

# Marine Early Triassic Osteichthyes from Spiti, Indian Himalayas

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Received: 12 March 2015 / Accepted: 11 August 2015 / Published online: 28 September 2015  
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**Abstract** A new, marine osteichthyan (bony fish) fauna from the Early Triassic of northern India is presented. The material was collected in situ at localities within Pin Valley (Lahaul and Spiti District, Himachal Pradesh, India) and is dated as middle-late Dienerian (one specimen possibly earliest Smithian). The new ichthyofauna includes a lower jaw of the predatory basal ray-finned fish *Saurichthys*, a nearly complete specimen of a parasemionotid neopterygian (cf. *Watsonulus* cf. *eugnathoides*), as well as further articulated and disarticulated remains (Actinopterygii indet., Actinistia indet.), and thus comprises the most complete Triassic fish fossils known from the Indian subcontinent. *Saurichthys* is known from many Triassic localities and reached a global distribution rapidly after the Late Permian mass extinction event. Parasemionotidae, a species-rich family restricted to the Early Triassic, also achieved widespread distribution during this epoch. Comparison of the Spiti material with other parasemionotid species reveals similarities with *Watsonulus eugnathoides* from Madagascar. However, taxonomic ambiguities within Parasemionotidae prevent a specific attribution of the Spiti specimen. The new material also includes an isolated actinistian urohyal exhibiting morphology distinct from any previously described urohyal. Marine Dienerian black shale deposited on continental shelves are common not only in the Himalayas but also in other geographic regions. Anoxic depositional settings provide ideal preservational conditions for vertebrate fossils, suggesting that additional ichthyofaunas could still be discovered in marine Dienerian

strata of other localities. The study of Early Triassic fish assemblages, including the presented one, is fundamental for our understanding of the great osteichthyan diversification after the Late Permian mass extinction event.

**Keywords** Neotethys · Northern Indian Margin · Gondwana · Anoxia · Biotic recovery · Urohyal

## Abbreviations

CMNFV Canadian Museum of Nature (Fossil Vertebrate), Ottawa, Canada  
MNHN.F Muséum National d’Histoire Naturelle, Paris, France  
PIMUZ Paläontologisches Institut und Museum, Universität Zürich, Zürich, Schweiz

## Introduction

Bony fishes flourished in the wake of the Late Permian mass extinction event, reaching a distinct diversity peak in the Middle Triassic (e.g. Romano et al. 2014a; Scheyer et al. 2014; Tintori et al. 2014; Friedman 2015). While research on Middle Triassic fishes recently experienced a renaissance following the discovery of new fossiliferous assemblages (e.g. Luoping biota, South China; Hu et al. 2010), knowledge of Early Triassic ichthyofaunas has been improving at a much slower pace. One reason for this discrepancy is the remote location of classical Early Triassic fish Lagerstätten, i.e. Greenland, Madagascar, Spitsbergen (Svalbard, Norway), and British Columbia (Canada), implicating logistically difficult and often expensive fieldwork (Scheyer et al. 2014). Moreover, for

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most of these Lagerstätten the pinnacle of research took place several decades ago (e.g. Stensiö 1921, 1925, 1932; Piveteau 1934, 1939–1940; Nielsen 1936; Lehman 1952; Lehman et al. 1959; Beltan 1968) and many of the described taxa are in need of revision and/or lack detailed biostratigraphic information. Even though other localities yielding marine and freshwater bony fishes of Early Triassic age are frequent (e.g. López-Arbarello 2004; Brinkmann et al. 2010; Romano et al. 2014a), most of them have not proven to be rich in well-preserved fossils. A geographic province that has a particularly poor record of Triassic fishes in spite of the widespread occurrences of suitable strata is the Himalayan Range (Deecke 1927; Chang and Miao 2004).

Here we present a previously unknown Early Triassic marine bony fish fauna from Pin Valley (Lahaul and Spiti District, Himachal Pradesh, India), a collection area which has the potential for further discoveries. Within Gondwana, the present-day Indian subcontinent includes some of the largest numbers of sites producing Early Triassic chondrichthyan and osteichthyan remains, but most localities yield only microfossils or rare and incomplete larger specimens, often with very limited biostratigraphic age constraints (see “Discussion”). The new ichthyofauna from Spiti not only includes the most complete macrofossils ever described from the Triassic of India (both marine and freshwater), it is also complemented with a detailed biostratigraphic framework based on ammonoids (Brühwiler et al. 2010; Ware et al. 2015, in production a, b) and conodonts (e.g. Goel 1977; Krystyn et al. 2004; Goudemand 2010, 2014). Future excavations in Spiti and neighbouring areas may thus help widen our understanding of Gondwanan fish faunas at the time of recovery after the end-Permian mass extinction event. The aim of this paper is to describe the first finds of Early Triassic fishes from Spiti, which have been recovered during two short field trips.

## Material and geological setting

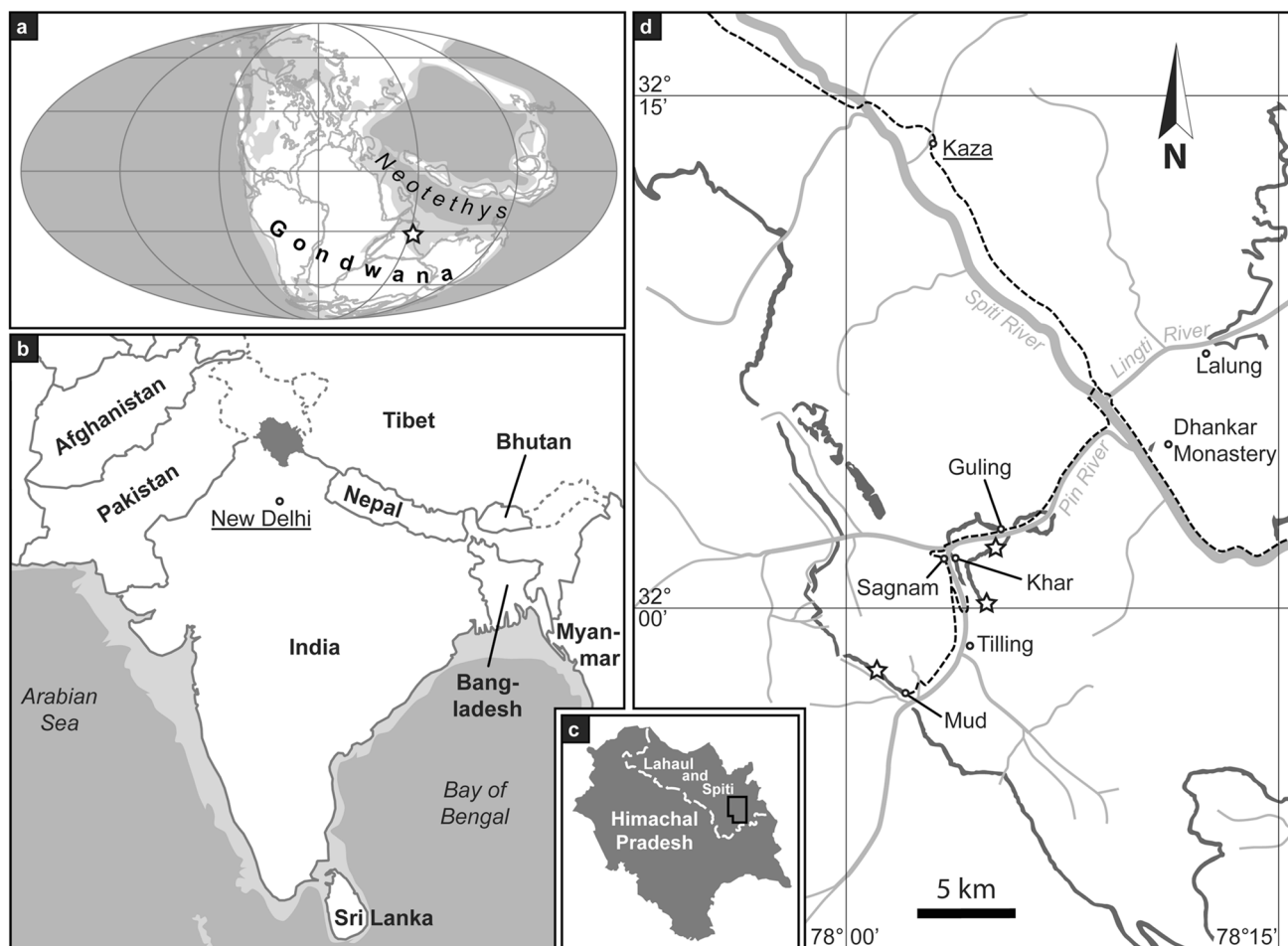
The specimens described below were recovered from different sites within Pin Valley, Spiti area, northern India (Fig. 1). The Spiti Subdistrict of Himachal Pradesh is famous for its well-exposed Early Triassic ammonoid- and conodont-rich sections (e.g. Diener 1897, 1912; Hayden 1904; Krafft and Diener 1909; Goel 1977; Krystyn et al. 2004; Goudemand 2010; Brühwiler et al. 2010, 2012; Ware et al. in production a), but the occurrence of fish macrofossils within these strata was unknown until 2009, when two articulated specimens were discovered near the village of Mud (cf. Fig. 1) in sediments of Dienerian age (late Induan, Early Triassic; we herein use the Early Triassic

subdivision of Tozer 1965). In 2010, additional fieldwork was conducted by members of the PIMUZ to explore the fish richness of Dienerian strata at three selected localities near the villages of Guling, Mud, and Tilling (Pin Valley, Fig. 1). The excursion was successful and yielded an additional articulated individual as well as numerous fragmentary remains. The material recovered during the 2009 and 2010 expeditions is curated by the PIMUZ.

All specimens were found in situ within the lower part of the Limestone and Shale Member of the Mikin Formation, which is dated as middle Dienerian to earliest Smithian on the basis of ammonoids (e.g. Brühwiler et al. 2010; Ware et al. 2015, in production a; Fig. 2). The stratigraphic interval from which the fishes come from is often referred to as the “*Meekoceras* beds” (e.g. Krafft and Diener 1909), the “*Gyronites* beds” (e.g. Krystyn et al. 2004) or the “*Ambites* beds” (Brühwiler et al. 2010). It consists of black shale layers rich in organic matter and pyrite with a few intercalated tempestitic limestone beds and large, early diagenetic, calcareous concretions (for references and further details concerning the lithostratigraphy of the Dienerian of Spiti see Ware et al. in production a). Articulated fish fossils usually occur in calcareous concretions, whereas the intercalated black shale layers frequently yield isolated remains, such as bones or incomplete fins. Black shale is typically deposited in an anoxic, reducing environment on the outer platform. During the Early Triassic, the study area was situated on the northern margin of Gondwana (Neotethys realm) at a palaeolatitude of ca. 30°S (Fig. 1a).

