Devonian vertebrate biostratigraphy of central Iran

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Abstract - Middle to Late Devonian fish faunas are known from different parts of central Iran. These faunas comprise thelodonts, acanthodians, actinopterygians, chondrichthyans, sarcopterygians, thelodonts and placoderms which are predominantly found in marine deposits. This study surveys previous and current work done on the biostratigraphy of micro and macro vertebrates from ten localities. These localities are: Soĥ limestone beds, north of Esfahan (hemiansatus to Early and Middle varcus Zones); Ab-e-Morad, Chanaruh (Bidou), Hutk and Tangile-ab-Garm (Ravar) localities in Kerman Province (Early varcus Zone to Early Frasnian); Chahriseh area of northeastern Esfahan (probably Late Givetian or Early Frasnian, jamieae, crepida to rhomboidea and postera to expansa Zones); Howz-e-Dorah and Niaz sections at the Shotori Range, Tabas region (falsiovalis, linguiformis, crepida, expansa to Middle praesulcata Zones); and the Garigoon Mountains in the Dalmeh area, northeastern Ardekan (triangularis to crepida and postera to Early expansa Zones). Faunal assemblages with their age constraints from these localities are described throughout the Bahram, Shishtu and other equivalent Formations.

INTRODUCTION

Rieben (1935) first recorded Devonian vertebrates from northwestern Iran (Zonus area, Azerbaijan), but the first report on Devonian vertebrates made in central Iran (Kerman) was by Huckriede et al. (1962), near thirty years later. The fish palaeontology was first studied by Golshani et al. (1972) and continued with many joint French -Iranian projects (e.g. Blieck and Goujet 1978; Janvier and Martin 1978, 1979; Lelievre et al. 1981). In recent years other workers have collected and studied Middle to Late Devonian fish materials from various localities (Figure 1), especially the Late Devonian successions of central, western and eastern central Iran (e.g. Hairapetian and Gholamalian 1998; Long and Adhamian 2000; Long and Hairapetian 2000; Yazdi and Turner 2000). These studies have provided new data on micro and macrovertebrates from central Iran with well constrained ages, useful for international correlation, based on fishes, specially in former Gondwana lands (Figure 2). Here, we provide a summary of micro and macrovertebrate faunas with their ages in order to increase our knowledge of Devonian vertebrates from northern Gondwana (Figure 3). Unpublished reports have not been included in this survey. The Late Devonian zonal scheme of Ziegler and Sandberg (1984, 1990) and the Devonian correlation chart of Weddige (1996) are used herein.

THE VERTEBRATE FAUNAS

1. Kerman fauna

One of the most important vertebrate faunas in the Middle East comes from the southeastern part of central Iran, named by Lelievre *et al.* (1993), as the Kerman fauna. They gave a summary of the fauna of Tangile – ab – Garm, Hutk, Ab – e – Morad and Chanbaruh (Bidou) localities (Figure 1). The component taxa of these areas seems to be as a mixture of Baltican and Gondwanan forms, with a larger number of widespread taxa (Lelievre *et al.* 1993). Lelievre *et al.* (1993) gives the faunal list from these localities as:

Thelodonti:

Turinia hutkensis Blieck and Goujet 1978

Acanthodi:

Persacanthus kermanensis Janvier 1977

? Climatiida gen. et sp. indet.

?Acanthodida gen. et sp. indet.

Placodermi:

Golshanichthys asiatica Lelievre, Janvier and Goujet 1981

Holonema cf. H. radiatum Obruchev 1933

Eastmanosteus sp.

Plourdosteus sp.

Asterolepis sp.

? Byssacanthus sp.

? Aspidichthys sp.



Figure 1 Map of Iran showing major localities for Devonian vertebrates.

Ptyctodontida aff. *Ptyctodus* sp. Ptyctodontida aff. *Rhynchodus* sp. ? Petalichthyida gen. et sp. indet. Dinichthidae gen. et sp. indet.

Chondrichthyes: Ctenacanthus sp. 'Cladodus' sp. Protacrodus sp.

Actinopterygii: Moythmasia sp.

Sarcopterygii: Onychodontiformes *Onychodus firouzi* Janvier and Martin 1978 *Strunius rolandi* Gross 1956 Osteolepiformes Osteolepididae gen. et sp. indet.

