A Middle Triassic thoracopterid from China highlights the evolutionary origin of overwater gliding in early ray-finned fishes

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Gliding adaptations in thoracopterid flying fishes represent a remarkable case of convergent evolution of overwater gliding strategy with modern exocoetid flying fishes, but the evolutionary origin of this strategy was poorly known in the thoracopterids because of lack of transitional forms. Until recently, all thoracopterids, from the Late Triassic of Austria and Italy and the Middle Triassic of South China, were highly specialized ‘four-winged’ gliders in having wing-like paired fins and an asymmetrical caudal fin with the lower caudal lobe notably larger than the upper lobe. Here, we show that the new genus Wushaichthys and the previously alleged ‘peltopleurid’ Peripeltopleurus, from the Middle Triassic (Ladinian, 235–242 Ma) of South China and near the Ladinian/Anisian boundary of southern Switzerland and northern Italy, respectively, represent the most primitive and oldest known thoracopterids. Wushaichthys, the most basal thoracopterid, shows certain derived features of this group in the skull. Peripeltopleurus shows a condition intermediate between Wushaichthys and Thoracopterus in having a slightly asymmetrical caudal fin but still lacking wing-like paired fins. Phylogenetic studies suggest that the evolution of overwater gliding of thoracopterids was gradual in nature; a four-stage adaption following the ‘cranial specialization–asymmetrical caudal fin–enlarged paired fins–scale reduction’ sequence has been recognized in thoracopterid evolution. Moreover, Wushaichthys and Peripeltopleurus bear hooklets on the anal fin of supposed males, resembling those of modern viviparious teleosts. Early thoracopterids probably had evolved a live-bearing reproductive strategy.

1. Introduction

Modern flying fishes are remarkable exocoetid teleosts that employ the overwater gliding strategy to presumably escape from predators [1–3]. This extraordinary gliding strategy, unlike those in terrestrial gliders, is energetically very expensive and has otherwise been hypothesized to occur only in a single stem group of the Neopterygii, the Thoracopteridae from the Late Triassic of Austria and Italy and Middle Triassic of South China [4–8]. Until recently, all known thoracopterids were suggested to be highly specialized ‘four-winged’ gliders because they have wing-like paired fins and an asymmetrical caudal fin with the lower caudal lobe notably larger than the upper lobe; movement of such a caudal fin could generate the power to launch the fish for overwater gliding as in modern flying fishes [1,7]. Owing to lack of transitional forms, the evolutionary origin of the overwater gliding strategy was poorly known in the thoracopterids. Here, we report the discovery of a new thoracopterid fish on the basis of six well-preserved specimens from the Ladinian (235–242 Ma) marine deposits of Xingyi in Guizhou Province, China. The new fish represents the most basal
thoracopterid; although it seems that it was not a glider, its nearly complete skeletons provide us new and more comprehensive anatomical information of early thoracopterids. Along with the new fish, other taxa known from the same fossil beds include plants, invertebrates, marine reptiles, ‘four-winged’ thoracopterids [7,8], and several other kinds of fishes; this taxonomically diverse fossil assemblage has been referred to the Xingyi biota [9]. Study of the new fish from the Xingyi biota stimulates re-examinations of contemporary material from the Monte San Giorgio area in southern Switzerland [10]. Our comparative studies resulted in a reinterpretation of the previously alleged ‘peltopleurid’ Peripeltopleurus [10] as a primitive thoracopterid. Peripeltopleurus and the new fish from China share with the type genus Thoracopterus of this family the specialization of the skull pattern and scale cover, but both taxa retain many primitive characters unknown in Thoracopterus and other derived thoracopterids. Studies of these taxa provide new insights into the early evolution of the Thoracopteridae.

2. Systematic palaeontology

Neopterygii Regan, 1923.
Wushaichthys exquisitus gen. et sp. nov.

(a) Etymology
The genus name refers to the town Wusha, where the fossils were collected. The species epithet is from Latin exquisitus, meaning exquisite.

(b) Holotype
A nearly complete skeleton in the collection of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP V19959). Standard length is 44 mm; total length is 52 mm.

(c) Referred specimens
Five topotypic specimens: IVPP V19960-19961; ZMNH (Zhejiang Museum of Natural History, Hangzhou, China) M1693, 1696 and 1699.

(d) Type locality and horizon
Wusha, Xingyi, Guizhou, China; Zhuganpo Member, Falang Formation, Middle Triassic.

(e) Diagnosis
A basal thoracopterid distinguished from others of this family by a combination of features: deep and narrow rostral; presence of rostral/frontal contact; anterior rim of orbit formed by nasal and antorbital; five pairs of branchiostegal rays; relatively short paired fins; 10 principal dorsal fin rays and presence of squamation formula of D25–26/P14, A20–21, C28–29/T32–34.