Within the Spiti Subdistrict, outcrops of the Lower Triassic and Anisian (lower Middle Triassic) Mikin Formation (cf. Bhargava et al. 2004) are widespread (Fig. 1). The prominent, cliff-forming Niti Limestone Member (Spathian, upper Olenekian, upper Lower Triassic) of the Mikin Formation is easily recognizable in the field. The Mikin Formation partly extends into remote areas and some sections may be difficult to access. Moreover, the fish-bearing beds of the Limestone and Shale Member are often covered by firn, rubble and/or vegetation. Some of the most accessible outcrops are found within the valleys of the Pin River and its tributary streams at roughly 3800 m above sea level (Fig. 1). There, sections near the villages of Mud (sometimes spelled Muth or Mudh) and Guling have been intensively exploited for ammonoids and conodonts (e.g. Diener 1897, 1908; Krafft and Diener 1909; Krystyn and Orchard 1996; Bhargava et al. 2004; Krystyn et al. 2004, 2007a, b; Brühwiler et al. 2010, 2012; Goudemand 2010, 2014; Ware et al. in production a).

Early Triassic ammonoids from Spiti are known since the late 19th century (Diener 1897). The taxonomy and biostratigraphy of Dienerian and Smithian ammonoids from the Spiti Subdistrict were recently revised by Ware



**Fig. 1** **a** Map of Early Triassic Pangaea (modified from PALEOMAP project, [www.scotese.com](http://www.scotese.com)), with indication of the approximate location of Spiti (white star) on the Northern Indian Margin (Gondwana, Neotethys realm), **b** map of present-day South Asia, with Himachal Pradesh of India indicated as dark grey area, **c** map of Himachal Pradesh (enlarged from **b**), with Lahaul and Spiti District

highlighted; **d** locality map of Pin Valley and surrounding areas within the Spiti Subdistrict (indicated as black frame in **c**). White stars in **d** indicate the three finding sites near the villages of Guling, Mud, and Tilling, where the described fish material was found. Exposures of the Early Triassic and Anisian Mikin Formation are indicated in dark grey and main roads of Spiti and Pin Valley by dashed lines in **d**

et al. (2015, in production a) and Brühwiler et al. (2010, 2012), respectively. Brühwiler et al. (2010) demonstrated the occurrence of typically Smithian ammonoid faunas lower than previously described in a section near Mud, which has recently been proposed as a GSSP for the base of the Olenekian stage by Krystyn et al. (2007a, b). We herein follow the definition of the Dienerian-Smithian substage boundary of Brühwiler et al. (2010), which is also supported by conodont data (Goudemand 2010, 2014). Within the Dienerian of Spiti, Ware et al. (in production a) recognised ten ammonoid zones, confirming the results obtained for faunas from the Salt Range in Pakistan (Ware et al. in production b) and the subdivision of the Dienerian into three parts (early, middle, and late; Ware et al. 2015).

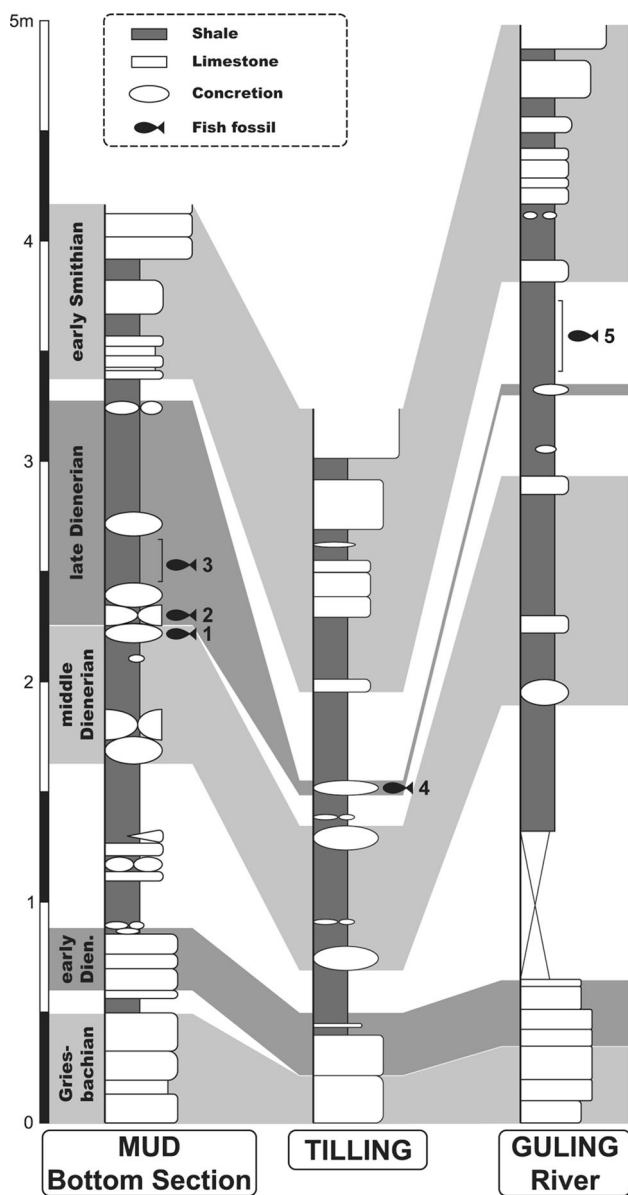
Actinopterygian bone terminology used herein is adopted from Lehman (1952). One fossil recovered from the Early Triassic of Spiti is identified as an actinistian

urohyal. Comparative studies have shown that the sarcopterygian ‘urohyal’ is not homologous with the teleostean urohyal and consequently some authors (e.g. Arratia and Schultze 1990) used inverted commas when referring to this element in lobe-finned fishes. We here follow most recent authors (e.g. Cavin et al. 2013; Dutel et al. 2015a, b) and refer to the actinistian urohyal without inverted commas, but no homology with the teleostean urohyal is implied. The use of open nomenclature in the present paper adheres to the recommendations of Bengtson (1988).

### Systematic palaeontology and description

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1887 (sensu Rosen et al. 1981)



**Fig. 2** Stratigraphic sections of the lower part of the Limestone and Shale Member (Mikin Formation) of the studied sections near the villages of Mud, Tilling, and Guling (Pin Valley, Spiti Subdistrict, Himachal Pradesh, India; cf. Fig. 1), with occurrences of the osteichthyan material described herein. 1 Unlabelled specimen (Actinopterygii indet.), 2 PIMUZ A/I 4361 (Actinopterygii indet.), 3 PIMUZ A/I 4145 (*Saurichthys* sp.), 4 PIMUZ A/I 4360 (cf. *Watsonulus* cf. *eugnathoides*), 5 PIMUZ A/I 4362 (Actinistia indet.). For more details on the stratigraphy see text and Ware et al. (2015, in production a, b)

Infraclass Actinopteri Cope, 1872, (sensu Patterson 1982)  
 Family Saurichthyidae Owen, 1860 (sensu Stensiö 1925)  
 Genus *Saurichthys* Agassiz, 1834 (sensu Mutter et al. 2008)

*Type species.* *Saurichthys apicalis* Agassiz, 1834 from the Middle Triassic of Bayreuth, Germany.

*Saurichthys* sp. (Fig. 3)

**Material and stratigraphy.** A single specimen, PIMUZ A/I 4145 (Fig. 3), which is an almost complete left lower jaw preserved on two slabs of black shale (parts a and b). Part a of A/I 4145 (Fig. 3a) is a body fossil and part b (Fig. 3b) a cast of the middle portion of part a, with impressions of the external ornamentation. A/I 4145 was found above the village Mud (“Bottom Section” of Ware et al. in production a) in Pin Valley (Lahaul and Spiti District, Himachal Pradesh, India; Fig. 1). The specimen originates from late Dienerian strata between the *Vavilovites meridialis* Zone and the *Kingites davidsonianus* Zone of Ware et al. (2015, in production a, b) within the lower part of the Limestone and Shale Member, Mikin Formation (Fig. 2).

**Description.** The hemimandible is anteriorly complete and bears several large teeth, which are best-seen on part a of PIMUZ A/I 4145 (Fig. 3a). Posteriorly, the left lower jaw is incomplete and it is unclear whether the angular and surangular bones are present. The length of the preserved part of A/I 4145a adds up to ca. 130 mm. The maximum height in the hind region of A/I 4145a measures ca. 15 mm. The straight superior margin and the gently S-curved inferior rim converge towards rostrally, giving the lower jaw a gracile, pointed front end.

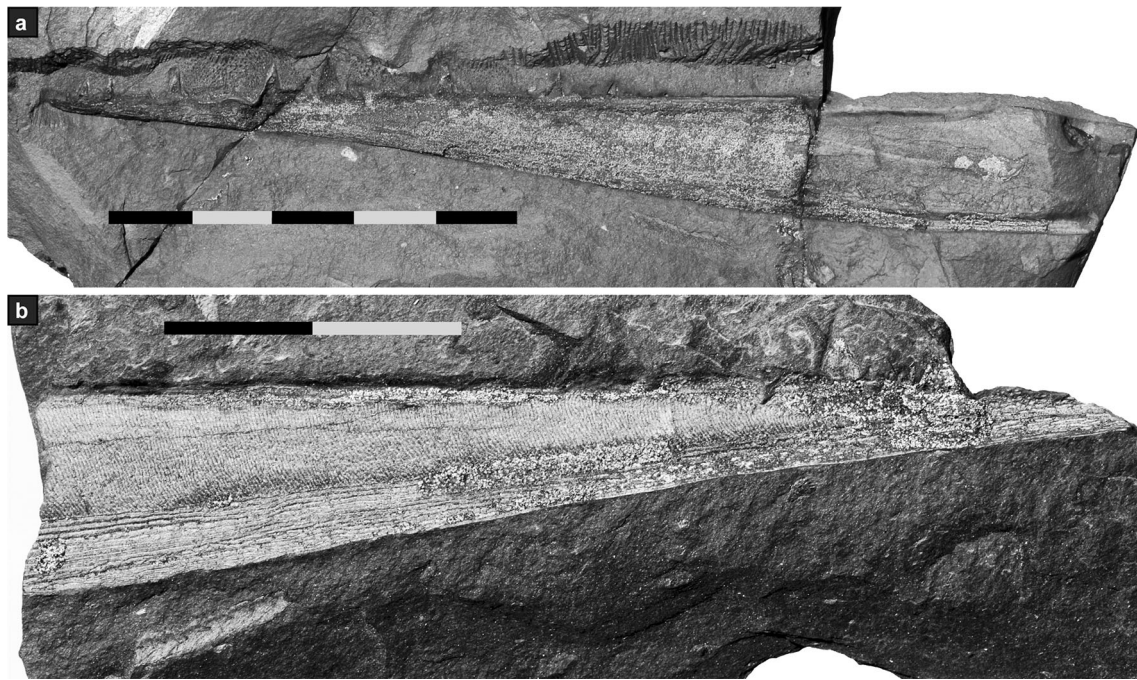
On the lateral surface, the upper part of the dentary bone is covered with parallel running, subvertical striae (A/I 4145b, Fig. 3b). In closer view, these fine striae are made up of oblong tubercles, some of which coalesce. The lower part of the external face of the mandible is ornamented with striae that run parallel to the ventral margin of the bone. These striae are much coarser than those in the upper part (Fig. 3b).

Several conical teeth of two size classes are developed in the anterior and middle portion of the dentary. There are about nine widely spaced larger teeth and at least thirteen smaller ones in between. The teeth possess a vertically striated basal portion and a smooth apical cap that, as far as can be seen on the larger teeth, measures a bit more than one third of the total tooth height.