Dipnoi:

Iranorhynchus seyedemanii Janvier and Martin 1978 *Rhinodipterus* sp.

- ? Dipterus sp.
- ? Chirodipterus sp.
- ? Rhynchodipteridae gen. et sp. indet.

Age constraints

Conodonts provide some age control on the Kerman fauna. According to the conodonts recovered by Huckriede *et al.* (1962), Kerman localities have age ranges from Late Givetian to Early Frasnian. Dastanpour (1990, 1996) examined some of the mentioned sections and additional ones on the basis of brachiopods and palynomorphs which he distinguished as Late Devonian (Frasnian). Useful fish elements for marine/ Devonian vertebrate biostratigraphy of central Iran

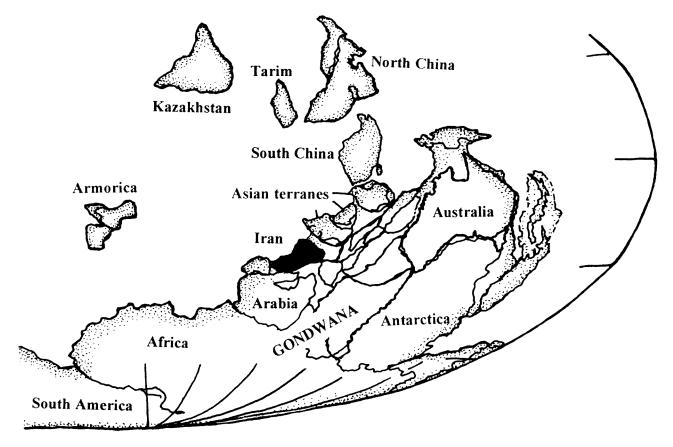


Figure 2 Palaeogeographic reconstruction for the Late Devonian (Famennian), showing the position of the Iran block (in black) with respect to the northern margin of Gondwana. After Li *et al.* (1993).

nonmarine correlation in Gondwanan lands are thelodont scales from Latest Silurian to early Late Devonian (Turner 1997). Blieck and Goujet (1978) suggested a late Early Devonian to Middle Devonian age for the thelodont *Turinia hutkensis* from limestone beds in Hutk section (part of the Bahram Formation). The lowermost limestone layer is attributed to the Givetian (Lower *varcus/disparilis* Zone) in Hutk area, based on conodonts (Wendt *et al.* 1997).

2. Soh fauna

The Middle Devonian (Givetian) successions in western central Iran are well exposed in the Soh area, northern Esfahan (Figure 1). This new locality has been yielded thelodonts, acanthodians and palaeoniscoids in a few limestone beds (Long and Adhamian 2000).

The identified microvertebrates from this area are as follows:

Thelodonti:

Turinia sp.

Acanthodi:

Cheiracanthoides cf. C. comptus Wells 1944

Actinopterygii:

Palaeoniscoidae gen. et sp. indet.

Age constraints

The upper Middle Devonian sediments of Soh was studied by Zahedi (1973), but further investigation in 1999 by Adhamian provided reliable age attributions. The age of the Soh fish bearing beds can be considered as Givetian stage, according to Adhamian (1999). The recovered shallow water conodonts from Soh section here indicate *hemiansatus* to early and middle *varcus* Zones (Adhamian 1999).

3. Chahriseh fauna

Palaeontological studies in the Chahriseh area were not reported on macro and micro vertebrates until 1998. Previous workers measured sections and mapped the area several times (e.g. Djafarian and Brice 1973; Shirani 1995 and Hamedani 1996). The probably Late Givetian, Frasnian and Famennian fish-bearing beds in this section are rich in thelodonts, placoderms, sarcopterygians, acanthodians and few shark microremains which were reported and studied by Hairapetian and Gholamalian (1998), and by Long and Harapetian (in press). Also recently, Golamalian et al. (2000), reported a considerable number of thelodont and acanthodian microremains. Based on these studies, the faunal list is as follows:

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Thelodonti: *Turinia hutkensis* Blieck and Goujet 1978 *Australolepis seddoni* Turner and Dring 1981

Acanthodi: cf. *Nostolepis gaujensis* Valiukevicius 1998

Placodermi:

Bothriolepis sp. Ptyctodontidae gen. et sp. indet. Arthrodira gen. et sp. Indet.

