First occurrence of the Ichnogenus Selenichnites from the Middle Jurassic Strata of the Skoura Syncline (Middle Atlas, Morocco); Palaeoecological and palaeoenvironmental context

Article *in* Comptes Rendus Palevol · February 2016

DOI: 10.1016/j.crpv.2015.09.013

C. R. Palevol 15 (2016) 461–471

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

First occurrence of the Ichnogenus *Selenichnites* from the Middle Jurassic Strata of the Skoura Syncline (Middle Atlas, Morocco); Palaeoecological and palaeoenvironmental context

Première découverte de l'ichnogenre Selenichnites *du Jurassique moyen dans le synclinal de Skoura (Moyen Atlas, Maroc) ; contexte paléoécologique et paléoenvironnemental*

Mostafa Oukassou [a,*], André Charrière [b], Abdelouahed Lagnaoui [c,d], Stacey Gibb [e], André Michard [f], Omar Saddiqi [g]

[a] *Laboratory "DBSCG", Department of Geology, Faculty of Sciences Ben M'sik, Hassan II University of Casablanca, BP 7955, Sidi Othman, Casablanca, Morocco*
[b] *University Toulouse III, 26, rue Jean-Pierre-Chabrol, 34740 Vendargues, France*
[c] *Laboratory of Geodynamic and Geoamatics, Department of Geology, Faculty of Sciences, Chouaïb Doukkali University, BP 20, 24000 El Jadida, Morocco*
[d] *Laboratory of Stratigraphy of Oil and Gas Bearing Reservoirs, Department of Paleontology and Stratigraphy, Institute of Geology and Petroleum Technologies, Kazan (Volga Region) Federal University, Kremlyovskaya str. 18, 420008 Kazan, Russian Federation*
[e] *Department of Earth & Atmospheric Sciences, University of Alberta, Edmonton, AB T6G 2E3, Canada*
[f] *Em. Pr. University Paris-Sud, 10, rue des Jeûneurs, 75002 Paris, France*
[g] *Laboratory "Géosciences", Department of Geology, Faculty of Sciences Aïn Chock, Hassan II University of Casablanca, BP 5366, Maârif, Casablanca, Morocco*

A R T I C L E   I N F O

Article history:
Received 17 March 2015
Accepted after revision 27 October 2015
Available online 13 February 2016

Handled by Danièle Grosheny

Keywords:
Selenichnites
Limulids
Subtidal palaeoenvironment
Middle Jurassic
Skoura
Middle Atlas

Mots clés :
Selenichnites

A B S T R A C T

Mesozoic strata of North Africa yield the first occurrence of the ichnogenus *Selenichnites*. The trace fossils occur on the top surface of a sandy carbonate deposit in the axis of a Middle Atlas syncline (Skoura Syncline, NE Morocco). The ichnofossil-bearing horizon belongs to the Late Bajocian–Early Bathonian Ich Timellaline/Bou Akrabene Formation. The trace fossils are crescent-shaped and the best preserved exhibits a posterior central axial impression (possible telson tail impression). They are interpreted as feeding burrows (fodinichnia) or hiding depressions of Xiphosurids or Limulids (horseshoe crabs) on a sandy carbonate substrate beneath a veneer of muddy deposits. The sedimentological character suggests a relatively protected shallow water subtidal palaeoenvironment preceding the Bathonian regression of the Atlas domain. This discovery provides the first evidence of xiphosurans or xiphosuran-like organisms inhabiting the southern shores of the Tethys in the Middle Jurassic.

R É S U M É

Des traces d'invertébrés, attribuées à l'ichnogenre *Selenichnites*, ont été découvertes dans les couches d'âge Bajocien supérieur–Bathonien inférieur (formation d'Ich Timellaline/Bou

* Corresponding author.
E-mail addresses: mostafa.oukassou@gmail.com, mostafa.oukassou@univh2m.ma (M. Oukassou).

http://dx.doi.org/10.1016/j.crpv.2015.09.013

Limulidés
Environnement littoral
Jurassique moyen
Skoura
Moyen Atlas

Akrabène) du synclinal de Skoura, dans le Moyen Atlas marocain. Conservées sur une dalle gréso-calcaire subhorizontale, ces traces montrent des formes en croissant ou fer à cheval avec, dans le spécimen le mieux conservé, une empreinte arrière selon l'axe médian (trace du telson caudal). Elles sont interprétées comme des traces d'enfouissement (fodinichnia) de Xiphosures (= Limules) cherchant leur nourriture sur le fond sablo-carbonaté ou sous un voile de vase le recouvrant. Les caractères sédimentologiques indiquent des dépôts subtidaux dans une zone peu profonde relativement abritée. Ces paléoenvironnements littoraux précèdent la régression bathonienne du domaine atlasique. Cette découverte permet d'établir la présence de Xiphosuridés sur les rivages sud de la Téthys dès le Jurassique moyen.

1. Introduction

Limulids (horseshoe crabs) are marine arthropods classified in the class Merostomata Woodward, 1866, subclass: Xiphosura Latreille, 1802 and order: Xiphosurida Latreille, 1802. The record of Limulids comprises the Early Cambrian, Ordovician and Devonian (Richter and Richter, 1929; Rudkin et al., 2008), and Triassic, when these organisms appear to have the highest diversity (Moore et al., 2007). The Devonian horseshoe crab morphotypes are the most similar to modern forms, hence, the limulids are considered "living fossils" (Barthel, 1974; Fischer, 1984; Gaillard, 2011). The ichnological record shows different behaviors of ancient limulids through time and they are, typically, assigned to four ichnogenera: *Paramphibius* Willard, 1935 (repichnia–digitate walking imprints), *Limulicubichnus* Miller, 1982 (cubichnia or resting traces), *Selenichnites* (domichnia or burrowing activity) (Romano and Whyte, 1990), a substitution for the junior homonym *Selenichnus* Romano and Whyte, 1987, and *Kouphichnium* Nopsca, 1923 (repichnia or very regular locomotion). *Kouphichnium* trackways are mainly reported from the Late Palaeozoic (Chisholm, 1985; Conti et al., 1991; Eagar et al., 1985; Gaillard, 2011; Hardy, 1970; Lucas and Lerner, 2005; Miller, 1982; Minter and Braddy, 2009; Willard, 1935), the Triassic (Bi et al., 1995; Caster, 1938, 1944; Linck, 1949; Nielsen, 1949; Wang, 1993), the Jurassic (Barthel, 1974; Barthel et al., 1990; Caster, 1941; Groiss, 1975; Harris and Lacovara, 2004; Kolb, 1963; Oppel, 1862; Peyer et al., 2014; Peyre de Fabregues and Allain, 2013; Romano and Whyte, 1987, 2003; Schweigert, 1998; Schweigert and Dietl, 2002; Viohl, 1998), and the Paleogene (Oishi et al., 1993; Xing et al., 2012).

Selenichnites is among the most stratigraphically and geographically widespread trace fossil of fossil limulid-like organisms: *S. tesiltus* Gibb et al., 2011 (Cambrian of Morocco); *S. scagliai* Poiré and Del Valle, 1996 (Cambrian/Ordovician of Argentina); *S. antarcticus* Weber and Braddy, 2004 (?Early Ordovician of Antarctica); *S. cordoformis* Fischer, 1978 (Ordovician of Colorado); *S. langridgei* Trewin and McNamara, 1995 (?Late Silurian of Western Australia); *Selenichnites* isp. Draganits et al., 2001 (Early Devonian of northern India); *Selenichnites* isp. Morrissey and Braddy, 2004 (Early Devonian of Southwest Wales); *Selenichnites* isp. Lucas and Lerner, 2005 (Early Pennsylvanian of Alabama); *S. rossendalensis* Hardy, 1970 (Carboniferous of the UK); *S. bradfordensis* Chisholm, 1985 (Carboniferous of the UK); *Selenichnites* isp. Wang, 1993 (Upper Triassic of the UK) and *S. hundalensis* Romano and Whyte, 1987 (Jurassic of the UK).

The record of the ichnotaxon *Selenichnites* from North Africa is sparse in comparison to the numerous occurrences in North and South America, Australia and Europe. Gibb et al. (2011) described a new ichnospecies assigned to *S. tesiltus* from the Middle Cambrian Azlag Formation of the Moroccan central Anti-Atlas. More recently, Riahi et al. (2014) published on *Selenichnites* isp. from the Oligocene–Miocene Numidian Formation of northern Tunisia.

