Multicuspidate shark teeth associated with chondrichthyan and acanthodian scales from the Emsian (Devonian) of southern Algeria

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KEY WORDS
Chondrichthyes,
Acanthodii,
teeth,
scales,
Devonian,
Algeria,
south Ahaggar,
new species,
new genus.

ABSTRACT

Previously undescribed Emsian vertebrates from southern Algeria (southern Ahaggar) include a new chondrichthyan *Tassiliodus lessardi* n. gen., n. sp. with multicuspidate teeth and scales with a distinctive histology. This is the first Emsian chondrichthyan taxon reported from the north-western margin of Gondwana. Rare acanthodian scales are assigned to *Milesacanthus* cf. *ancestralis* Burrow, Lelièvre & Janjou, 2006, an Emsian species also known from Saudi Arabia, reinforcing the Gondwanan faunal affinity.

MOTS CLÉS
Chondrichthyes,
Acanthodii,
dents,
écailles,
Algérie,
sud Hoggar,
espèce nouvelle,
genre nouveau.

RÉSUMÉ

Dents multicuspides de requin associées à des écailles de Chondrichthyen et d'Acanthodien de l'Emsien (Dévonien) du sud de l'Algérie.

Du matériel inédit de vertébrés provenant du sud Hoggar (sud Algérie) comprend deux dents multicuspides d'un nouveau Chondrichthyen, *Tassiliodus lessardi* n. gen., n. sp. accompagnées d'écailles présentant un nouveau dispositif histologique. Il s'agit du premier enregistrement de Chondrichthyens d'âge Emsien sur la marge Nord-Ouest Gondwana. Quelques écailles de *Milesacanthus* cf. *ancestralis* Burrow, Lelièvre & Janjou, 2006 (Acanthodien), décrites auparavant dans l'Emsien d'Arabie Saoudite, renforcent les affinités gondwaniennes du matériel.

INTRODUCTION

Palaeozoic early vertebrate remains from Algeria are sparse, and generally only briefly mentioned in the current literature. A Silurian calcareous level from Ougarta (Fig. 1 [1]) (Oued Ali) yielded remains of armoured "agnathans" (Massa *et al.* 1965 *in* Fabre 1976: 107; Fabre 2005: 214) also reported by Nedjari *et al.* (2007: 37). Blieck (1982) recorded the only putative, but doubtful, heterostracan of Africa from the Pridoli of Ougarta. Acanthodian scales have also been reported from the Siluro-Devonian boundary of southern Algeria (Ougarta, Oued Ali section) (Blieck *et al.* 1984).

Devonian remains are more abundant. The Devonian fish faunal list for Algeria mentioned some Lower Devonian shark scales in the Idekel sandstone (Edikel sandstone, southern Algeria) doubtfully placed in southern Ahaggar (Lelièvre *et al.* 1993: fig. 7.2 [D5]). Numerous arthrodire remains associated with acanthodian scales assigned to *Haplacanthus* and Acanthodii indet. have been described and reported from the Emsian of Béchar Basin (Béni Abbès region; Lelièvre 1988; km 30, Nedjari *et al.* 2007: 71) (Fig. 1 [2]). Lehman (1964) described placoderms and *Machaeracanthus* Newberry, 1857 spines from southern Ahaggar and the Béni Abbès area, whereas associated acanthodian scales, partly corresponding to the material published here, were only mentioned. In Ajjers (Illizi Basin, Fig. 1 [7, 8]) Emsian levels have yielded "fishes" and arthrodires (Fabre 2005: 277).

Lehman (1951, 1952a, b) mentioned remains of arthrodires from the Upper Devonian near Béni Abbès, Adrar Ahnet (Fig. 1 [5]), Adrar Mouydir (Lower Famennian) (Fig. 1 [6]) and Fort Polignac (now Illizi, Fig. 1 [7]). Famennian arthrodires are recorded from the Saoura valley (Fig. 1 [1, 2]) (Fabre 1976: 129). More recently, Ginter *et al.* (2002) published chondrichthyan, acanthodian and actinopterygian microremains from the Upper Devonian of Gour Bedda (250 km east of In Salah; Fig. 1 [3], 26°32'7"N, 4°24'17"E).

In the Carboniferous of Béchar (Fig. 1 [1]), isolated scales, possibly actinopterygians, have been reported (Fabre 1976: 190, 192). In the Permo-Carboniferous of Ajjers Basin (Fig. 1 [8]), a level in the upper Tournaisian containing fish bones (Issendjel Formation, 27°N, 8-9°E) and three levels with many fish remains (paleoniscids and selachians) (Tiguentourine Formation) are dated as latest Carboniferous or basal Permian (Fabre 1976: 196, 204). Later, Attar *et al.* (1981) recognized this material as elasmobranchians, acanthodians and actinopterygians, and confirmed a Stephanian-Autunian age. The Carboniferous of the Reggane Basin (Fig. 1 [4]) also yields fish scales (Fabre 1976: 214).

Lessard (1961) published sections from southern Ahaggar, along the Algeria-Mali-Niger borders. He reported *Ctenacanthus major* Agassiz, 1837, identified by J. P. Lehman, from the Carboniferous of the In Debirène syncline in the western part of the area (west of In Guezzam; Figs 1 [11]; 2 [2]). He also mentioned arthrodires in the Tin Seririne syncline (at the In Ateï-Taberia section, east of In Guezzam; Fig. 1 [9]) and in Oued Felaou (in front of In Guezzam; Fig. 1 [10]) from a level denoted F3 (Devonian). Later on, the mentions of an antiarch placoderm (*Bothriolepis* Eichwald, 1840) and a selachian (*Ctenacanthus major*) have been credited to Lessard (1961) by Fabre (1976: 230) in the Iullemmeden Basin, Taberia Formation (Upper Devonian-Lower Carboniferous) in the same area, but this time east of In Guezzam. Fabre probably mistook the location for *Ctenacanthus major* (essentially Carboniferous in age; Maisey 1981: 9), because Lessard organized the logs in his correlation table (1961: fig. 4) from left to right; that is, in the opposite way of his map (NE-SW and E-W directions).

MATERIAL AND METHODS

The specimens were collected in the Tassili, southern Oua-n-Ahaggar. According to Lehman (1964), the sample contains plates of Dolichothoraci and spinal plates of Petalichthyida, along with scales referred to acanthodians. In the same locality, occur conularids, tentaculites and spiriferids.

Two chondrichthyan teeth (MNHN.F.ALD-15, 16), 126 chondrichthyan scales and nine acanthodian scales have been extracted from the same sample (MNHN.F.ALD-12) by DG.

