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► **To cite this version:**

Donald Davesne, Jorge Mondéjar-Fernández, Vachik Hairapetian, Martin Rücklin, Jobst Wendt, et al.. A new large tetrapodomorph sarcopterygian from the Late Devonian of Iran. *Paläontologische Zeitschrift*, 2015, 89 (3), pp.661-667. 10.1007/s12542-015-0255-7 . hal-04228525

HAL Id: hal-04228525

<https://hal.science/hal-04228525>

Submitted on 6 Oct 2023

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A new large tetrapodomorph sarcopterygian from the Late Devonian of Iran

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Abstract Remains of a large sarcopterygian were collected in the Middle-Late Devonian Zarand Formation of Southeastern Iran. These remains consist of incomplete jaw bones of uncertain identification, preserved in a dense and heterogeneous rock matrix. The use of CT-scan microtomography and 3D visualization enabled to unravel their overall anatomy, as well as the microstructure of one tooth. This large tooth shows eusthenodont-type plicidentine, found only in Devonian tetrapodomorph sarcopterygians and more specifically suggesting affinities with the family Tristichopteridae. This discovery constitutes the first occurrence of a large tetrapodomorph in the Devonian of Iran and the Middle East.

Keywords Sarcopterygii, Tetrapodomorpha, Middle East, Palaeozoic, Gondwana, CT-scan, tooth microstructure, Tristichopteridae

Kurzfassung Die Reste eines großen Sarcopterygiers wurden in der mittel- bis oberdevonischen Zarand Formation des südöstlichen Iran gefunden. Diese Reste umfassen fragmentäre Kieferknochen ungewisser Identifikation in einer dichten und heterogenen Gesteinsmatrix. Mithilfe von MikroCT und 3D Visualisierung konnten die allgemeine Anatomie sowie die Mikrostruktur eines Zahnes rekonstruiert werden. Dieser große Zahn zeigt Plicidentin des eusthenodonten Typs, welches nur in devonischen tetrapodomorphen Sarcopterygiern vorkommt und auf eine Affinität zur Familie Tristichopteridae aufweist. Diese Entdeckung stellt das erste Auftreten eines großen Tetrapodomorphen im Devon des Irans und Mittleren Ostens dar.

Schlüsselwörter Sarcopterygii, Tetrapodomorpha, Mittlerer Osten, Paläozoikum, Gondwana, Computertomographie, Zahnmikrostruktur, Tristichopteridae

Introduction

Our understanding of the vertebrate faunas that populated the Northern coasts of Gondwana at the end of the Devonian remains largely elusive. Few Upper Devonian vertebrate-bearing localities are known from regions considered as part of Northern Gondwana. Among these, sites from Morocco, Afghanistan, Iraq and Iran (e.g., Blicek et al. 1982; Lelièvre et al. 1993; and references therein) have provided a diverse set of sarcopterygian (lobe-finned vertebrates) remains such as onychodontids, coelacanth and dipnomorphs, but tetrapodomorphs are poorly represented, except in the case of Morocco – from which several cranial remains have been assigned to an “*Eusthenopteron*-like” tristichopterid (Lehman 1977; Lelièvre and Janvier 1986) – and Iran (Janvier and Martin 1979).

In most palaeogeographical models of the Late Devonian (Wendt et al. 2002; Ruban et al. 2007), Central Iran is treated as a terrane located on the Northern margin of Gondwana (Fig. 1a). The Paleo-Tethys Ocean, evident in Iran by the presence of ophiolites (Wendt et al. 2002), separated this terrane from Euramerica. The Devonian of Iran has yielded a diverse vertebrate fauna (Golshani et al. 1973; Golshani and Janvier 1974; Hairapetian et al. 2000) comprising thelodonts, “acanthodians” (Hairapetian et al. 2006), chondrichthyans (Long and Hairapetian 2000; Hairapetian et al. 2008), “placoderms” (Schultze 1973; Janvier 1979; Lelièvre et al. 1981; Lelièvre et al. 1993), actinopterygians and sarcopterygians. The sarcopterygian fauna is composed of onychodontids, actinistians (Janvier and Martin 1979) and rhipidistians. Among rhipidistians, dipnomorphs are represented by dipnoan tooth plates and skull fragments and by a putative porolepiform cleithrum (Janvier and Martin, 1978). Tetrapodomorphs are only represented by isolated scales and a fragment of a cosmine-covered maxilla attributed to an undetermined “osteolepidid” (Janvier and Martin 1979).