In this paper, we describe trace fossils assigned to *Selenichnites*, from the Middle Jurassic of the Skoura Syncline (Middle Atlas, Morocco). This adds to the understanding of Mesozoic limulids entrancing for the specimens in the northern region of Africa, with forms that have mainly or exclusively been known from the northern regions of the Tethys and Atlantic oceans. Thus, they provide further evidence of the palaeogeographical distribution of Limulids and/or limulid-like organisms.

2. Geological and biostratigraphic setting

The Middle Atlas is a northeast-trending mountain range extending between the western-Central Moroccan Meseta in the west and the High Moulouya and High Plateaus in the east (Fig. 1A). The Middle Atlas belongs to the Atlas system of intracontinental belts erected through the Alpine inversion of the Triassic–Liassic rifts at the northern fringe of the African plate (Frizon de Lamotte et al., 2008). The belt is characterized by northeast-trending faults inherited from the major structures of the Variscan basement (Fig. 1B). The northern Middle Atlas Fault (NMAF) separates the faulted Tabular Middle Atlas in the NW from the Folded Middle Atlas in the SE (Choubert, 1956; Martin, 1973, 1981). The latter consists of narrow anticlinal ridges associated with longitudinal faults and extrusions of Triassic evaporites, which are separated by wide, open synclines (Colo, 1961). The synsedimentary activity of most of these faulted ridges during the Jurassic has been repeatedly demonstrated (Charrière, 1990; Duée et al., 1977; Fedan et al., 1989; Fedan, 1993; Laville and Fedan, 1989; Rhrib, 1997; Scheele, 1994).

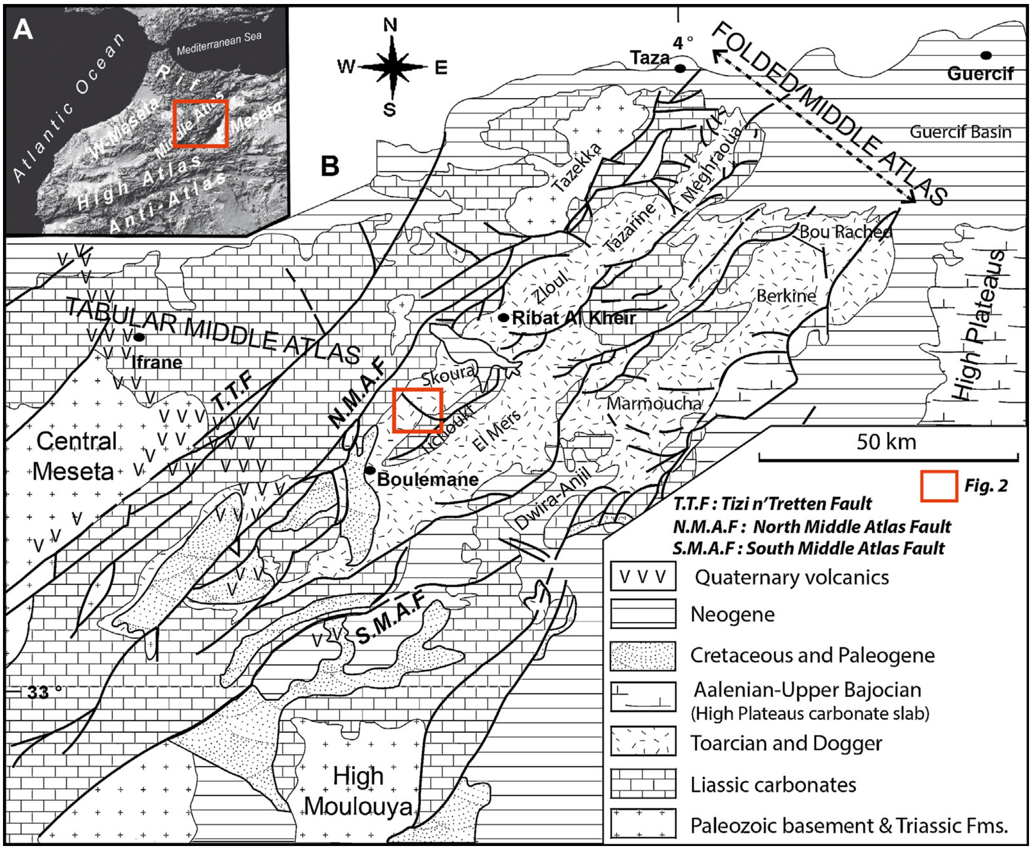

Fig. 1. A. Location of the Middle Atlas, B. Geological sketch map of the Middle Atlas and location of the study area (modified after Fedan et al., 1989).
Fig. 1. A. Localisation du Moyen Atlas. B. Carte géologique simplifiée du Moyen Atlas et localisation du secteur étudié (modifiée d'après Fedan et al., 1989).

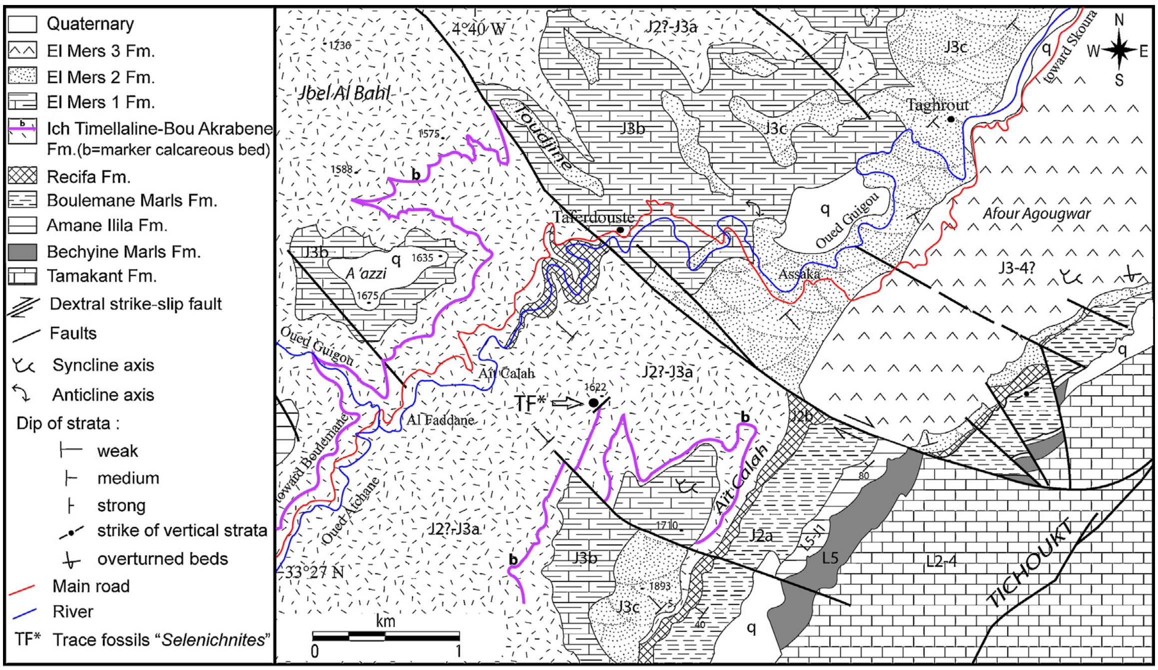

Fig. 2. Simplified geological map of the Skoura syncline (Middle Atlas, Morocco) after Charrière (1990), with additional field data.
Fig. 2. Carte géologique simplifiée du synclinal de Skoura (Moyen Atlas, Maroc), d'après Charrière (1990), avec de nouvelles données de terrain.

The Skoura syncline extends between the NMAF and the Jbel Tichoukt ridge (Fig. 1B) and exposes formations ranging from Lower Liassic limestones to late Middle Jurassic regressive deposits (Benshili, 1989; Charrière, 1992; Charrière et al., 1994; Dresnay, 1963, 1969, 1975; Fedan, 1993). The strata exhibit a gentle dip on the northwestern flank of the syncline whereas they are vertical or even overturned on the southeastern flank underlying the Jebel Tichouk transverse fault. The ichnofossil-bearing section is located at the axis of the syncline between two transverse faults (Fig. 2).

The biostratigraphy of the section can be summarized as follows, after Dresnay (1963) and Charrière (1989) (Figs. 2 and 3):

Recifa Formation Fm: This major morphogenic formation corresponds to the "Corniche Limestones", which include two thick sections of massif limestones. The uppermost unit is particularly rich in brachiopods and branching of corals. This peri-reefal platform is dated as Late Bajocian based upon the brachiopods and (scarce) ammonites.