**Remarks.** The overall morphology and the peculiar lateral ornamentation pattern of PIMUZ A/I 4145 are well in agreement with those of the Triassic predatory actinopterygian *Saurichthys* (e.g. Stensiö 1925; Lehman 1952; Griffith 1959; Lehman et al. 1959), but the incomplete preservation of the Spiti specimen precludes a determination to species level (see “Discussion”). The dimensions of A/I 4145 suggest an estimated total length range of ca. 400–600 mm for the animal (cf. Griffith 1959; Romano et al. 2012). A/I 4145 was already mentioned in Romano et al. (2012).

Series Neopterygii Regan, 1923

Superdivision Holostei Müller, 1845 (sensu Grande 2010)



**Fig. 3** *Saurichthys* sp. (PIMUZ A/I 4145): left lower jaw with teeth from the late Dienerian (lower part of the Limestone and Shale Member, Mikin Formation) of Mud Bottom Section (Pin Valley, Spiti

Division Halecomorphi Cope, 1972 (sensu Grande and Bemis 1998)

Family Parasemionotidae Stensiö, 1932

Genus *Watsonulus* Brough, 1939

*Remarks.* *Watsonulus* is the replacement name for *Watsonia* Piveteau, 1934, which is preoccupied (Brough 1939: p. 91).

*Type and only species.* *Watsonia eugnathoides* Piveteau, 1934 from the Early Triassic of northwest Madagascar.

**cf. *Watsonulus* cf. *eugnathoides*** (Figs. 4, 5, 6)

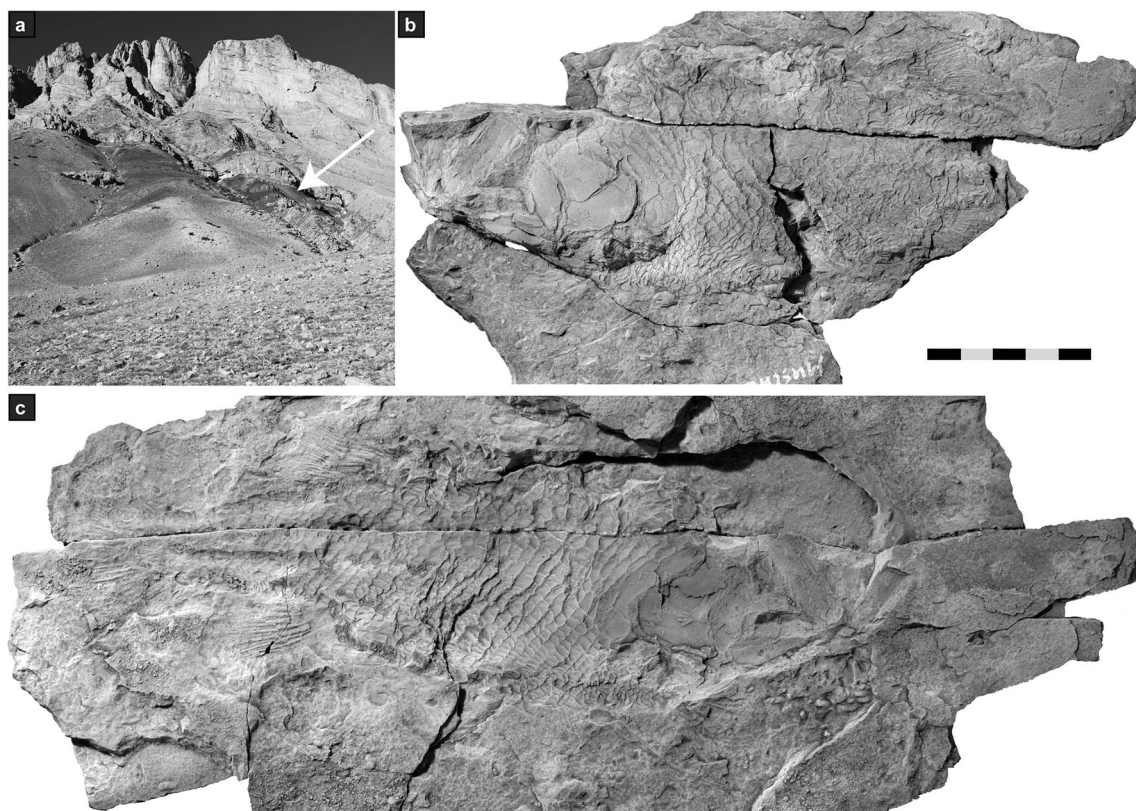
*Material and stratigraphy.* A single specimen, PIMUZ A/I 4360 (Figs. 4, 5, 6), which is a complete fish preserved within a calcareous nodule as part (A/I 4360a; Figs. 4b, 5, 6a) and counterpart (A/I 4360b; Figs. 4c, 6b). The specimen is exposed in left lateral view in part a, whereas part b mostly contains the impressions of the bones preserved in part a. A latex peel cast of A/I 4360b was prepared for this study. A/I 4360 was found about halfway between the villages of Khar and Tilling (Pin Valley, Lahaul and Spiti District, Himachal Pradesh, India), high above the valley floor at ca. 4030 m altitude (“Tilling Section” of Ware et al. in production a, N32°00′46.2″/E78°05′04.5″; Figs. 1, 4a). It was recovered from the late Dienerian *Kingites davidsonianus* Zone of Ware et al. (2015, in production a, b), lower part of the Limestone and Shale Member, Mikin Formation (Fig. 2).

Subdistrict, Himachal Pradesh, India). **a** Part a of A/I 4145 (scale bar measures 50 mm); **b** part b of A/I 4145 showing details of the distinct lateral ornamentation pattern (scale bar measures 20 mm)

*Description.* PIMUZ A/I 4360 is flattened, but the three-dimensional shape of the skull and the body are still discernible. For the most part, the bones are weathered away and usually only their medial impression is preserved. For this reason, no comments can be made about the external ornamentation. A/I 4360 has a standard length of ca. 210 mm, whereas the head (including gill cover) measures ca. 60 mm.

The dermal skull roof of A/I 4360 (Fig. 5) is preserved as one unit in dorsal view (Fig. 5). Its postorbital portion is better preserved than the anterior one. The posterior part of the dermal skull roof is shaped by two paired elements: the parietals medially and the large dermopterotics laterally. Extrascapulars are not preserved in situ, but a small fragment situated posterior to the dermal skull roof may belong to the left extrascapular bone (Fig. 5). The parietals are antero-posteriorly relatively short and of subquadrangular shape. These bones are bounded by fairly straight caudal and lateral margins. Their medial borders are distinctly undulating, whereas their anterior confinements are gently oblique, running from antero-medial to postero-lateral. The dermopterotics are nearly twice as long as the parietals. Each dermopterotic is bounded by four margins: a very short and gently oblique posterior one, a convex medial border, a short, concave antero-lateral margin, and a relatively straight postero-lateral border.

The central portion of the dermal skull roof is occupied by the large, paired frontal bones and the very small, paired



**Fig. 4** *cf. Watsonulus cf. eugnathoides* (PIMUZ A/I 4360) from the late Dienerian (lower part of the Limestone and Shale Member, Mikin Formation) of Tilling Section (Pin Valley, Spiti Subdistrict, Himachal Pradesh, India). **a** Photo of the eastern slope of Pin Valley between

the villages of Khar and Tilling (cf. Fig. 1), with indication of the approximate location where A/I 4360 was found (*white arrow*), **b** part a of A/I 4360, **c** part b of A/I 4360. *Scale bar* in **b** and **c** measures 50 mm

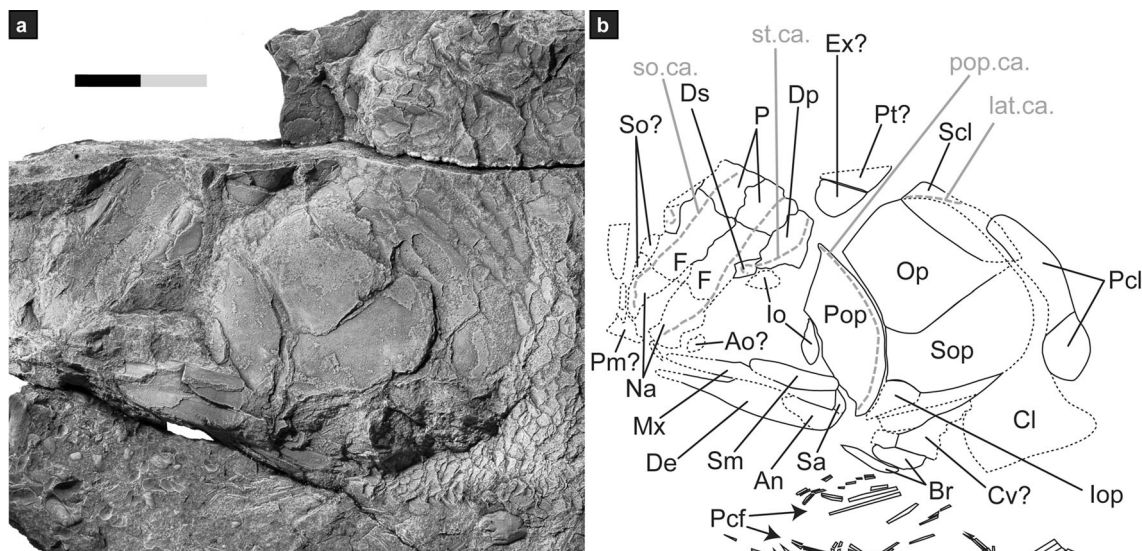
dermosphenotics (Fig. 5). The rhomboidal dermosphenotics are firmly incorporated into the dermal skull roof and posterolaterally adjoin the dermopterotics. The frontal is the largest bone of the dermal skull roof. It is distinctly longer than wide and possesses a notch in the lateral margin, which houses the neighbouring dermosphenotic. The medial margin of the frontal is sinuous. Rostrally, the frontals border the paired nasal bones. The confinement between these elements is seemingly mildly curved. As far as can be seen, the anterior ends of the left and right frontal are medially separated and the nasal bones are medially not in contact with each other. Antero-laterally to the right frontal and postero-laterally to the right nasal lie about two serially arranged supraorbital bones (Fig. 5).

The dermal skull roof is distinctly three-dimensionally bent (Fig. 5). Within its posterior portion, up to the level of the orbit, the dorsal surface of the dermal skull roof is concave along its median axis but convex along its lateral flanks. At the level of the anterior supraorbital, the dermal skull roof is relatively flat. Further rostrally, however, the external surface of the dermal skull roof becomes increasingly convex anteriorly and laterally. The curvature of the dermal skull roof of A/I 4360 is bilaterally symmetrical, suggesting that it reflects the

original shape, but some taphonomic deformation cannot be excluded.

The cheek region is mainly occupied by the large, slightly anteriorly inclined praeoperculum. This bone is higher than long and bounded by four margins: a long, convex posterior one, straight antero-dorsal and antero-ventral borders, and a short, concave anterior confinement. The lateral surface of the praeoperculum is gently convex. The circumorbital series is incompletely preserved and only represented by three elements. Next to the left dermosphenotic lies a poorly preserved bone that likely corresponds to an infraorbital. A further, teardrop-shaped infraorbital bone is found in situ between the praeoperculum and the supramaxilla. In addition, two fragmentary elements that are antero-laterally bordering the nasal bones may belong to the antorbitals. A sclerotic ring is not preserved.