Here we describe remains of a large tetrapodomorph from the Late Devonian of Southeastern Iran. Due to the heterogeneity of the surrounding siliciclastic matrix, a

preparation using conventional, mechanical techniques was not suitable. It was thus decided to study the specimen by means of X-ray tomographic techniques (CT-scan) and 3D-visualization. The scanning was performed at the AST-RX platform, MNHN, Paris (1965 transversal slices with an inter-slice spacing of 76,61 μm) and provided the basis for a digital reconstruction using the medical visualization software Mimics (version 14.0), which enabled to reconstruct structures that were hidden by the rocky matrix (Fig. 2b–d) and provided useful information on bone morphology and tooth microstructures (Fig. 3).

Institutional Abbreviations—MNHN, Muséum national d’Histoire naturelle, Paris, France

Systematic palaeontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

Tetrapodomorpha Ahlberg, 1991

cf. Tristichopteridae Cope, 1889 (Figs. 2–3)

Remarks—The presence of eusthenodont plicidentine in a Middle-Late Devonian sarcopterygian suggests an attribution of the specimen to the tetrapodomorph family Tristichopteridae (see below). However, despite the presence of an unusual combination of features, due to the incompleteness of the material we do not attempt to assign this specimen to any existing species or genus nor do we establish it as a new taxon.

Referred specimen—MNHN.F.URP 550, ensemble of jaw bones bearing teeth.

Locality and age—The specimen studied here, MNHN.F.URP 550, was collected during field work in 2001 by one of us (J.W.) in the Kerman region, Southeastern Iran (Fig. 1b). The specimen was discussed (although unnamed) by Wendt et al. (2002:138), first—by mistake from an earlier manuscript version—as an “acanthodian” and later corrected in the same

publication as a sarcopterygian (Wendt et al., 2002:153, fig. 12). The specimen (Fig. 2a) comes from the sandstones of the Gask syncline, Zarand Formation (Fig. 1b, c), which is considered to be Devonian in age (Wendt et al. 2002) due to the presence of Frasnian brachiopods in the upper part of the formation (Huckriede et al. 1962). According to Wendt et al. (2002:153), the Zarand Formation is probably Givetian to Frasnian in age, spanning the Middle-Late Devonian boundary. The sedimentological model proposes that the Zarand Formation corresponds either to a shallow marine, possibly estuarine platform, or to a sebkha deposition, alternating with two episodes of marine regression that would explain the time gaps above and below the Zarand Formation (Wendt et al. 2002).

Description

External morphology – Externally, MNHN.F.URP 550 appears as an elongate and narrow jaw bone association bearing teeth and measuring around 16 cm in length (Fig. 2a). The 3D reconstruction (Fig. 2b–d) shows that the specimen is divided in two parts separated by a transversal crack. This crack might match a transverse suture between two bones (hereafter called anterior and posterior bones). The overall labial curvature is sinusoidal. The labial surface lacks dermal ornamentation and, giving the rendering of the 3D model, appears smooth and unornamented. This indicates that it most probably corresponds to an internal surface of contact between bones rather than to an outer surface.

The bones appear as incompletely preserved. The anterior portion of the anterior bone is lacking and presents a longitudinal crack in its lingual margin, exposing the root of a large fang and its replacement fossa. The posterior portion of the posterior bone is also lacking and it appears that the bone has been fractured along its midline. In lingual view this fracture exposes a deep groove that could correspond to the lateral wall of a canal, possibly nervous,

running throughout the bone. The anterior and posterior bones are separated by a depression that probably fitted the fangs of the opposite jaw when the mouth of the animal was shut.

The anterior bone bears a fang pair in which the posterior fang is entirely preserved; it is conical, with no remarkable curvature, and slightly compressed medially in its distal region resulting in a carinated profile (Fig. 2c). A replacement fossa, or pit, lies just anterior to it. The posterior bone bears two fangs that are distally broken. They have roughly the same size and diameter, which suggests that they might have started growing at the same time. They are separated by a socket that presumably corresponds to a replacement fossa. This configuration can be defined as a fang triplet (two fangs and an intervening replacement fossa).

Laterally to the fang series the specimen bears a row of small teeth that spread along a vertical lamina, lining the fangs of both the anterior and posterior bones. There are six small teeth in the anterior bone and 13 in the posterior bone. The teeth series is incomplete in certain parts where teeth have been shed leaving one or two adjoining sockets with evidences of radial attachment bone at the base (Figs. 2c, 3a). The close proximity of this row of teeth with the series of large fangs, as well as the lack of a visible suture in tomography images (Fig. 3a), suggest that both the fangs and the small teeth were part of the same bone(s) and thus the small teeth can be described as marginal teeth.