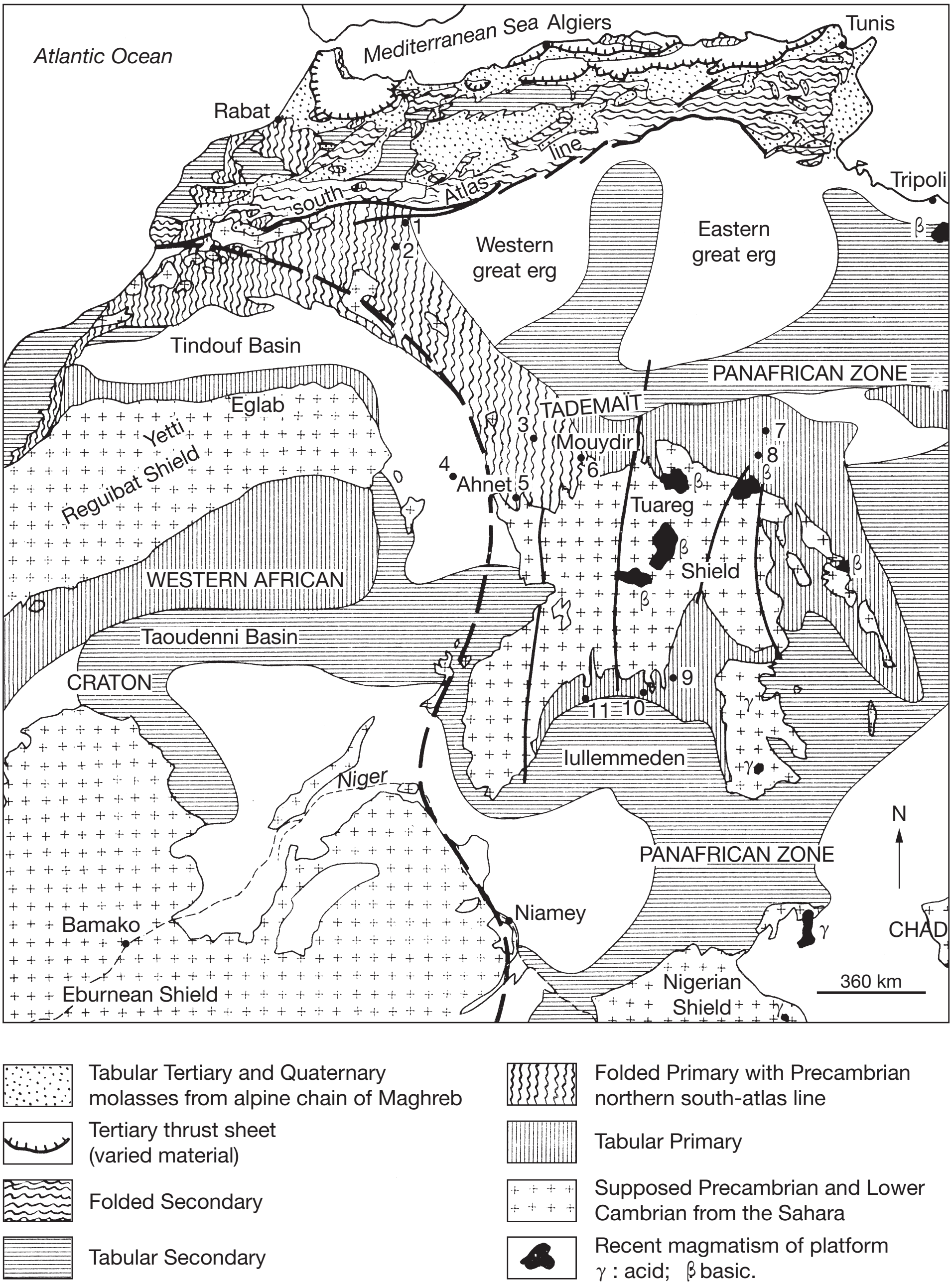

Fig. 1. — Geological map of North-West Africa after Fabre (1976: 13). Numbers correspond to localities: **1**, Bechar; **2**, Béni Abbès; **3**, In Salah (Gour Bedda); **4**, Reganne; **5**, Ahnet; **6**, Mouydir; **7**, Illizi (Fort Polignac); **8**, Ajjers; **9**, Tin Seririne Syncline (Anou In Ateï-Taberia); **10**, Oued Felaou; **11**, In Debirène.

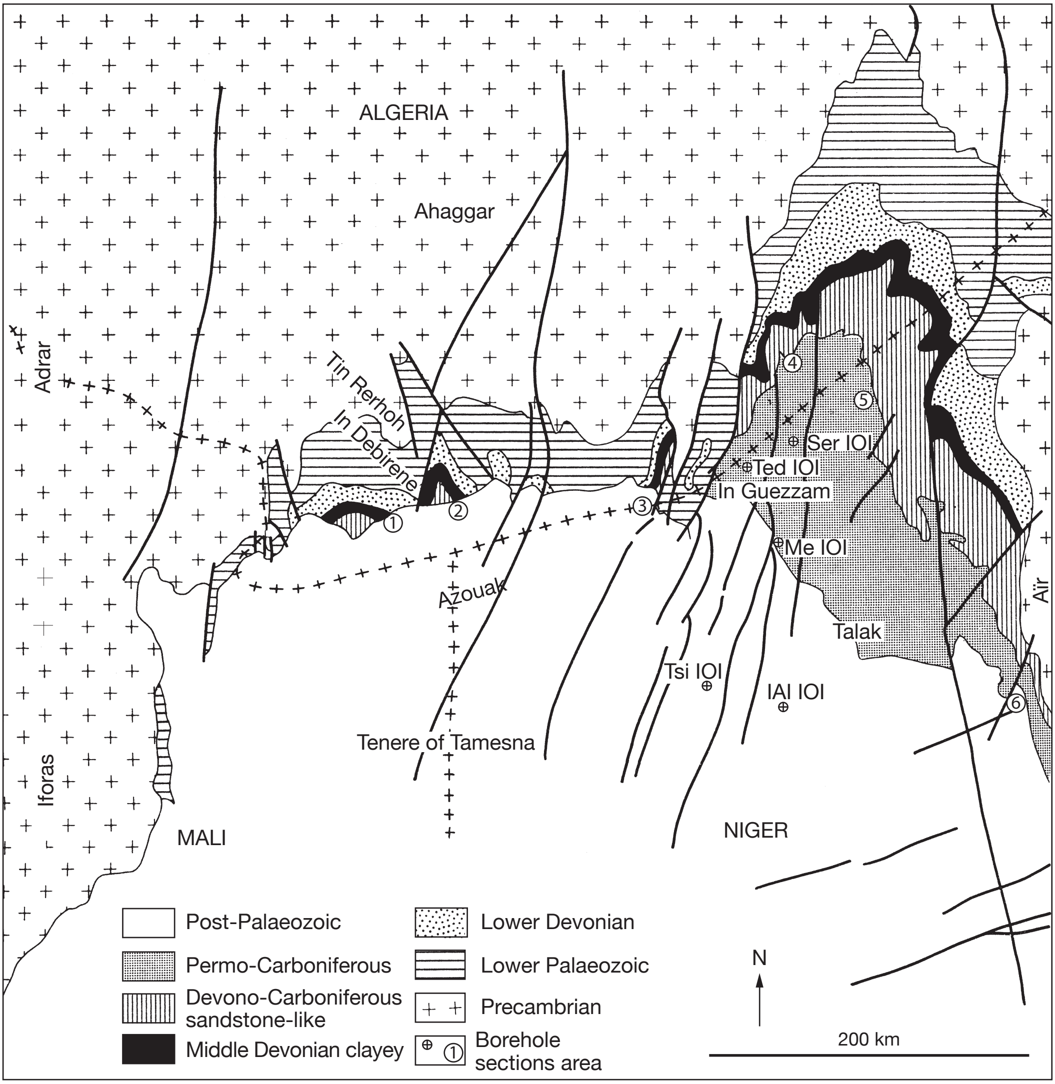

Fig. 2. — Geological map of the Devonian and Carboniferous in southern Ahaggar after Fabre (1976: 154). Localities: **1**, In Debirène; **2**, Tin Rerhoh; **3**, Oued Felaou; **4**, Anou Izileg; **5**, Touaret-Tim Mersoï; **6**, Talak.

Determination of age and locality

The only indication for the location of the material provided by Lessard was "sandstones from southern Oua-n-Ahaggar, Tassili" of supposed Pragian age (ex Siegenian) (Lehman 1964). The Petalichthyida published by Lehman is now considered as Emsian or Eifelian in age. Acanthodian scales derived from the sample, are here compared to *Milesacanthus ancestralis* Burrow, Lelièvre & Janjou, 2006 from the Jawf formation (Saudi Arabia), dated as early Emsian (Burrow *et al.* 2006). The material was found with *Arduspirifer* (*"Acrospirifer"*) *arduennensis* Mittmeyer, 1972 (Lehman 1964), also Emsian in age (Nicollin & Ouali Mehadji pers. comm.).