Ich Timellaline/Bou Akrabene Fm: This formation mainly consists of oolitic and bioclastic limestone alternating with marly limestone. Thus far, it has yielded abundant and diverse marine fauna including small-branched corals, echinoids, bivalves and endemic brachiopods (Rhynchonellids, Terebratulides, Zeilleriids; see Colo, 1961). As a whole, this formation corresponds to an open sea, exhibiting relatively shallow water environments. Brachiopods and (rare) ammonoids from the lower part of the formation indicate a Late Bajocian age. In the middle of the section, next to the Taferdoust-Boulemane road, a fragment of *Parkinsonia* sp. was collected (Choubert and Faure-Muret, 1967), which confirms the Late Bajocian-Bathonian age (Fig. 3, point 1). These sequences represent the last stages of the Middle Atlas carbonate platform. The first subsequent detrital deposits occurred in the "Aïn Brel Sandstones", which marks the upper part of the formation (Fig. 3).

El Mers Group: It consists of three formations: ***i)*** The *El Mers 1 Fm* is characterized by its reddish purple marls indicating the first continental influences. It is renowned for its abundance of dinosaur remains (Dresnay, 1963; Lapparent, 1955; Marinheiro et al., 2014). *Cadomites bremeri*, an endemic ammonite (Fig. 3, point 2), indicates a Middle Bathonian age (Fedan, 1993). ***ii)*** The *El Mers 2 Fm* unconformably overlies the *El Mers 1 Fm* and displays internal bed obliquities reflecting the synsedimentary deformation of the basin (Charrière, 1989, 1990; Dresnay, 1969; Fedan, 1993). It consists of alternating marl to sandstone deposits. The sequence consists of proximal platform marls and is capped by intertidal sandstones. The final sequence contains foraminifers, *Pseudocyclammina maynci* (Fig. 3, point 3), an index fossil of the Middle Bathonian-Callovian interval (Charrière, 1990). ***iii)*** The *El Mers 3 Fm* consists of evaporite deposits that represent the Latest Jurassic deposits prior to the Early Cretaceous transgression.

3. Material and substrate conditions

The data presented represents seven specimens of invertebrate ichnofossils from one locality (FSBM locality 1) discovered during fieldwork in 2014 by the senior

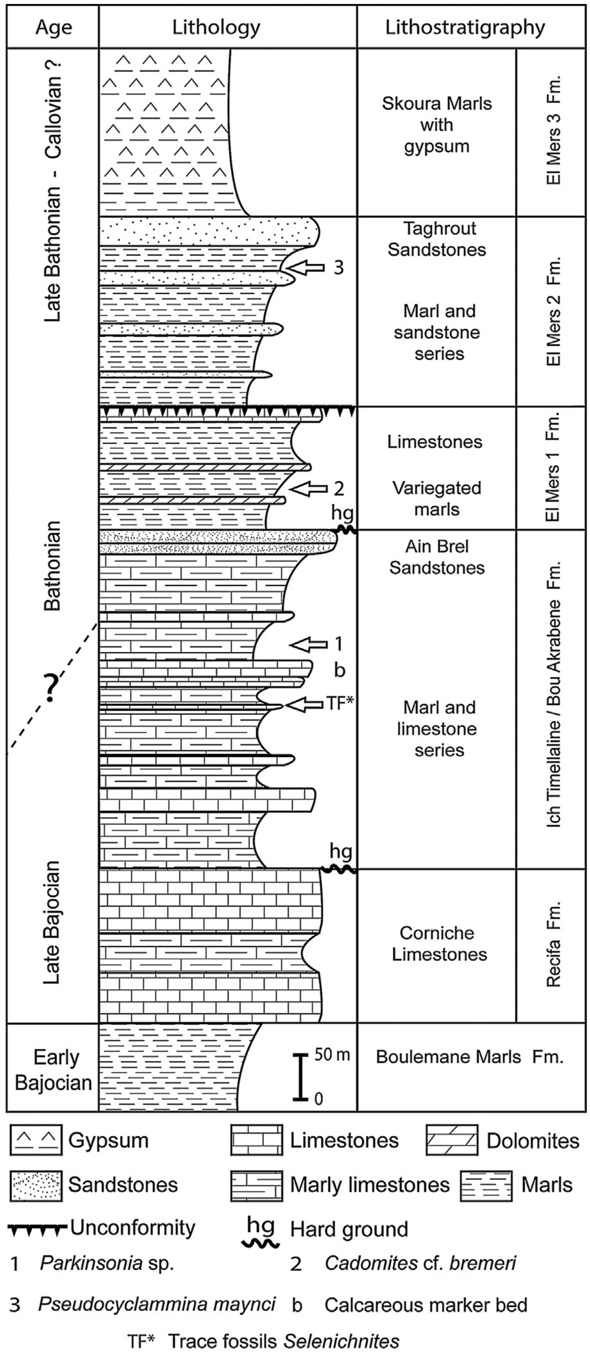

Fig. 3. Lithostratigraphic subdivision of the Middle Jurassic strata of the Skoura syncline at FSBM locality 1 (Middle Atlas, Morocco), with position of biostratigraphic markers and ichnofossil-bearing bed.

Fig. 3. Subdivision lithostratigraphique des couches du Jurassique moyen dans la localité FSBM 1 du synclinal de Skoura (Moyen Atlas, Maroc), avec localisation des repères biostratigraphiques et du banc contenant les ichnofossiles.

Table 1
Primary measurements of the described ichnofossils (in centimetres). *l*: length of trace; *w*: width of trace; *l/w*: length to width ratio of trace fossil.
Tableau 1
Principales mesures réalisées sur les ichnofossiles (en centimètres). *l* : longueur de trace ; *w* : largeur de trace ; *l/w* : rapport longueur et largeur de trace fossile.

FSBM locality number	Coordinates	IchnofossilsFSBM specimen number	*l*	*w*	*l/w*
FSBM Loc. 1	N33′27.528′	FSBM 1	50	25	2
		FSBM 2	70	38	1.84
		FSBM 3	20	14	1.4
		FSBM 4	–	25	–
Taferdouste	W4′39.170′	FSBM 5	–	8	–
		FSBM 6	–	8	–
		FSBM 7	–	26	–

author. The trace fossils described herein are located in the SE block of the Taferdouste dextral thrust, south of the mapped point 1622 (Fig. 2). The trace fossils are preserved on the upper bedding planes of a limestone bed, ten meters below the thick calcareous bed marker that forms approximately 2/3 of the Ich Timellaline/Bou Akrabene Fm (Figs. 2 and 3). The analyses are based upon outline drawings, photographs and measurements of the best-preserved specimens. Drawings were carried out on transparency film and digitalized with a vector-based drawing software. Photographs were taken in the field with natural light. Measurements in the field are documented in Table 1. The specimens are housed in the FSBM-Department of Geology, Faculty of Science Ben M'sik, Casablanca, Morocco, along with the locality data.

3.1. *Substrate conditions*

The ichnofossil-bearing horizon corresponds to a fill mesosequence comprising 20 m of marls and marly limestones overlain by 5 m of thickening-upwards limestone deposits (Fig. 4B and C). The overlying mesosequence correlates to the topographic point 1622 (Fig. 2) slightly above the ichnofossil-bearing horizon that forms a cornice about ten meters below. North of hill 1622, the horizon is fairly well exposed and consists of borings and a ferruginous encrustation defining a hard ground sequence at the top (Fig. 4G and H). South of hill 1622, next to a N20° trending fault, the top surface of the same horizon is widely exposed (approximately 20 m^2) and displays several trace fossils (GPS N 33′27.528′, W 4′39.170′; Figs. 5–7).

The studied horizon displays a relatively homogeneous microfacies of calcareous grainstone, with a microsparite cement and well-graded calcareous pellets and ooids ranging from 50 to 150 μm in size. Rare bipyramidal quartz grains are the nuclei for some ooids. A pellet-rich microfacies (pelmicrosparite) dominates in the lower part of the sequence, and becomes subordinate in the upper part with respect to the intraclast and bioclast-rich facies (intrabiomicrosparite). Ooids are common in the upper part of the beds and they most often have a micritic cortex (bahamite) encased by a single layer. The ichnofossil-bearing horizon contains different types of fragmented shells (bivalves, brachiopods and echinoderms), benthic foraminifers (miliolids, uniserial arenaces) and rare phosphatic fragments of bone or teeth (Fig. 4F). The associated lithophase is dominated by intraclasts and bahamites lacking spherical oolith laminations (alpha-type ooliths).

4. Systematic ichnology

Due to poor preservation, the majority of the described invertebrate trace fossils cannot be assigned to a specific ichnotaxon. Among the better-preserved material, we identify specimens that can be assigned at least to two morphotypes of the ichnogenus *Selenichnites* Romano and Whyte, 1990.