In front of the anterior fang pair, two large teeth are visible, although in a shedding process. These teeth are larger and stouter than the other marginal teeth. A small, older tooth is being evicted by a larger, younger tooth protruding underneath. The small tooth left an impression in the posterior margin of the larger one, which suggests that both teeth might belong to the same or to closely adjacent replacement pits. An incompletely preserved concavity in the anterior most margin of the anterior bone might correspond to a socket housing the next tooth of the marginal row.

Tooth microstructure – The internal microstructure of the complete anterior fang was revealed by the CT-scan data (Fig. 3). It shows a folded structure of the dentine (i.e., plicidentine).

The superficial orthodentine is folded with primary and secondary bends (Fig. 3a–b). The folds are complex and subdivided in secondary folds towards the surface of the tooth (Fig. 3b). In the basal part of the tooth the bone of attachment extends between the dentine folds (Fig. 3c). In the centre there is a wide pulp cavity filled with matrix (in black), whereas in higher sections (Fig. 3a–b) the pulp cavity is filled by osteodentine, appearing less dense than the surrounding matrix. However, the osteodentine appears not to fill the pulp cavity completely, but is limited to its central part. This combination of structures matches the eusthenodont pattern, defined by Schultze (1969, 1970) in the fang of the genus *Eusthenodon*.

Discussion

The external and internal features displayed by MNHN.F.URP 550 and its virtual tomographic data are too partial and lack diagnostic characters that could undisputedly confirm whether the bones belong to an upper or a lower jaw. Given the state of the preservation and nature of the specimen, comprising two dermal jaw bones, two interpretations are possible (Fig. 2):

- the specimen corresponds to an upper jaw. The anterior bone then would probably correspond to a portion of the dermopalatine bone, while the posterior bone would be the ectopterygoid.
- the specimen corresponds to a lower jaw. In this case, the two bones would be better interpreted as two successive coronoids.

Both interpretations will be taken into account for the forthcoming discussion.

External morphology – The anterior most portion of the specimen has proven difficult to interpret. There is no evidence of a choana, or of a lower jaw parasymphysial plate, but the anterior most portion of the bone complex is possibly lacking altogether. The enlarged anterior teeth, caught in a replacement process, are intriguing. They can correspond to a fang triplet on the dermopalatine/anterior coronoid. If the specimen is a lower jaw, a close resemblance can be signalled with the enlarged marginal teeth, anterior to the first coronoid, that are found in Gondwanan tetrapodomorphs such as *Gogonasus* (Long et al. 1997, fig. 38) and *Mandageria* (Johanson and Ahlberg 1997).

The occurrence of a marginal dentition in the lingual jaw bones is a variable feature in tetrapodomorphs. Marginal teeth are always present on the dermopalatine/ectopterygoid complex, except on the anterior portion of the dermopalatine in some Gondwanan tristichopterids such as *Mandageria* (Johanson and Ahlberg 1997). On the coronoids, marginal teeth are unambiguously present in *Eusthenopteron* (Jarvik 1944; Zupinš 2008), *Notorhizodon* (G. C. Young et al. 1992), *Langlieria* (Clément et al. 2009), *Heddleithys* (Snitting 2009), *Bruehnopteron* (Schultze and Reed 2012) and in “elpistostegalians” (Ahlberg and Clack 1998; Daeschler et al. 2006). On the other hand, they are absent in the tristichopterids *Cabonnichthys* (Ahlberg and Johanson 1997), *Eusthenodon* (Johanson 2004) and *Hyneria* (J. M.-F. pers. obs.).

The depression that separates anterior and posterior bones is reminiscent of the intercoronoid fossae, typical in the lower jaw of tetrapodomorphs (e.g. Ahlberg and Johanson 1997; Parfitt et al. 2014). In contrast, there is rarely a fossa separating the dermopalatine from the ectopterygoid.

The posterior bone bears only one fang triplet. There is classically only one fang pair or triplet on the middle coronoid and two on the posterior coronoid in tristichopterids (Ahlberg

and Johanson 1998). There are also two fang pairs/triplets on the ectopterygoids in tristichopterids – except *Tristichopterus* and *Spodichthys* (Snitting 2008). The latter configuration might contrast with our specimen if it is interpreted as an upper jaw, but the ectopterygoid could also be posteriorly broken, explaining the absence of a second fang pair.

All fangs preserved in MNHN.F.URP 550 are straight, as clearly seen in the completely preserved anteriormost fang, which also shows two carinae or cutting edges. This condition approaches that of tristichopterids in which the fangs are usually straight and show carinated margins, at least in the dermopalatine-ectopterygoid complex and in the lower jaw (Jarvik 1944).