Actinopterygii:

Moythomasia durgaringa Gardiner and Bartram 1977

Chondrichthyes:

Thrinacodus ferox (Turner 1982) Phoebodus sp. (Hairapetian pers. obs.) Protacrodus sp. Stethacanthus sp. "Cladodus" sp.

Dipnoi:

Adololopas sp. Campbell and Barwick 1998 Chirodipterus sp. aff. C. australis Miles 1977 Dipteridae gen. et. sp. Indeterminate.

Crossopterygii:

Onychodus sp. Osteolepididae gen. et sp. indet.

Age constraints

The age of the thelodont assemblage from a calcareous sandstone bed can be attributed to Early Frasnian on the basis of conodonts and palynomorphs. But the presence of one incomplete doubtful element of the genus Bippenathus suggests an older age than Early Frasnian time for this horizon (Gholamalian et al. 2000). The presence of Australolepis seddoni associated with Turinia hutkensis is a most remarkable feature of. These new data on the stratigraphical position of T. hutkensis can be used a thelodont zone for world-wide as biostratigraphic correlation in the Early Frasnian (Gholamalian et al. 2000). The large and wellpreserved placoderm, crossopterygian and dipoan remains were found and studied by Long and Hairapetian (in prep). These all come from thin bedded fossiliferous limestone which can be considered a Middle Frasnian age (jamieae Zone), based on conodonts (Hairapetian and Gholamalian 1998). A microvertebrate fauna of Early and Middle Famennian age occurs in the upper part of the Chahriseh section, but has not yielded many specimens of fish microremains.

4. Tabas (Shotori Range) fauna

The Shotori Range in Tabas vicinity (eastern central Iran) comprises two main sections in Late Devonian age (Howz-e-Dorah and Niaz sections). These have been measured and studied, and dated by conodont biostratigraphy (M. Yazdi, pers. comm. 1999). The well-exposed Late Devonian sections in both localities have been yielded Frasnian and Famennian vertebrates, throughout the Bahram and Shistu Formations (e.g. Schultze 1973; Yazdi and Turner 2000). The fauna is:

Thelodonti:

Australolepis seddoni Turner and Dring 1981

Placodermi:

Aspidichthys cf. ingens Koenen 1883 Holonema cf. H. rugosum Claypole 1883 Eastmanosteus sp. Dunkleosteus sp.

Acanthodi:

'Acanthodes' sp. Chondrichthyes: Phoebodus rayi Ginter and Turner 1999 Protacrodus sp. Symmoriida gen. et sp. indet. ? Stethacanthus sp. ? "Cladodus" sp.

Sarcopterygii:

? Onychodus sp.

Age constraints

The thelodont Australolepis seddoni confirms an Early Frasnian age (falsiovalis Zone) in the base of the Bahram Formation (e.g. Turner 2000). Large Late Devonian arthrodires are abundant in the Tabas fauna which can be considered as a key bed in the linguiformis Zone, below the F/F boundary.

The phoebodont teeth occur with many conodont species/subspecies in the Shotori Range samples are of confirmed *crepdia* Zone (Early Famannian) through the Shishtu Formation (e.g. Yazdi and Turner 2000). A small microvertebrate fauna from Howz-e-Dorah samples in the age of *expansa* – Middle *praesulcata* Zone (Late Famennian) has been recognised by Yazdi (pers. comm.).

5. Dalmeh Fauna

The present of Famennian vertebrates is documented in northeastern Ardekan, Garigoon Mountains by Long and Hairapetian (2000). This section is slightly metamorphosed, but has yielded many well-preserved microvertebrates. The new locality is extremely rich in shark and palaeoniscoid remains. Based on Long and Hairapetian (2000), the faunal content is as follows:

Chondrichthyes:

Thrinacodus ferox (Turner 1982) *Phoebodus gothicus* Ginter 1990 *Stethacanthus* sp.