4.1. *Ichnospecies Selenichnites tesiltus*

Ichnogenus *Selenichnites* Romano and Whyte, 1987
Ichnospecies *Selenichnites tesiltus* Gibb, Chatterton and Pemberton, 2011 (Fig. 5)

Type ichnospecies: *S. hundalensis* (Romano and Whyte, 1987) from the Jurassic Scarborough Formation of Yorkshire, United Kingdom.

Referred material: FSBM 3, 4 and 7, isolated crescent-shaped trace fossils from FSBM locality 1. All specimens are preserved in a concave epirelief form.

Description: Irregularly ridged crescent-shaped concave epirelief trace fossils. Morphological dimensions up to 20 cm long, 14–26 cm wide (Table 1). The length to width ratio is labile and is not be a useful ichnotaxonomic parameter in this case (Table 1). Shallow to deep concavities (depth from 2 to 8 cm). Specimen FSBM 7 (Fig. 5), maximum width (≈26 cm) with shallow lunate impression. Depth of specimens varies from shallow to moderately deep, deepest (FSBM 4) measures 21 cm long, 16 cm wide and approximately 6 cm deep, typically slightly widen than long.

Discussion: The trace fossils described herein display the morphological features of the *S. tesiltus* Gibb et al., 2011, from the Middle Cambrian Azlag Formation of Zagora (Anti-Atlas, Morocco). The significant character strate is the horseshoe simple shape. The type ichnospecies, *S. hundalensis*, (Romano and Whyte, 1987) displays a relatively flat and subtriangular morphology between two crescent-shaped paired lobes. Hardy (1970) described *S. rossendalensis*as lunate impressions associated with appendages, or posteriorly projecting morphological imprint and defined lateral edges to anterior and lateral edge of trace fossil. The heart-shaped doublure and telson imprints of *S. cordiformis* (Fischer, 1978) are not observed in these specimens. *S. bradfordensis* also displays more

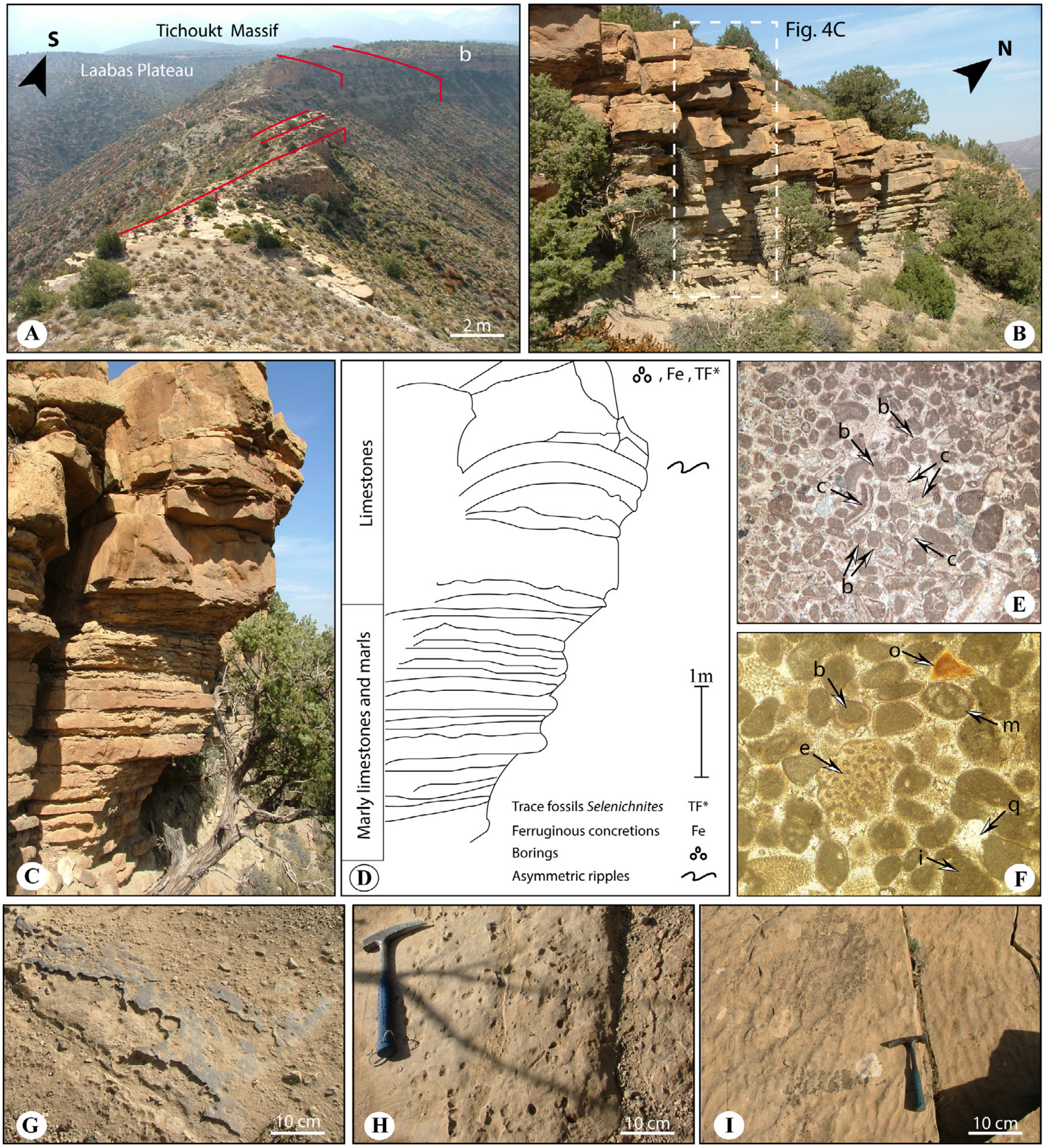

Fig. 4. Observations at FSBM Locality 1 (studied area) in the Ich Timellaline/Bou Akrabene Fm of the Skoura Syncline. A. View from hill 1662, looking southward; notice the calcareous marker bed "b" (Figs. 2 and 3) in the foreground. B–D. Strata-growing sequence at FSBM locality 1 (overview, detail, and sketch with position of the trace fossils, respectively). E–F. Thin sections of the substrate of the ichnofossil-bearing bed: (E) view of intrabiopelmicrosparitic grainstone microfacies and (F) zoom on biopelmicrosparitic grainstone microfacies with punctuated echinoderm plate in the center. (*b*) Bahamite; (*c*) undetermined shell fragment; (*e*) echinoderm test fragment; (*i*) carbonate intraclast; (*q*) rounded quartz grain; (*m*) miliolid foraminifer; (*o*) phosphatic fragments of bone or teeth. G–I. Detail views of bedding surface from the ichnofossil-bearing bed showing muddy deposits and hard ground, ferruginous concretions (G), borings (H) and current ripples (I).

Fig. 4. Situation dans la localité FSBM 1 (zone d'étude) de la formation d'Ich Timellaline/Bou Akrabene dans le synclinal de Skoura. A. Vue panoramique de la localité FSBM 1 ; remarquer la couche calcaire repère « b » (Fig. 2 et 3). B–D. Coupe de la formation d'Ich Timellaline/Bou Akrabene dans la localité FSBM 1, avec la position des traces fossiles dans le dessin de la section (D). E–F. Lames minces dans la couche substratum des ichnofossiles : (E) vue d'ensemble d'un microfaciès grainstone intrabiopelmicrosparite et (F) vue détaillée d'un microfaciès *grainstone* biopelmicrosparite avec une plaque d'échinoderme ponctué au centre. (*b*) : Bahamite ; (*c*) : fragment coquillier indéterminé (*e*) : fragment de test d'échinoderme ; (*i*) : intraclaste carbonaté ; (*q*) : grain de quartz émoussé ; (*m*) : foraminifère miliolide ; (*o*) : fragment phosphaté d'un os ou d'une dent. G–I. Surfaces contenant les ichnofossiles avec des incrustations de fer (G), des perforations (H) et des rides de courant (I).