A more accurate location of the outcrop may now be proposed. In southern Ahaggar, Palaeozoic outcrops

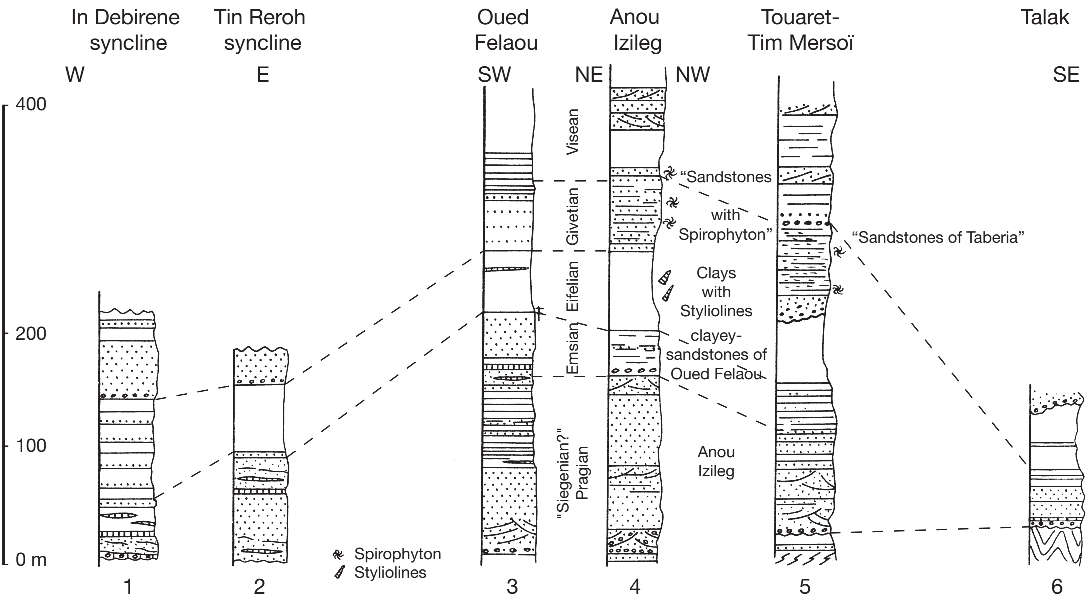

Fig. 3. — Stratigraphical sections of the Devonian and Carboniferous in southern Ahaggar after Fabre (1976: 155). Numbers of sections correspond to numbers of localities of Figure 2.

are fringing north of the Tamesna Basin or are located in the Tin Seririne syncline (western Aïr) (Fig. 2). The brachiopod *Arduspirifer arduennensis*, has also been found in Anou Izileg (Figs 2 [4]; 3 [4]), cut I (Tin Seririne syncline), where clay-sandstone levels named Oued Felaou (from the type locality) are dated as late Emsian (Claret & Tempere 1965). A level denoted "F3" and dated as Pragian (ex Siegenian)-Emsian, and containing arthrodires, spiriferids, corals, and tentaculites, was mentioned by Lessard (1961) in two sections of the Tin Seririne syncline (cut I In Ateï-Taberia, east In Guezzam; Fig. 1 [9]) and Oued Felaou (cut J, north In Guezzam; Fig. 1 [10]). According to Fabre (1976: 153-155), two sections in South Ahaggar (Oued Felaou and Anou Izileg, eastern In Guezzam) show Emsian levels (Figs 2; 3). Tin Seririne (17°25'0"N, 6°16'60"E) and Anou Izileg (wilaya Tamanghasset, 20°19'60"N, 6°4'0"E) sections – the latter also mentioned by Claret & Tempere (1965) – are located about 120 km east of In Guezzam and are close to each other. This restricted the possibilities of location to less than 150 km from In Guezzam; i.e. the material must come from Oued Felaou (Figs 1 [10]; 2 [3]), In Ateï-Taberia, Tin Seririne syncline, or Anou Izileg (Fig. 1 [9]). The presence of Emsian levels containing "fishes" (arthrodires) is confirmed in sandstones (Oued Felaou Formation) east of In Guezzam (Fabre 2005: 279).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Sub-class ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Order *incertae sedis*
Family *incertae sedis*

Genus *Tassiliodus* n. gen.

Type species. — *Tassiliodus lessardi* n. sp. (MNHN.F.ALD-15, Fig. 4A).

Etymology. — From Tassili, origin of the material, and -odus, tooth.

Diagnosis. — Crown with three diverging main cusps, the middle one being shorter than the two diverging lateral ones, intermediate cusplets in a more labial position than the main ones, rugose base oriented lingually. Scales with a flat base, a high neck and ridges on the crown, histological structure with an extensive network of wide vascular canals through the neck and base, box-in-box pattern, pallial dentine and mesodentine.

Tassiliodus lessardi n. sp.
(Fig. 4)

?*Haplacanthus* sp. – Lelièvre 1988: 300, fig. 5.

?*Phoebodus* sp. – Forey *et al.* 1992: 31, fig. 7.

Nogueralepis sp. – Burrow *et al.* 2006: 554, fig. 11: 12-17, 23, 24.

"Chondrichthyan teeth, scales" – Derycke & Goujet 2009: 87.

Tassiliodus lessardi "nomen nudum"– Derycke & Goujet 2010: 145.

TYPE LOCALITY. — Near In Guezzam, Oued Felaou or Anou Izileg, southern Ahaggar (Algeria).

ETYMOLOGY. — After L. Lessard, a hydrogeologist who discovered the material in the 1960's.

DIAGNOSIS. — As for genus.

SYNTYPES. — Teeth, MNHN.F.ALD-15 (Fig. 4A) and MNHN.F.ALD-16 (Fig. 4B); scales MNHN.F.ALD-17 to 35; thin sections MNHN.F.ALD-30-32, 34, 35.

OTHER MATERIAL EXAMINED. — 107 scales, same origin as the syntypes (see Material and methods).

DESCRIPTION OF THE TEETH
The tooth crown of MNHN.F.ALD-15 (Fig. 4A) bears 8 cusps and cusplets. Among the three main cusps, the middle one is half the height of the lateral cusps, that diverge at an angle of about 50°. The main cusps have a rounded tip. Five cusplets are visible, three on one side of the central cusp and two on the other side. Lateral cusplets are not in the same plane, and the smallest ones are in a more labial position. The smooth crown is probably covered with enameloid, and only one ridge is visible in the middle of a main cusp (right side in Fig. $4A_1$).

The base is perpendicular to the crown and expanded lingually. Its internal structure is revealed by a fracture surface showing bone or osteodentine (Fig. $4A_3$) with a rugose external aspect (Fig. $4A_4$). There is apparently no regular organization of the foramina in the base (Fig. $4A_4$, A_5).

The crown of the second, smaller tooth MNHN.F.ALD-16 (Fig. 4B) is only visible in lingual aspect and made up by four cusps with 3 diverging main cusps (angle around 50°). The tip of the cusps are more pointed and slender than in MNHN.F.ALD-15. The rugose base shows a kind of lingual bulge behind the central cusp (Fig. $4B_4$). One cusplet is visible but is not in the same plane, it is situated more labially, like in MNHN.F.ALD-15. The base is poorly developed and the cusps are oriented or curved lingually. Tiny foramina are visible in the lingual part of the base.

