



Andrea Tintori  
Zuo-Yu Sun  
Cristina Lombardo  
Da-Yong Jiang  
Cheng Ji  
Ryosuke Motani

## A NEW "FLYING" FISH FROM THE UPPER LADINIAN (MIDDLE TRIASSIC) OF WUSHA (GUIZHOU PROVINCE, SOUTHERN CHINA)

UN NUOVO PESCE "VOLANTE" DAL LADINICO SUPERIORE (TRIASSICO MEDIO) DI WUSHA (PROVINCIA DEL GUIZHOU, CINA MERIDIONALE)

**Riassunto breve** - La distribuzione dei pesci "volanti" fossili, con 4 specie appartenenti al genere *Thoracopterus*, era finora ristretta all'area alpina (corrispondente alla Tetide occidentale durante il Triassico) e all'intervallo di tempo compreso tra il Carnico inferiore di Raibl-Cave del Predil (Udine, Friuli) e il Norico medio-superiore del Calcare di Zorzino (Lombardia). Nuovi ritrovamenti sono venuti alla luce durante lo scavo sistematico di un'ampia superficie del livello fossilifero del Ladinico superiore nel Membro Zhuganpo della Formazione Falang che ha fornito la famosa "Xingyi Fauna" dominata dal pachipleurosaur *Keichousaurus*. Essi permettono di ampliare la distribuzione, sia areale che stratigrafica, di *Thoracopterus*, anticipando la comparsa di questo particolare pesce "subolosteo" alla fine del Triassico Medio, cioè nel Ladinico superiore. Lo scavo si sta svolgendo nei pressi del villaggio di Nimaigu (Distretto di Wusha, Xingyi City, provincia del Guizhou, Cina Meridionale) e interessa globalmente una superficie di strato di quasi 1000 mq; tuttavia lo scavo di dettaglio per la ricerca soprattutto dei piccoli pesci si svolge su una superficie variabile tra i 10 e i 20 mq. La nuova specie di *Thoracopterus* che viene qui descritta è simile a *T. telleri*, conosciuto nel Carnico Inferiore di Lunz (Austria), sia nelle dimensioni che nella quasi totale assenza di scaglie sul corpo; questo carattere peraltro è comune anche alle due specie del Norico, *T. martinisi* e *T. magnificus*, nelle quali le scaglie sono però totalmente assenti. La nuova specie cinese si differenzia da *T. telleri* per la presenza di un campo relativamente ampio di piccole scaglie sub-quadrato subito dietro il cranio e un altro a supporto del lobo ventrale della caudale. Le scaglie della regione dorso-toracica hanno la superficie ornamentata da sottili e brevi strie di ganoina. Come in molti Peltopleuriformes la nuova specie di *Thoracopterus* presenta dimorfismo sessuale sulla base di una differenziazione della pinna anale. I supposti maschi hanno ossa craniche e pinne pettorali più robuste, mentre le femmine mostrano una ornamentazione delle scaglie dorso-toraciche più sviluppata e la pinna anale modificata con parte posteriore formata da raggi molto sottili e dotati di una serie di uncini terminali.

**Parole chiave:** Triassico Medio, Nuova specie, *Thoracopterus wushaensis*, Subolostei, Pesce "volante", Cina.

**Abstract** - Fossil "flying" (gliding) fishes have been known since the XIX century from the Late Triassic of northern Italy and Austria. So far, four species have been ascribed to the genus *Thoracopterus*. Now a new species is erected on well preserved specimens from a new extensive and detailed excavation started in the summer 2011 near the village of Nimaigu (Wusha District, Xingyi City, Guizhou Province, southern China). The investigation concerns a rich vertebrate level in the Late Ladinian Zhuganpo Member of the Falang Formation. This vertebrate-bearing section is famous because it contains an assemblage made of abundant specimens of the pachipleurosaur *Keichousaurus*, as well as nothosaurs, ichthyosaurs and a few fish genera (Xingyi Fauna). During the bed by bed excavation several specimens of a new "flying" fish have been collected; mainly on the basis of a peculiar partial scale covering, limited to the antero-dorsal and ventral caudal regions, we erect a new species. As for several other peltopleuriformes, the new species shows a sexual dimorphism that allows the differentiation, mainly base on the anal fin modifications, in "males" and "females". This new species is closer to the Carnian *Thoracopterus telleri* than to any of the other three species and it is the oldest known "flying" fish.

**Key words:** Middle Triassic, New species, *Thoracopterus wushaensis*, Subholosteans, "Flying fish", China.

### Introduction

"Flying" fishes are a well-known, small group of modern teleosts (Exocoetidae) that had a Triassic analogous in the subholostean genus *Thoracopterus* (TINTORI & SASSI 1992). Actually, *Thoracopterus* had a gliding way of flying, like the modern "biplane"

(four winged) flying fishes: the genus *Cypselurus*, for example, whose pectoral and pelvic fins are elongated and structured to be very stiff when kept laterally open (TINTORI & SASSI 1992).

Fossil "flying" fishes have been known for a long time, as BRONN (1858) described *Thoracopterus niederristi* from the lower Carnian of Raibl (now Cave del Predil, Udine,



Fig. 1 - The site of the bed by bed excavation near the village of Nimaigu (Wusha District, Xingyi City, Guizhou Province, China). This quarry will become a field museum being roofed and prepared for tourist visits. In the oval a man for scale. The rectangle shows the area for lamina by lamina searching.

- Il sito di scavo sistematico presso il villaggio di Nimaigu (Wusha District, Xingyi City, Guizhou Province, China). Lo scavo verrà attrezzato con una copertura e predisposto per le visite. Nell'ovale, una persona per scala. Nel rettangolo l'area interessata dalle ricerche lamina per lamina.

Italy) more than 150 years ago. The type species was re-described by GRIFFITH (1977) using specimens from the Carnian of Polzberg (Lunz, Austria). ABEL (1906) erected a new genus and species (*Gigantopterus telleri*) on a specimen from Polzberg; however, TINTORI & SASSI (1992) considered *Gigantopterus* a junior synonym of *Thoracopterus* because the only difference from the type species of *Thoracopterus* is the scale covering, while the general anatomical pattern is the same. Actually, specimens of *T. telleri* are on the average somewhat larger than those of *T. niederristi*, whereas both the Norian species, *T. magnificus* and *T. martinisi*, show a wide size range (TINTORI & SASSI 1987; 1992).

In August 2011 a scientific excavation was started at the village of Nimaigu (Wusha District, Xingyi City, Guizhou Province, China); during the bed by bed collecting (fig. 1), over 300 reptilian remains as well as dozens of fishes have been so far collected in the 28 units (layer 26 to layer 53) of the 5.5 m-thick vertebrate-bearing section. They belong to the 96 m thick Zhuganpo Member of the Falang Formation (JI et al. 2012). This Late Ladinian vertebrate assemblage (JIANG et al. 2009, M. Balini, pers. com. 2012) has been

known since the half of the last century when YOUNG (1958) described the pachipleurosaur *Keichousaurus hui* and SU (1959) erected two new genera and three species of fish (*Asialepidotus shingyiensis*, *Sinoeugnathus kueichowensis*, and *Peltopleurus orientalis*). Since then, very little attention has been paid to the fishes preserved in these beds, because research was focused on the numerous *Keichousaurus* specimens.

The vertebrate-bearing section has been intensively excavated in the last 10 years by local farmers over a wide area encompassing the Guizhou (Dinxiao and Xingyi-Wusha localities) and Yunnan provinces (Fuyuan and Luoping localities). Generally, only medium to large sized *Asialepidotus* were collected, while those whose length is less than 10 cm have not been detected at all. A few other genera and species have been added to this fauna (see LIU et al. 2003) but the validity of some of them needs confirmation. LIN et al. (2011) ascribed *Peltopleurus orientalis* to the genus *Habroichthys* on the basis of the typical squamation shown by the holotype and by a couple of other known specimens.