The bones of the upper and lower jaw are located on either side of the dermal skull roof (Fig. 4). On the left side of the cranium (Fig. 5), the jaw bones are preserved in situ. The upper jaw consists of the long and slender maxilla, the supramaxilla, and possibly a pair of praemaxillae. The latter may be preserved anterior to the nasals (Fig. 5), but



**Fig. 5** cf. *Watsonulus* cf. *eugnathoides* (PIMUZ A/I 4360) from the late Dienerian (lower part of the Limestone and Shale Member, Mikin Formation) of Tilling Section (Pin Valley, Spiti Subdistrict, Himachal Pradesh, India). **a** Close-up view of the skull and anterior body portion of part a of A/I 4360, **b** drawing of the bones of the cranium and pectoral girdle of A/I 4360a, with indication of the bones and sensory canals (dashed grey lines). *An* angular, *Ao* antorbital bone, *Br* branchiostegal ray, *Cl* cleithrum, *Cv* clavicle, *De* dentary, *Dp*

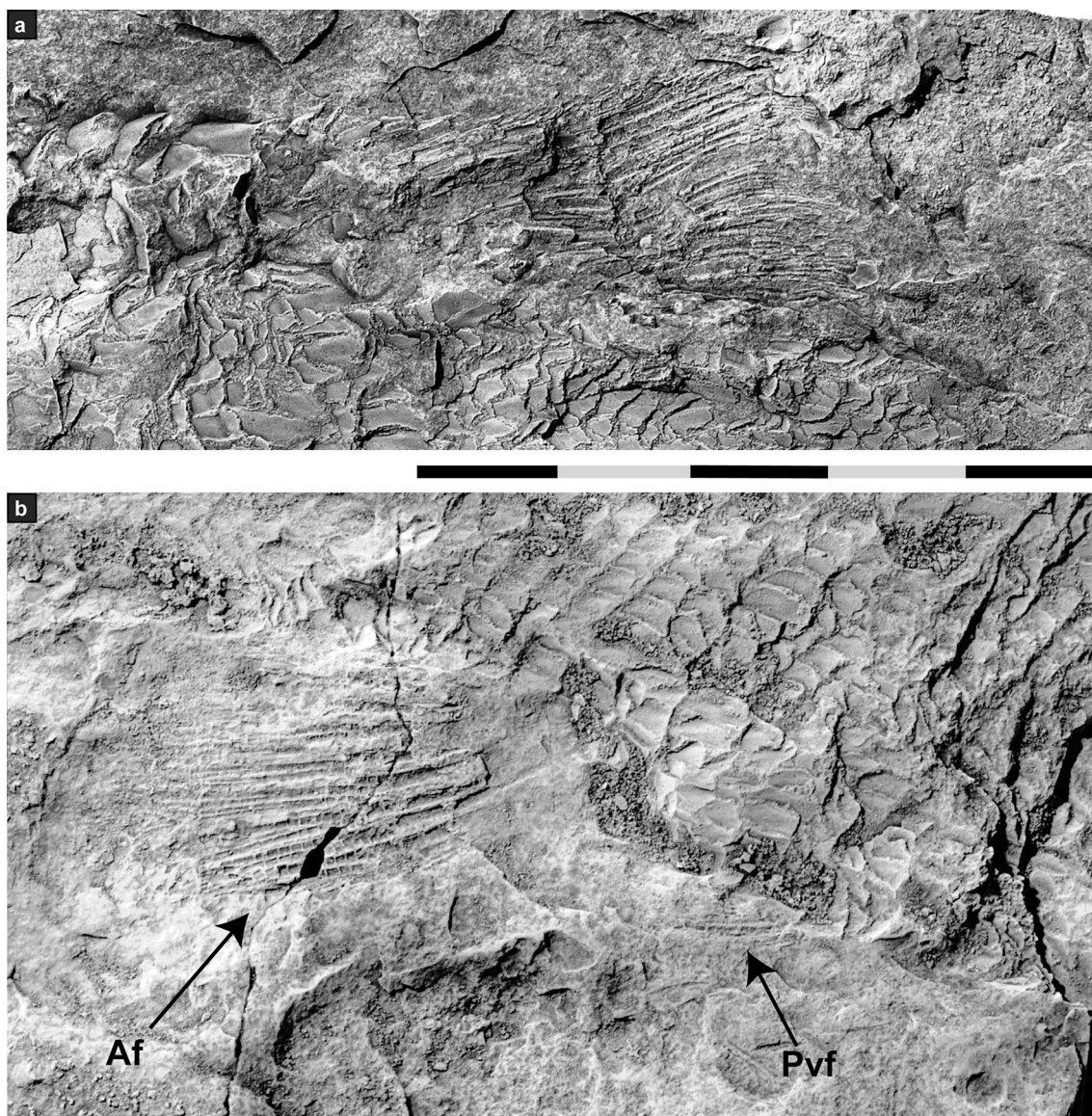
dermopterotic, *Ds* dermosphenotic, *Ex* extrascapular, *F* frontal, *Io* infraorbital bone, *Iop* interoperculum, *lat.ca.* lateral line sensory canal, *Mx* maxilla, *Na* nasal, *Op* operculum, *P* parietal, *Pcf* pectoral fin, *Pcl* postcleithrum, *Pm* premaxilla, *Pop* praeoperculum, *pop.ca.* praeopercular sensory canal, *Pt?* posttemporal, *Scl* supracleithrum, *Sm* supramaxilla, *So?* supraorbital, *so.ca.* supraorbital sensory canal, *Sop* suboperculum, *st.ca.* supratermporal sensory canal

the poor state of preservation of these bones precludes a description. The left maxilla is preserved in two separate segments in A/I 4360a (Fig. 5). The rostral portion and most of the ventral margin of the maxillary bone are missing and teeth have not been observed. The left mandibular branch is largely complete and only its rostral end is lacking. The boundaries between the dentary, the angular, and surangular bones are barely visible. The dentition of the lower jaw is not preserved.

Of the bones of the operculogular series only the operculum, suboperculum, and a few branchiostegal rays are visible (Fig. 5). Gulars are not preserved. The operculum and suboperculum are both large, plate-like bones that shape most of the lateral gill cover. The operculum is a roughly five-sided bone bounded by a gently concave antero-ventral border, a straight antero-dorsal margin, a long, deeply convex postero-dorsal border, a straight postero-ventral margin, and a short, convex ventral confinement. The postero-dorsal border is damaged and mostly preserved as an impression. The suboperculum adjoins the operculum ventrally. This bone is longer than high and confined by five margins: a slightly concave anterior, a deeply concave dorsal, a distinctly convex posterior, a nearly straight postero-ventral, and a short, concave antero-ventral. The suboperculum borders the interoperculum antero-ventrally and a branchiostegal ray ventrally, but both of these elements are only preserved fragmentarily. Two additional radii branchiostegii are located further ventrally (Fig. 5).

Most elements of the shoulder girdle are present, but the majority of them are poorly preserved. A fragmentary bone attached to the putative left extrascapular may correspond to the left posttemporal (Fig. 5). The supracleithrum is found in situ and is best visible in part b of A/I 4360 (Fig. 4c). It is an elongate, four-sided bone that in vivo was partially overlapped by the adjacent operculum. The cleithrum is probably preserved in place but heavily damaged. The endoskeletal shoulder girdle cannot be traced. A fragmentary, plate-like bone neighbouring the branchiostegal rays could correspond to the clavicle. There are two postcleithra, an elongate upper one that is anteriorly in contact with the supracleithrum and cleithrum, and a smaller, teardrop-shaped lower one (Fig. 5).

All fins are present but in different preservational conditions. The pectoral fin is largely disarticulated, but several isolated lepidotrichial segments are found ventrally to the skull and shoulder girdle (Figs. 4b, c, 5). The length of some fin rays (up to ca. 50 mm) and the distribution pattern of the lepidotrichial segments suggests that the pectoral fin of A/I 4360 was of rather large size. The pelvic fins, even though poorly preserved, lie closer to the anal fin than to the pectoral girdle (Figs. 4b, c, 6b). At least four fin rays are observed in situ. The first lepidotrichium of the pelvic fin is thicker than the subsequent ones and distally segmented into very short units (Fig. 6b). Furthermore, its leading edge is equipped with small fringing fulcra (A/I 4360a). Several isolated fin ray



**Fig. 6** *cf. Watsonulus cf. eugnathoides* (PIMUZ A/I 4360) from the late Dienerian (lower part of the Limestone and Shale Member, Mikin Formation) of Tilling Section (Pin Valley, Spiti Subdistrict, Himachal

Pradesh, India). **a** Close-up view of the dorsal fin of A/I 4360a, **b** magnified detail of the pelvic and anal fin of A/I 4360b. Scale bar for **a** and **b** measures 50 mm. *Af* anal fin, *Pvf* pelvic fin

segments in close proximity to the pelvics may also belong to these fins. The pelvic fins were seemingly short-based and generally small. The virtually opposed dorsal and anal fins are placed closer to the caudal fin than to the cranium (Fig. 4). The dorsal fin begins a very short distance ahead of (but a few scale rows behind) the anal fin and both fins contain about twelve lepidotrichia each. Each fin ray of the dorsal and anal fin consists of a relatively long basal segment and numerous, very short distal ones (Fig. 6). At least those lepidotrichia terminating at the posterior fin margin are once or twice distally bifurcated. The anterior margin of the first lepidotrichium of the dorsal and anal fin is edged with fringing fulcra. A few basal fulcra are probably developed

in front of the dorsal fin (Fig. 6a). The caudal fin is relatively poorly preserved and the distal parts of its upper and lower lobes are missing (Fig. 4c). The number of lepidotrichia in the caudal fin cannot be determined. As far as can be seen, the tail fin is only weakly heterocercal and at least the leading edge of the dorsal caudal lobe is armed with fulcra.

The entire body of A/I 4360 (Fig. 4) is covered with rhombic scales. Hence, the endoskeletal support of the fins and the elements of the axial skeleton cannot be studied. The squamation consists of oblique scale rows. At least 35 scale rows are counted along the lateral line. Scales on the side of the body are usually higher than long, whereas those situated more dorsally and ventrally are usually longer than



high. The largest scales are found behind the upper postcleithrum (Fig. 5a). The ornamentation of the scales is not preserved.

The lateral line sensory canal can be traced across multiple scales along the flank of the body (best seen in the cast of A/I 4360b). Anteriorly, the lateral line canal pierces the supracleithrum through its posterior margin and traverses this bone just above the area covered by the neighbouring operculum (Fig. 5). Sensory canals can also be spotted on the dermal skull roof. The supratemporal section of the lateral line runs through the dermosphenotic before it enters the dermosphenotic. Due to limited preservation the canal cannot be traced within the infraorbital series and the antorbital bones. The left and right branches of the supraorbital sensory canal are well visible in the parietal, frontal, and nasal bones. The praeopercular sensory canal is seen near the posterior margin of the praeoperculum. It closely follows the caudal margin of the praeoperculum in its upper part, whereas the distance to the hind border increases towards the ventral portion of the bone. The mandibular canal, which usually runs along the posterior and ventral margins of the lower jaw, could not be detected in the studied specimen.

*Remarks.* PIMUZ A/I 4360 shows many similarities with *Watsonulus eugnathoides* (Piveteau 1934) and can, thus, be referred to Parasemionotidae Stensiö (1932). However, taxonomic problems within Parasemionotidae presently impede a definite determination of the Spiti specimen (see “Discussion”).