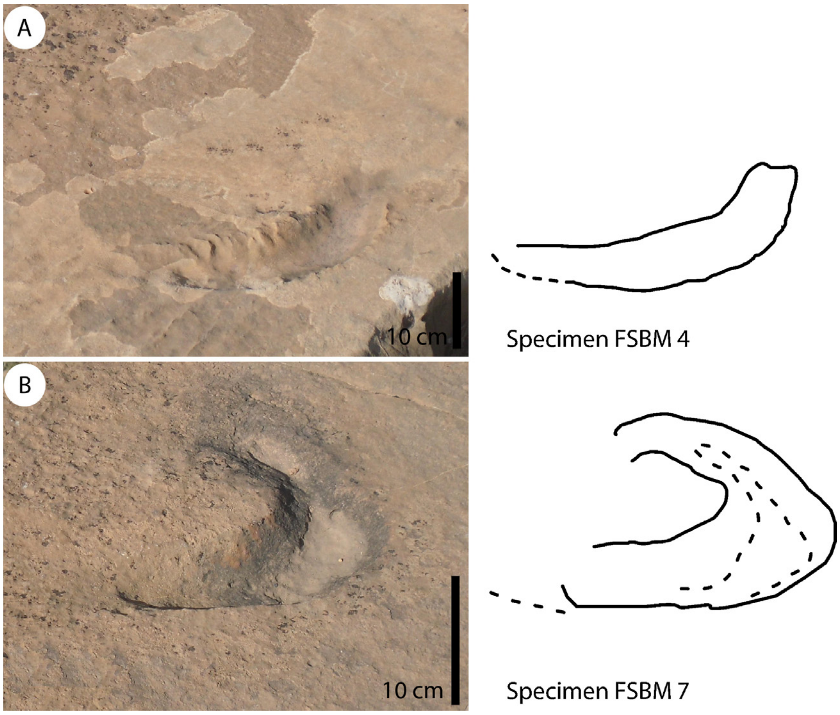

Fig. 5. The ichnospecies *Selenichnites tesiltus* Gibb, Chatterton and Pemberton, 2011 from the FSBM locality 1 with (A) specimen FSBM 4 and (B) specimen FSBM 7.

Fig. 5. L'ichnoespèce *Selenichnites tesiltus* Gibb, Chatterton et Pemberton, 2011 de la localité FSBM 1 avec (A) le spécimen FSBM 4 et (B) le spécimen FSBM 7.

complex morphological character states, such as transverse or chevron markings and a defined median furrow. *S. scagliai* (Poiré and Del Valle, 1996) was discussed and synonymised by Gibb et al. (2011) to the ichnogenus *Selenichnites*. SG, in Late 2011, had the opportunity to visit the collection in Argentina and now the synonomization is called into question. This assignment will be addressed in a future publication anon. Further ichnospecies identified within the ichnogenus *Selenichnites* are discussed in Gibb et al. (2011).

4.2. Selenichnites isp.

Ichnogenus *Selenichnites* (Romano and Whyte, 1987)
***Selenichnites* isp.** (Figs. 6 and 7)

Referred material: FSBM 1–2 and 5–6, isolated crescent-shaped invertebrate traces from FSBM locality; all specimens are preserved in concave epirelief.

Description: Small to medium size elongate crescent-shaped (more than half circle) with defined anterior and lateral edges, preserved in concave epirelief measuring 50–70 cm long and 8–38 cm width (Table 1). Ratio of length to width is less than 2 ($2 > l/w > 1.4$) for the specimens FSBM 1–3 (Table 1). Specimen FSBM 3 represents only the telson trace with very shallow crescentic form. Generally, all the specimens studied here correspond as well to horseshoe-like segments with locally elevated margins and arc of circle-like feature exceeding sometimes the half circle (specimens FSBM1-2; Fig. 6). The depth of the traces varies from 2 to 10 cm, with the specimen FSBM 2 as the deepest and larger trace. The last one shows the maximum length size ($\approx$70 cm) with deep lunate imprints and possible telson trace (Fig. 6B). Specimens, FSBM 1-2, could be subdivided in two parts, i.e., the lunate part in the front and the telson imprint behind. Furthermore, the same morphological characters are present in the specimens FSBM 5–6 (Fig. 7), which moderately incise the bedding surface with the smallest length and width, showing sometimes three shallow lobes (FSBM 5) and measuring 8 cm in width. Generally, the invertebrate traces described herein are slightly twice as long as large, except the specimens FSBM 5–6 that we could not estimate their true length. Telson trace mark is seemingly also present in specimen FSBM 5.

Discussion: Specimens FSBM 1–3, 5–6 show the features given in the diagnosis of the ichnogenus *Selenichnites* (Draganits et al., 2001; Fischer, 1978; Gibb et al., 2011; Hardy, 1970; Romano and Whyte, 1987, 2013; Wang, 1993). Romano and Whyte (1987) evoked in their diagnosis the presence or absence of prosomal imprint and scratch/telson traces. The lack of several morphological features similarly prevented several other authors from suggesting any definite ichnospecies, i.e., the *Selenichnites* isp. of Wang (1993), Thomson and Weber (1999), Draganits et al. (2001), Morrissey and Braddy (2004), Lucas and Lerner (2005), Romano and Whyte (2013), and Riahi et al. (2014). Assignment to a distinct ichnospecies is not given here, taking into account that the type species *S. bradfordensis* (Chisholm, 1985) is basically described as *Aulichnites?bradfordensis* with short furrow marks. We are aware that the Skoura material might even comprise

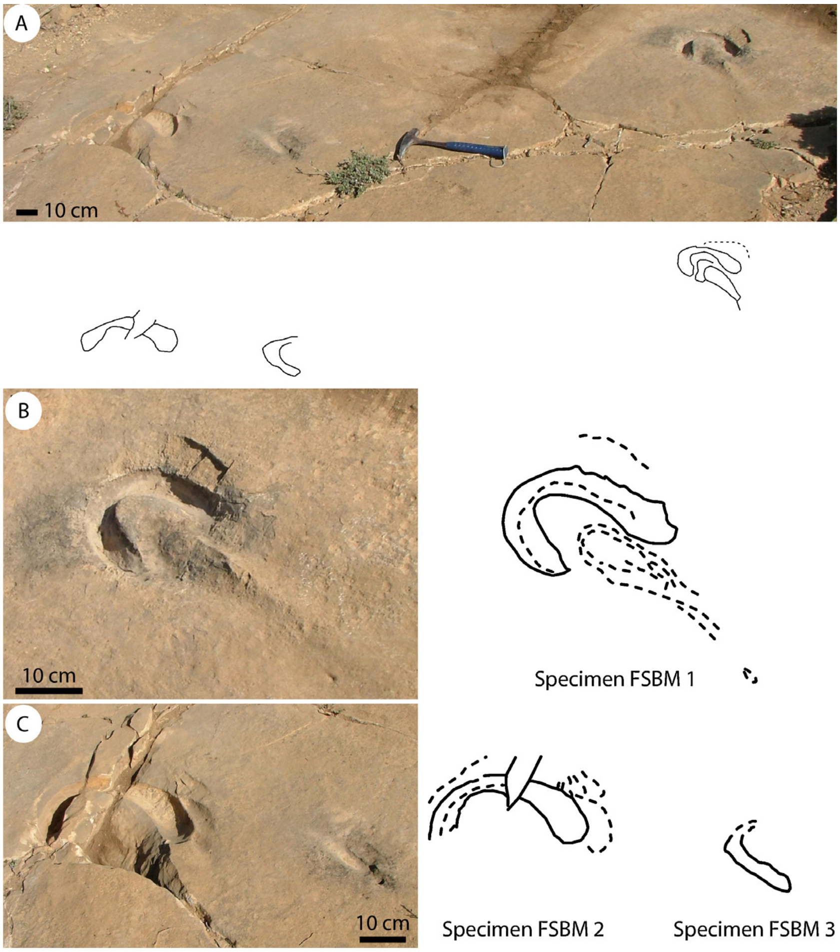

Fig. 6. The ichnotaxon *Selenichnites* isp. from the FSBM locality 1with (A) the ichnofossil-bearing surface, (B) Specimen FSBM 1 and (C) specimen FSBM 2. All figures assisted with interpretative sketches.

Fig. 6. L'ichnotaxon *Selenichnites* isp. de la localité FSBM 1 avec (A) surface contenant les ichnofossiles, (B) le spécimen FSBM 1 et (C) le spécimen FSBM 2. Toutes les figures sont accompagnées des dessins interprétatifs.

different ichnospecies. However, considering the fact that the ichnotaxonomy of *Selenichnites* (Romano and Whyte, 1987) is still problematic, we refrain from determining distinct ichnospecies or naming a new ichnotaxon. Therefore, we herein prefer an open nomenclature referring it to *Selenichnites* isp.

4.3. Potential tracemakers

According to the available research and publications, the possible tracemaker of *Selenichnites* is commonly attributed to Xiphosurids (Chisholm, 1985; Draganits et al., 2001; Fischer, 1978; Hardy, 1970; Lucas and Lerner, 2005; Riahi et al., 2014; Romano & Whyte, 1987, 1990, 2013; Wang, 1993) though Trewin and Mc Namara (1995) suggested that *S. langridgei* could be the behaviour of euthycarcinoids and Weber and Braddy (2004) attributed *S. antarcticus* to crustaceans. No body fossils are known from the Skoura syncline. Based on morphological character states of *Selenichnites* and the observed morphology, functional morphology and behaviours of modern limulids, the rounded prosoma and musculature to drive the prosoma into sandy substrate, we suggest limulids are the possible tracemakers for *Selenichnites*.