This late Ladinian fauna corresponds to the fauna contained in the Kalkschieferzone (Calcare di Meride,

Monte San Giorgio, Switzerland and Italy) on the western side of the Tethys. It must be stressed that the Kalkschieferzone fauna is quite rich in fishes (LOMBARDO 1999; 2001; 2002; LOMBARDO & TINTORI 2004; TINTORI 1990a,b; TINTORI & LOMBARDO 1999; 2007) but to date has yielded only *Lariosaurus* among reptiles (TINTORI & RENESTO 1990). The composition of the two fish faunas is rather different: so far they share only the genus *Saurichthys*, but this is not significant because this genus is widely spread across the whole Triassic. Only a few fish genera of the Xingyi Fauna are shared with fish-bearing sites of eastern and western Tethys if we consider the whole Middle/Late Triassic interval (*Peripeltolepus*, *Habroichthys*, *Marcopoloichthys*, *Thoracopterus* itself, and possibly a few others). During the Anisian, eastern and western Tethys shared many actinopterygian genera, but later those fishes appeared to differentiate in the two regions. The same result is obtained considering marine reptiles: only *Lariosaurus* is present in both regions at the end of the Ladinian, while *Nothosaurus youngi*, *Keichousaurus hui*, the thalattosaur *Anshunsaurus wushaensis*, the pistosaur *Yiunguisaurus liae*, the protosaurus *Macrocnemus* cf. *M. fuyuanensis* and *Tanystropheus* cf. *T. longobardicus* occur in the Xingyi Fauna (Ji et al. 2012). Finally, it is worth remembering that excavations in the Kalkschieferzone did not reach 100 square meters and concerned at least two different fossiliferous levels, only one of them yielding reptiles remains; the excavation near Wusha alone it is up to 1000 square meter wide, so the Italian sample is much smaller than the Chinese one.

Before this recent excavation near Wusha, both reptiles and fish fossils of the Xingyi Fauna were hardly given a precise stratigraphic position; though, we think that most of them came from the *Keichousaurus* richest beds (n. 26 to 35 in our excavation). Actually, the detailed research carried out in the last months has provided a nice stratigraphic sequence both for reptiles (Ji et al. 2012) and fishes (authors' pers. obs.). Among others, several "flying" fish specimens have been collected from bed 42 to bed 47, thus above the main *Keichousaurus*-bearing interval. We consider this "flying" fish as a new species of *Thoracopterus*, thus becoming the oldest "flying" (gliding) fish so far known: however it must be pointed out that the new species could be only one-two My older than *Thoracopterus niederristi*, the type species, even if further detailed stratigraphical investigations must be done on both Wusha and Cave del Predil sections. Furthermore, the geographical range of the genus *Thoracopterus* results greatly enlarged, at least to most of the Tethys. On the other hand, modern "flying" fishes (Exocoetidae) are also widespread, and taxa such as *Cypselurus* or *Exocoetus* occur with different species in almost all the tropical and subtropical marine environments. Also single species can be cosmopolitan, like *Exocoetus volitans* (www.fishbase, 2012).

## Material and methods

About ten specimens have been prepared, totally or only partially. Preservation quality varies, depending on the source bed, but also on the sex of the fish, supposed female skeleton being lighter than that of males. A few bed surfaces show structures related to pressure-solution, affecting also the preservation of fossils. This is especially true for the body, since the new species is almost totally naked and the endoskeleton elements are not covered by the very hard ganoine that may somehow protect the bone during the diagenetic processes: thus it is more easily destroyed. As for most fish specimens recovered from those beds, the skeletal elements are often dislocated. The distal part of the fins in *Thoracopterus* are lacking or disarticulated; the same is for scales, which probably simply overlapped each other rather than showing the usual peg and socket articulation of typical ganoid scales. However, almost all the recovered specimens can be considered as complete. They have been mechanically prepared by means of steel needles under microscope (Nikon SMZ645). Pictures were taken by Nikon D200 and D3100 with micro lens Nikkor 60mm, Sony NEX 5N. Microscope pictures were taken by photo device mounted on Nikon SMZ1500.

## Abbreviations

GMPKU-P-, Geological Museum of the Peking University, Paleontological collection.

AF, anal fin; CFD, dorsal lobe of the caudal fin; CFV, ventral lobe of the caudal fin; DF, dorsal fin; DS, antero-dorsal scales; Fr, frontal; HA, haemal arch; HYO, hyomandibular; IOP, infraorbitals process; MMNS, modified median neural spine in the ural region; MNS, median neural spine; Mx, maxilla; Op, opercle; PCT, pectoral fin; PNA, paired neural arches; Pop, preopercle; PV, pelvic fin; PVP, pelvic fin endoskeletal plate; Ro, rostral; SCL, supracleithrum; SN, supraneurals.

## Systematic Palaeontology

Subclass Actinopterygii COPE, 1871

Order Peltopleuriformes GARDINER, 1967

Family Thoracopteridae GRIFFITH, 1977

**Emended diagnosis:** Small to medium-sized fishes. Skull roof with broad paired frontals; large dermopterotics sometimes fused together; no distinct parietals. Nasals separated by a large convex rostral. Supraorbital single or few in number. One suborbital. Opercular series with opercular, subopercular, several branchiostegal rays, lateral and median gulars. Vertical, very narrow preopercular abutting the rear edge of the maxilla with the infraorbital process. Maxilla extending

beyond posterior border of orbit and with large postero-ventral plate. Mandible with very low coronoid process. Spiracular bones present. Large otoliths are usually present. Sensory canal system reduced. Body totally or partially scaled or naked. Tail hemietercercal with more than ten epaxial rays. Caudal fin deeply forked with lower lobe larger than upper. Pectoral fins very large. Pelvic fins well developed. Anal and dorsal fin well posteriorly inserted and with lepidotrichia usually reduced in length.

Genus *Thoracopecterus* BRONN, 1858

Type species: *Thoracopecterus niederristi* BRONN, 1858

Diagnosis: As for the family, because it includes only a single genus.

Age and geographical distributions: Late Ladinian (Middle Triassic) to late Norian (Late Triassic) of Western Tethys (northern Italy - Bergamo and Udine provinces - and Austria) and Eastern Tethys (Southern China).

*Thoracopecterus wushaensis* sp.n.

Diagnosis (\*are considered apomorphic characters): large-sized *Thoracopecterus* (s.l. between 85 and 120mm). Lower jaw with almost straight oral margin and well ornamented with large tubercles\*. Preopercle with long pointed infraorbital process\*. Most skull dermal bones ornamented with small tubercles. Proximal segments of the pectoral fin ornamented mainly with short and thin ridges. Last lepidotrichium of the pectoral fin expanded with polygonal proximal segments. Pectoral fins of 52-55% of the standard length, pelvic fins around 27% of

the standard length. Anal fins modified in "females", with hooks at the end of thin posterior rays. Supposed females with lighter bones and paired fins lepidotrichia. Antero-dorsal field of small scales just behind the skull\*: ornamentation stronger on "female" specimens than on "males", even if the "males" scales appear thicker and more squarish. Four rows with ten-twelve scales each as support to the ventral lobe of the tail\*: large patches of ganoine in "males", mostly covered by a smooth layer of ganoine in "females". No peg and socket articulation. No or very small otoliths\*.

Etymology: From Wusha, the administrative district where the excavation has been carried out.

Holotype: GMPKU-P-3061, a complete "male" specimen from layer 43 (fig. 2).

Paratypes: GMPKU-P-3060 ("male" from layer 43), GMPKU-P-3071 ("female" from layer 42, fig. 3), GMPKU-P-3072 (from layer 44f- scattered bones and pectoral fin rays), GMPKU-P-3073 (from layer 45, weathered complete specimen).

Type locality: Village of Nimaigu, Wusha District, Xingyi City, Guizhou Province, China.