Tooth microstructure – The CT-scan data revealed the presence of eusthenodont-type plicidentine in the large anterior fang of MNHN.F.URP 550 (Fig. 3). Plicidentine is present in different vertebrate taxa: extant lepisosteiforms and several other predatory actinopterygians (Meunier et al. 2014), most fossil non-tetrapod sarcopterygians (Schultze, 1969, 1970), most of the first tetrapods (colloquially known as “labyrinthodonts”), and several amniotes (Maxwell et al. 2011). Amongst Devonian vertebrates, plicidentine is found only in sarcopterygians, but not in onychodontids and actinistians (Vorobyeva 1977). The polyplocodont plicidentine is the most general one amongst sarcopterygians as demonstrated by its presence in the early dipnomorphs *Powichthys* and *Youngolepis* (Clément and Janvier 2004). The dendrodont plicidentine of porolepiforms, the eusthenodont plicidentine and the labyrinthodont plicidentine of *Panderichthys* and tetrapods are certainly derived forms of polyplocodont plicidentine (Schultze, 1970).

Eusthenodont plicidentine is exclusively found in Devonian tetrapodomorph sarcopterygians such as *Litoptychus* (Schultze 1969) and – most specifically – in the tristichopterids *Eusthenodon* (Schultze 1969), *Platycephalichthys* (Vorobyeva 1977), an

isolated tooth from Belgium, possibly belonging to the genus *Langlieria* (Clément 2002; Clément et al. 2009), and in the large Gondwanan tristichopterid *Edenopteron* (B. Young et al. 2013).

The reconstructed position of central Iran during the Middle-Late Devonian times is at the Northern margin of Gondwana (Wendt et al. 2002; Ruban et al. 2007). Given this palaeobiogeographic context, the only other coeval Gondwanan taxon showing a tooth microstructure similar to the one of our specimen is the tristichopterid *Edenopteron* from Australia (B. Young et al. 2013).

Conclusions

The highly incomplete nature of the specimen MNHN.F.URP 550 renders a detailed anatomical description difficult, and a precise systematic attribution nearly impossible. However, the overall morphology of the specimen – such as the presence of large fangs paralleled by smaller, marginal teeth – suggests that it corresponds to the remains of a tetrapodomorph sarcopterygian. More specifically, the tooth microstructure matches the eusthenodont pattern, suggesting an affinity with the Devonian family Tristichopteridae for the specimen. This identification would not be surprising in the context of the reconstructed localisation of Iran at this time: right between Eastern (Australia) and Western Gondwana (Morocco) tristichopterid-bearing localities.

Although further fieldwork might retrieve more complete sarcopterygian remains from the region that would help to confirm the systematic position of MNHN.F.URP 550, this discovery adds up possible tristichopterids to the already diverse fauna of the Zarand Formation. This discovery is also significant because all other Gondwanan tristichopterids were found either in the eastern part of the supercontinent (G. C. Young 2008; B. Young et al.

2013), or in North Africa (Lelièvre and Janvier 1986). It showcases the need of further research on the Devonian faunas of the Middle East, with potential implications on the comprehension of biogeography and biodiversity patterns at this time.

Acknowledgements The authors thank Arnaud Mazurier (Université de Poitiers) and the MNHN AST-RX platform ‘Accès Scientifique à la Tomographie à Rayons X’ (UMS 2700 ‘Outils et Méthodes de la Systématique Intégrative’ CNRS-MNHN) for access to CT-scanning facilities. Florent Goussard (MNHN) is warmly thanked for his support in 3D visualisation and software training. Philippe Loubry (CNRS-MNHN) took the photograph of Fig. 2a. Philippe Janvier (CNRS-MNHN), Per Ahlberg and Daniel Snitting (Uppsala University), Martin Brazeau (Imperial College, London), Zerina Johanson (Natural History Museum, London) and Jonathan Jeffery kindly provided helpful comments and discussions on jaw morphology. We warmly thank the editor Oliver Rauhut, as well as John Long and Hans-Peter Schultze for their thorough reviews of the manuscript. The specimen was discovered by J.W. during a fieldwork for the joint project initiated in 1995 by the Geological Survey of Iran (GSI), Tehran, and the Department of Geology of the University of Tübingen (Germany). We are indebted to the past and present directors of the GSI, Prof. Dr. M. Ahmadzadeh-Heravi and Dr. M. T. Korehie, and to Dr. M. Ghorashi (GSI Teheran) for their cooperation as well as the logistic and financial support of this project. Funding for the German counterparts was provided by the Deutsche Forschungsgemeinschaft (DFG, grant We 239/13-1-4). M. R. was supported by funds awarded to M. D. Brazeau from the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013) / ERC Grant Agreement number 311092. J. M.-F. was supported by ‘La Caixa’ Foundation (Spain). This work is a contribution to the TERRES project (n° ANR-2010-BLAN-607-0) of the French National Research Agency (ANR).

