings' to gain lift owing to functional limitations of pectoral girdles/fins and the associated muscles (see discussion by Davenport [12]). Instead, exocoetid flying fishes generate thrust underwater, and launch themselves out of the water by swift movement of their asymmetrical caudal fin. Fishes with greatly expanded pectoral fins are commonly presumed to be 'flying fishes', but these judgements should be treated with caution. These alleged 'flying fishes' with enlarged pectoral fins, but lacking an asymmetrical caudal fin, such as extant gasteropelicid hatchet fishes and pantodontid butterfly fish (*Pantodon*), are neither powered flyers nor even true gliders [36,37]. On the other hand, greatly expanded pectoral fins have been independently evolved for other strategies (e.g. startling predators), such as marine 'flying gurnards', which possess wing-like pectoral fins, but in fact cannot launch themselves out of water. Thus, wing-like pectoral fins are not indicative of gliding. Indeed, the key character to identify over-water gliding strategy in fishes is an asymmetrical caudal fin, with the ventral lobe noticeably stronger than the dorsal lobe. Establishing this criterion is especially important for extinct taxa whose behaviour cannot be directly examined. For example, the fossil fish *Icarealcyon* from the Early Triassic of Madagascar was previously regarded as a 'flying fish' [38] (but see [10]) because of its expanded pectoral fins. However, this alleged 'flying fish' lacks an asymmetrical caudal fin. Furthermore, it has a relatively deep and laterally compressed body shape, with long dorsal and anal fins, quite different from extant flying fishes, which have a laterally expanded skull roof, broadly cylindrical bodies and short dorsal and anal fins. These differences in body plan between *Icarealcyon* and exocoetids cause us to question whether *Icarealcyon* was a true glider. In contrast to *Icarealcyon*, but similar to exocoetids, these features associated with gliding are observed in both *Potanichthys* and European thoracopterids. Thus, *Potanichthys* and European thoracopterids are interpreted as over-water gliders.

(c) Ecological implication

The discovery of *Potanichthys* extends the stratigraphic range of the Thoracopteridae from the Late Triassic to the Middle Triassic, and enriches our knowledge of morphological and taxonomic radiation of non-teleostean neopterygians after the end-Permian mass extinction. The end-Permian mass extinction was the most remarkable event to impact ecological systems on Earth, and recovery from this extinction has long been viewed as more prolonged than the recoveries following other mass extinctions [1]. Based primarily on

studies of terrestrial tetrapods [39], it was suggested that a low level of taxonomic diversity and ecological complexity was sustained through to the Early–Middle Triassic. However, the recovery of marine ecosystems appears to have been more rapid than that of terrestrial ecosystems, as indicated by recently discovered fossil Lagerstätten from the Middle Triassic (Anisian) of southwestern China [40]. Vast outcrops from the Middle Triassic (Anisian–Ladinian) of China have yielded diverse assemblages of invertebrates, fishes and marine reptiles [17,18,22,26,40,41], demonstrating that both the taxonomic diversity and the ecological complexity of top predators and prey in the Middle Triassic were much higher than those in the Early Triassic. As the earliest evidence of over-water gliding in vertebrates, the discovery of *Potanichthys* significantly adds to our knowledge of the ecological complexity in the Middle Triassic (Ladinian) of the Palaeotethys Ocean. This discovery lends support to the hypothesis that the recovery of marine ecosystems after the end-Permian event was more rapid than previously thought.

Potanichthys represents the first record of the Thoracopteridae in Asia, extending the geographical distribution of this clade from the western to the eastern rim of the Palaeotethys Ocean. The Palaeotethys would have provided an east–west corridor for dispersal, and biological exchanges of aquatic vertebrates between the East and West Palaeotethys Ocean have previously been suggested [17,22,41]; *Potanichthys* provides new evidence supporting these exchanges in the Middle Triassic.

In modern ecosystems, flying fishes are commonly limited to surface waters warmer than 20–23°C. In addition, owing to limitations of muscle function, flying fishes are unlikely to be capable of flight at temperatures below 20°C [12]. We can reasonably apply similar limitations to the thoracopterids, which are inferred to have inhabited the epipelagic zone in the eastern Palaeotethys Ocean, and therefore implying surface water temperatures warmer than 20°C. A global hot climate in the Triassic period with no evidence of glaciation at or near either pole has been suggested by previous palaeoclimate studies [42], and *Potanichthys* adds new data supporting a generally hot climate in the Middle Triassic eastern Palaeotethys Ocean.