Age and horizon: Lower part of Zhuganpo Member of Falang Formation, Late Ladinian (Middle Triassic).

## Description

### The skull

The dermal bones of the skull are very similar to those of other *Thoracopecterus* species (TINTORI & SASSI 1992) and do not deserve detailed description (fig. 4).

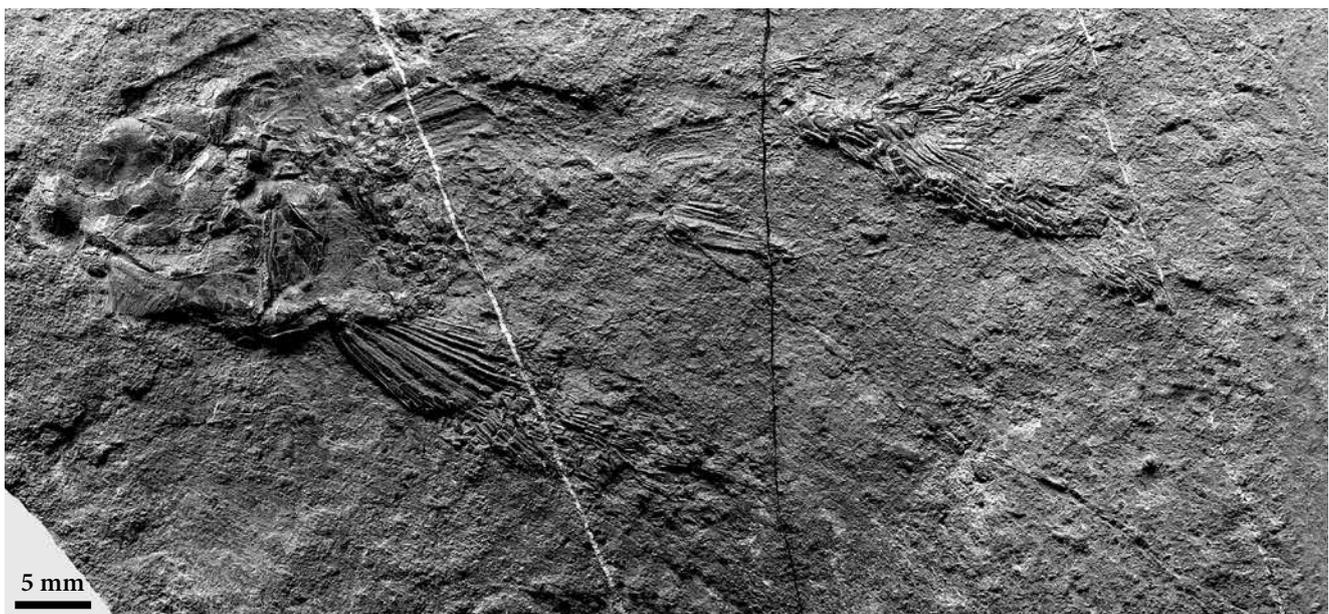


Fig. 2 - Specimen GMPKU-P-3061, *Thoracopecterus wushaensis* sp. n., the holotype.  
- Esemplare GMPKU-P-3061, *Thoracopecterus wushaensis* sp. n., l'olotipo.

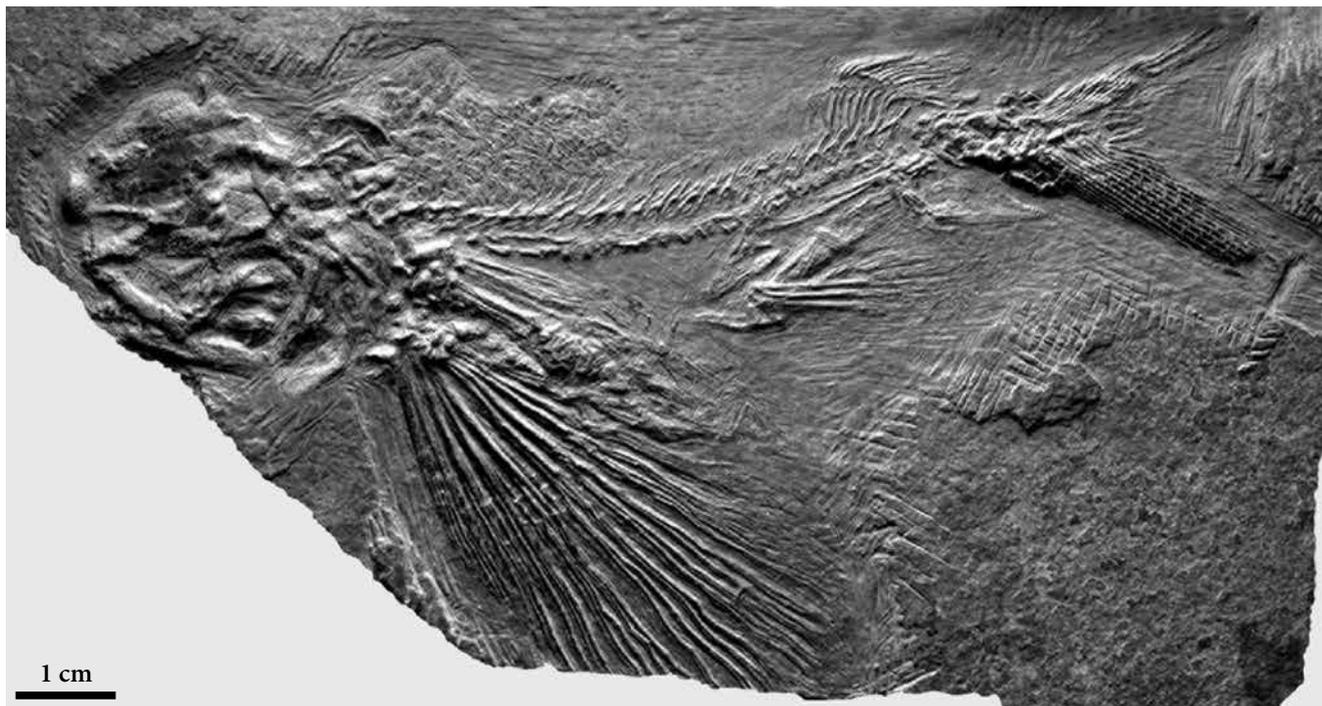


Fig. 3 - *Thoracopecterus wushaensis* sp. n., specimen GMPKU-P- 3071, paratype, "female".  
 - *Thoracopecterus wushaensis* sp. n., esemplare CMPKU-P-3071, paratipo, "femmina".