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Fauna	Occurrence (central Iran)	Stage	Dating	Formation
			E.expansa-postera	01.1.4
Dalmeh	central	Famennian	crepida-triangularis	Shishtu equivalent
Shotori Range	eastern	Famennian	M.praesulcata- expansa	Shishtu
			crepida	
		Frasnian	linguiformis	
			E. falisovalis	Bahram
Chariseh	western	Famennian	postera-expansa	-
			rhomboidea-crepida	Shishtu equivalent
		Frasnian	jamieae	
		Frasnian- ?Givetian	<i>falisovalis-</i> ?Late Givetian	Bahram equivalent
Kerman (Hukt, Tangil-e- ab-Garm, Ab-e-Morad, Chanaruh)	south- eastern	Frasnian	Early Frasnian	Bahram
		Givetian	<i>disparilis-</i> E. varcus	
Soh	western	Givetian	M. varcus- hemiansatus	Bahram equivalent

Figure 3 Chart showing the distribution of Middle-Late Devonian vertebrate faunas of central Iran.

Dalmehodus turnerae Long and Hairpetian 2000 Protacrodus sp.

Orodontidae gen. et sp. indet.

Actinopterygii:

Moythmasia durgaringa

Palaeoniscoidae gen. et. sp. indet.

A minor locality has also been found in Anjireh, near Yazd (Figure 1) which yielded Frasnian fish beds (e.g. Janvier 1980; Lelievre *et al.* 1993), but faunal content is unknown to the authors.

Age constraints

Hairapetian (2000) studied a section in northwestern Dalmeh area in which, on the basis of conodonts, a carbonate section was dated from Late Frasnian to Late Famennian. Famennian successions in the Dalmeh area have yielded many fish horizons associated with submarine basic volcanic rocks. The most important fish-bearing beds belong to *triangular's* – *crepida* and *postera* – Early *expansa* Zones, but very few vertebrate remains occur in the Middle Famennian.

Concluding Remarks

Many of the faunas are currently still being studied, and only provisional results are summarised herein. Devonian vertebrate studies of central Iran are providing new knowledge on the evolutionary, biogeographic and biostratigraphic patterns of former Gondwanan terranes. From this review, it is clear that most of the Givetian to Early Frasnian successions in central Iran (except the Dalmeh section) have yielded thelodont taxa. The thelodont scales are recognised as an important taxa for biostratigraphy (Turner 1997) that can be used for correlation of Middle and early Late Devonian marine/nonmarine sections in most of Central Iran. The phoebodont-based zonation chart of Ginter and Ivanov (1995) is useful for biostratigraphy in the Late Devonian (especially Famennian) of central Iran. Finally, the macrovertebrate faunas will also prove to be valuable for biostratigraphy once detailed studies of them have been completed.

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REFERENCES

- Adhamian, A. (1999). Biostratigraphy of the Middle Devonian rocks in the Soh area (North of Esfahan, Iran), based on conodonts. University of Esfahan, Iran, unpublished M.Sc. thesis, 96 pages.
- Bartram, A.W. (1981). Late Devonian fishes from Central Iran, Part II: Actinopterygii. Geological Survey of Iran, Reports 49: 165–171.
- Blieck, A. and Goujet, D. (1978). A propos de nouveau matériel de Thelodontes (Vertèbres, Agnathes) d' Iran et de Thaïlande: aperçu sur la répartition géographique et stratigraphiques des Agnathes des "régions gondwaniennes" au Paléozoïque moyen. Annales de la Société géologique du Nord. Lille 97: 363– 372.
- Blieck, A., Golshani, F., Goujet, D., Hamdi, A., Janvier, P., Mark-kurik, E. and Martin, M. (1980). A new vertebrate locality in the Eifelian of the Khush-Yeilagh Formation, Eastern Alborz, Iran. *Palaeovertebrata* 9: 133-154.
- Dashtban, H. (1966a). Late Devonian (Famennian) Dipterus tooth plate from the Geirud Formation in Central Alborz. Geosciences Scientific Quarterly Journal 19: 68–71.
- Dashtban, H. (1996b). Study of fossil fishes from Geirud Formation and recognition of the genus *Rhinodipterus*. *Geosciences Scientific Quarterly Journal* **20**: 48–57.
- Dashtban, H. (1996b). Investigation on the actinopterygian fish-scales of the Geirud Formation

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(Central Alborz). *Geosciences Scientific Quarterly Journal* 23, 24: 57–66.