Remarks
Our specimens have been compared with other Emsian chondrichthyans: *Doliodus* Traquair, 1893, known from an articulated specimen (Turner & Miller 2005: fig. 6) as well as isolated teeth, *Protodus* Woodward, 1892 (Turner & Miller 2008), *Pucapampella* Janvier & Suarez-Riglos, 1986 (Maisey & Anderson 2001), and possible Emsian *Antarctilamna* Young, 1982 (e.g., Forey *et al.* 1992).

Devonian levels of Saudi Arabia have yielded early vertebrate material. A tooth referred to *Phoebodus* sp. (Forey *et al.* 1992: fig. 7) has been described from the Jauf Formation (Saudi Arabia) and dated as Pragian to Early Emsian. Although it is only illustrated by a drawing and in lingual aspect, it is possibly an antarctilamnid, a family mainly known from the Givetian-Frasnian (type genus *Antarctilamna*). However this tooth appears smooth and shows fewer vascular foramina than *Antarctilamna* and is not comparable to *Tassiliodus* n. gen. which shows no big foramina. *Antarctilamna* is also represented by spines and scales in the Wajid Formation (Saudi Arabia, Pragian to Early Emsian) (Forey *et al.* 1992). Other "shark" material corresponds to "*Cladodus*" teeth, that are not identifiable according to Ginter (2004). One species, *A. seriponensis*, was also described from the Emsian of Bolivia (Gagnier *et al.* 1988) based on fin spines. *Antarctilamna* teeth are characterized by many ridges on the cusps (Young 1982; Long & Young 1995), a feature that is absent in our specimens.

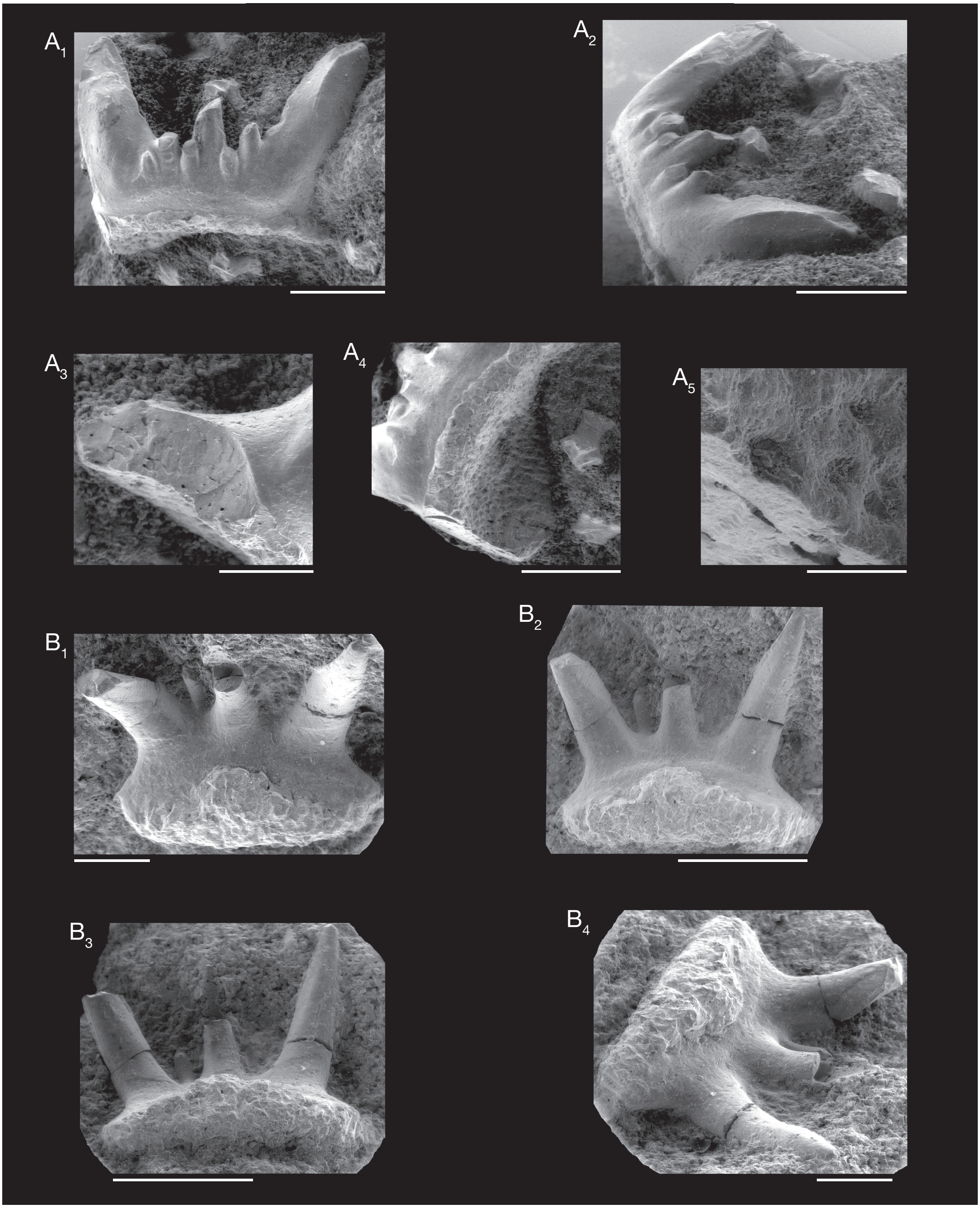

FIG. 4. — Chondrichthyan teeth of *Tassiliodus lessardi* n. gen., n. sp. from the Emsian (Devonian) of southern Algeria: **A**, MNHN.F.ALD-15; $\mathbf{A_1}$, labial view; $\mathbf{A_2}$, labio-lateral view; $\mathbf{A_3}$, enlargement of the base; $\mathbf{A_4}$, basal view; $\mathbf{A_5}$, enlargement of the basal view; **B**, MNHN.F.ALD-16, lingual views. Scale bars: A_1, A_2, A_4, B_2, B_3, 2 mm; A_3, B_1, B_4, 1 mm; A_5, 200 µm.

Pucapampella first found in Bolivia (Janvier & Suarez-Riglos 1986) is also known from the upper Emsian in South Africa (Anderson *et al.* 1999; Maisey & Anderson 2001 *in* Maisey 2004). It is only known by its braincase and no teeth have been yet described (Maisey 2001).

Doliodus problematicus Woodward, 1892, is early Emsian in age (Canada) and shows trunk scales (Miller *et al.* 2003: 503) that resemble those of *Antarctilamna* from the Jauf Formation. *Doliodus* teeth have cusps similar to some xenacanthiform ones and have been included in the Omalodontida (Miller *et al.* 2003). Known as one of the oldest articulated chondrichthyans, *Doliodus* possesses paired fin-spines, a character long considered as a synapomorphy of acanthodians, but now as a gnathostome symplesiomorphy (Miller *et al.* 2003). Turner (2004) described the teeth of *Doliodus* in detail. The main difference with *Tassiliodus* n. gen. concerns their base, which is oriented labially in *Doliodus*, hence its inclusion in the Omalodontida. The crowns are also different: in *Doliodus* one of the main lateral cusps is larger than the other, the proportions in length of cusps are different, and intermediate cusplets are in the same plane as the main cusps.

Protodus jexi Woodward, 1892 from New Brunswick (Canada) (late Pragian/early Emsian) is quite different, as it has monocuspid teeth (Turner & Miller 2008).

Finally among Emsian chondrichthyans, the *Tassiliodus* n. gen. teeth show a unique morphology.

Leonodus Mader, 1986, first described by Mader (1986) from Lochkovian-Pragian levels of Spain, is considered as the oldest unequivocal chondrichthyan teeth (Turner 2004; Turner & Miller 2005). It is bicuspid, more acute when sharpened by wear (Botella *et al.* 2009), and is the first indication of a dental lamina (Botella 2006, except for placoderms according to Smith & Johanson 2003, even there is a regular tooth addition without a true dental lamina, M. M. Smith pers. comm.).