References

1. Hallam A, Wignall PB. 1997 *Mass extinctions and their aftermath*. Oxford, UK: Oxford University Press.

2. Motani R. 2010 Warm-blooded 'sea dragons'? *Science* **328**, 1361–1362. (doi:10.1126/science.1191409)

3. Nelson JS. 2006 *Fishes of the world*, 4th edn. Hoboken, NJ: John Wiley & Sons Inc.

4. Bürgin T. 1992 Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). *Schweiz. Paläont. Abh.* **114**, 1–164.

5. Abel O. 1906 Fossile Flugfische. *Jahrbuch Geol. Reichsanstalt* **56**, 1–93.

6. Bronn HG. 1858 Beiträge zur Triassischen Fauna und Flora der bituminösen Schiefer von Raibl. *Neues Jahrb. Min. Geol. Petrefaktenk.* **1**, 1–32.

7. Griffith J. 1977 The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zool. J. Linn. Soc.* **60**, 1–93. (doi:10.1111/j.1096-3642.1977.tb00834.x)

8. Lehman JP. 1979 Note sur les Poissons du Trias de Lunz. I. Thoracopterus Bronn. *Ann. Naturhistor. Mus. Wien* **82**, 53–66.

9. Tintori A, Sassi D. 1987 Pesci volanti del genere *Thoracopterus* nel Norico Lombardo. *Nota preliminar. Riv. Ital. di Paleontol. e Stra.* **93**, 337–345.

10. Tintori A, Sassi D. 1992 *Thoracopterus* Bronn. (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. *J. Vert. Paleontol.* **12**, 265–283. (doi:10.1080/02724634.1992.10011459)

11. Müller AH. 1985 *Lehrbuch der Paläozoologie, Band 3, Teil 1, 2. Auflage.* Jena, Germany: VEB Gustav Fischer.

12. Davenport J. 1994 How and why do flying fish fly? *Rev. Fish Biol. Fish.* **4**, 184–214. (doi:10.1007/BF00044128)

13. Lewallen EA, Pitman RL, Kjartanson SL, Lovejoy NR. 2011 Molecular systematics of flyingfishes (Teleostei: Exocoetidae): evolution in the epipelagic zone. *Biol. J. Linn. Soc.* **102**, 161–174. (doi:10.1111/j.1095-8312.2010.01550.x)

14. Fish F. 1991 On a fin and a prayer. *Scholars* **3**, 4–7.

15. Kutschera U. 2005 Predator-driven macroevolution in flyingfishes inferred from behavioural studies: historical controversies and a hypothesis. *Ann. Hist. Phil. Biol.* **10**, 59–77.

16. Kutschera U. 2009 Symbiogenesis, natural selection, and the dynamic Earth. *Theory Biosci.* **128**, 191–203. (doi:10.1007/s12064-009-0065-0)

17. Li J-L. 2006 A brief summary of the Triassic marine reptiles of China. *Vert. PalAsia.* **44**, 99–108.

18. Jin F. 2006 An overview of Triassic fishes from China. *Vert. PalAsia.* **44**, 28–42.

19. Woodward AS. 1901 *Catalogue of the fossil fishes in the British Museum (NH), Part IV.* London, UK: Longmans and Co.

20. Regan CT. 1923 The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proc. Zool. Soc. Lond.* **1923**, 445–461.

21. Gardiner BG, Schaeffer B. 1989 Interrelationships of lower actinopterygian fishes. *Zool. J. Linn. Soc.* **97**, 135–187. (doi:10.1111/j.1096-3642.1989.tb00550.x)

22. Rippel O, Liu J, Li C. 2006 A new species of the thalattosaur genus *Anshunsaurus* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou Province, southwestern China. *Vert. PalAsia.* **44**, 285–296.