3. Description and discussion

Wushaichthys shows certain derived features of the Thoracopteridae in the skull. The skull roof is laterally expanded, formed by a pair of trapezoidal frontals and enlarged dermopterotics, along with small triangular extrascapulans (figure 1). The supraorbital sensory canal enters the frontal from the nasal and ends at the posterior portion of this bone. No distinct parietals are present, as in other thoracopterids; the parietals were probably lost by fusion with the dermopterotics according to the presence of a transverse pit-line on the dermopterotics. The extrascapular contacts the post-temporal posteroomedially and is separated from contact with its counterpart by paired post-temporals. A similar condition is also present in Peripeltopleurus [10] and Potanichthys [7], and probably in Thoracopterus as well [4,5]. No post-temporals were identified in Thoracopterus from Austria [4,5], but the previously alleged ‘median suprascapular’ (= median extrascapular) appears more reasonably interpreted as the post-temporal because of its relationships with the supracleithrum and absence of a supratemporal commissural sensory canal on this bone. The preopercle, resembling other thoracopterids, has a narrow vertical bar and a tapering anterior process that ventrally contacts the maxilla (figure 1). The operculogular series includes a large and tall opercle, a much smaller subopercle, five pairs of elongate branchiostegal rays, a pair of trapezoidal lateral gulars and a subcircular median gular. A dermothyal is obviously absent, as in other thoracopterids and more derived neopterygians [7,11,12].

A notable feature is the presence of hooklets (claws) on the anal fin of supposed males (figure 1b,c), suggesting that Wushaichthys was a viviparous fish. Viviparity occurs in 14 families of living teleosts and two coelacanth species, which together account for only 2–3% of species of extant bony fishes [13]. The Triassic Peltopleuriformes (probably paraphyletic [14]) have independently evolved the viviparity because they show hooklets in the supposed male anal fin [15,16]. These hooklets might have played an important role in sperm transfer to females; a study of the living viviparous guppy (Poecilia) showed that up to threefold more sperm were transferred when males had hooklets compared with those with hooklets removed [17]. The supposed female anal fin of Wushaichthys consists of about 10 principal fin rays, whereas the male anal fin is modified and can be divided into two portions; the anterior ‘supporting structure’ consists of four segmented fin rays, whose proximal portions are covered by a large scute on each of side, and the posterior ‘holdfast structure’ includes five or six stout proximal segments that articulate with dense long and slender brush-like rays; each of five posterior brush-like rays bears a recurved hooklet at its tip. A similar condition is also present in Peripeltopleurus (figures 1j and 2b; [10]) and Thoracopterus wushaensis [8] (see the electronic supplementary material for taxonomic comments on this taxon). This condition indicates that early thoracopterids probably had evolved a live-bearing reproductive strategy.

Wushaichthys possesses a combination of features that distinguish it from other thoracopterids. First, the median rostral is deep and narrow, resembling that in Peripeltopleurus [10]; by contrast, the rostral is broad and short in Thoracopterus and more derived thoracopterids [4–7]. In addition, this bone contacts the frontals posterodorsally and separates the nasal from contact with its counterpart in Wushaichthys, Peripeltopleurus, Potanichthys and Thoracopterus from Italy [4–7]. However, the rostral/frontal contact is lost, and the paired nasals meet each other medially in Thoracopterus and Gigantopterus from Austria [4,5]. Second, the supraorbital sensory canal ends at the posterior portion of the frontal in Wushaichthys, resembling those of Thoracopterus and...
Gigantopterus from Austria. However, this canal ends at the anterior-middle portion of the frontal in Peripeltopleurus, Potanichthys and Thoracopterus from Italy [6]. Third, the nasal is slightly deeper than the antorbital, and the anterior rim of the orbit is formed by both bones in Wushaichthys. However, in other thoracopterids, the antorbital is more enlarged, and the anterior rim of the orbit is formed mainly by the antorbital, without contribution from the nasal [7]. Last, Wushaichthys has a fully scale-covered body with the lateral line scales conspicuously deeper than wide in the anterior flank region, showing a condition resembling those of Peripeltopleurus [10] and Thoracopterus [4,5]. However, Potanichthys [7] and Gigantopterus [4] show great reduction of body scales, and the two thoracopterids from Italy are characterized by the total loss of body scales [6]. A progressive reduction of scales, probably providing the advantage of manoeuvrability and energy efficiency for the overwater gliding, is a notable feature in the thoracopterid evolution [7].