- Dastanpour, M. (1990). The Devonian stratigraphy of Kerman, south east central Iran. University of Bristol, unpublished PhD thesis: 1–234.
- Dastanpour, M. (1996). The Devonian system in Iran: a review. *Geological Magazine* **133**: 159–170.
- Djafarian, M.A. and Brice, D. (1973). Biostratigraphie des brachiopodes dans le Famennian supérieur de la région d'Ispahan (Iran central). *Comptes rendus de'l Academie des sciences* **276**: 2125–2128.
- Gholamalian, H., Turner, S., Burrow, C.J. and Yazdi, M. (2000). Recovery of Late Devonian (Frasnian) microvertebrates and conodonts from the Chahriseh area, North East Esfahan, Iran. *In* G. Wilson and J. Laurie, (eds), Abstract book, Sydney meeting of AUSCOS-2, 3–7 July, 2000.
- Ginter, M. (1990). Late Famennian shark teeth from the Holy Cross Mts, Central Poland. Acta Geologica Polonica 40: 69-81.
- Ginter, M. (1999). Palaeozoic chrondricththyan microfossils as facies indicators. pp. 20–21. *In* R. Feist, J.A. Talent, and B. Orth (eds), Abstract Book, Errachidia Meeting of SDS-IGCP project 421, North Gondwanan Mid-Paleozoic bioevent/biogeography patterns in relation to crustal dynamics, April 23rd– May 1st, 1999.
- Ginter, M. and Ivanov, A. (1995). Middle/Late Devonian Phoebodont – based ichthyolith zonation. *Geobios* **19**: 351–355.
- Ginter, M. and Ivanov, A. (1992). Devonian phoebodont shark teeth. Acta Geologica Polonica 37: 55–75.
- Ginter, M. and Turner, S. (1999). The Early Famennian recovery of phoebodont sharks. *Acta Geologica Polonica* 49: 105–117.
- Golshani, F. and Janvier, P. (1974). Some aspects of the fish fauna in the Late Devonian seas of Iran. *Geological Survey of Iran Reports* **31**: 49–54.
- Golshani, F., Janvier, P., Brice, D., Corsin, P. and De Lapparent, A.F. (1972). Découverte d'une faune de poissons et de restes de végétaux dans le Dévonien supérieure de Bidu, en Iran central. *Comptes rendus de'l Academie des sciences* **275**: 2103–2106.
- Golshani, F., Janvier, P., Brice, D., and P., De Lapparent, A.F. (1973). Sur la paléogéographie et la paleobiologie du Dévonien dans la région de Kermân, en Iran. *Comptes rendus de'l Academie des sciences* 276: 697–700.
- Haghipour, A., Valeh, N., Pelissier, G. and Davoudzadeh, M. (1977). Explanatory text of the Ardekan quadrangle map, 1:250000. Geological Survey of Iran, Reports H8: 1-121.
- Hairapetian, V. (2000). Biostratigraphy of Late Devonian sediments in the Dalmeh area, northeastern Ardekan, based on conodonts and vertebrate-remains. University of Esfahan, Iran, unpublished M.Sc. thesis, 141 pages.
- Hairapetian, V. and Gholamalian, H. (1998). First report of Late Devonian fish remains in micro vertebrate fragments in the Chahriseh area, North East of Esfahan. In R. Mawson, J.A. Talen, G. Wilson and P. Cockle, (eds). Abstracts book, Esfahan meeting of UNESCO-IGCP Project 421, North Gondwanan mid-

Devonian vertebrate biostratigraphy of central Iran

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Palaeozoic bioevent/biogeography patterns in relation to crustal dynamics, 5–20 December 1998: 15.