23. Coates MI. 1999 Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. *Phil. Trans. R. Soc. Lond. B* **354**, 435–462. (doi:10.1098/rstb.1999.0396)

24. Gardiner BG, Schaeffer B, Masserie JA. 2005 A review of the lower actinopterygian phylogeny. *Zool. J. Linn. Soc.* **144**, 511–525. (doi:10.1111/j.1096-3642.2005.00181.x)

25. Xu G-H, Gao K-Q. 2011 A new scanilepiform from the Lower Triassic of northern Gansu Province, China, and phylogenetic relationships of non-teleostean Actinopterygii. *Zool. J. Linn. Soc. Lond.* **161**, 595–612. (doi:10.1111/j.1096-3642.2010.00645.x)

26. Xu G-H, Wu F-X. 2012 A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. *Chin. Sci. Bull.* **57**, 111–118. (doi:10.1007/s11434-011-4719-1)

27. Gardiner BG, Maisey JG, Littlewood DTJ. 1996 Interrelationships of basal neopterygians. In *Interrelationships of fishes* (eds MLJ Stiassney, LR Parenti, GD Johnson), pp. 117–146. San Diego, CA: Academic Press.

28. Cloutier R, Arratia G. 2004 Early diversification of actinopterygians. In *Recent advances in the origin and early radiation of vertebrates* (eds G Arratia, MVH Wilson, R Cloutier), pp. 217–270. München, Germany: Verlag Dr Friedrich Pfeil.

29. Pinna MCC. 1996 Teleostean monophyly. In *Interrelationships of Fishes* (eds MLJ Stiassney, LR Parenti, GD Johnson), pp. 147–162. San Diego, CA: Academic Press.

30. Grande L, Bemis WE. 1998 A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy: an empirical search for interconnected patterns of natural history. *Soc. Vertebr. Paleontol. Mem.* (*Suppl. J. Vertebr. Paleontol.*) **4**, 1–690.

31. Grande L. 2010 An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of holostei. *Copeia* **10** (Suppl.), 1–871.

32. Swofford DL. 2003 PAUP*. Phylogenetic analysis using parsimony (*and other methods)*, v. 4.0b10. Sunderland, MA: Sinauer Associates.

33. Dudley R, Byrnes G, Yanoviak SP, Borrell B, Brown RM, McGuire JA. 2007 Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annu. Rev. Ecol. Evol. Syst.* **38**, 179–201. (doi:10.1146/annurev.ecolsys.37.091305.110014)

34. Rayner JMV. 1986 Pleuston: animals which move in water and air. *Endeavour* **10**, 58–64. (doi:10.1016/0160-9327(86)90131-6)

35. Collette BB, Parin NV. 1998 Flying fishes and their allies. In *Encyclopaedia of fishes* (eds JR Paxton, WN Eschmeyer), pp. 144–147. Sydney, Australia: UNSW Press.

36. Wiest FC. 1995 The specialized locomotory apparatus of the freshwater hatchetfish family Gasteropelecidae. *J. Zool. Lond.* **236**, 571–592. (doi:10.1111/j.1469-7998.1995.tb02733.x)

37. Saidel WM, Strain GF, Fornari SK. 2004 Characterization of the aerial escape response of the African butterfly fish, *Pantodon buchholzi* (Peters). *Environ. Biol. Fish.* **71**, 63–72. (doi:10.1023/B:EBFI.0000043153.38418.cd)

38. Beltan L. 1984 A propos d'un poisson volant biplan de l'Eotrias du NW de Madagascar: *Icarealcyon malagasium* Beltan. *Ann. Soc. Geol. Nord.* **103**, 75–82.

39. Sahney S, Benton MJ. 2008 Recovery from the most profound mass extinction of all time. *Proc. R. Soc. B* **275**, 759–765. (doi:10.1098/rspb.2007.1370)

40. Hu S-X, Zhang Q-Y, Chen Z-Q, Zhou C-Y, Lü T, Xie T, Wen W. 2011 The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proc. R. Soc. B* **278**, 2274–2282. (doi:10.1098/rspb.2010.2235)

41. Lombardo C, Sun Z-Y, Tintori A, Jiang D-Y, Hao W-C. 2011 A new species of the genus *Perleidus* (Actinopterygii: Perleidiformes) from the Middle Triassic of southern China. *Boll. Soc. Paleont. Ital.* **50**, 75–83.

42. Preto N, Kustatscher E, Wignall PB. 2010 Triassic climates: state of the art and perspectives. *Palaeogeogr. Palaeoclimatol. Paleoecol.* **290**, 1–10. (doi:10.1016/j.palaeo.2010.03.015)