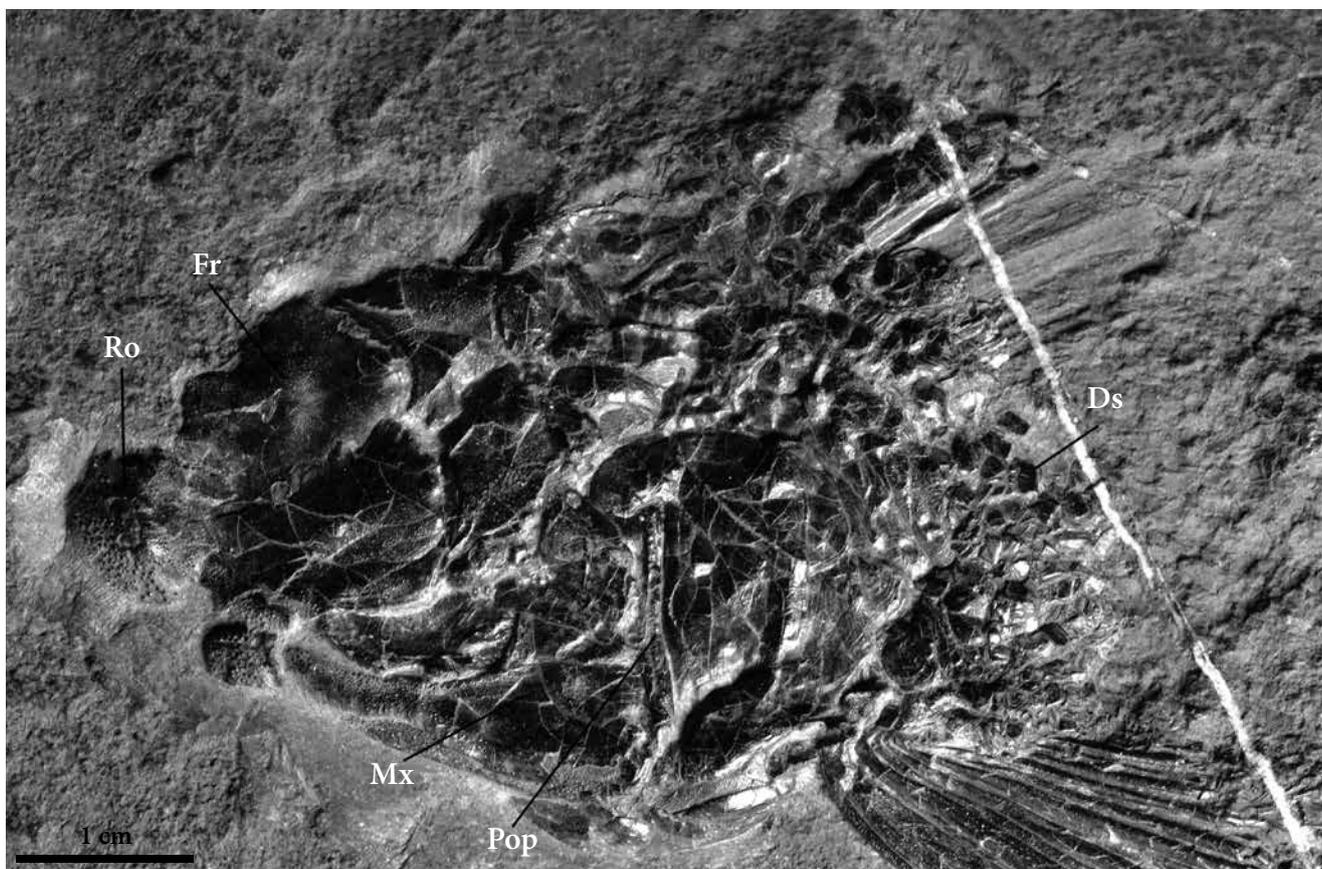


Fig. 4 - *Thoracopecterus wushaensis* sp. n., the skull of the holotype GMPKU-P-3061, in dorso-lateral view (left side) showing also the antero-dorsal scales. Left pectoral fin proximal segments are also visible.  
 - *Thoracopecterus wushaensis* sp. n., il cranio dermico dell'olotipo GMPKU-P-3061, in vista dorso-laterale (lato sinistro), con evidenti anche le scaglie antero-dorsali e i robusti segmenti prossimali della pinna pettorale sinistra.

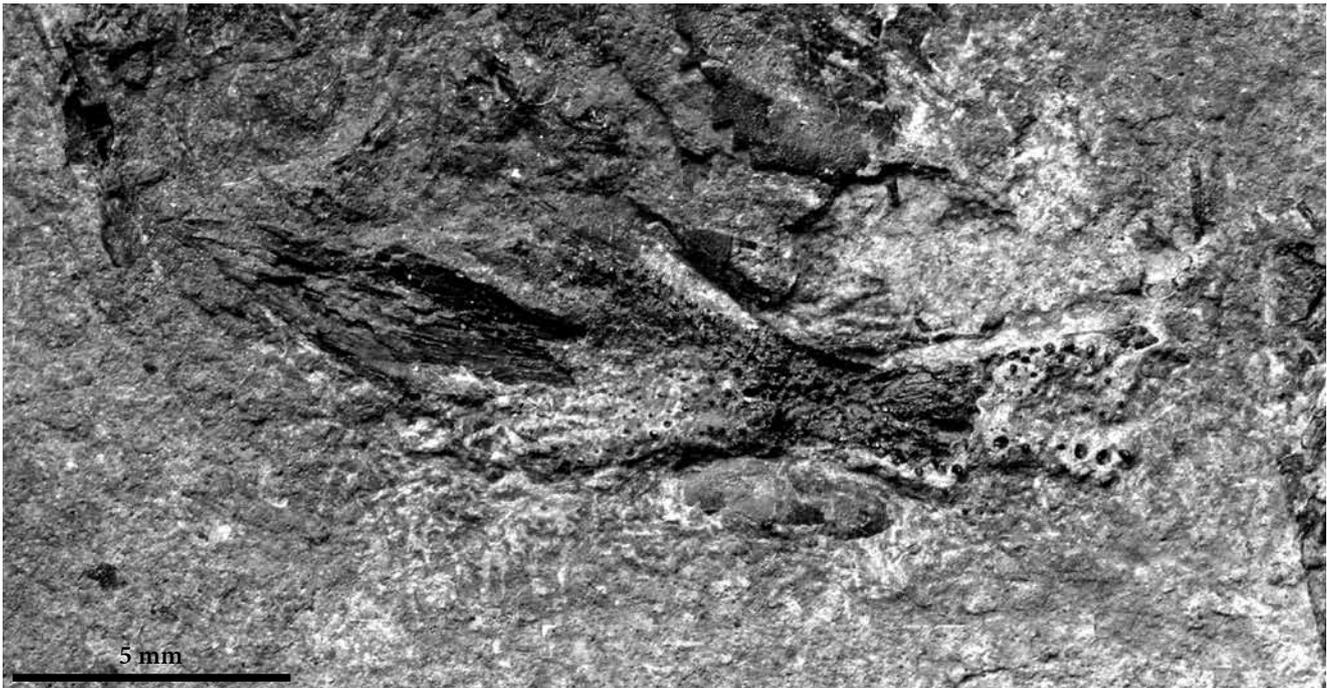


Fig. 5 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3072, the parasphenoid in ventral view; the anterior part is to the right. Portions of the anterior region was weathered away and teeth are not preserved.

- *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3072, il parasfenoide in vista ventrale; la parte anteriore si trova a destra. Una porzione della regione anteriore è priva di denti a causa della alterazione superficiale (vedi anche il colore chiaro della matrice).

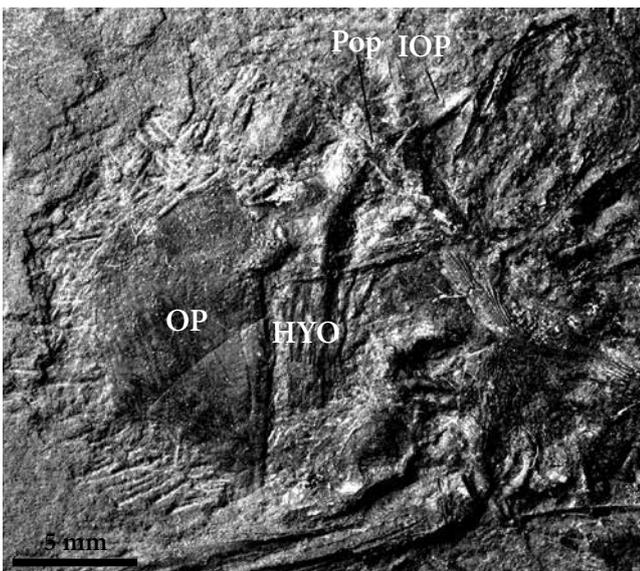


Fig. 6 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3072, close up of some of the scattered dermal bones.

- *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3072, dettaglio di alcune delle ossa dermiche del cranio-disarticolate.