Figure 1. Wushaichthys exquisitus gen. et sp. nov. and Peripeltopleurus vexillipinnis. (a–h) Wushaichthys exquisitus gen. et sp. nov.; complete skeleton (a) and close-up of anal fin (b), IVPP V19959 (holotype), male; complete skeleton (c) and close-up of anal fin (d), IVPP V19960, female, (e) close-up of anal fin, ZMNH M 1696, male; (f) skull and pectoral girdle of holotype (a); (g) skull and pectoral girdle, ZMNH M 1699, female; (h) reconstruction of skull and pectoral girdle. (i) Peripeltopleurus vexillipinnis; (i) complete skeleton, PIMUZ A/I 3687, female, and (j) close-up of anal fin, PIMUZ T4332, male. Arrow indicates hooklets on anal fin. ao, antorbital; br1, first branioiostegal ray; cl, cleithrum; cla, clavicle; dpt, dermopterotic; dsp, dermosphenotic; es, extrascapular; fr, frontal; ju, jugal; la, lachrymal; lg, lateral gular; md, mandible; mg, median gular; mx, maxilla; n, nasal; op, opercle; pas, parasphenoid; pcl, postcleithrum; pmx, premaxilla; pop, preopercle; pscl, presupracleithrum; pt, post-temporal; r, rostral; sd, supracleithrum; scr, sclerotic ring; so, suborbital; sop, subopercle. (Online version in colour.)
**Peripeltopleurus** is reinterpreted as a primitive thoracopterid because it possesses five synapomorphies of this group: (i) a pair of laterally expanded frontals, (ii) absence of distinct parietals, (iii) a supraorbital sensory canal ending at the frontal, (iv) an extrascapular contacting the post-temporal posteromedially and being separated from contact with its counterpart by paired post-temporals and (v) a preopercle with a narrow vertical bar and a tapering anterior process. Additionally, more derived than *Wushaichthys*, *Peripeltopleurus* like *Thoracopterus* and other thoracopterids has an asymmetrical caudal fin with the lower lobe larger than the upper lobe. An asymmetrical caudal fin was previously identified in one of three species of the genus *Peripeltopleurus*, *P. hypsisomus* (figure 2a and [10]), but personal examinations.

**Figure 2.** *Peripeltopleurus* and phylogenetic placement of *Peripeltopleurus* and *Wushaichthys*. (a) Reconstruction of *Peripeltopleurus hypsisomus* (from Bürgin [10]) and (b) line-drawing of anal fin of *Peripeltopleurus vexillipinnis* (from Bürgin [10]), PIMUZ T4332, male. (c) Strict consensus of the six most parsimonious trees (MPTs) (tree length, TL = 142 steps; consistency index, CI = 0.6127; retention index, RI = 0.7901; rescaled consistency index, RC = 0.4841), illustrating phylogenetic placement of *Peripeltopleurus* and *Wushaichthys* within the Neopterygii. Numerical values immediately below the nodes denote Bremer decay indices. (d) Comparison of caudal fin in *Wushaichthys*, *Peripeltopleurus* and *Potanichthys*, illustrating a progressive elongation of the lower lobe relative to the upper lobe in thoracopterid evolution; pf, principal fin ray. For character description and coding of the characters for the sampled taxa, see the electronic supplementary material. (Online version in colour.)
of the type specimens showed that this feature is also present in *P. vexillipinnis* (figure 1i), although it is unknown in another *Peripeltopleurus* species because of poor state of preservation. However, *Peripeltopleurus* lacks some synapomorphies of *Thoracopterus* and other derived thoracopterids: presence of wing-like paired fins and absence of fringing fulcra. The intermedium condition of *Peripeltopleurus* between *Wushaichthys* and *Thoracopterus* indicates that an asymmetrical caudal fin was evolved before the wing-like paired fins in thoracopterid evolution. Studies of modern flying fishes [1] have shown that possession of an asymmetrical caudal fin in the absence of wing-like paired fins provides some ‘halfbeaks’ (Hemiramphidae) with limited gliding performance relative to the gliding abilities of exocoetid ‘flying fishes’.

Our phylogenetic studies suggest that overwater gliding adaptations of thoracopterids were gradual in nature. Four stages can be recognized in the thoracopterid evolution (figure 2c): the first stage (represented by *Wushaichthys*) is defined by cranial specialization (see descriptions above), the second stage (represented by *Peripeltopleurus* [10]) is characterized by acquisition of an asymmetrical caudal fin, the third stage (represented by *Thoracopterus* [4,5]) by evolution of wing-like paired fins and the last stage (represented by *Potanichthys* [7], *Gigantopecterus* [4] and two *Thoracopterus* species from Italy [6]) by evolution of flank scales.

Data accessibility. All data used for analysis have been uploaded as the electronic supplementary material.

Acknowledgements. We thank M.-M. Chang, K.-Q. Gao and F. Jin for constructive suggestions, L. Cavin, M. V. H. Wilson and two anonymous reviewers for helpful comments on the manuscript, T. Bürgin for providing important references, H. Furrer and M. Richter for access to comparative fossil material in the Paläontologisches Institut und Museum, Universität Zürich (Zürich), and the Natural History Museum (London), respectively, and Z.-Y. Li for specimen preparation.

Author contributions. G.-H. Xu designed the research, wrote the main manuscript text and prepared the figures. G.-H. Xu and L.-J. Zhao undertook the fieldwork. C.-C. Shen and L.-J. Zhao contributed to the discussion of the results.

Funding statement. The research was supported by the National Natural Science Foundation of China (41272002 and 40902010), and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; 143114).

Competing financial interests. The authors declare no conflict of interest.

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