References

- Ahlberg, Per Erik, and Jennifer A. Clack. 1998. Lower jaws, lower tetrapods—a review based on the Devonian genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 89: 11–46.
- Ahlberg, Per Erik, and Zerina Johanson. 1997. Second tristichopterid (Sarcopterygii, Osteolepiformes) from the Upper Devonian of Canowindra, New South Wales, Australia, and phylogeny of the Tristichopteridae. *Journal of Vertebrate Paleontology* 17: 653–673.
- Ahlberg, Per Erik, and Zerina Johanson. 1998. Osteolepiforms and the ancestry of tetrapods. *Nature* 395: 792–794.
- Blieck, Alain, Philippe Janvier, Hervé Lelièvre, B. Mistiaen, and C. Montenat. 1982. Vertébrés du Dévonien supérieur d’Afghanistan. *Bulletin du Muséum national d’Histoire naturelle, Paris* 4C: 3–19.
- Clément, Gaël. 2002. Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the Late Famennian Evieux Formation of Belgium. *Palaeontology* 45: 577–593.
- Clément, Gaël, and Philippe Janvier. 2004. *Powichthys spitsbergensis* sp. nov., a new member of the Dipnomorpha (Sarcopterygii, lobe-finned fishes) from the Lower Devonian of Spitsbergen, with remarks on basal dipnomorph anatomy. *Fossils and Strata* 50: 92–112.
- Clément, Gaël, Daniel Snitting, and Per Erik Ahlberg. 2009. A new tristichopterid (Sarcopterygii, Tetrapodomorpha) from the Upper Famennian Evieux Formation (Upper Devonian) of Belgium. *Palaeontology* 52: 823–836.
- Daeschler, Edward B., Neil H. Shubin, and Farish A. Jenkins. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440: 757–763.
- Golshani, Farrokh, and Philippe Janvier. 1974. Some aspects of the fish fauna in the late Devonian of Iran. *Geological Survey of Iran Report* 31: 49–54.
- Golshani, Farrokh, Philippe Janvier, Denise Brice, and Albert F. De Lapparent. 1973. Sur la paléogéographie et la paléobiologie du Dévonien dans la région de Kerman, en Iran. *Comptes rendus de l’Académie des sciences, Paris, Série D* 276: 697–700.
- Hairapetian, Vachik, Michał Ginter, and Mehdi Yazdi. 2008. Early Frasnian sharks from central Iran. *Acta Geologica Polonica* 58: 173–179.
- Hairapetian, Vachik, Juozas Valiukevičius, and Carole J. Burrow. 2006. Early Frasnian acanthodians from central Iran. *Acta Palaeontologica Polonica* 51: 499–520.

- Hairapetian, Vachik, Mehdi Yazdi, and John A. Long. 2000. Devonian vertebrate biostratigraphy of central Iran. *Records of the Western Australian Museum* supplement: 241–247.
- Huckriede, M., M. Kürsten, and H. Venzlaff. 1962. Zur Geologie des Gebietes zwischen Kerman und Sagand (Iran). *Beihefte zum Geologischen Jahrbuch* 51: 1–197.
- Janvier, Philippe. 1978. Les vertébrés dévoniens de l’Iran central I : Dipneustes. *Geobios* 11: 819–833.
- Janvier, Philippe. 1979. Les vertébrés dévoniens de l’Iran central III : Antiarches. *Geobios* 12: 605–608.
- Janvier, Philippe, and Michel Martin. 1979. Les vertébrés dévoniens de l’Iran central II - Coelacanthiformes, Struniiformes, Osteolepiformes. *Geobios* 12: 497–511.
- Jarvik, Erik. 1944. On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *Kungliga Svenska Vetenskapsakademiens Handlingar* 21: 1–48.
- Johanson, Zerina. 2004. Late Devonian sarcopterygian fishes from eastern Gondwana (Australia and Antarctica) and their importance in phylogeny and biogeography. In *Recent Advances in the Origin and Early Radiation of Vertebrates*, ed. Gloria Arratia, Mark V. H. Wilson, and Richard Cloutier, 287–308. Munich: Verlag Dr. Friedrich Pfeil.
- Johanson, Zerina, and Per Erik Ahlberg. 1997. A new tristichopterid (Osteolepiformes: Sarcopterygii) from the Mandagery Sandstone (Late Devonian, Famennian) near Canowindra, NSW, Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 88: 39–68.
- Lehman, Jean-Pierre. 1977. Sur la présence d’un Ostéolépiforme dans le Dévonien supérieur du Tafilalet. *Comptes rendus de l’Académie des sciences, Paris, Série D* 285: 151–153.
- Lelièvre, Hervé, and Philippe Janvier. 1986. L’Eusthénoptéridé (Osteichthyes, Sarcopterygii) du Famennien (Dévonien supérieur) du Tafilalet (Maroc) : nouvelle description. *Bulletin du Muséum national d’Histoire naturelle, Paris* 3C: 351–365.
- Lelièvre, Hervé, Philippe Janvier, and Alain Blicek. 1993. Silurian-Devonian vertebrate biostratigraphy of western Gondwana and related terranes (South America, Africa, Armorica-Bohemia, Middle East). In *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, ed. John A. Long, 139–173. London: Belhaven.
- Lelièvre, Hervé, Philippe Janvier, and Daniel Goujet. 1981. Les vertébrés dévoniens de l’Iran central IV : Arthroires et ptyctodontes. *Geobios* 14: 677–709.
- Long, John A., Richard E. Barwick, and Kenton S. W. Campbell. 1997. Osteology and functional morphology of the osteolepiform fish *Gogonassus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* Suppl. 53: 1–89.