A/I 4360 is associated with several internal moulds of indeterminable bivalves (Fig. 4b–c). A dense accumulation of clams is found just ventrally to the skull and partially also on the lower jaw of the fish (cf. A/I 4360b). The bivalves seem disarticulated but otherwise undamaged, which suggests that this accumulation is neither a regurgitalite of the fish nor a coprolite of a different animal.

#### **Actinopterygii indet.** (Fig. 7)

*Material and stratigraphy.* Two articulated specimens preserved in limestone nodules from the lower part of the Limestone and Shale Member of the Mikin Formation. Both individuals were recovered in 2009 at a site above the village of Mud (“Bottom Section” of Ware et al. in production a), Pin Valley, Lahaul and Spiti District, Himachal Pradesh, India (Fig. 1). The first specimen, PIMUZ A/I 4361 (Fig. 7), is preserved on two complementary plates (a and b) and originates from the late Dienerian *Vavilovites meridialis* Zone (Ware et al. in production a, b) (Fig. 2). The second specimen, which is from the middle Dienerian *Ambites lilangensis* Zone (Ware et al. 2015, in production a, b; Fig. 2), requires preparation and is thus not taken further into account herein. A/I 4361 is described below but

is treated in open nomenclature due to the absence of diagnostic features.

*Description.* PIMUZ A/I 4361 (Fig. 7) is a relatively large, slender actinopterygian with only its body preserved, including the pectoral fin and a few lepidotrichia of the caudal fin. The skull and shoulder girdle are entirely missing and the remaining fins cannot be traced. The length of the preserved body portion of A/I 4361 (without caudal fin rays) measures ca. 275 mm. The postero-ventrally directed pectoral fin (Fig. 7a) is peculiarly long (at least 55 mm) and slender. The number of fin rays and the segmentation pattern are difficult to determine, but the count of lepidotrichia seems to be low. Fringing fulcra are seemingly absent on the pectoral fin. The endoskeletal part of the pectoral fin is not preserved.

The trunk is covered with relatively small, rhombic scales. Most scales are poorly preserved but the oblique scale rows can still be traced. About 67 scale rows are counted in total. Some scales still have their lateral ornamentation preserved, especially those on the flanks of the caudal peduncle. The ornamentation consists of thick horizontal striae (Fig. 7b).

*Remarks.* PIMUZ A/I 4361 and the second, unlabelled specimen are both assigned to Actinopterygii based on the presence of oblique rows of rhombic scales.

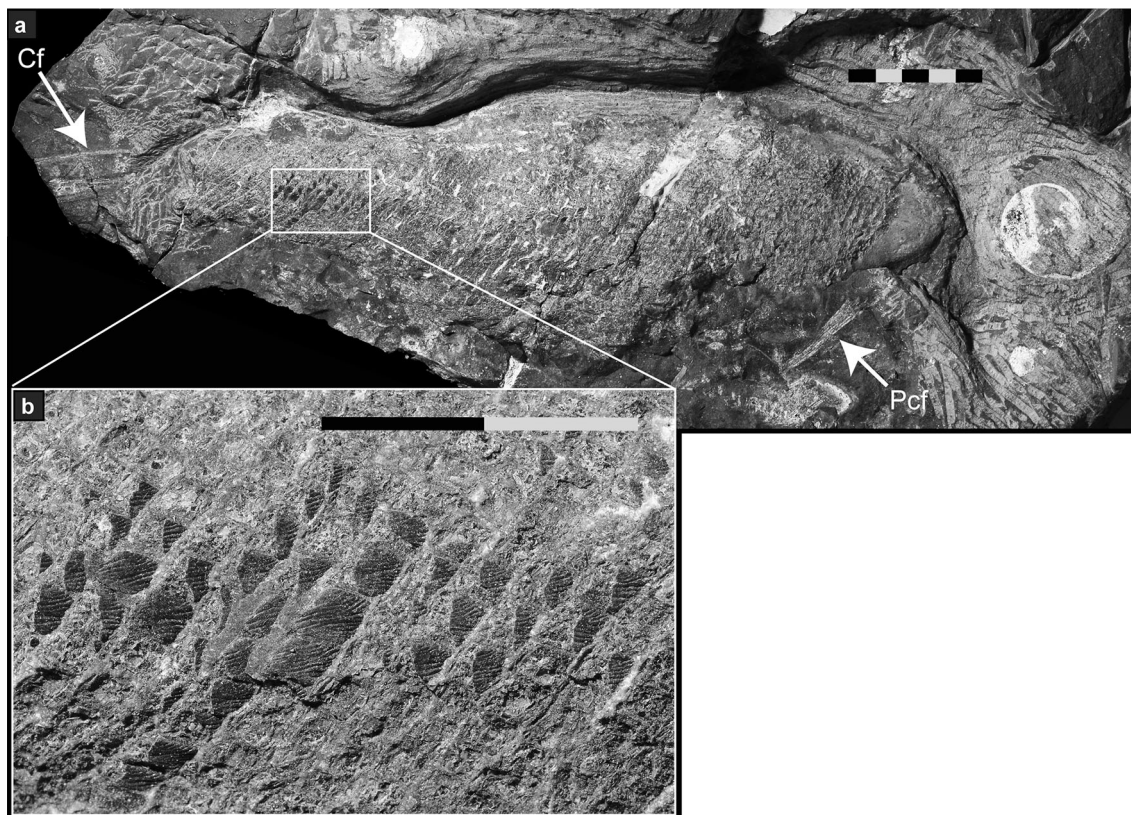
Subclass Sarcopterygii Romer, 1955 (sensu Rosen et al. 1981)

Infraclass Actinistia Cope, 1871 (sensu Forey 1998)

#### **Actinistia indet.** (Fig. 8)

*Material and stratigraphy.* A single, largely complete actinistian urohyal, PIMUZ A/I 4362, preserved in dorsal aspect on two rock hand samples of black shale, part a (A/I 4362a; Fig. 8a) and its counterpart b (A/I 4362b; Fig. 8b), with the fracture plane going through the element. The most posterior part of the bone is incomplete. A/I 4362 was collected near Guling on the opposite side of the Pin River Valley (“Guling River” section in Ware et al. in production a), Lahaul and Spiti District, Himachal Pradesh, India (Fig. 1). It is derived from the lower part of the Limestone and Shale Member of the Mikin Formation (Fig. 2) and was recovered in situ from black shale layers between the late Dienerian *Kingites davidsonianus* Zone and the earliest Smithian *Flemingites bhargavai* Zone of Brühwiler et al. (2010) and Ware et al. (2015, in production a, b).

*Description.* PIMUZ A/I 4362 (Fig. 8) is a thin, elongate element with a pronounced slender shape. It is dorso-ventrally flat and horizontally broad. The form of the urohyal in the horizontal plane roughly resembles that of an hourglass possessing unequally sized lobes: a short anterior one (ca. 7 mm long) and a longer posterior one (at least 16 mm). A



**Fig. 7** Actinopterygii indet. (PIMUZ A/I 4361) from the late Dienerian (lower part of the Limestone and Shale Member, Mikin Formation) of Mud Bottom Section (Pin Valley, Spiti Subdistrict, Himachal Pradesh, India). **a** Part a of A/I 4361 representing a nearly

complete fish lacking the skull and most fins (*scale bar* measures 50 mm), **b** close-up view of the squamation of the caudal peduncle with preserved ornamentation (*scale bar* measures 20 mm). *Cf* caudal fin, *Pcf* pectoral fin

distinct constriction analogous to the neck of an hourglass is developed within the rostral portion of this bone.

The short anterior segment of the urohyal is rostrally broad, reaching a maximum width of ca. 3 mm. The front end is blunt and the terminal margin is marked by a small central notch (Fig. 8). The long caudal segment of the urohyal is posteriorly forked and thereby tapers off as two wings, each of which probably had an acute hind end. The caudal wings of the urohyal reach their greatest horizontal width (ca. 7 mm) about halfway between the constricted portion of the bone and its hind end. Caudally, the two posterior rami are separated by a distinct interspace. Anteriorly, the wings are connected via a wedge-shaped median portion. The hind part of this medially placed segment is incompletely preserved but it seems to have extended halfway between the level of greatest width of the urohyal and the posterior end of the bone (Fig. 8c). The preserved total length of the urohyal is about 23 mm.

For the most part, the urohyal is plate-like, especially in its elongate posterior portion. Two fine ridge-like structures are detected along the lateral confinements of the anterior segment (A/I 4362; Fig. 8). Just behind the constricted portion, the bone is distinctly dorsally arched. This curvature of the dorsal

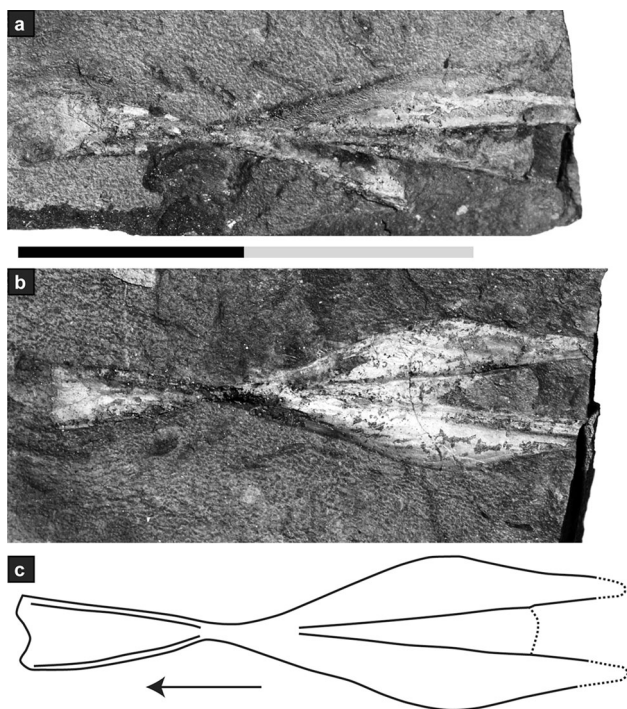
surface continues along the lateral margins within the rostral part of the posterior wings of the urohyal. The flat, triangular median portion between the caudal wings is separated from the latter by two distinct ridges. These ridges continue posteriorly along the medial margins of the caudal wings of the urohyal. In dorsal view, the triangular median portion appears slightly lowered relative to the posterior wings (A/I 4362b; Fig. 8b).

*Remarks.* The distinct shape and morphology of PIMUZ A/I 4362 allows a confident identification of this element as an actinistian urohyal. However, due to limited knowledge of the urohyal of fossil ‘coelacanth’ fishes, including most Early Triassic forms, we currently refrain from a determination at low taxonomic rank (see “[Discussion](#)” section).