5. Palaeobiogeographic and palaeoecologic implications

5.1. Palaeoenvironmental and palaeogeographic conditions

The ichnofossil-bearing layer belongs to the Middle Jurassic "Gulf of Skoura" of the South Tethyan margin (Frizon de Lamotte et al., 2008). The combination of sedimentological data and microfacies analyses provides evidence that the deposition environment of the Ich Timellaline/Bou Akrabene Formation was a regressive coastal environment in a relatively warm and low-energy setting that was periodically open sea. The horizon is conformably overlain by marls that contain spines of sea urchins and fragments of tabular i.e. isolated corals, providing further confirmation of a warm fully marine environment.

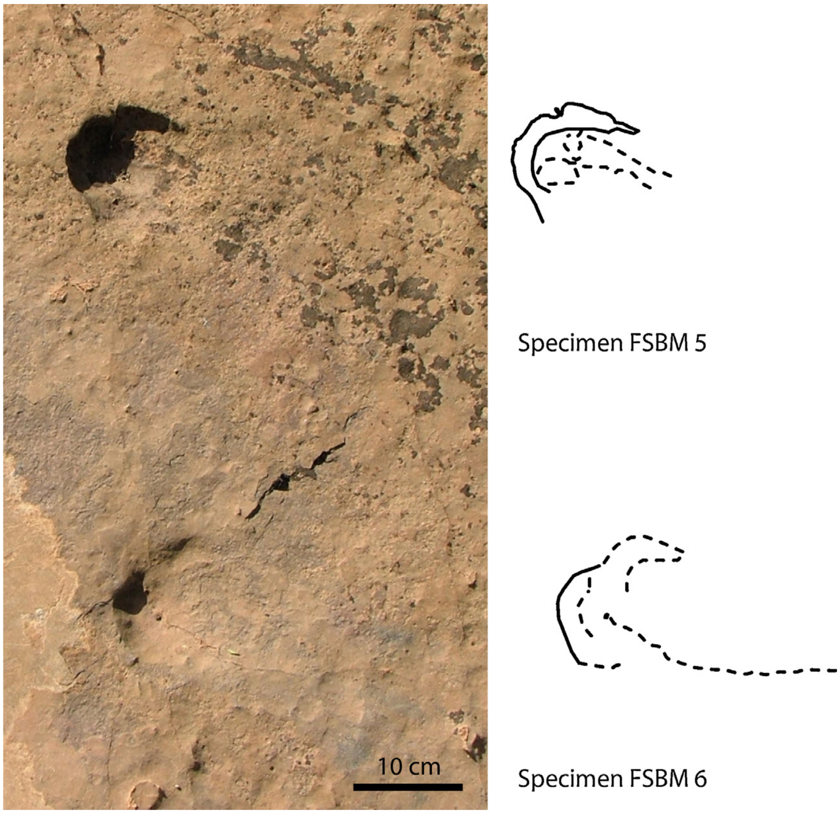

Fig. 7. The ichnotaxon *Selenichnites* isp. from the FSBM locality 1 showing the specimen FSBM 5–6 assisted with interpretative sketches.
Fig. 7. L'ichnotaxon *Selenichnites* isp. de la localité FSBM 1 montrant les spécimens FSBM 5–6 accompagnés des dessins interprétatifs.

Despite the variable lithology including pellets, intraclasts, bioclasts and ooids, the entire deposit is very well sorted at 50–150 μm. This type of limestone is almost exclusively derived from fine-grained, well sorted carbonate sands, which indicates regular and prolonged wave action apparently undisturbed by storms. The presence of bahamites also provides evidence that the Ich Timellaline/Bou Akrabene Formation formed in a protected environment.

The presence of borings suggests shallow water depth during depositional/early diagenetic processes, as these borings are supported by ferruginous concretions indicating the formation of a hard ground during a period of low sedimentation (Fig. 4G). We note the absence of current ripples on the ichnofossil-bearing surface, while the presence of sinuous ripples atop the two underlying beds indicates subtidal conditions (Fig. 4I). As concluded from sedimentological, palaeontological and palaeoichnological data, a warm humid climate in a shallow marine environment is inferred as the depositional environment of the ichnofossil-bearing layer.

5.2. Palaeobiogeographic interest

Xiphosurans are marine group of chelicerate arthropods, based on their supposed stem lineage. They are known from the Ordovician to the present day (Martin et al., 2015; Moore et al., 2007; Rudkin et al., 2008; Van Roy et al., 2010, 2015). Van Roy et al. (2010, 2015) and Garassino et al. (2008) reported undetermined xiphosurid specimens from the Early Ordovician and the Late Cretaceous respectively in Morocco. The record of Xiphosurid-like trace fossils from Africa is sparse in comparison to numerous occurrences on other continents with only rare limulid-like trackways from the Late Palaeozoic Great Karoo Basin (South Africa) assigned to the ichnogenus *Kouphichnium* (Anderson, 1975). Indeed, *Selenichnites* has only recently been recorded in North Africa from the Middle Cambrian strata of the Anti-Atlas (southern Morocco; Gibb et al., 2011) and from Oligocene–Miocene deposits in northern Tunisia (Riahi et al., 2014). New decapod assemblages were studied from the Late Cretaceous (Cenomanian–Turonian) of Gara Sbaa (Kem Kem region, Anti-Atlas, southeastern Morocco), including the first report of xiphosuran fossils in North Africa (Garassino et al., 2008). The trace fossils discussed in this paper broadens the geographical distribution of possible xiphosurans on the South Tethyan margin.

Selenichnites from the Anti-Atlas Middle Cambrian deposits (Morocco) are associated with the transgression of the Rheic Ocean on the West African Craton margin (Michard et al., 2008; Nance et al., 2012). Likewise, the Turonian xiphosurids of the Kem Kem region (Morocco) are associated with a global transgression that occurred on the northern African continent. Conversely, the Middle Atlas *Selenichnites* of Late Bajocian–Early Bathonian age correspond to the end of the Jurassic carbonate platform and the onset of the Middle Jurassic regression (El Mers Fm) prior to the complete emersion of the region (Charrière, 1992). In every case, *Selenichnites* is found in what is a shallow marine, relatively warm marine environment. Xiphosurid-like ichnofossils are well known in the northern part of the Tethys especially from Ordovician to the present day. However *Selenichnites* has been interpreted as a burrowing activity of horseshoe crab-like organisms searching for food such polychaete worms and/or soft-shelled molluscs that live within muddy sediments (Gibb et al., 2011; Romano and Whyte, 1987; Wang, 1993). Four limulid burrowing behaviours were proposed by Eldredge (1970) and Wang (1993) and the *Selenichnites* would consist of the beginning of the burrowing process.

6. Conclusion

We describe the first occurrence of trace fossils of possible limulids from the Middle Jurassic deposits of the Atlas domain (Skoura Syncline, Middle Atlas). These ichnofossils are assigned to *S. tesiltus* and *Selenichnites* isp., and represent the second occurrence of this ichnogenus in Morocco. The trace fossils can be inferred to be those of horseshoe crab tracemakers. According to the fossil and stratigraphic interpretations, their occurrence may be of great importance for the reconstruction of the ecosystems of the southern Tethys margin. The described trace fossils are also important for other reasons: they suggest subtidal palaeoenvironments with relatively warm water; the traces highlight the presence of possible xiphosurans in the Middle Atlas during the Middle Jurassic, just prior to major regression that caused the emergence of the Jurassic carbonate platform. Essentially, the above reported data underlines the significance of northwestern Africa for the reconstruction of littoral fauna behaviour during the Mesozoic. Moreover, the discovery of *Selenichnites* in the Middle Jurassic strata of the Skoura Syncline could be considered a palaeoecological predictor of the possible presence of body fossils in adjacent beds. Therefore, exploration of the Skoura Syncline should be continued and extended to other North African Jurassic deposits to refine it trace fossil and body fossil record.

Acknowledgments

The authors thank the Editor-in chief, Andrew K. Rindsberg and Davide Olivero for their constructive reviews.

References

Anderson, A.M., 1975. Limulid trackways in the Late Palaeozoic Ecca sediments and their palaeoenvironmental significance. S. Afr. J. Sci. 71, 249–251.

Barthel, K.W., 1974. *Limulus*: a living fossil: Horseshoe crabs aid interpretation of an Upper Jurassic environment (Solnhofen). Naturwissenschaften 61, 428–433.