- Long, John A., and Vachik Hairapetian. 2000. Famennian microvertebrates from the Dalmeh area, central Iran. *Records of the Western Australian Museum Suppl.* 58: 211–221.
- Maxwell, Erin E., Michael W. Caldwell, and Denis O. Lamoureux. 2011. The structure and phylogenetic distribution of amniote plicidentine. *Journal of Vertebrate Paleontology* 31: 553–561.
- Meunier, François J., Diogo Mayrinck, and Paulo M. Brito. 2014. Presence of plicidentine in the labial teeth of *Hoplías aimara* (Erythrinidae; Ostariophysii; Teleostei). *Acta Zoologica*. doi:10.1111/azo.12065.
- Parfitt, Matthew, Zerina Johanson, Sam Giles, and Matt Friedman. 2014. A large, anatomically primitive tristichopterid (Sarcopterygii: Tetrapodomorpha) from the Late Devonian (Frasnian) Alves Beds, Upper Old Red Sandstone, Moray, Scotland. *Scottish Journal of Geology* 50: 79–85.
- Ruban, Dmitry A., Moujahed I. Al-Husseini, and Yumiko Iwasaki. 2007. Review of Middle East Paleozoic plate tectonics. *GeoArabia* 12: 35–56.
- Schultze, Hans-Peter. 1969. Die Faltenzähne der Rhipidistiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung Lepisosteus. *Palaeontographia Italica* 65: 64–136.
- Schultze, Hans-Peter. 1970. Folded teeth and the monophyletic origin of tetrapods. *American Museum Novitates* 2408: 1–10.
- Schultze, Hans-Peter. 1973. Large Upper Devonian arthrodires from Iran. *Fieldiana: Geology* 23: 53–78.
- Schultze, Hans-Peter, and John W. Reed. 2012. A tristichopterid sarcopterygian fish from the upper Middle Devonian of Nevada. *Historical Biology* 24: 425–440.
- Snitting, Daniel. 2008. A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. *Journal of Vertebrate Paleontology* 28: 637–655.
- Snitting, Daniel. 2009. *Heddeleithys* - a new tristichopterid genus from the Dura Den Formation, Midland Valley, Scotland (Famennian, Late Devonian). *Acta Zoologica* 90: 273–284.
- Vorobyeva, Emilia J. 1977. Evolutionary modifications of the teeth structure in the Palaeozoic Crossopterygii. *Journal of the Paleontological Society of India* 20: 16–20.
- Wendt, Jobst, Bernd Kaufmann, Zdzislaw Belka, Noor Farsan, and Alireza Karimi Bavandpur. 2002. Devonian/Lower Carboniferous stratigraphy, facies patterns and palaeogeography of Iran. Part I. Southeastern Iran. *Acta Geologica Polonica* 52: 129–168.

- Young, Ben, Robert L. Dunstone, Timothy J. Senden, and Gavin C. Young. 2013. A gigantic sarcopterygian (tetrapodomorph lobe-finned fish) from the Upper Devonian of Gondwana (Eden, New South Wales, Australia). *PLoS ONE* 8: e53871.
- Young, Gavin C. 2008. Relationships of tristichopterids (osteolepiform lobe-finned fishes) from the Middle-Late Devonian of East Gondwana. *Alcheringa* 32: 321–336.
- Young, Gavin C., John A. Long, and Alex Ritchie. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum* Suppl. 14: 1–77.
- Zupiņš, Ivars. 2008. A new tristichopterid (Pisces, Sarcopterygii) from the Devonian of Latvia. *Proceedings of the Latvian Academy of Sciences. Section B* 62: 40–46.