The rostral is typically preserved as a conical structure: tubercles are much larger on the ventral side than on the dorsal one. Nasals are T-shaped, with an anterior narrow region, showing well-developed nostril notches, and a larger posterior one. The frontals are very broad and subrectangular. The supraorbital sensory canal extends till about the mid-length of the frontals and it is followed by two short pit-lines lying at about 45° respect to the median suture. This latter is usually quite indented. The squarish large dermopterotics (sensu TINTORI & SASSI 1992) follow the frontals: the suture with the frontals is concave and somewhat wavy. The sensory canal made a regular arch, the anterior part being totally included in the bone while the posterior part lay in a groove ending well before the posterior margin of the bone. Presupracleithra and four extrascapulars (sensu TINTORI

& SASSI 1992) follow. Presupracleithra are oval and are inserted postero-laterally to the dermopterotics. The small lateral extrascapulars show possible traces of the sensory canal in the lining of shallow ridges with antero-posterior direction and possibly for the supratemporal commissure. Median extrascapulars are much larger and meet along the mid line.

All bones are ornamented with small, round, and flat tubercles made of ganoine, much smaller on average than on maxilla/lower jaw. On the posterior region of the skull roof shallow ridges and patches of ganoine are also present and tubercles tend to be more elongated antero-posteriorly.

The maxillae have a narrow anterior region, where most of the stout teeth are present. The dentigerous region is covered by strong tubercles, while the expanded

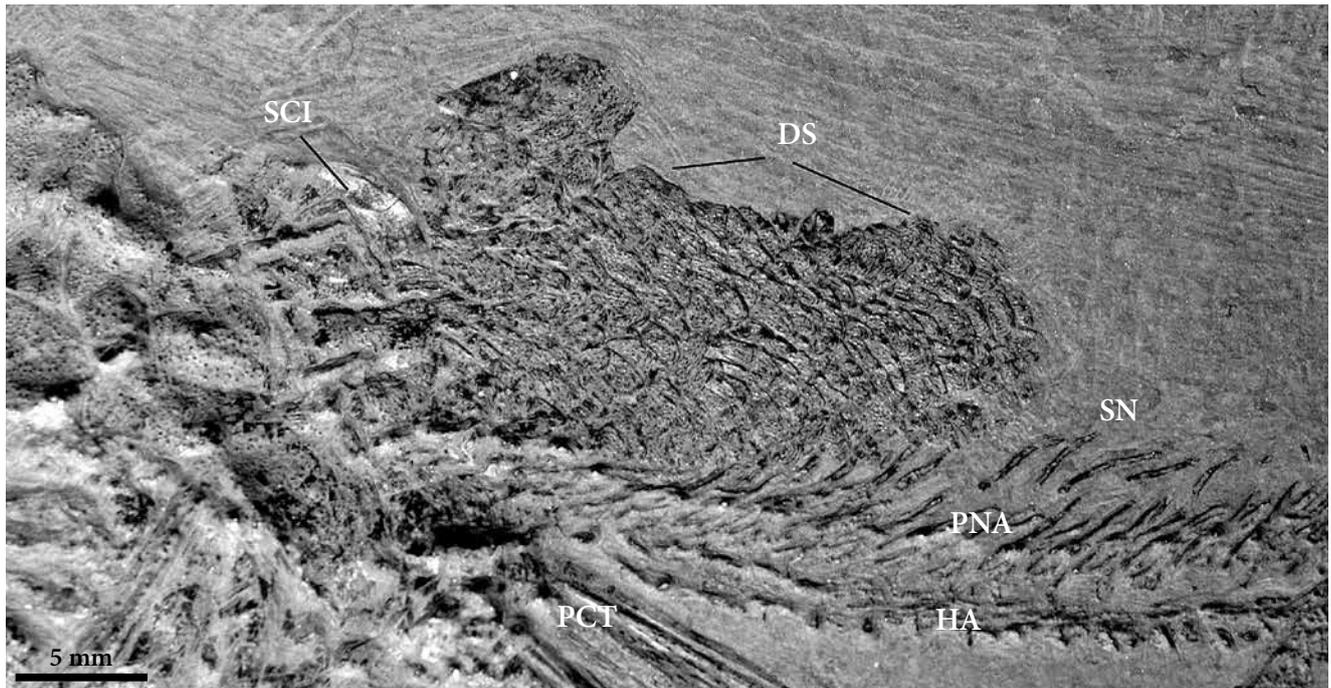


Fig. 7 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3071, the anterior trunk region with the antero-dorsal scale field and the vertebral column elements.  
 - *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3071, la regione anteriore del tronco con il campo antero-dorsale di scaglie e la colonna vertebrale.

posterior part is almost smooth. Premaxilla can seldom be seen and it is so far impossible to state whether it is median, like in *T. magnificus*, or paired. Teeth borne by this bone are smaller than those on maxilla and lower jaw. The lower jaws are powerful, with an almost straight oral margin bearing at least 20 stout conical teeth in the outer row. A large articular notch is visible at the postero-dorsal corner. The external surface shows a smooth area just below the oral margin, while the ventral region is densely covered by large round tubercles. A few small pores from the sensory canals are visible especially in the anterior region.

The parasphenoid (fig. 5) is very wide: its ventral surface is well visible although it is not perfectly preserved (specimen GMPKU-P-3072 is the only one so far collected consisting only in scattered skull bones and a few pectoral fin remains and allows the ventral view of the parasphenoid; furthermore, it has been found on an exposed weathered surface). The anterior region is quite large and it is followed by a median narrow region. The posterior one enlarges again before tapering to the posterior end. Apart from the middle posterior region, the ventral surface is covered by small sharp teeth, the largest being arranged in two lateral longitudinal rows on the anterior region.

Preopercles are straight, narrow but thick. The infraorbital process is an elongate narrow triangle, almost splint-like, and its length is about 40% of the height of the preopercle itself (fig. 6). Pores of the sensory canal can be detected along the posterior margin of the ventral

region: they are large, but their wideness decreases dorsally. No pores can be seen in the dorsalmost part. Ganoine tubercles are present all along the bone, except on the infraorbitals process.

Opercles are quite large, with a round upper edge. They are about three times higher than the subopercles. The suture between opercle and subopercle is forward inclined. The subopercles are trapezoidal in shape and their anterior part is higher than the posterior. The surface of the opercular bone is covered by a thin layer of ganoine and it is almost smooth a part from very small sparse tubercles in the uppermost region.

Branchiostegal rays are broad and at least seven elements have been counted. The median gular is small and oval. Their surface appear to be smooth.

As usual for *Thoracopterus*, data on the circumorbital series are scarce. A large suborbital is certainly present as for supraorbitals, although the number and shape of these latter cannot be stated. Nothing can be said about the infraorbitals series.

Large, elongate semicircular supracleithra are present, but there are no traces of the sensory canal. The cleithra are stout and L-shaped. Their ornamentation consists of longitudinal ridges covering the whole surface of the bone. Three-four postcleithrals are present on each side. Their ornamentation is quite different depending on the sex: "males" bones are almost smooth with only faint radial ridges and some concentric ones close to the edges, while "females" show stronger ridges running almost dorso-ventrally.

No clear evidence of otholits can be detected: if present, they must be quite small compared to the body size of the fish.

The general appearance of the dermal skull bones is different in the supposed males and females. Though, only a “female” has been so far identified with certainty (GMPKU-P-3071): its bones seem to be lighter than in other specimens of comparable size, which we consider as “males” (see below).

### Scales

Scale covering is quite peculiar, even for a very specialized fish like *Thoracopterus*. Most of the body is naked apart from two regions, one antero-dorsal and one ventral just in front of the caudal fin.