Barthel, K.W., Swinburne, N.H.M., Conway Morris, S., 1990. Solnhofen study in Mesozoic palaeontology. Cambridge Univ. Press, Cambridge.

Benshili, Kh., 1989. Lias-Dogger du Moyen Atlas plissé (Maroc), sédimentologie, biostratigraphie et évolution paléogéographique. Doc. Lab. Géol., Lyon 106.

Bi, D.C., Guo, P.X., Qian, M.P., 1995. Discovery of limulid tracks from Qinglong Formation (Lower Triassic) in Nanling, Anhui. Acta Palaeontol. Sinica 34 (6), 714–721 (in Chinese, with English abstract).

Caster, K.E., 1938. A restudy of the tracks of *Paramphibius*. J. Paleontol. 12, 3–60.

Caster, K.E., 1941. Trails of *Limulus* and supposed vertebrates from the Solnhofen lithographic limestone. Pan-American Geol. 76, 241–258.

Caster, K.E., 1944. Limuloid trails from the Upper Triassic (Chinle) of the Petrified Forest National Monument, Arizona. Am. J. Sci. 242, 74–84.

Charrière, A., 1989. Carte géologique à 1/100 000. Feuille de Sefrou. Notes et Mém. Serv. géol. Maroc, 354.

Charrière, A., (Thèse d'État) 1990. Héritage hercynien et évolution géodynamique alpine d'une chaîne intracontinentale : le Moyen Atlas au SE de Fès (Maroc). Univ. Toulouse III.

Charrière, A., 1992. Discontinuités entre les « Couches rouges » du Jurassique moyen et du Crétacé inférieur dans le Moyen-Atlas (Maroc). C.R. Acad. Sci. Paris, Ser. II 315, 1389–1393.

Charrière, A., Dépêche, F., Feist, M., Grambast-Fessard, N., Jaffrezo, M., Peybernès, B., Ramalho, M., 1994. Microfaunes, microflores et paléoenvironnements successifs dans la Formation d'El Mers (Bathonien-? Callovien) du synclinal de Skoura (Moyen-Atlas, Maroc). Geobios 27 (2), 157–174.

Chisholm, J.I., 1985. Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of WestYorkshire. Palaeontology 28, 619–628.

Choubert, G., 1956. Carte géologique du Maroc, feuille de Rabat au 1/500 000. Notes Mem. Serv. Geol. Maroc, 70.

Choubert, G., Faure-Muret, A., 1967. Le Jurassique de la région d'El Mers-Skoura. Notes Mem. Serv. Geol. Maroc 200, 1–32.

Colo, G., 1961. Contribution à l'étude du Jurassique du Moyen Atlas septentrional. Notes Mem. Serv. Geol. Maroc 139.

Conti, M.A., Leonardi, G., Manni, R., Venturini, C., 1991. Limuloid tracks into the Meledis Fm. (Upper Carboniferous, Kasimovian) of the Carnic Alps. Giornale di Geologiaser 3a (53), 151–159.

Draganits, E., Braddy, S.J., Briggs, D.E.G., 2001. A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, northern India): Paleoenvironment and tracemaker behavior. Palaios 16, 126–147.

Dresnay, R., 1963. Données stratigraphiques complémentaires sur le Jurassique moyen des synclinaux d'El Mers et de Skoura (Moyen-Atlas, Maroc). Bull. Soc. geol. France 7 (6), 883–900.

Dresnay, R., 1969. Discussions stratigraphiques sur les conditions de gisements de bois fossiles mésozoïques du Maroc étudiés par Melles Y. Attims, F. Cremier et F. Gazeau. Bois fossiles mésozoïques du Maroc, 210. Notes Mem. Serv. du Maroc Geol., pp. 121–178.

Dresnay, R., 1975. Données topographiques, stratigraphiques et paléontologiques concernant une ammonite citée dans la Formation d'El Mers (Moyen-Atlas, Maroc) et leurs conséquences sur l'âge attribué à cette formation. Bull. Soc. géol. France (7), XVII (6), 1144–1146.

Duée, G., Hervouet, T., Laville, E., Luca, P., Robillard, D., 1977. L'accident nord moyen-atlasique dans la région de Boulemane (Maroc) : une zone de coulissement synsédimentaire. Ann. Soc. Géol. Nord, Lille XCVIII, 145–162.

Eagar, R.M.C., Baines, J.G., Collinson, J.D., Hardy, P.G., Okolo, S.A., Pollard, J.E., 1985. Trace fossil assemblages and their occurrence in Silesian (mid-Carboniferous) deltaic sediments of the Central Pennine Basin, England. In: Curran, H.A. (Ed.), Biogenic structures: their use in interpreting depositional environments. Society of Economic Paleontologists and Mineralogists, Spec. Publ., 35, pp. 99–149.

Eldredge, N., 1970. Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. American Museum Novitates 2436, 1–17.

Fedan, B., 1993. Évolution géodynamique d'un bassin intraplaque sur décrochements : Le Moyen Atlas (Maroc) durant le Méso-Cénozoique (Thèse Doctorat État), 18. Trav. Instit. Sci., Rabat (1989), sér. Géologie–Géographie physique.

Fedan, B., Laville, E., El Mezgueldi, A., 1989. Le bassin jurassique du Moyen Atlas (Maroc) : un exemple de bassin sur relais de décrochements. Bull. Soc. geol. France, V 6, 1123–1136.

Fischer, D.C., 1984. The Xiphosurida: archetypes of bradytely? In: Eldredge, E., Stanley, S.M. (Eds.), Living Fossils. Springer, Berlin, pp. 196–213.

Fischer, W.A., 1978. The habitat of the early vertebrates: trace and body fossil evidence from the Harding Formation (Middle Ordovician), Colorado. The Mountain Geologist 15, 1–26.

Frizon de Lamotte, D., Zizi, M., Missenard, Y., Hafid, M., El Azzouzi, M., Maury, R.C., Charrière, A., Taki, Z., Benammi, M., Michard, A., 2008. I Continental evolution: The Geology of Morocco, chap. 4. In: Michard, A., Saddiqi, O., Chalouan, A., Frizon de Lamotte, D. (Eds.), The Atlas system. Lect. Notes Earth Sci., 116, pp. 133–202.

Gaillard, C., 2011. A giant limulid trackway (*Kouphichnium lithographicum*) from the Lithographic Limestones of Cerin (Late Kimmeridgian,