Figure captions

Fig. 1 Geographical and stratigraphical context. **a** Palaeogeographical map of the Late Devonian, modified from Blakey (2014). White star illustrates the position of the Gask locality (Iran) in the Northern margin of Gondwana. **b** Map of Iran, showing the position of the Gask locality. **c** Stratigraphy of the Gask fossil site modified from Wendt et al. (2002: fig. 12)

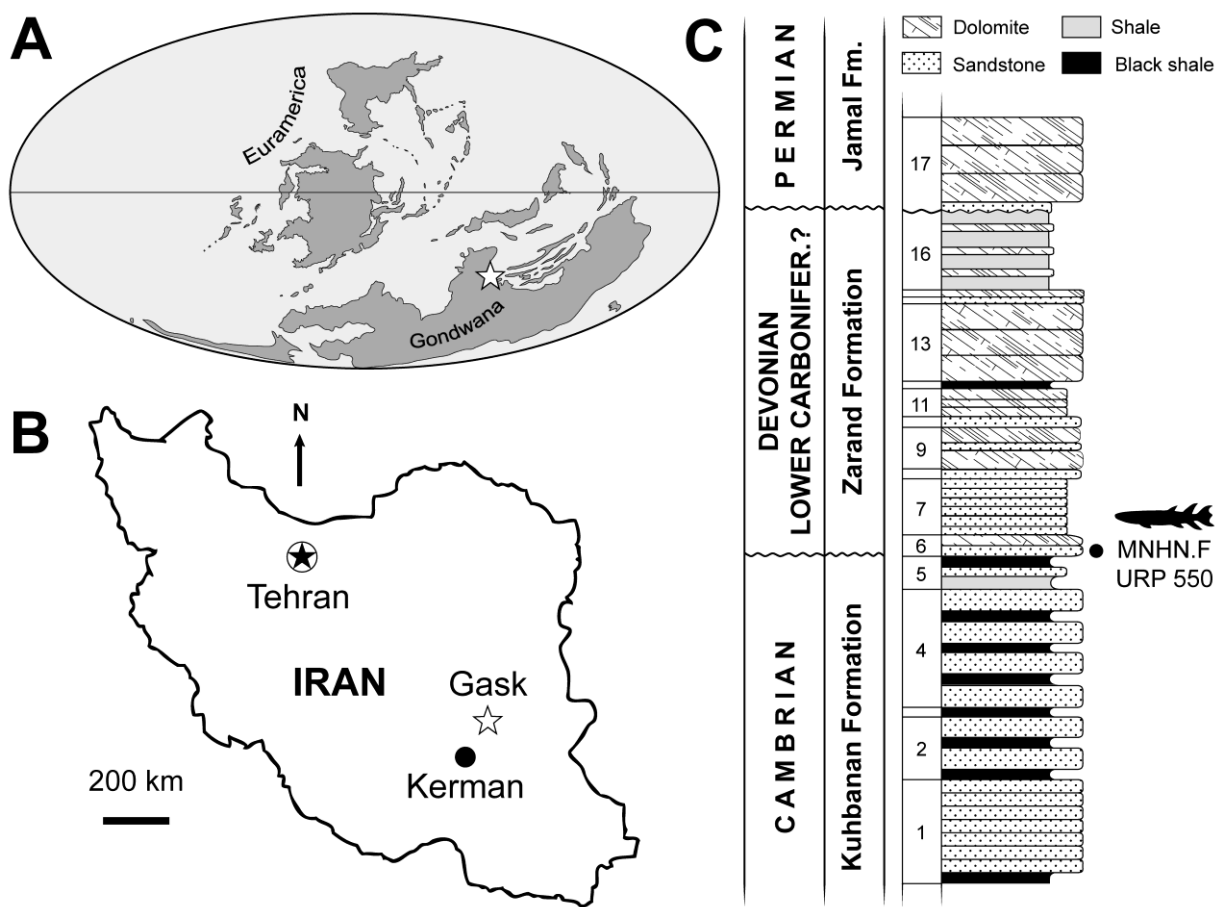


Fig. 2 cf. Tristichopteridae gen. et sp. indet., MNHN.F.URP 550. **a** Fossil specimen in lingual view, embedded in the rocky matrix. **b** 3D model in lingual view, **c** upper view, **d** labial view. Scale bar equals 1 cm. Arrow points anteriorly. *ant.f* anterior fang, *d/co1* anterior bone – dermopalatine or first coronoid, *e.m.t* enlarged marginal tooth, *ect/co2* posterior bone – ectopterygoid or middle coronoid, *m.t* marginal teeth, *m.t.s* marginal teeth socket, *r.f* replacement fossa