Description of the scales

From the *c.* 126 scales, six morphotypes have been identified as belonging to the squamation of *Tassiliodus lessardi* n. gen., n. sp.

High-neck scales, almost 58 scales (Fig. 5A-D)

These four scales share a crown that shows wide grooves intercalated with converging thin, sometimes nodose, ridges in the middle, an elongate neck and a flat base, that is narrower than the crown. These scales are generally higher than wide.

The crown of MNHN.F.ALD-17 (Fig. 5A) bears six main tuberculated ridges converging at the top. One ridge is divided near the crown margin (right on Fig. $5A_1$). One intermediate ridge seems to merge on the opposite side. This round scale has a high neck and a flat base with one basal pore and a notch near its margin (Fig. $5A_2$). In the scale MNHN.F.ALD-18 (Fig. 5B), more numerous ridges begin in the vertical part of the crown, converging at the top, nipped-in waist and high neck with one foramen at the extreme basal part of the neck.

In the scale MNHN.F.ALD-19 (Fig. 5C), one foramen in the middle of the base and one tiny lateral foramen, could correspond in position to the "pulp" cavity "openings" described in *Elegestolepis grossi* Karatajute-Talimaa, 1973 (Karatajute-Talimaa 1973: taf. 3), but in our scale there is no pulp cavity, so they are strictly vascular foramina.

A bigger scale, MNHN.F.ALD-20 (Fig. 5D), shows about nine ridges converging and reaching the top and slightly displaced. Smaller ridges starting at the margin of the crown are intercalated between them. The crown outline is oval and the margin crenulated. The elliptical base has the same orientation as the crown. In basal view (Fig. $5D_2$), a tenuous limit underlines the boundary between the crown and the neck.

Flat-crowned scales (Fig. 5E-G)

The scales MNHN.F.ALD-21 to 23 are flatter. The upper crown is ornamented with 4-7 ridges converging backward and separated by wide grooves. The lower lateral crown is either smooth (Fig. $5E_1$), or with ridges parallel or perpendicular (Fig. $5F_1$) to the central crown ridges. The flat base, narrower than the crown, may show two foramina in MNHN.F.ALD-22 (Fig. $5F_2$): one near the centre and one near the margin.

The morphology of the scales is similar to that of *Wetteldorfia triangula* Vieth-Schreiner, 1983 (Vieth-Schreiner 1983: taf. 1. 1-9; Emsian-lower

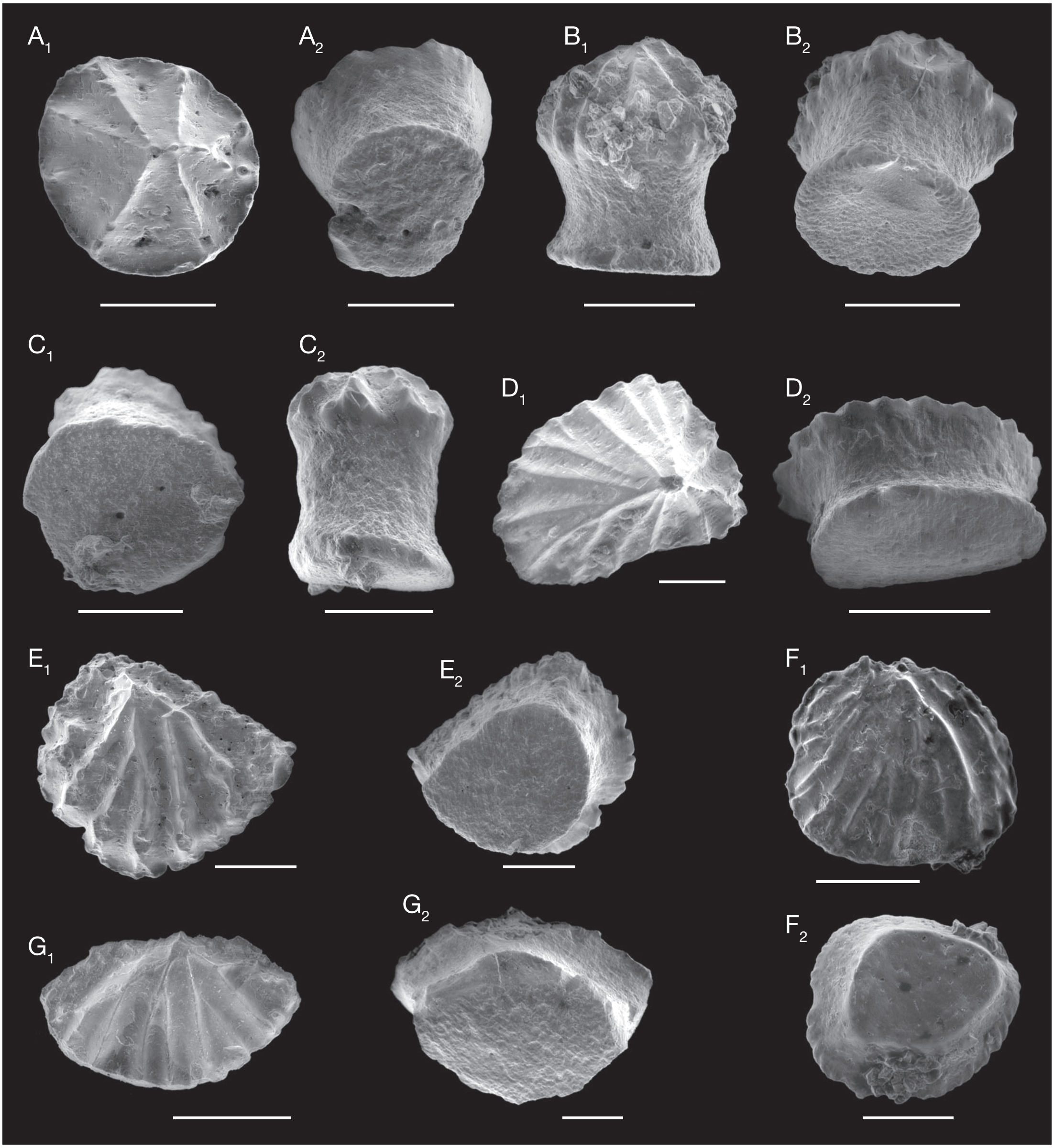

FIG. 5. — Chondrichthyan scales of *Tassiliodus lessardi* n. gen., n. sp. from the Emsian (Devonian) of southern Algeria: **A**, MNHN.F.ALD-17; $\mathbf{A_1}$, crown view; $\mathbf{A_2}$, basal view; **B**, MNHN.F.ALD-18; $\mathbf{B_1}$, lateral view; $\mathbf{B_2}$, basal view; **C**, MNHN.F.ALD-19; $\mathbf{C_1}$, basal view; $\mathbf{C_2}$, lateral view; **D**, MNHN.F.ALD-20; $\mathbf{D_1}$, crown view; $\mathbf{D_2}$, basal view; **E**, MNHN.F.ALD-21; $\mathbf{E_1}$, crown view; $\mathbf{E_2}$, basal view; **F**, MNHN.F.ALD-22; $\mathbf{F_1}$, crown view; $\mathbf{F_2}$, basal view; **G**, MNHN.F.ALD-23; $\mathbf{G_1}$, crown view; $\mathbf{G_2}$, basal view. Scale bars: A, B, C_2, D_1, E, F, G2, 500 µm; C_1, 400 µm; D_2, G_1, 1 mm.