The anterior scale-field is just behind the skull, probably reaching the base of the pectoral fin from the dorsal midline (figs 4 and 7). Scales are present in between the extrascapulars along the midline, extending back to approximately the 12<sup>th</sup> vertebral segment. Though not totally clear on the available specimens, this field seems to have a triangular shape with the maximum extension along the mid-dorsal edge and a ventral tip at the base of the pectoral fins. Again, some differences appear to be related to sexual dimorphism: “female” specimens have thinner scales (fig. 7), with a rounded posterior margin, and fairly marked ornamentation consisting of several short ridges on each scale. Nonetheless, a narrow smooth surface borders the exposed area. The scales are embriated. In “male” specimens these scales are more rhomboidal and thicker than in “female” specimens

and their ornamentation is lighter. No peg and socket articulation is visible; the scales appear juxtaposed.

Shape and thickness of scales are the same in the caudal area for both sexes, but “males” have stronger ornamentation than “females”. In fact their surface is almost totally covered by narrow patches of ganoine, while “females” show this ornamentation only on the most anterior scales. The remaining ones have only a smooth ganoine covering. So far only one specimen shows articulated scales in the caudal region, the “female” GMPKU-P-3071. This fish, though, has a possible fracture in the vertebral column, just behind the dorsal fin; its tail is gently bent downward and is not aligned to the anterior part of the body. Furthermore, the lepidotrichia of the caudal fin lack their posterior part, which cannot be seen anywhere around the specimen as scattered segments. Thus, even though in other specimens the scales are mainly settled on the ventral region, we are not totally sure about the scale rows position. In specimen GMPKU-P-3071 scales are arranged in four rows made of 12 scales each. The rows, postero-ventrally directed, seem to cover the ventral area in front of the caudal fin, leaving the ural part of the body uncovered.

### Vertebral column

The notochord is uncostricted. Dorsally, there are 23-25 paired neural arches: they are slender rectangular elements, dorso-ventrally elongated, each one showing a transversal stout ridge at about half of its length, possibly making the roof of the neural canal: the distal part may

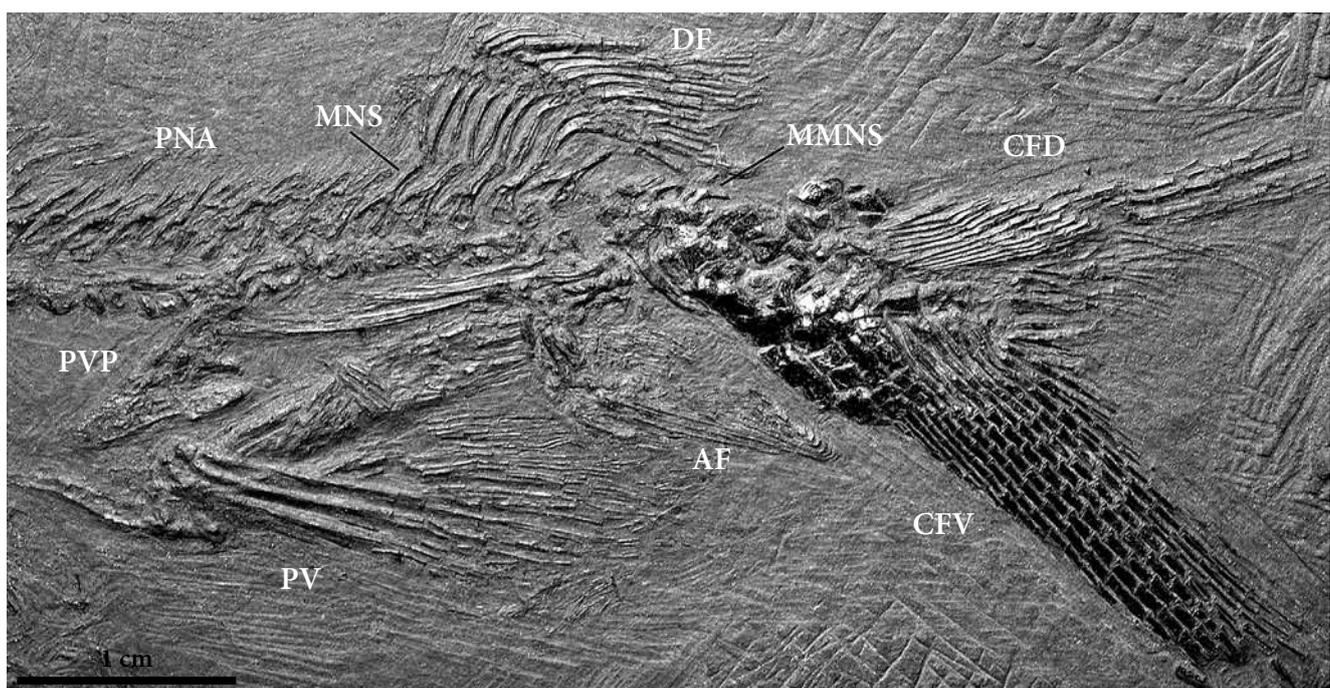


Fig. 8 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3071, the caudal region.  
- *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3071, la regione caudale.

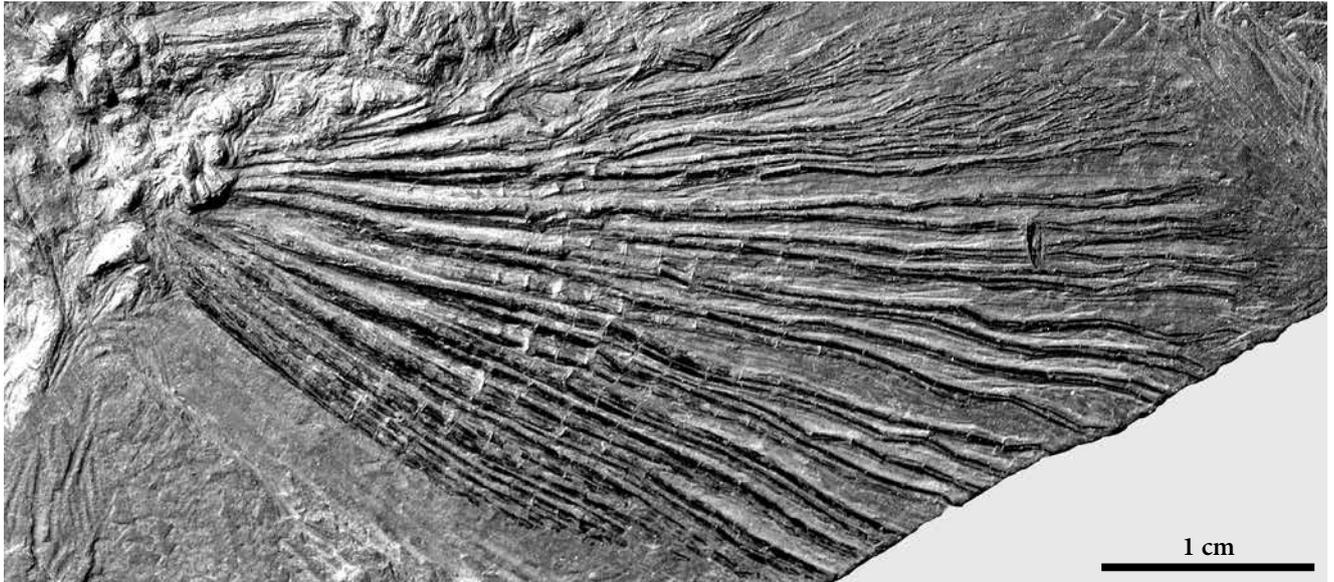


Fig. 9 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3071, the left pectoral fin in dorsal view.  
- *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3071, la pinna pettorale sinistra in vista dorsale.