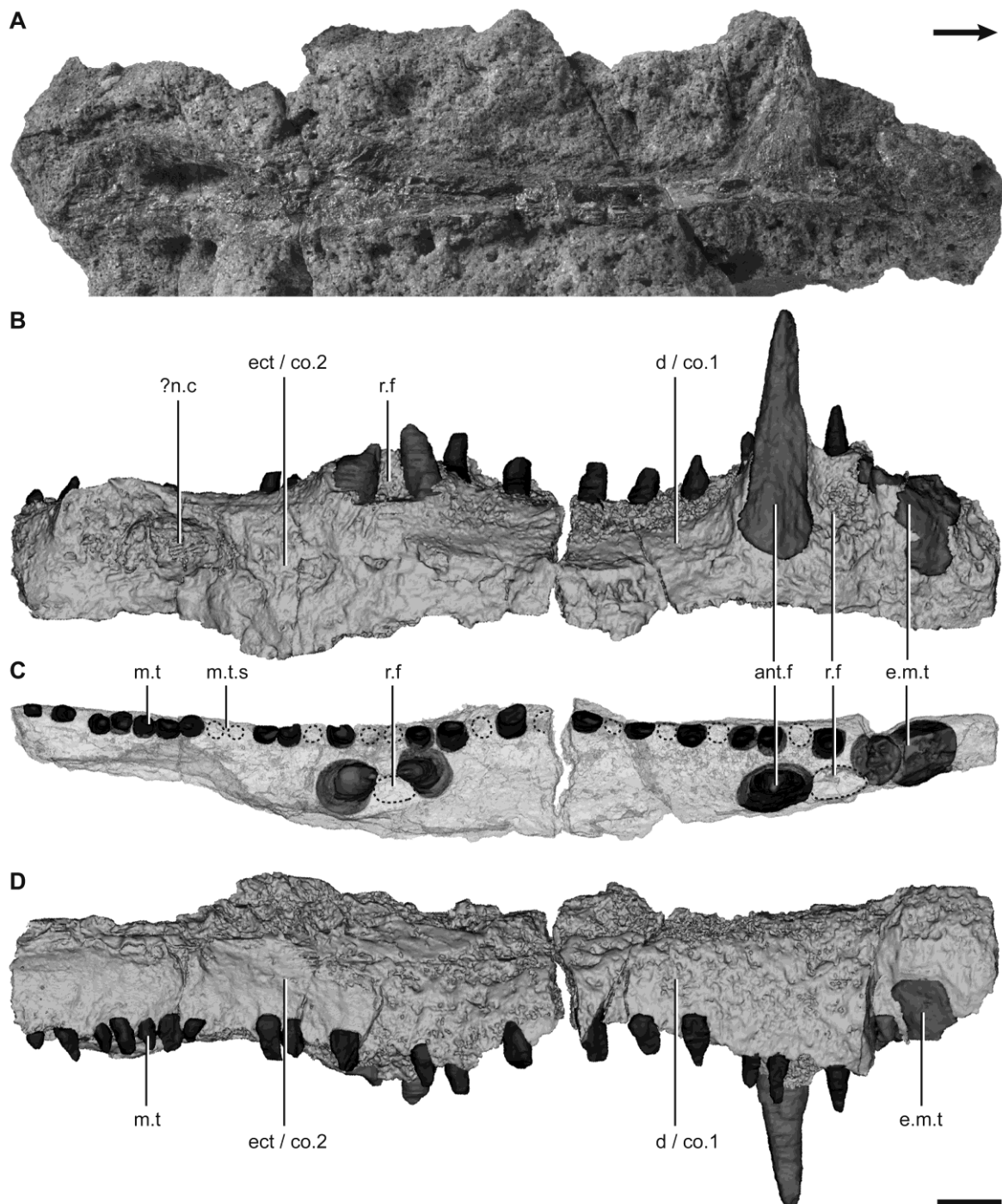


Fig. 3 cf. *Tristichopteridae* gen. et sp. indet., MNHN.F.URP 550, microtomographic virtual coronal section of the anterior fang, at different heights, from the tip (**a**), to the midheight (**b**), to the basal attachment of the fang (**c**). The color pattern is inverted. Scale bar equals 5 mm. *m.t* marginal teeth, *p.c* pulp cavity, *ort* orthodentine, *ost* osteodentine, *r.f* replacement fossa