Eifelian), which is considered as an acanthodian. Here the circular base is smaller than the crown whereas *Wetteldorfia* Vieth-Schreiner, 1983 shows a forwardly displaced, diamond-shaped base. The scales are smaller (1-1.5 mm) than those of *Wetteldorfia* (3 mm). The histological structure of some scales of *Wetteldorfia* from the Eifel (Vieth-Schreiner 1983: abb. 7, 8) recalls that of the high-neck scales (Figs 5A-D; 7E_2), with a box-in-box structure with only two or three growth lines in the crown, which do not continue in the base. In Vieth-Schreiner's drawings, internal growth zones seem to terminate before the surface. Furthermore, the same tissues are visible in the same position. Usually, in the center of the crown of acanthodian scales, a primordium is visible. It is present neither in the thin sections of *Wetteldorfia* from the Eifel, nor in our material (morphologically more closely corresponding to Figure 5A-D; the material that shows the external morphology of *Wetteldorfia* has not been sectioned). *Wetteldorfia* is also described from the Emsian of Saudi Arabia (Burrow *et al.* 2006: figs 4.12, 13, 15, 16) but is different from the type species, and Burrow *et al.* (2006: 544) proposed a revised diagnosis of the genus.

Leaf-shaped scales (Fig. 6A, B)
These flat diamond-shaped scales show ridges converging in the centre of the convex crown, some very worn (ALD-25; Figs 6B_1; 7B_2) and others less so (ALD-24; Fig. 6A1). Shorter ridges appear on the lateral sides of the crown (Fig. 6A_2, B_2). The flame outline corresponds to two concave opposite sides and two other more convex ones (Fig. 6A_1). The base is flat (Fig. 6A_2) or slightly convex (Fig. 6B_2). The neck is short and nipped-in waist (Fig. 6A_2). These scales are wider than high.

Spiny scale (Fig. 6F)
A spiny crowned scale, MNHN.F.ALD-29, has a nipped-in waist, high neck and a flat base (Fig. 6F_2). Three broad spines are distributed with one at the top of the crown and two on one side (Fig. 6F_1). Smaller, more irregularly distributed, spines may be joined by a crest to the highest spine in two files (Fig. 6F_1). It resembles isolated tubercles of the scale MNHN.F.ALD-17 (Fig. 5A_1).

Scales with parallel ridges on the crown (Fig. 6C, D)
The two scales MNHN.F.ALD-26, 27 have a flat, posteriorly elongated crown. The crown is ornamented with four, strong, subparallel ridges – the biggest one in the middle – separated by wide grooves (Fig. 6C_1). The second scale MNHN.F.ALD-27 shows seven ridges beginning in the anterior part, and two supplementary ones intercalated in the posterior part (Fig. 6D_2). The bases are different in these two scales: more flat for MNHN.F.ALD-26 (Fig. 6C_2) and more convex and diamond-shaped for MNHN.F.ALD-27 (Fig. 6D_1) with a foramen in a lateral position.

The scale MNHN.F.ALD-26 (Fig. 6C_1) evokes a scale of *Elegestolepis grossi* Karatajute-Talimaa, 1973, from the Silurian of Tuva (Karatajute-Talimaa 1973: taf. 3, figs 5c, 6a), with a high neck and a flat base, and is associated with scales showing a more diamond-shaped base, like that in MNHN.F.ALD-27 (Fig. 6D1).

Broken scale (Fig. 6E)
The broken scale MNHN.F.ALD-28 shows a rounded convex base protruding forward of the crown (Fig. 6E_1). One foramen is visible on the high neck. The fore-crown displays ridges that are inserted low on the base.

Scales histology
Thin section 1 MNHN.F.ALD-30 (Fig. 7A_2), thin section 3 MNHN.F.ALD-32 (Fig. 7C_2) and thin section 5 MNHN.F.ALD-35 (Fig. 7H_2) are vertical sections of scales with a high neck, converging crown ridges and a flat base (Fig. 5A-D). Thin sections 2 MNHN.F.ALD-31 (Fig. 7B_1) and 4 MNHN.F.ALD-34 (Fig. 7E_2) are of flatter scales like MNHN.F.ALD-24 and 25 (Fig. 6A, B). Thin section 4 MNHN.F.ALD-34 (Fig. 7E_2) is of a scale that is wider than high, but also with wide grooves and thin ridges converging at an eccentric apex. In the Figure 7, each thin section corresponds to the nearest scale morphology and bears the same letter.

Almost the entire scale internal structure comprises a network of meandering canals emerging in any part of the scale; canals can open out on the base (Figs 7A_2, C_2; 5A_2, C_1), the neck (Figs 7C_2; 5B_1) or on the crown (Fig. 7C_2, H_1, H_2). It consists of a distinctive type of mesodentine (Ørvig 1967).