Fig. 10 - *Thoracopterus wushaensis* sp. n., specimen GMPKU-P-3073, close up of the modified last lepidotrichium of the right pectoral fin in dorsal view (the remaining part of the fin is in ventral view). The anterior part is to the right.  
- *Thoracopterus wushaensis* sp. n., esemplare GMPKU-P-3073, dettaglio dell'ultimo lepidotrichio della pinna pettorale destra, in vista dorsale mentre il resto della pinna è in vista ventrale. La base del lepidotrichio si trova a destra.

then be considered as paired neural spines (fig. 7). At the beginning of the dorsal fin median neural spines suddenly appear. Five occur before the point where the spines start to shorten and bend backward, becoming also very stout. About 8 of these modified neural spines are present (fig. 8). Supraneurals are present up to the 18-20<sup>th</sup> vertebral segment: the last three sharply decrease in size and they do not reach the beginning of the dorsal fin (and the arising of the median neural spine). This condition is quite unusual and can be here related to the very posterior position of the dorsal fin itself.

Paired, elongated, haemal arches forming a kind of gutter occur ventral to the notochord up to the beginning of the anal fin. Each pair has strong paraphophyses

with short ribs articulated, at least in the most anterior region. In the posterior abdominal region they become somewhat shorter and more rounded. Short haemal spines are present in the preural region: they suddenly become much larger and stout just in front of the caudal scale field, where also the median neural spines start to modify. There are eight to nine modified haemal spines, the first four-five being very long but still quite narrow, while the last four are much expanded. The last two elements are somewhat shorter than the preceding ones and the last is almost flat and triangular. All these modified haemal spines are really packed. It's impossible to determine which ones could be considered as hypurals.

### Paired fins

Each pectoral fin is made of at least 11 lepidotrichia, whose long proximal segments (fig. 9) have an elongate ventral wing giving support to the following ray. The first element is huge and consists of a splint-like part making up the anterior base of the fin. The first short unbranched lepidotrichium is abutted to it and it is followed by the second one that branches very soon twice in its anterior part and once more distally. These three elements seem to be strictly connected and have a single, strongly enlarged articulating base. The following lepidotrichia are the longest, giving the fin its typical fan shape: they branch four times. Branching is asymmetrical (anterior first) in the anterior lepidotrichia but tends to become symmetrical in the central and posterior ones. The most posterior element (the 12<sup>th</sup>?) is again very peculiar, giving rise to a wide thin area (inner scaly lobe in TINTORI & SASSI 1992) made up of subpentagonal segments (MGPKU-P-3073, fig. 10). These soon become elongate like the usual distal segments in the other lepidotrichia. All the lepidotrichia show a strongly bent proximal end articulating to the endoskeletal supports. The long proximal segments, as well as some of the larger following ones, are well ornamented with short ridges on both dorsal and ventral sides. It is impossible to describe them in detail, but we can say that at least four very stout radials are present.

In the largest “male” specimens the length of the lepidotrichia possibly reached about 60% of the s.l., even though the recorded measurements give a range between 52% and 57%, apparently independent of the actual size of the fish.

The pelvic fins are much smaller than the pectorals, not reaching 30% of the standard length, but showing the same arrangement of the lepidotrichia, apart from a very large saber-like first element. Probably less than 10 lepidotrichia are present. Large, sub-triangular plates make the endoskeletal support of these fins. Their ornamentation is very similar to that of the pectoral fins.

The “female” specimen MGPKU-P-3071 shows more lightly built pectorals and pelvics; their ratio to the s.l. is somewhat lower than that of the supposed “males” of comparable size (MGPKU-P-3061-2).

### Median fins

Dorsal and anal fins are small and inserted very close to the caudal fin; the dorsal fin occurs at about 75% of the standard length.

The dorsal fin is made up of three basal fulcra and 11 lepidotrichia, which distally branch probably only once. The proximal segment is elongated, two-three times the distal ones, which are also quite long. The endoskeleton consists of nine proximal radials (so far it is not clear if there are also distal radials), the first one having a very

expanded distal region apparently originated from the fusion of two radials. This first element does not support any part of the fin. The second radial supports the three basal fulcra; each of the following six radials articulates to a single lepidotrichium. The last radial is boomerang-shaped and gives support to the last five lepidotrichia. The anal fin is inserted near the end of the dorsal fin. So far, we could observe this fin only in the “female” specimen MGPKU-P-3071. It is usually very small and delicate also in the other *Thoracopterus* species, and is frequently covered by the distal part of the pelvic fins. In specimen MGPKU-P-3071, on which this description is based, the endoskeleton is not visible. In the anterior part of the fin there are 5-6 large proximal segments, followed by very small scattered elements connecting to the distal part of the anterior lepidotrichia, which are short-segmented. The posterior part is made up of about 15 very thin, long rays, which are unsegmented, tightly grouped together and ending with large medially directed hooklets. A single (on the right side) large scale is present lateral to the proximal long segments of the anterior rays.

The ventral lobe of the deeply forked caudal fin is much stronger than the dorsal one. A real body lobe cannot be distinguished. However, if we consider the proximal part of lepidotrichia where ganoine is lacking, we can trace out the body outline which looks almost perfectly symmetrical. Actually, the lepidotrichia of both dorsal and ventral lobes were deeply inserted in the body because most long proximal segments are ganoine-free. The caudal fin is formed by 30 lepidotrichia, comprising very short but segmented elements on both dorsal and ventral edges. In the ventral lobe there are five segmented rays in front of four major lepidotrichia, the stouter ones: these latter branch very distally. Then, there are three less robust lepidotrichia which branch proximally at least twice. The central part of the fin is made of nine very short lepidotrichia that branch probably two or three times. Twelve lepidotrichia form the dorsal lobe: they are much thinner than those of the ventral lobe but they were deeply inserted in the body dorsal to the notochord too, and must then be considered as epaxial rays. Large patches of ganoine cover several segments of the major ventral lobe lepidotrichia. As the actual length of lepidotrichia is hardly measurable owing to the scattered distal parts, the ventral lobe length vs. standard length ratio and the dorsal lobe vs. ventral lobe length ratio must be regarded as just preliminary. The first ratio ranges from 26% to 38% (only two specimens); the second ranges from 60% to 84% (in the same two specimens).

### Discussion

“Flying” fishes from the family Thoracopteridae have been thoroughly discussed by TINTORI & SASSI (1992),

who regarded *Thoracopterus* as the only valid genus on the basis of a very similar anatomical pattern of the skull and endoskeleton elements. Apart from the different average size, the four species considered by TINTORI & SASSI (1992) can be easily identified by the differences in the scale covering and/or in the paired fins proportion.

*T. niederristi*, the type species from lower Carnian, has a complete scale covering (GRIFFITH 1977; Tintori, pers. obs) while the new specimens show a very partial covering with only two small areas covered by scales. *T. niederristi* is also somewhat smaller than the new specimens, with an average standard length (s.l.) of about 70 mm (GRIFFITH 1977). The Norian *T. magnificus* and *T. martinisi*, (TINTORI & SASSI 1987; 1992) totally lack any body scale covering. *T. magnificus* is also usually smaller: most specimens are around 50 mm in standard length, only a few reach 120 mm s.l. *T. martinisi* shows a wider size range (45 mm to 150 mm), the average standard length being around 90 mm (TINTORI & SASSI 1992). The new specimens display a relatively narrow size range (87 mm to 117 mm s.l.) with an average of about 100 mm s.l.

The comparison between the new taxon and *T. telleri* is not easy, due to the scanty available material of the latter (GRIFFITH 1977, Tintori, pers. obs.). *T. telleri* is almost totally naked, but it has at least one scale row in front of the ventral edge of the caudal fin, similarly to the new specimens. Even though GRIFFITH (1977) did not mention them, scales are possibly present in the antero-dorsal region (Tintori, pers. obs.), again similarly to the new material from Wusha. Complete specimens of *T. telleri* are not known, but their size, inferred from the 30 to 40 mm skull length, is comparable to that of the new specimens. Also similar is the strong tuberculation (Tintori, pers. obs.) on the lower jaw, though *T. telleri* shows ridges that are lacking in the new material. Major differences concern the pectoral fins length, which is up to 70% of the s.l. in *T. telleri* (GRIFFITH 1977) but do not even reach 60% in our material. In *T. telleri* there are 9-10 lepidotrichia, with a few sparse small tubercles; specimens from Wusha have 11-12 lepidotrichia and they are well ornamented, prevalently by short ridges, without round tubercles. The same difference in the ornamentation is observed in the caudal and in the pelvic fins. Concerning the dorsal fin, in *T. telleri* it is made of at least 15 lepidotrichia (see GRIFFITH 1977) but only 11 are present in our specimens. One last remark about the large otoliths that are probably present in *T. telleri* (GRIFFITH 1977) like in the other *Thoracopterus* species (TINTORI & SASSI 1992). They usually make paired bumps in the head although they are seldom exposed: these bumps are never observed in our new specimens.