## Discussion

### Record of Triassic fishes from the Indian subcontinent

Despite the long history of palaeontological and geological research in Spiti (e.g. Diener 1897, 1908, 1912; Hayden 1904; Krafft and Diener 1909; Krystyn and Orchard 1996;



**Fig. 8** *Actinistia* indet. (PIMUZ A/I 4362): Urohyal of a ‘coelacanth’ fish from the late Dienerian (possibly earliest Smithian) of Guling River section (lower part of the Limestone and Shale Member, Mikin Formation, Spiti Subdistrict, Himachal Pradesh, India), seen in dorsal view. **a** Part a of A/I 4362, **b** counterpart (A/I 4362b), **c** drawing of A/I 4362b. Arrow points anteriorly. Scale bar measures 20 mm

Krystyn et al. 2004; Bhargava et al. 2004; Brühwiler et al. 2010), fish macrofossils have hitherto not been reported from this region (see also below). Merely Goel (1977) mentioned the occurrence of microscopic fish remains (teeth and scales) in a section of the Mikin Formation near the village of Khar (cf. Fig. 1), but this material was neither described nor figured. The fact that fish macrofossils have not yet been reported is surprising given our own experience during fieldwork in Spiti. Within only a couple of days we were able to find several isolated remains and even some articulated specimens. Considering the vast exposures of the Mikin Formation (cf. Fig. 1) compared with the small number of localities so far explored for fish remains, it is likely that further explorations in Spiti will yield more material.

The Indian subcontinent bears numerous sites producing Early Triassic fish fossils, as a matter of fact more than most other former Gondwanan provinces (cf. López-Arbarelo 2004; Brinkmann et al. 2010). Outcrops within the peninsular part of India are all freshwater settings and yield only ichthyoliths (Panchet Formation, e.g. Chatterjee and Roy-Chowdhury 1974; Bandyopadhyay 1999; Bandyopadhyay et al. 2002; Gupta 2009), whereas those from the extrapeninsular part (Northern Indian Margin) all represent

marine deposits (e.g. Chang and Miao 2004; Brinkmann et al. 2010). Younger Triassic fish assemblages from the Indian subcontinent are mainly freshwater (e.g. the Middle Triassic Yerrapalli Formation or the Upper Triassic Tiki and Maleri formations), rarely marine (e.g. Misra et al. 1973; Chhabra and Mishra 2002), and usually typified by isolated skeletal remains (e.g. Agarwal and Singh 1981; Bandyopadhyay 1999; Bandyopadhyay et al. 2002; Chang and Miao 2004; Prasad et al. 2008).

Early Triassic marine chondrichthyan and osteichthyan fishes from the Northern Indian Margin (Neotethys realm, Fig. 1a) have been described from the Salt Range in northwest Pakistan (e.g. De Koninck 1863a, b; Waagen 1895; Romano et al. 2014b) as well as from the Himalayas of Jammu and Kashmir (e.g. Sahni and Chhabra 1976; Agarwal and Singh 1981; Srivastava and Mehrotra 1986), India (e.g. Sahni and Chhabra 1976; Mehrotra et al. 1983a, b; Mishra et al. 1990), Nepal (Beltan and Janvier 1978), and South Tibet (Zhang 1976; Brinkmann et al. 2010). However, most of this material consists of isolated remains, such as teeth or scales, which are valuable for chondrichthyan parataxonomy but only of limited use for osteichthyan taxonomy. Merely two finds from the Northern Indian Margin are more complete, i.e. a tooth whorl fragment of the edestid chondrichthyan *Sinohelicoprion gomolangma* Zhang, 1976 from South Tibet and a partial skull of *Saurichthys nepalensis* Beltan and Janvier, 1978 from the Nepalese Annapurna (Chang and Jin 1996; Chang and Miao 2004; Jin 2006; Brinkmann et al. 2010). Precise biostratigraphic data for the aforementioned fish fossils is, in many cases, wanting (e.g. Beltan and Janvier 1978). The new ichthyofauna from Spiti includes the most complete fish macrofossils ever described from the Triassic of India and benefits from a detailed biostratigraphic framework (e.g. Ware et al. 2015, in production a).

### Taxonomic discussion of the Spiti ichthyofauna

The presented Early Triassic fish assemblage from Spiti comprises material of *Saurichthys* Agassiz, 1834, a parasemionotid (cf. *Watsonulus* cf. *eugnathoides*), as well as further actinopterygian and actinistian remains. The Spiti ichthyofauna thus includes taxa also known from several other coeval assemblages (see below), highlighting the similarities of fish biocoenoses during the Early Triassic (see e.g. Romano et al. 2014a for a recent summary and references). Cosmopolitanism at that time may have been the combined result of the devastating effects of the end-Permian mass extinction event, of poorly differentiated habitats, and of the simple Pangaeian supercontinent configuration, facilitating faunal exchange of the surviving and newly evolved taxa.

*Saurichthys* is a common component of Triassic fish assemblages and usually very easily identifiable due to its peculiar anatomy (e.g. Romano et al. 2012). During the Early Triassic, *Saurichthys* had a worldwide distribution and this taxon has previously also been described from the Northern Indian Margin (Beltan and Janvier 1978), even though with poor age control. The presence of *Saurichthys* in the Dienerian of Spiti underlines the successful circum-pangaean dispersal of this highly specialised predator within only a couple of hundred thousand years (Galfetti et al. 2007; Burgess et al. 2014; Ovtcharova et al. 2015) after the end-Permian mass extinction event (Mutter et al. 2008; Romano et al. 2012; Scheyer et al. 2014).

*Watsonulus* Brough, 1939 was first described from the Early Triassic of Ambilobe Basin in northwest Madagascar (Piveteau 1934, 1939–1940; Lehman 1952; Beltan 1968; Olsen 1984; Grande and Bemis 1998), but was later also discovered in strata of similar age in southwest Madagascar (Morondava Basin) studied by Lehman et al. (1959). The material from both northwest and southwest Madagascar is referred to a single species, *Watsonulus eugnathoides* (Piveteau, 1934). However, based on minor morphological differences several types of *W. eugnathoides* have been distinguished (A, B, and C of Piveteau 1934; 1, 2, and 3 of Lehman 1952). Furthermore, from the earliest Triassic (Griesbachian substage) of East Greenland, Nielsen (1936) also mentioned specimens referable to *Watsonulus*, but a description of this material was never published.

*Watsonulus* belongs to Parasemionotidae Stensiö, 1932 (=Ospiidae Stensiö, 1932; see e.g. Nielsen 1936), a very speciose and cosmopolitan family known only from the marine Early Triassic (Grande and Bemis 1998). Morphological and cladistic analyses suggest that these fishes are basal halecomorph neopterygians (e.g. Patterson 1973; Grande and Bemis 1998; Xu et al. 2014; Friedman 2015). Besides India, parasemionotids are known from Greenland, Madagascar, China, and Canada, and at least 17 species have been described, most of which belong to monotypic genera (Table 1). In addition, Patterson (1973) included several other Triassic taxa within Parasemionotidae, amongst others the Early Triassic genera *Tungusichthys* Berg, 1941 (Siberia, Russia) and *Paracentrophorus* Piveteau, 1939–1940 (northwest Madagascar), but his proposition was later rejected by Grande and Bemis (1998). Grande and Bemis (1998) list the Early Triassic *Helmolepis* Stensiö, 1932 as a parasemionotid, which is erroneous (see e.g. Nielsen 1936; Neuman and Mutter 2005). A parasemionotid-like fish, *Peia* Li, 2009, was described from the Early Triassic of Jiangsu Province, China. Interestingly, parasemionotids are absent at the Spitsbergen Lagerstätte (Svalbard, Arctic Norway), in spite of the otherwise similar ichthyofaunal composition to other Early Triassic sites (e.g. Nielsen 1936; Brinkmann et al. 2010).

Although a few authors have expressed confidence regarding the validity of several parasemionotid genera (e.g. Nielsen 1936), many taxa are distinguished by relatively small morphological differences, some of which could reflect ontogenetic or individual variation (Patterson 1973, 1975; Grande and Bemis 1998). Parasemionotidae is in need of thorough taxonomic revision, but such a task is beyond the scope of this study. The high number of parasemionotid species as well as current uncertainties regarding the validity of several of them renders the taxonomic interpretation of PIMUZ A/I 4360 (Figs. 4, 5, 6) difficult. A/I 4360 is herein referred to cf. *Watsonulus* cf. *eugnathoides* due to similarities with the type specimens of *W. eugnathoides* (MNHN.F.MAE 11, MNHN.F.MAE 33, MNHN.F.MAE 34, MNHN.F.MAE 42, MNHN.F.MAE 108) figured by Piveteau (1934). In the following, A/I 4360 is compared with other parasemionotids, where the taxa are listed respectively in the sequence of publication of their names (cf. Table 1).

Based on the literature and personal observations (CR), the most notable differences between parasemionotid species concern (1) the anatomy of the brain case, (2) the proportions of the skull and body, (3) the shape and fragmentation pattern of the praeoperculum, (4) the number of branchiostegal rays, (5) the size of the pectoral fins, (6) the relative position of the pelvic fins, and (7) the number of lepidotrichia as well as presence or absence of fringing fulcra. Regarding point (1) no comparisons can be made because the endocranium is not preserved in A/I 4360. This also precludes comparisons with *Devillersia* Beltan, 1968 and *Piveteaunotus* Beltan, 1968, both of which are primarily known from brain cases. The proportions between the head and body (point 2) of A/I 4360 mostly resemble those of *Watsonulus*, *Lehmanotus* Beltan, 1968, *Jurongia* Liu in Liu et al., 2002, and *Suius* Liu in Liu et al., 2002. In these taxa and A/I 4360, the length of the head (tip of snout to hind margin of gill cover) usually measures about one-fourth or more of the standard length (Fig. 4; Piveteau 1934; Beltan 1968; Liu et al. 2002; Tong et al. 2006). By contrast, A/I 4360 differs from taxa such as *Parasemionotus* or *Qingshania* Liu in Liu et al., 2002, which have a smaller head to body length ratio (e.g. Priem 1924; Piveteau 1934). In addition, specimen A/I 4360, as well as *Ospia*, *Watsonulus* (especially type C of Piveteau 1934) and *Jurongia*, are characterized by a long lateral gill cover (operculum plus suboperculum) relative to the length of the anterior part of the skull (Fig. 5; Stensiö 1932; Piveteau 1934; Liu et al. 2002). However, the lateral gill cover is distinctly shorter with respect to the rest of the skull in *Stensionotus* Lehman, 1952, *Jacobulus* Lehman, 1952, *Thomasinotus* Lehman, 1952, *Albertonia*, *Lehmanotus*, and *Suius* (e.g. Beltan 1968; Schaeffer and Mangus 1976; Liu et al. 2002).