- Hamedani, A. (1996). Neue biostratigraphische Daten aus dem Palozoikum (Devon-Karbon) von Isfahan, Iran. Neues Jahrbuch für Geologie und Pälaontologie, Monatshefte, **1996**: 309–323.
- Hampe, O. (1998). Remains of *Phoebodus* from the Upper Devonian (Middle Famennian) of Northwestern Iran (Chondrichthyes: Elasmobranchii). *In* R. Mawson, J.A. Talent, G. Wilson, and P. Cockle, (eds). Abstracts book, Esfahan meeting of UNESCO-IGCP Project 421, North Gondwanan mid-Palaeozoic bioevent/ biogeography patterns in relation to crustal dynamics, 5–20 December 1998: 16.
- Hamdi, B. and Janvier, P. (1981). Some conodonts and fish remains from the Lower Devonian (Lower part of the Khush-Yeilagh Formation), North East Shahrud. *Geological Survey of Iran, Reports* **49**: 195–212.
- Huckriede, R., Kursten, M. and Venzlaff, H. (1962). Zur Geologie des Gebietes zwischen Kerman and Sagand (Iran). *Beihefte des Geologischen Jahrbuch* **51**: 1–197.
- Janvier, P. (1974). Preliminary report on Late Devonian fishes from Central and Eastern Iran. *Geological Survey of Iran Reports* **31**: 5–47.
- Janvier, P. (1977). Les vertebres Dévoniens de L'Iran Central et de L'Afghanistan. *Mémoires de la Société Géologique du France*, 8: 277–289.
- Janvier, P. (1980). Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle. In A.L. Panchen (ed.), The Terrestrial environment and the original of the Land Vertebrates. Academic Press, London: 223–254.
- Janvier, P. and Martin, M. (1978). Les vertebres Dévoniens de L'Iran Central i: Dipneustes. *Geobios* 11: 819–833.
- Janvier, P. and Martin, M. (1979). Les vertebres Dévoniens de L'Iran Central II: Coelacanthiformes, Struniformes, Osteolepiformes. *Geobios* **12** : 497–511.
- Janvier, P. and Pan, J. (1982). Hyrcanaspis bliecki n. g. n. sp., a new primitive euantiarch (Antiarcha, Placodermi) from the Middle Devonian of northeastern Iran, with a discussion on antiarch phylogeny. Neues Jahrbuch für Geologie und Paläontologie. Ahandlungen **164**: 364-392.
- Lelievre, H., Janvier, P. and Goujet, D. (1981). Les vertebres Dévoniens de L'Iran Central. IV: Arthrodires et Ptyctodontes. *Geobios* **14**: 677–709.
- Lelievre, H., Janvier, P. and Blieck, A. (1993). Siluro-

Devonian vertebrate biostratigraphy of Western Gondwana and related terranes (South American, Africa, Armorica-Bohemia, Middle East). In J.A. Long (ed), Palaeozoic vertebrate Biostratigraphy and Biogeography. Belhaven press, London: 139–173.

- Li, Z-X., Powell, C. McA and Trench, A. (1993). Palaeozoic global reconstructions. In Palaeozoic Vertebrate Biostratigraphy and Biogeography, Long, J. (ed), Belhaven Press, London: 25–53.
- Long, J.A. and Adhamian, A. (2000). Givetian microvertebrate remains from the Soh area, northern Esfahan, Iran. *Records of the Western Australian Museum*, Supplement No. 58: 191–196.
- Long, J.A. and Hairapetian, V. (2000). Famennian microvertebrates from Dalmeh area, central Iran. *Records of the Western Australian Museum*, Supplement No. 58: 211–221.
- Rieben, H. (1935). Contribution a la geologie de l'Azerbaidjan persan. Bulletin de la Societe Narcothérapie de Sciences naturelle **59**: 19–144.
- Schultze, H.P. (1973). Large Upper Devonian arthrodires from Iran. *Feildiana Geology* 23: 53–78.
- Shirani, K. (1995). Palynostratigraphy and paleobiogeography of Upper Devonian sediments in the Chariseh area, Northeast of Esfahan. University of Teacher Education, Tehran, unpublished M.Sc. thesis: 1–190.
- Turner, S. (1982). Middle Palaeozoic Elasmobranch remains from Australia. Journal of Vertebrate Paleontology 2: 117-131.
- Turner, S. (1993). Palaeozoic micro vertebrate biostratigraphy of Eastern Gondwana. In J.A. Long (ed), Palaeozoic vertebrate Biostratigraphy and Biogeography. Belhaven press, London: 174–207.
- Turner, S. (1997). Sequence of Devonian thelodont scale assemblages in East Gondwana. *Geological Society of America, Special Paper* **321**: 295–315.
- Turner, S. and Janvier, P. (1979). Middle Devonian Thelodonti (Agnatha) from the Khush-Yeilagh Formation, North-East Iran. *Geobios* 12: 889–892.
- Yazdi, M. and Turner S. (2000). Late Devonian and Carboniferous vertebrates from the Shishtu and Sardar Formations of the Shotori Range, Iran. *Records* of the Western Australian Museum, Supplement No. 58: 223–240.

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