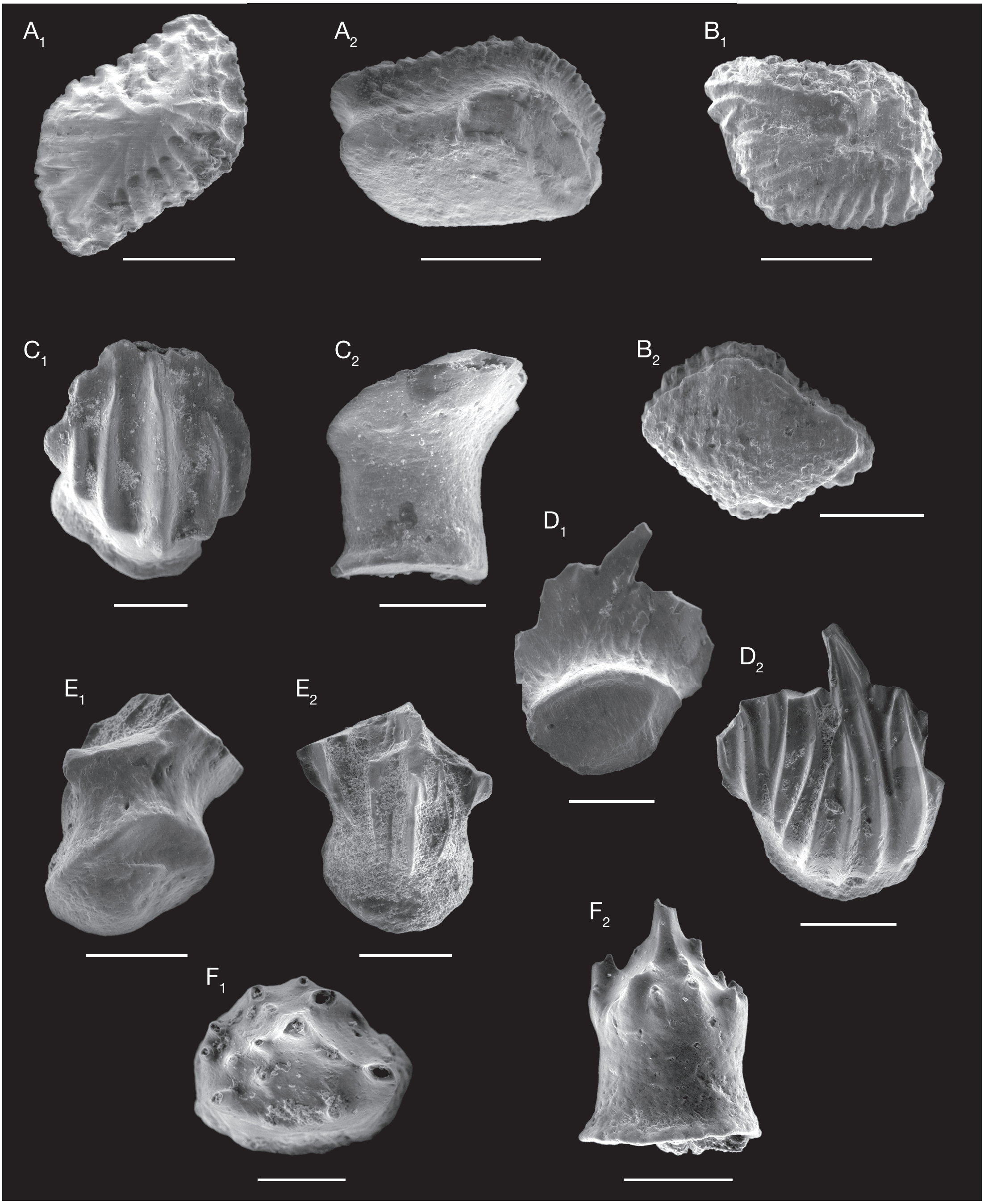

FIG. 6. – Chondrichthyan scales of *Tassiliodus lessardi* n. gen., n. sp. from the Emsian (Devonian) of southern Algeria: **A**, MNHN.F.ALD-24; **A$_1$**, crown view; **A$_2$**, basal view; **B**, MNHN.F.ALD-25; **B$_1$**, crown view; **B$_2$**, basal view; **C**, MNHN.F.ALD-26; **C$_1$**, crown view; **C$_2$**, lateral view; **D**, MNHN.F.ALD-27; **D$_1$**, basal view; **D$_2$**, crown view; **E**, MNHN.F.ALD-28; **E$_1$**, latero-basal view; **E$_2$**, front view; **F**, MNHN.F.ALD-29; **F$_1$**, crown view; **F$_2$**, lateral view. Scale bars: A, B, 1 mm; C$_1$, F$_1$, 200 µm; C$_2$, F$_2$, 300 µm; D, 500 µm; E, 400 µm.

A kind of box-in-box pattern is visible in the crown, but some elements of the previous generations of the scale may appear at the surface. Whereas thin section 3 MNHN.F.ALD-32 (Fig. 7C_2) only shows one growth zone, thin sections 1, 2 and 5 show two growth stages (Fig. 7A_2, B_1, H_2), with possibly more for thin section 4 MNHN.F.ALD-34 (Fig. 7E_2), based on the undulating ridges. The first stage, mainly invaded by the vascular canal network, emerges on the right side on MNHN.F.ALD-35 (Fig. 7H_2) and on the left one in MNHN.F.ALD-34 (Fig. 7E_2). It may correspond to the intermediate external shorter ridges at the crown base (Fig. 7E_1). It means that the overlapping by the second growth stage is not complete and that this histology does not exactly correspond to a real box-in-box pattern.

Resorption-remobilization phenomena are observed: on the left side of the tip of MNHN.F.ALD-30 (Fig. 7A_2), in the middle part and right side of MNHN.F.ALD-34 (Fig. 7E_2) and in the middle bulge of the first stage MNHN.F.ALD-35 (Fig. 7H_2). Resorption was never found before in chondrichthyans, except in *Ctenacanthus* sp. from the Namurian (Derycke-Khatir 2005).

More classically, bushes of pallial dentine (Radinsky 1961) radiate from vascular canals under the crown surface, sometimes lined by a thin refringent layer. Two levels of dentine may appear inside the crown, for example in thin sections 1 MNHN.F.ALD-30, 4 MNHN.F.ALD-34 and 5 MNHN.F.ALD-35 (Fig. 7A_2, E_2, H_2). Sharpey's fibers and osteocytes are localized in the extreme basal part of the scales, and may be particularly dense in thin sections 1 MNHN.F.ALD-30 and 5 MNHN.F.ALD-35 (Fig. 7A2, H2). In thin section 4 MNHN.F.ALD-34 (Fig. 7E2) the osteocytes are not randomly organized, surrounding vascular canals. The density and the organization of Sharpey's fibers and osteocytes are variable, possibly reflecting the maturity of the scale.

In two thin sections (1 MNHN.F.ALD-30 and 2 MNHN.F.ALD-31, Fig. 7A_2, B_1), a short canal joining an aperture in the posterior part and in the basal part of the base corresponds to the openings and the notch visible on MNHN.F.ALD-17 (Fig. 5A_2).

Scale histology appears almost identical in the material of Algeria and in the "*Nogueralepis* sp." scales from the Jauf Formation of Saudi Arabia (Burrow *et al.* 2006: fig. 11: 12-17, 23, 24). Crown ridges converge backwards or are subparallel in "*Nogueralepis* sp.", and the scales have the same morphology as those of *Tassiliodus lessardi* n. gen., n. sp., with a very high neck and a flat base. They strickingly differ from those of the type-species of *Nogueralepis* Wang, 1993 from the Lochkovian of Spain (Wang 1993), particularly in their histology. The scales from Saudi Arabia were probably misidentified and may in fact belong to our new taxon *Tassiliodus* n. gen., reinforcing the close biogeographic affinity between these two areas.

Thin section 4 MNHN.F.ALD-34 (Fig. 7E_2) evokes a thin section of a tiny adult scale of *Elegestolepis grossi* from the Silurian of Tuva (Karatajute-Talimaa 1973: 42, abb. 3, E), but also the thin section of *Wetteldorfia* from Saudi Arabia, except for the growth zones of the base (Burrow *et al.* 2006: fig. 4: 16).

Conclusion for chondrichthyan scales

Scales with the morphology shown by MNHN.F.ALD-17, 19 (Fig. 5A-D) and histology with the network of meandering canals as in MNHN.F.ALD-30, 32 (Fig. 7A_2, C_2) resemble those of "*Nogueralepis* sp." from Saudi Arabia (Burrow *et al.* 2006: fig. 11: 12-17, 23, 24). The scales MNHN.F.ALD-21-23 (Fig. 5E-G) morphologically resemble *Wetteldorfia* scales (Vieth-Schreiner 1983: taf. 1.1-9), but the different morphotype of scales MNHN.F.ALD-17-19 (Fig. 5A-D) corresponds to the histology of *Wetteldorfia* (Fig. 7E_1, E_2). Thin section MNHN.F.ALD-34 (Fig. 7E_2) also evokes the histology of *Elegestolepis*, except for the lack of a pulp cavity and its finer calibre canals (Karatajute-Talimaa 1973: 42, abb. 3, E). Two other scales, MNHN.F.ALD-26, 27 (Fig. 6C, D), resemble the morphology of *Elegestolepis* (Karatajute-Talimaa 1973: taf. 3, figs 5c, 6a).

The distinctive histological structure indicates that all these scales may belong to the squamation of the same chondrichthyan.