France): ethological and environmental implications. Swiss J. Geosci. 104 (Suppl. 1), 57–72.
Garassino, A., De Angeli, A., Pasini, G., 2008. New decapod assemblage from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, south-eastern Morocco. Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano 149, 37–67.
Gibb, S., Chatterton, B.D.E., Pemberton, S.G., 2011. Prod traces (*Selenichnites*) from the Middle Cambrian of Morocco, with hypotheses on the ethology of the tracemaker(s). Ichnos 18, 156–165.
Groiss, J.T., 1975. Eine Spurenplattemit *Kouphichnium* (*Mesolimulus*) *walchi* (Desmarest 1822) aus Solnhofen. Geologische Blätterfür Nordost-Bayern 25, 80–95.
Hardy, P.G., 1970. New xiphosurid trails from the Upper Carboniferous of northern England. Palaeontology 13, 188–190.
Harris, J.D., Lacovara, K.J., 2004. Enigmatic fossil footprints from the Sundance Formation (Upper Jurassic) of Bighorn Canyon national recreation area, Wyoming. Ichnos 11, 151–166.
Kolb, A., 1963. Riesige *Limulus*-Fährteaus den lithographischen Schiefern-bei Pfalzpaint. Geol. Bl. NO-Bayern 13, 73–78.
Lapparent, A.F., 1955. Etude paléontologique des vertébrés du Jurassique d'El Mers (Moyen Atlas). Notes Mém. Serv. Géol. Maroc 124, 1–36.
Latreille, P.A., 1802. Histoire naturelle, générale et particulière, des Crustacés et des Insectes, vol. 3. Dufart, Paris.
Laville, E., Fedan, B., 1989. Le système atlasique marocain au jurassique : évolution structurale et cadre géodynamique. Sci. Géol. Mém. Strasbourg 84, 3–28.
Linck, O., 1949. Lebens-Spurenausdem Schifsandstein (Mittl, Keuper km 2) NW-Württemberg und ihre Bedeutung für die Bildungsgeschichte der Stufe. Jahreshefte des Vereins fur Vaterlandische Naturkunde in Württemberg 97 (101), 1–100.
Lucas, S.G., Lerner, A.J., 2005. Lower Pennsylvanian invertebrate ichnofossils from the Union Chapel Mine, Alabama: a preliminary assessment. In: Buta, R.J., Rindsberg, A.K., Kopaska-Merkel, D.C. (Eds.), Pennsylvanian Footprints in the Black Warrior Basin of Alabama. Alabama Paleontological Society Monograph no. 1, pp. 147–152.
Marinheiro, J., Mateus, O., Alaoui, A., Amani, F., Nami, M., Ribeiro, C., 2014. New Quaternary fossil site from the middle Atlas of Morocco. Comunicações Geológicas 101 (Especial I), 485–488.
Martin, E.L.O., Pittet, B., Gutiérrez-Marco, J.C., Vannier, J., El Hariri, K., Lerosey-Aubril, R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R.A., Van Roy, P., Vaucher, R., Lefebvre, B., 2015. The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: age, environment and evolutionary perspectives. Gondwana Res., http://dx.doi.org/10.1016/j.gr.2015.03.009.
Martin, J., 1973. Carte géomorphologique du Moyen Atlas central à 1/100 000. Notes Mém. Serv. géol. Maroc 258, 5 feuilles.
Martin, J., 1981. Le Moyen Atlas Central, étude géomorphologique. Notes Mém. Serv. géol. Maroc 258 bis.
Michard, A., Frizon De Lamotte, D., Saddiqi, O., Chalouan, A., 2008. An Outline of the Geology of Morocco. In: Michard, A., Saddiqi, O., Chalouan, A., Frizon de Lamotte, D. (Eds.), Continental evolution: The Geology of Morocco. Lecture Notes in Earth Sciences, 116. Springer Verlag, Berlin Heidelberg, pp. 1–31.
Miller, M.F., 1982. *Limulicubichnus*: a new ichnogenus of limulid resting traces. J. Paleontol. 56, 429–433.
Minter, N.J., Braddy, S.J., 2009. Ichnology of an Early Permian intertidal flat: the Robledo Mountains Formation of southern New Mexico, USA. Spec. Paper Palaeontol. 82, 1–107.
Moore, R.A., Mckenzie, S.C., Lieberman, B.S., 2007. A Carboniferous synziphosurine (Xiphosura) from the Bear Gulch Limestone, Montana, USA. Palaeontology 50, 1013–1019.
Morrissey, L.B., Braddy, S.J., 2004. Terrestrial trace fossils from the Lower Old Red Sandstone, southwest Wales. Geol. J. 39, 315–336.
Nance, R.D., Alonso, G.G., Keppie, J.D., Linnemann, U., Murphy, J.B., Quesada, C., Strachan, R.A., Woodcock, N.H., 2012. A brief history of the Rheic Ocean. Geosci. Front. 3, 125–135.
Nielsen, E., 1949. On some trails from the Triassic beds of East Greenland. Meddelelserom Grønland 149, 1–44.
Nopsca, F., 1923. Die Familien der Reptilien. Fortschritte der Geologie und Paläontlogie 2, 1–210.
Oishi, H., Matsukuma, A., Aihara, A., 1993. Limulid trace fossils from the Oligocene of Takeo, Saga Prefecture, Japan, 18. Science Reprints, Department of Earth and Planetary Science, Kyushu University, pp. 73–84.
Oppel, A., 1862. Über Färhtenimlithographischen Schiefer (*Ichnites lithographicus*). Museum des Königlich Bayerischen Staates. Paläeontol. Mittheilungen 2, 121–125.
Peyer, K., Charbonnier, S., Allain, R., Läng, E., Vacant, R., 2014. A new look at the Late Jurassic Canjuers conservation Lagerstätte (Tithonian, Var, France). C. R. Palevol 13, 403–420.
Peyre de Fabregues, C., Allain, R., 2013. A limulid trackway from the Late Jurassic (Tithonian) Lagerstatte of Canjuers (Var, France). C. R. Palevol 12, 181–189.
Poiré, D.G., Del Valle, A., 1996. Trazas fosiles en barras submareales de la Formacion Balcarce (Cambrico/Ordovicico), cabocorrientes, Mar del Plata, Argentina. Asoc. Paleontol. Argentina, Publ. Espec. 4, 89–102.
Rhrib, J., 1997. Die Störungszonen des Mittleren Atlas (Zentralmarokko) Strukturelle Entwicklung in einem intrakontinentalen Gebirge. Berliner Geowiss. Abh., A 194, 1–221.
Riahi, S., Uchman, A., Stow, D., Soussi, M., Ben Ismail Lattrache, K., 2014. Deep-sea trace fossils of the Oligocene–Miocene Numidian Formation, northern Tunisia. Palaeogeogr. Palaeoclimatol. Palaeoecol., http://dx.doi.org/10.1016/j.palaeo.2014.08.010.
Richter, R., Richter, E., 1929. *Weinberginaopitzi*, n g., n. sp., einSchwertträger (Merost, Xiphos) aus dem Devon (Rheinland). Senckenbergiana 11, 193–209.
Romano, M., Whyte, M.A., 1987. A limulid trace fossil from the Scarborough Formation (Jurassic) of Yorkshire: its occurrence, taxonomy and interpretation. Proc. Yorkshire Geol. Soc. 46, 85–95.
Romano, M., Whyte, M.A., 1990. *Selenichnites*, a new name for the ichnogenus *Selenichnus* Romano & Whyte, 1987. Proc. Yorkshire Geol. Soc. 48, 221.
Romano, M., Whyte, M.A., 2003. The first record of Xiphosurid (Arthropod) trackways from the Saltwick Formation, Middle Jurassic of the Cleveland basin, Yorkshire. Palaeontology 46, 257–269.
Romano, M., Whyte, M.A., 2013. A new record of the trace fossil *Selenichnites* from the Middle Jurassic Scably Formation on the Cleveland Basin Yorkshire. Proc. Yorkshire Geol. Soc. 59, 203–210.
Rudkin, D.M., Young, G.A., Nowlan, G.S., 2008. The oldest horseshoe crab: a new xiphosurid from Late Ordovician Konservat-Lagerstätten deposits, Manitoba, Canada. Palaeontology 51, 1–9.
Scheele, J., 1994. Vom frühmesozoischen Riftgraben zum intrakontinen Gebirge: Konvergente Blattveschiebungstektonikimzentralen Mittleren Atlas (Marokko). Berliner Geowiss. Abh. (A)., pp. 160.
Schweigert, G., 1998. Die Spurenfauna des Nusplinger Plattenkalks (Oberjura, SchwäbischeAlb). Stuttgarter Beiträgezur Naturkunde Serie B 262, 1–47.
Schweigert, G., Dietl, G., 2002. Miscellanea ausdemNusplinger Plattenkalk (Ober-Kimmeridgium, Schwäbische Alb). 4. Limuliden. Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins NF 84, 323–331.
Thomson, M.R.A., Weber, B., 1999. Discovery of an Ordovician invertebrate fauna in the Blaiklock Glacier Group, Shackleton Range, Antarctica. Terra Antarctica 6, 241–248.
Trewin, N.H., Mc Namara, K.J., 1995. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (? Late Silurian) of Kalbarri, Western Australia. Trans. Royal Soc. Edinburgh: Earth Sci. 85, 177–210.
Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., El Hariri, K., Briggs, D.E., 2010. Ordovician faunas of Burgess Shale type. Nature 465, 215–218.
Van Roy, P., Derek, E., Briggs, G., Gaines, R.R., 2015. The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. J. Geol. Soc., http://dx.doi.org/10.1144/jgs2015-017.
Viohl, G., 1998. Die Solnhofener Plattenkalke–Entsthehung und Lebensräume. Archaeopteryx 16, 37–68.
Wang, G., 1993. Xiphosurid trace fossils from the Westbury Formation (Rhaetian) of southwestern Britain. Palaeontology 36, 111–122.
Weber, B., Braddy, S.J., 2004. A marginal marine ichnofauna from the Blaiklock Glacier Group (? Lower Ordovician) of the Shackleton Range, Antarctica. Trans. Royal Soc. Edinburgh: Earth Sci. 94, 1–20.
Willard, B., 1935. Chemung tracks and trails from Pennsylvania. J. Paleontol. 9, 43–56.
Woodward, H., 1866. On the species of the genus *Eryon*, Desm., from the Lias and Oolite of England and Bavaria (with parts of 2 plates). Quart. J. Geol. Soc. London 22, 494–502.
Xing, L.-D., Lockley, M.G., Qind, H., Matsukawa, M., Persons, I.V., Xiao, W.S., Zhang, Y.-W.J.-P., 2012. Forgotten Paleogene limulid tracks: *Xishuangbanania* from Yunnan, China. Palaeoworld 21, 217–221.