**Table 1** Taxa referred to Parasemionotidae Stensiö, 1932 (=Ospiidae Stensiö, 1932)

| Genus                   | Species                        | Locality                             | References   |
|-------------------------|--------------------------------|--------------------------------------|--|
| <i>Parasemionotus</i>   | <i>P. labordei</i>             | Madagascar (northwest and southwest) | Priem (1924), Piveteau (1929), Lehman et al. (1959), Uyeno (1978)  |
|                         | <i>P. besairiei</i>            | Madagascar (southwest)               | Lehman et al. (1959)   |
|                         | <i>Parasemionotus</i> sp.      | Greenland                            | Nielsen (1936)   |
| <i>Ospia</i>            | <i>O. whitei</i>               | Greenland                            | Stensiö (1932)   |
|                         | <i>Ospia</i> sp.               | Madagascar (northwest)               | Beltan (1968)  |
| <i>Broughia</i>         | <i>B. perleidoides</i>         | Greenland                            | Stensiö (1932)   |
|                         | <i>Broughia</i> sp.            | Madagascar (northwest)               | Beltan (1968)  |
| <i>Watsonulus</i>       | <i>W. eugnathoides</i>         | Madagascar (northwest and southwest) | Piveteau (1934, 1939–1940), Brough (1939), Lehman (1952), Lehman et al. (1959), Beltan (1968), Olsen (1984), Grande and Bemis (1998) |
|                         | <i>Watsonulus</i> sp.          | Greenland                            | Nielsen (1936)   |
|                         | cf. <i>W. cf. eugnathoides</i> | India, Himachal Pradesh              | This study   |
| <i>Stensionotus</i>     | <i>S. intercessus</i>          | Madagascar (northwest)               | Lehman (1952)  |
|                         | <i>S. dongchangensis</i>       | China, Jiangsu                       | Liu et al. (2002)  |
| <i>Jacobulus</i>        | <i>J. novus</i>                | Madagascar (northwest)               | Lehman (1952)  |
| <i>Thomasinotus</i>     | <i>T. divisus</i>              | Madagascar (northwest)               | Lehman (1952)  |
|                         | <i>Thomasinotus</i> sp.        | Madagascar (southwest)               | Lehman et al. (1959)   |
| <i>Albertonia</i>       | <i>A. cupidinia</i>            | Canada, British Columbia and Alberta | Lambe (1916), Gardiner (1966), Schaeffer and Mangus (1976), Neuman (2015)  |
|                         | <i>Albertonia</i> sp.          | Canada, British Columbia and Alberta | Davies et al. (1997)   |
| <i>Lehmanotus</i>       | <i>L. markubai</i>             | Madagascar (northwest)               | Beltan (1968)  |
| <i>Devillersia</i>      | <i>D. madagascariensis</i>     | Madagascar (northwest)               | Beltan (1968)  |
| <i>Piveteaunotus</i>    | <i>P. ifasiensis</i>           | Madagascar (northwest)               | Beltan (1968)  |
| <i>Icarealcyon</i>      | <i>I. malagasium</i>           | Madagascar (northwest)               | Beltan (1980, 1984)  |
| <i>Jurongia</i>         | <i>J. fusiformis</i>           | China, Jiangsu and Anhui             | Liu et al. (2002), Tong et al. (2006)  |
| <i>Qingshania</i>       | <i>Q. cercida</i>              | China, Jiangsu and Anhui             | Liu et al. (2002), Tong et al. (2006)  |
| <i>Suius</i>            | <i>S. brevis</i>               | China, Jiangsu                       | Liu et al. (2002)  |
|                         | <i>S. cf. brevis</i>           | China, Anhui                         | Tong et al. (2006)   |
| Parasemionotidae indet. | –                              | Greenland                            | Patterson (1973, 1975)   |
| Parasemionotidae indet. | –                              | Canada, British Columbia and Alberta | Schaeffer and Mangus (1976), Neuman (2015)   |

Genera are sorted in the respective order of publication of their first description

The praeoperculum (point 3) is a single, relatively large and subvertically arranged bone in AJI 4360, much like in *Parasemionotus*, *Ospia*, *Broughia*, *Watsonulus*, and *Jurongia* (Fig. 5; Priem 1924; Stensiö 1932; Piveteau 1934; Liu et al. 2002). By contrast, the antero-dorsal part of the praeoperculum is subdivided into smaller plates in *Stensionotus*, *Jacobulus*, *Thomasinotus*, and *Lehmanotus* (Lehman 1952; Beltan 1968). However, Lehman (1952) referred specimens to *Parasemionotus* and *Watsonulus* that showed a few very small “praeopercular plates” (anamnetic bones) dorsally to the main praeoperculum. There also seems to be variation of the antero-posterior extension of the praeoperculum between taxa (e.g. Stensiö 1932; Piveteau 1934; Lehman 1952). The number of branchiostegal rays (point 4) seems to vary between

parasemionotid species (e.g. Piveteau 1934; Lehman 1952; Lehman et al. 1959; Olsen 1984; Li 2009), although this character is often not well known. Also, differences in counts of radii branchiostegii could be due to ontogenetic variation as the number of these elements usually increases during growth (Arratia and Schultze 1990).

The size of the pectoral fin (point 5) appears to be a distinctive feature that separates *Watsonulus*, *Albertonia* Gardiner, 1966, and *Icarealcyon* Beltan, 1980 from other parasemionotids. Whereas the pectoral fins of most parasemionotids are usually small or only slightly enlarged (e.g. *Parasemionotus*, *Ospia*, *Jacobulus*, *Lehmanotus*, *Jurongia*; Stensiö 1932; Piveteau 1934; Lehman 1952; Beltan 1968; Liu et al. 2002), these fins possess a considerable size in *Watsonulus* (MNHN.F.MAE 11, Piveteau

1934: pl. 9 Figs. 1, 1a), *Albertonia* (CMNFV 757, Lambe 1916: pl. 2; CMNFV 12330; Schaeffer and Mangus 1976: Fig. 18a), and *Icarealcyon* (MNHN.F.MAE 576, Beltan 1984: pl. 3a, b). Although incompletely preserved, the pectoral fin of A/I 4360 appears to have been of fairly large size (Figs. 4, 5), hence being similar to that of *Watsonulus*, *Albertonia*, or *Icarealcyon*. Nevertheless, whether the size of the pectoral fin has taxonomic value or whether alternative explanations such as preservational bias, ontogenetic variation or sexual dimorphism can account for it requires detailed comparative analysis.

The pelvic fins (point 6) are small and short-based in all parasemionotids and they are normally placed approximately midway between the pectoral girdle and the anal fin. In some taxa, such as *Watsonulus* or *Albertonia*, the pelvic fins seem to be slightly nearer to the anal fin than to the shoulder girdle (e.g. MNHN.F.MAE 11, Piveteau 1934: pl. 9 Figs. 1, 1a; CMNFV 757, Lambe 1916: pl. 2; CMNFV 12330, Schaeffer and Mangus 1976: Fig. 18a), whereas in others like *Parasemionotus* (e.g. MNHN.F.MAE 122; Priem 1924; Piveteau 1934) the pelvic fins appear to be slightly closer to the pectoral girdle than to the anal fin. In this respect, A/I 4360 shows more resemblance to *Watsonulus* or *Albertonia* than with most other taxa.

Some variation has been noted in the distribution of fringing fulcra and the count of lepidotrichia (point 7). For instance, whereas fringing fulcra have been detected on the leading margin of the fins of most parasemionotids (e.g. *Parasemionotus*, *Watsonulus*, *Albertonia*; Lambe 1916; Piveteau 1934; Lehman 1952), such elements are reportedly absent on the leading edge of the pectoral and pelvic fins of *Icarealcyon* (Beltan 1984). Differences in the number of lepidotrichia are small in some cases but more distinct in others. For example, Beltan (1984) counted in *Icarealcyon* about 35 pectoral fin rays, four to six pelvic fin rays, approximately 20 dorsal fin rays, roughly 12 anal fin rays, and 26 caudal fin rays. By contrast, *Albertonia* has about 21 pectoral fin rays, nine or ten pelvic fin rays, about 17 dorsal fin rays, roughly 18 anal fin rays, and about 30 caudal fin rays (Schaeffer and Mangus 1976). Although differences in fin ray counts are potentially useful to separate taxa, the precise number of lepidotrichia is sometimes difficult to determine in fossil actinopterygians.

Additionally, with a standard length of ca. 210 mm, A/I 4360 has a comparable body size to specimens of *Ospia* or *Watsonulus* (cf. Stensiö 1932; Piveteau 1934), but differs, for instance, from *Parasemionotus*, *Lehmanotus*, *Qingshania*, and *Suius*, which seemingly only achieved maximum standard lengths of ~120 mm or less (Priem 1924; Lehman 1952; Lehman et al. 1959; Beltan 1968; Liu et al. 2002; Tong et al. 2006). The body of A/I 4360 is slender as in most parasemionotids, with the exception of the more

hypsosomatic *Albertonia* (Schaeffer and Mangus 1976; Davies et al. 1997; Neuman 2015). Based on the preceding comparisons with other parasemionotids, we conclude that A/I 4360 from Spiti shows the most similarities with *Watsonulus*.

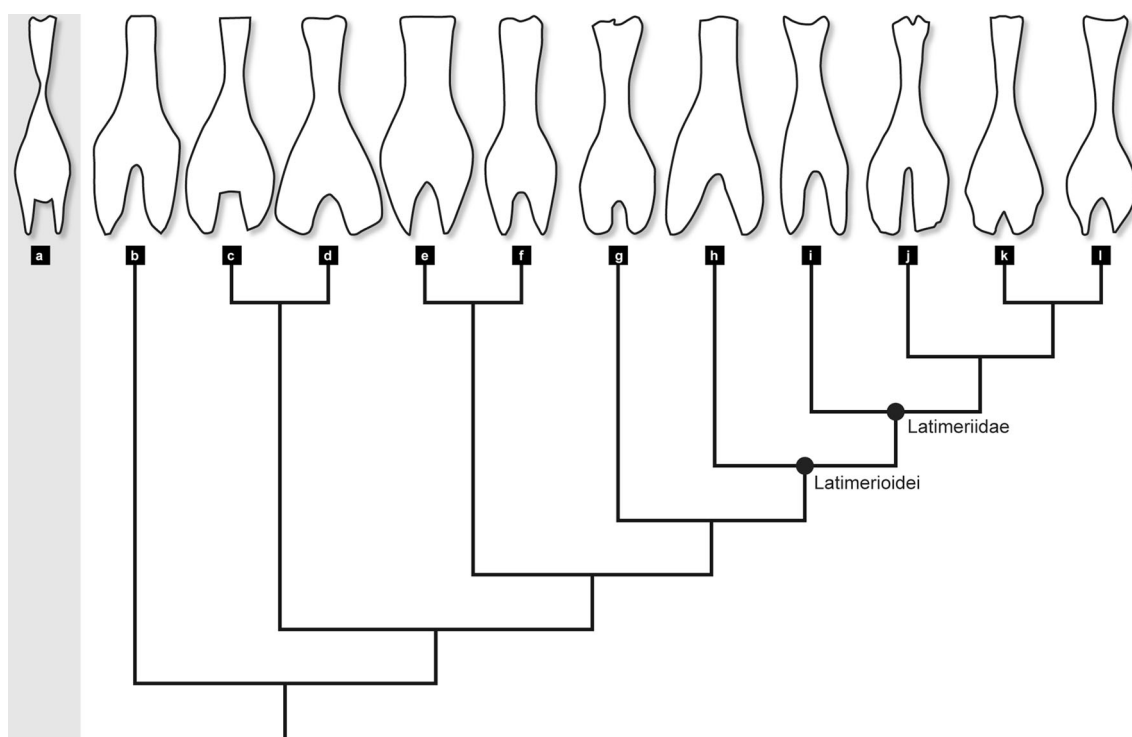
Among the new osteichthyan material from Spiti is a bone (PIMUZ A/I 4362; Fig. 8) that without doubt can be identified as an actinistian urohyal. The urohyal of actinistians is usually dorso-ventrally flattened and has the shape of an inverted Y when seen from above or below, with a narrow anterior end and a broad, bifid posterior portion. In addition, the centre part of the actinistian urohyal is bilaterally constricted (Millot and Anthony 1958; Lehman 1966; Schultze 1993; Forey 1998). The morphology of A/I 4362 is, on the other hand, well-distinguished from that of the actinopterygian urohyal. In ray-finned fishes, this element is normally either plate-like and vertically expanded (e.g. *Birgeria nielsenii*; Lehman 1952; Arratia and Schultze 1990) or rod-like in both dorso-ventral and lateral view (teleosts; Arratia and Schultze 1990). Additionally, it may, in some cases, exhibit a repeatedly notched hind margin, which gives it a fringe-like appearance (Kusaka 1974). The urohyal of dipnoans is poorly researched (Arratia and Schultze 1990) but seemingly different from that of actinistians (see e.g. Miles 1977; Bemis et al. 1987). The urohyal occurs in various shapes and its very distinct morphology is highly diagnostic not only at higher taxonomic levels but also at the species rank (Kusaka 1974; Forey 1998).