We have thus stated that *T. telleri* is the closest species to our new specimens: nonetheless, the few different

characters are sufficient to erect a new species, *T. wushaensis* sp.n. on the late Ladinian specimens from the Wusha region.

Once more, it is proved that our models of radiation and/or evolution inside a group (TINTORI & SASSI 1992) are deeply influenced either by the discovery of new sites (as in the case of the Luoping Fauna, LOMBARDO et al. 2011; SUN et al. 2012) or just by the improvement in the quality and detail of collecting in already known localities, like the new bed by bed excavation in Wusha. We must always take account of the geological setting and of the uneven chances of marine vertebrates to be preserved (preservation windows): not finding them does not mean they were not present!

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## References

- ABEL, O. 1906. Fossile Flugfische. *Jahrb. der Geolog. Bundesan. Wien* 56: 1-88.
- BRONN, H.G. 1858. Beiträge zur triassischen Fauna und Flora der bituminösen Schiefer von Raibl. *Neues Jahrb. für Min., Geol. und Paläont.* 1: 1-32.
- GRIFFITH, J. 1977. The Upper Triassic Fishes from Polzberg bei Lunz, Austria. *Zoological Journal of Linnean Society* 60: 1-93.
- Ji, C., W.L. SANG, G.W. DIAO, R. MOTANI & A. TINTORI. 2012. Biodiversity and stratigraphic distribution of the first late Ladinian (Middle Triassic) marine vertebrate fauna (Xingyi Fauna) from south China. *Jour. Vert. Paleont.* 32, 3 suppl.: 131.
- JIANG, D.Y., R. MOTANI, W.C. HAO, O. RIEPPEL, Y.L. SUN, A. TINTORI, Z.Y. SUN & L. SCHMITZ. 2009. Biodiversity and Sequence of the Middle Triassic Panxian marine Reptile Fauna, Guizhou Province, China. *Acta Geol. Sinica* 83: 451-59.
- LI, H.Q., Z.Y. SUN, A. TINTORI, C. LOMBARDO, Q.Y. JIANG & W.C. HAO. 2011. A new species of *Habroichthys* BROUGH, 1939 (Actinopterygii; Peltopleuriformes) from the Pelsonian (Anisian, Middle Triassic) of Yunnan Province, South China. *Neues Jahrb. für Geol. und Paläont. Abh.* 262, n. 1: 78-89.
- LIU, G.B., G.Z. YIN, X.H. WANG, Y.M. LUO & S.Y. WANG. 2003. New discovered fishes from *Keichousaurus* bearing horizon of Late Triassic in Xingyi of Guizhou. *Acta Paleontologica Sinica* 42, n. 3: 346-66.
- LOMBARDO, C. 1999. Sexual dimorphism in a new species of the actinopterygian *Peltopleurus* from the Triassic of northern Italy. *Palaeontology* 42, n. 4: 741-60.

- LOMBARDO, C. 2001. Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): anatomical descriptions and nomenclatural problems. *Riv. It. Paleont. Strat.* 107, n. 3: 345-69.
- LOMBARDO, C. 2002. *Caelatichthys* gen. n.: a new palaeonisciform from the Middle Triassic of Northern Italy and Canton Ticino (Switzerland). *Riv. It. Paleont. e Strat.* 108, n. 3: 399-414.
- LOMBARDO, C., & A. TINTORI. 2004. New perleidiforms from the Triassic of the Southern Alps and the revision of *Serrolepis* from the Triassic of Wüttemberg (Germany). In *Mesozoic Fishes 3 - Systematics, Paleoenvironments and biodiversity*, cur. G. ARRATIA & A. TINTORI, 179-96.
- LOMBARDO, C., Z.Y. SUN, A. TINTORI, D.Y. JIANG & W.C. HAO. 2011. A new species of the genus *Perleidus* (Actinopterygii: Perleidiformes) from the Middle Triassic of southern China. *Boll. Soc. Paleont. It.* 50, n. 2: 75-83.
- SU, T.T. 1959. Triassic fishes from Kueichow. *Vertebrata Palasiatica* 3, n. 4: 205-12.
- SUN, Z.Y., C. LOMBARDO, A. TINTORI, D.Y. JIANG, W.C. HAO, Y.L. SUN & H.Q. LIN. 2012. *Fuyuanperleidus dengi* GENG et al., 2012 (Osteichthyes, Actinopterygii) from the Middle Triassic of Yunnan Province, South China. *Riv. It. Paleont. Strat.* 118, n. 3: 359-73.
- TINTORI, A. 1990a. The actinopterygian fish *Prohalecites* from the Triassic of N. Italy. *Palaeontology* 33, n. 1: 155-74.
- TINTORI, A. 1990b. *Dipteronotus olgiatii* sp.n. (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' del Frate (N. Italy). Preliminary note. *Atti Tic. Sc. Terra* 33: 191-97.
- TINTORI, A., & C. LOMBARDO. 1999. Late Ladinian fish faunas from Lombardy (N-Italy): stratigraphy and paleobiology. In *Mesozoic fishes 2 - Systematics and the fossil record*, cur. G. ARRATIA & H.-P. SCHULTZE, 495-504.
- TINTORI, A., & C. LOMBARDO. 2007. A new early Semionotidae (Semionotiformes, Actinopterygii) from the Upper Ladinian of Monte San Giorgio area (Southern Switzerland and Northern Italy). *Riv. It. Paleont. Strat.* 113: 369-81.
- TINTORI, A., & S. RENESTO. 1990. A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese-N. Italy). *Boll. Soc. Paleont. It.* 29, n. 3: 309-19.
- TINTORI, A., & D. SASSI. 1987. Pesci volanti del genere *Thoracopterus* nel Norico Lombardo. Nota preliminare. *Riv. It. Paleont. Strat.* 93, n. 3: 337-46.
- TINTORI, A., & D. SASSI. 1992. *Thoracopterus* BRONN (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. *Jour. Vert. Paleont.* 12, n. 3: 265-83.
- YOUNG, C.C. 1958. On the new *Pachypleurosauroidea* from Keichow, South-West China. *Vertebrata Palasiatica* 2: 69-81.

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Authors' addresses - Indirizzi degli Autori:

- Andrea TINTORI  
Dipartimento di Scienze della Terra "A. Desio"  
Università degli Studi di Milano  
via Mangiagalli 34, I-20133 MILANO  
e-mail: andrea.tintori@unimi.it
- Zuo-Yu SUN  
Department of Geology and Geological Museum  
Beijing University  
Yiheyuan Str. 5, Haidian District, BEIJING 100871, P.R. China
- Cristina LOMBARDO  
Dipartimento di Scienze della Terra "A. Desio"  
Università degli Studi di Milano  
via Mangiagalli 34, I-20133 MILANO  
e-mail: cristina.lombardo@unimi.it
- Da-Yong JIANG  
Department of Geology and Geological Museum  
Beijing University  
Yiheyuan Str. 5, Haidian District, BEIJING 100871, P.R. China
- Cheng Ji  
Department of Geology and Geological Museum  
Beijing University  
Yiheyuan Str. 5, Haidian District, BEIJING 100871, P.R. China
- Ryosuke MOTANI  
Department of Geology  
University of California  
DAVIS, California 95616, USA