Below, A/I 4362 (Figs. 8, 9a) is compared with the urohyal of several actinistians. Concerning the validity as well as the chronological and spatial occurrence of the included taxa we mostly adhere to Cloutier and Forey (1991) and Forey (1998). Within Actinistia, the urohyal is well-documented in the following taxa: *Diplocercides kayseri* (Koenen, 1895) (Fig. 9b), *Rhabdoderma elegans* (Newberry, 1856) (Fig. 9c), *Rhabdoderma (Synaptotylus?) newelli* (Hibbard, 1933) (Fig. 9d), *Whiteia woodwardi* Moy-Thomas, 1935 (Fig. 9e), *Wimania sinuosa* Stensiö, 1921 (Fig. 9f), *Coelacanthus granulatus* Agassiz, 1833–1843 (Fig. 9g), *Trachymetopon liassicum* Hennig, 1951 (Fig. 9h), *Ticinepomis* cf. *T. peyeri* (Fig. 9i), *Megaloelacanthus dobiei* Schwimmer, Stewart and Williams, 1994 (Fig. 9j), *Macropoma lewesiensis* (Mantell, 1822) (Fig. 9k), and the recent *Latimeria chalumnae* Smith, 1939 (Fig. 9l). Additionally to the aforementioned species, incompletely preserved urohyalia have been described in several other fossil taxa, including (in alphabetical order) *Diplurus newarki* (Bryant, 1934) from the Late Triassic of North America (Schaeffer 1952: pl. 6 Fig. 4; presumed urohyal), *Dobrogeria aegyssensis* Cavin and Grădinaru, 2014 from the late Early Triassic of Romania (Cavin and Grădinaru 2014: Fig. 14; fragmentary preservation),

*Laugia groenlandica* Stensiö, 1932 from the Early Triassic of East Greenland (Stensiö 1932: pl. 3; urohyal not well visible), and *Undina penicillata* Münster 1834 from the Late Jurassic of Germany (Reis 1888: pl. 1 Fig. 57; Reis 1892: pl. 2 Fig. 10). However, the available data on the urohyalia of most of the aforementioned taxa is not suitable for comparison.

Comparison of the Spiti specimen with the urohyal of other taxa reveals notable differences. Most strikingly, A/I 4362 has a generally more slender shape than the urohyal of most actinistians (Fig. 9). Additionally, the hind segment of the urohyal of *Coelacanthus*, *Latimeria*, *Megalocoelacanthus*, *Undina*, and *Wimania* is relatively shorter than in A/I 4362 (Reis 1888, 1892; Stensiö 1921; Moy-Thomas and Westoll 1935; Millot and Anthony 1958; Adamicka and Ahnelt 1976; Forey 1998; Brandt 2007; Dutel et al. 2012; Fig. 9). In *Rhabdoderma*

(including *Synaptotylus*), *Trachymetopon*, and *Whiteia* the posterior portion of the urohyal is also distinctly wider than in A/I 4362 (Aldinger 1931; Hennig 1951; Lehman 1952; Dutel et al. 2015a). In all other taxa the constriction between the front and the hind segment of the urohyal is less pronounced compared to A/I 4362 (e.g. Stensiö 1921; Moy-Thomas and Westoll 1935; Lehman 1952, 1966; Millot and Anthony 1958; Adamicka and Ahnelt 1976; Forey 1998; Dutel et al. 2012; Cavin et al. 2013; Cavin and Grădinaru 2014; Dutel et al. 2015a; Fig. 9). In *Coelacanthus*, *Diplocercides*, *Macropoma*, *Megalocoelacanthus*, *Rhabdoderma* (including *Synaptotylus*), and *Undina* the tips of the posterior wings are broad (Reis 1888, 1892; Stensiö 1922, 1937; Aldinger 1931; Moy-Thomas and Westoll 1935; Forey 1998; Brandt 2007; Dutel et al. 2012), whereas in A/I 4362 and some other taxa they are acute (Fig. 9). A clear phylogenetic pattern



**Fig. 9** Morphological comparison of actinistian urohyalia (bone outlines in dorso-ventral aspect redrawn from the literature, anterior is on top) in a phylogenetic context (cladogram modified from Dutel et al. 2015a: Fig. 6b). **a** PIMUZ A/I 4362 (Actinistia indet., this study) from the Early Triassic of India, **b** *Diplocercides kayseri* (Koenen, 1895) from the Devonian of Germany (after Stensiö 1922: Fig. 8, pl. 3 Fig. 3, pl. 4 Figs. 1, 2; Stensiö 1937: pl. 1, pl. 8 Fig. 2); **c** *Rhabdoderma elegans* (Newberry, 1856) from the Carboniferous of Europe (after Aldinger 1931: Fig. 5, pl. 6; Forey 1998), **d** *Rhabdoderma* (*Synaptotylus*?) *newelli* (Hibbard, 1933) from the Carboniferous of North America (after Echols 1963: Fig. 5; see also Forey 1998); **e** *Whiteia woodwardi* Moy-Thomas, 1935 from the Early Triassic of northwest Madagascar (after Lehman 1952: Fig. 12b; Lehman 1966: Fig. 24b), **f** *Wimania sinuosa* Stensiö, 1921 from the

Early Triassic of Spitsbergen (after Stensiö 1921: Fig. 29, pl. 4 Fig. 2, pl. 7 Fig. 3); **g** *Coelacanthus granulatus* Agassiz, 1833–1843 from the Lopingian of Germany and England (after Moy-Thomas and Westoll 1935: Fig. 5; Brandt 2007: Fig. 10), **h** *Trachymetopon liassicum* Hennig, 1951 from the Early Jurassic of Germany (after Hennig 1951: pl. 8 Fig. 5; Dutel et al. 2015a: Figs. 1, 4–5); **i** *Ticinepomis* cf. *T. peyeri* from the Middle Triassic of Switzerland (after Cavin et al. 2013: Fig. 5); **j** *Megalocoelacanthus dobiei* Schimmer, Stewart and Williams, 1994 from the Late Cretaceous of the USA (after Dutel et al. 2012: Fig. 16b), **k** *Macropoma lewesiensis* (Mantell, 1822) from the Late Cretaceous of England (after Forey 1998: Fig. 7.7), **l** *Latimeria chalumnae* Smith, 1939 from present-day western Indian Ocean (after Millot and Anthony 1958: Figs. 15, 17, pl. 47; Adamicka and Ahnelt 1976: Fig. 3; Forey 1998: Fig. 7.6b)

in the outline of the actinistian urohyal (using the cladogram of Dutel et al. 2015a: Fig. 6b) is not apparent based on the available data (Fig. 9).

In summary, the morphology of A/I 4362 (Figs. 8, 9a) is distinct from the urohyal of the taxa listed above. A/I 4362 most prominently differs from other known actinistian urohyalia in its pronounced slender, elongate habitus and the extreme narrowness of its constricted portion. We therefore conclude that the specimen from Spiti does not belong to any actinistian species of which the urohyal is known.

The sarcopterygian urohyal, which is formed from cartilage, is not homologous to the teleostean urohyal, which is an ossification of the tendon of the sternohyoideus muscle (e.g. Millot and Anthony 1958; Arratia and Schultze 1990; Forey 1998). The urohyal of actinistians is a relatively large, bilaterally symmetrical median element placed postero-ventrally to the unpaired basibranchial of the hyoid arch. The urohyal articulates with the basibranchial via its broad, flat anterior end (Forey 1998). Despite its name, the urohyal does not form part of the hyoid arch. In Actinistia, the urohyal plays an important role as the point of origin of several muscles involved with mandibular depression, lowering of the buccal floor, and retraction of the shoulder girdle (Millot and Anthony 1958; Adamicka and Ahnelt 1976; Dutel et al. 2015b).

## Concluding remarks

Deecke (1927) already noticed the paucity of the Himalayan record of Triassic fishes and, regrettably, our knowledge about these faunas has not significantly improved since that time. The herein presented, new Early Triassic (mainly middle-late Dienerian) marine osteichthyan fauna from Pin Valley of Spiti Subdistrict (Himachal Pradesh, India) includes the most complete fish specimens so far described from the marine and continental Triassic of India (cf. Jain and Roychowdhury 1987; Bandyopadhyay 1999; Chang and Miao 2004; Prasad et al. 2008; Gupta 2009). Regarding the wide extent of exposures and how little of it has been previously explored specifically for fish fossils there is great potential that future fieldwork in Spiti will yield more specimens. The quality of preservation is good and reveals fine morphological details (e.g. bone ornamentation and fin ray segmentation patterns). Additionally, the fish remains co-occur with abundant index fossils (ammonoids, conodonts) for precise biochronological dating. In this perspective, research on the Spiti fishes could considerably enhance our understanding of Himalayan Triassic ichthyofaunas.

Widespread marine anoxia on continental shelves during the middle and late Dienerian (Hermann et al. 2011; Ware et al. 2011) provided excellent preservational conditions for fishes and other vertebrates (e.g. Tintori 1992) and complete specimens could still be concealed in Dienerian strata of other localities that have not yet been specifically explored for such fossils (see e.g. Brinkmann et al. 2010; Ware et al. 2011). Evidently, the study of new fish faunas is vital for the advancement of palaeoichthyology and new Early Triassic assemblages can provide further insight into the evolutionary dynamics of fishes in the aftermath of the end-Permian mass extinction, a time of major osteichthyan radiation (Cavin et al. 2013; Romano et al. 2014a; Scheyer et al. 2014; Tintori et al. 2014).

**Acknowledgments** We greatly appreciate discussions with Ilja Kogan (Department of Palaeontology, Geological Institute, TU Bergakademie Freiberg, Germany), Piotr and Roksana Skrzycki (Krakow, Poland), as well as Thodoris Argyriou, Richard Hofmann, and Michael Hautmann (all PIMUZ) during preparation of the manuscript. Gaël Clément and Monette Véran (both MNHN.F) are thanked for their hospitality and help during visit of the Madagascar collection at the Paris museum in 2012. We thank Lui Unterrassner (Zürich) for assistance during field work in 2009. Rosi Roth (PIMUZ) is thanked for photographs and preparation of the cast of PIMUZ A/I 4360 and Ashley Latimer (PIMUZ) for correcting the English. We highly appreciate critical remarks by Adriana López-Arbarello (Bayerische Staatssammlung für Paläontologie, Munich, Germany) and a second, anonymous reviewer, which helped to improve the quality of this contribution. We deeply acknowledge support by the Swiss National Science Foundation (project numbers 120311/135075 and 144462 to W.B. and H.B., and 200021/135446 to H.B.).

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