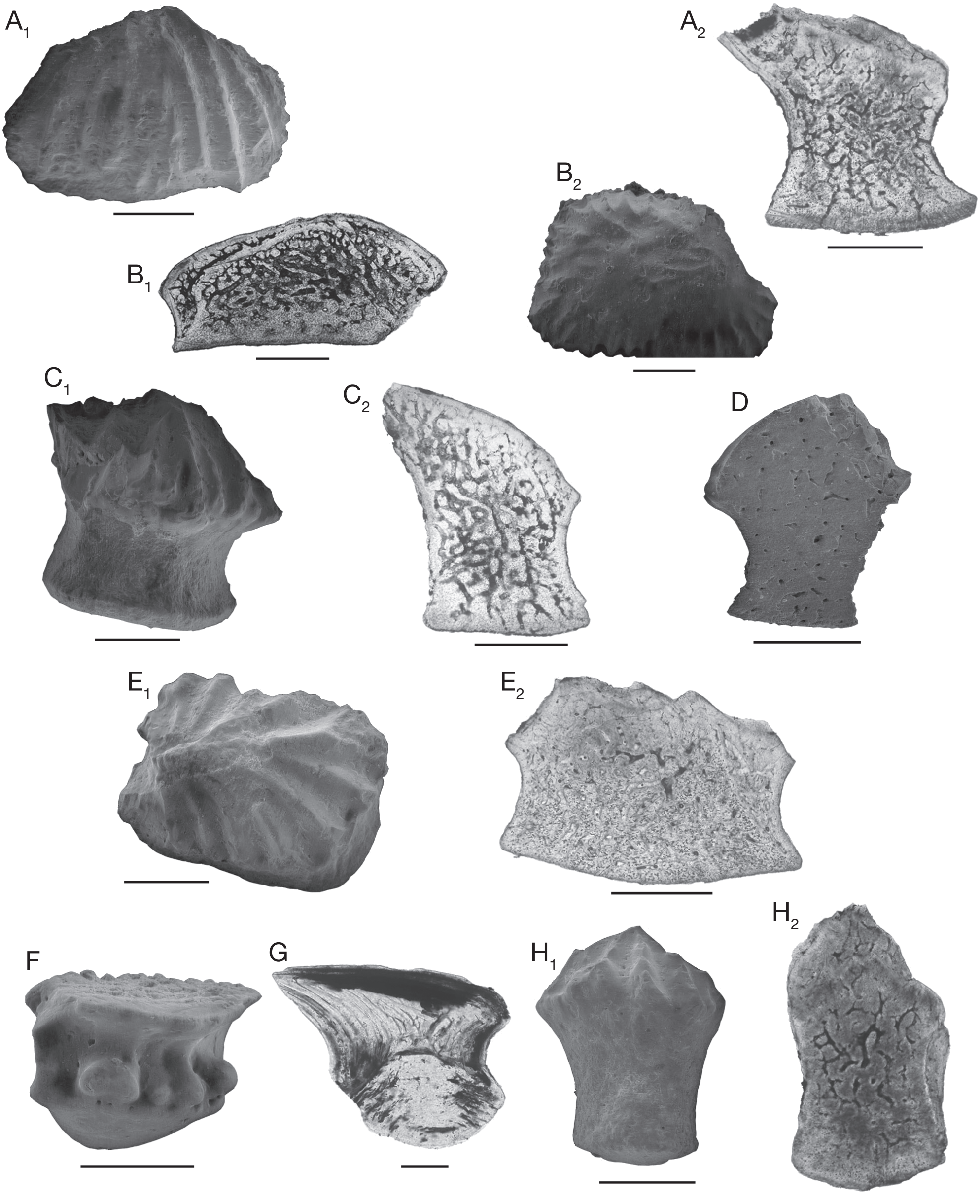

FIG. 7. — Histology and corresponding morphology of chondrichthyan scales from the Emsian (Devonian) of southern Algeria: **A**-**E**, **H**, *Tassiliodus lessardi* n. gen., n. sp.; **F**, **G**, *Milesacanthus* cf. *ancestralis*; identical letters refer to the same scale in morphology and in thin section (except for **D**, corresponding to an internal view of a broken scale photographed by SEM, and for **F**, which was lost in the SEM); **A**, crown view and sagittal thin section 1 of a scale with converging ridges posteriorly and high-neck (MNHN.F.ALD-30); **B**, thin section 2 and crown view of a dumpy scale with radiating ridges only fringing the crown (MNHN.F.ALD-31); **C**, lateral view of a high-neck scale and thin section 3 (MNHN.F.ALD-32); **D**, SEM micrograph of internal view of a high-necked scale (MNHN.F.ALD-33); **E**, crown view of a dumpy scale with radiating ridges reaching the middle of the scale, and thin section 4 (MNHN.F.ALD-34); **H**, lateral view of a scale with converging ridges in the middle of the scale and a high neck, and thin section 5 (MNHN.F.ALD-35); **F**, postero-lateral view (MNHN.F.ALD-40); **G**, thin section 9 (MNHN.F.ALD-41). Scale bars: A-E, H, 500 µm; F, 300 µm; G, 100 µm.

Class ACANTHODII Owen, 1846
Order Indeterminate
Family DIPLACANTHIDAE Woodward, 1891

Genus *Milesacanthus* Young & Burrow, 2004

TYPE SPECIES. — *Milesacanthus antarctica* Young & Burrow, 2004: 26-38, figs 1-5, 6h, o-r.

Milesacanthus* cf. *ancestralis
(Fig. 8)

MATERIAL. — Nine scales, one of which is lost (MNHN.F.ALD-40), and one thin section MNHN.F.ALD-41.

DESCRIPTION

The crown of these four scales is diamond-shaped and its anterior part may be more rounded as in MNHN.F.ALD-38 (Fig. $8C_2$). The convex base, also diamond-shaped, and with anterior and rounded posterior edges is located anteriorly.

The scales with a flat crown show sub-parallel grooves (18 for Fig. $8A_1$, B_2 and possibly more), diverging in the front part (Fig. $8C_2$), like in the material of *Milesacanthus ancestralis* from Saudi Arabia. The grooves are not really deep but narrower than the ridges. Both grooves and ridges run along the entire crown length of the scale. In the scale MNHN.F.ALD-36 (Fig. $8A_1$), grooves and ridges start just at the front edge of the scale, whereas in the scale MNHN.F.ALD-37 (Fig. $8B_2$) the ridges start at the vertical edge of the crown and the posterior edge is more crenulated.

One scale (ALD-38) shows 13 larger grooves (Fig. $8C_2$), but only in its anterior part. Pore openings, located mainly at the beginning of the grooves, connect to an ascending canal system. The grooves begin after the anterior edge of the crown and most lateral grooves undulate, slightly converging in the beginning, then parallel to the diagonal, and stop in the posterior third of the crown. The neck is well marked with a row of foramina posteriorly and anteriorly (Fig. $8A_2$, B_2, C_2). Furthermore, wart-like protuberances are visible on the posterior neck (Fig. $8A_2$; more evident on Fig. 7F), visible on "young" scales according Burrow *et al.* (2006: 547).

HISTOLOGY

The thin section 9 MNHN.F.ALD-41 (Fig. 7G) shows a classical pattern for an acanthodian, with a primordium in the middle of the crown that is made of dentine covered with thin box-in-box growth zones continuing from the crown into the acellular bone base. Contrary to *Milesacanthus ancestralis* and *M. antarctica* (Young & Burrow 2004), no vascular canal was found, but only one thin section has been made.

DISCUSSION

The number and the development of ridges on the crown recalls the scales of *M. antarctica*, but the presence of wart-like bumps in the posterior part of the neck is more suggestive of *M. ancestralis*. Although wide canals were not detected here, they are present in both *M. ancestralis* and *M. antarctica*, and pore openings are visible at the surface of the scale MNHN.F.ALD-38 (Fig. $8C_2$). The cone of the base inserted in the crown is, in our material, more developed. In conclusion, some acanthodian scales are closer to *M. antarctica* and the others to *M. ancestralis* but their histology is different.

DISCUSSION

PALAEOBIOLOGY

The earliest chondrichthyans are considered to have been toothless, with a gap of about 50 millions of years between the first putative scales and the first teeth (Turner 2004). The first undoubted chondrichthyan teeth belong to *Leonodus* (diplodont or bicuspid) from the Lochkovian/Pragian of Spain. Multicuspidate "cladodont" teeth are considered to appear later (Maisey & Melo 2005: 500). Until now, three other undisputed Emsian chondrichthyan genera were known: *Pucapampella* without described teeth, *Doliodus* with articulated remains and *Protodus* (monocuspid) only known from teeth (Turner & Miller 2005, 2008). *Protodus* is the first to show predator style teeth according to Turner & Miller (2008: 140). *Doliodus* with its diplodont teeth (Maisey & Melo 2005) is included in the Omalodontidae (Turner 2004; Turner & Miller 2008). Some Emsian bicuspid teeth with intermediate cusplets

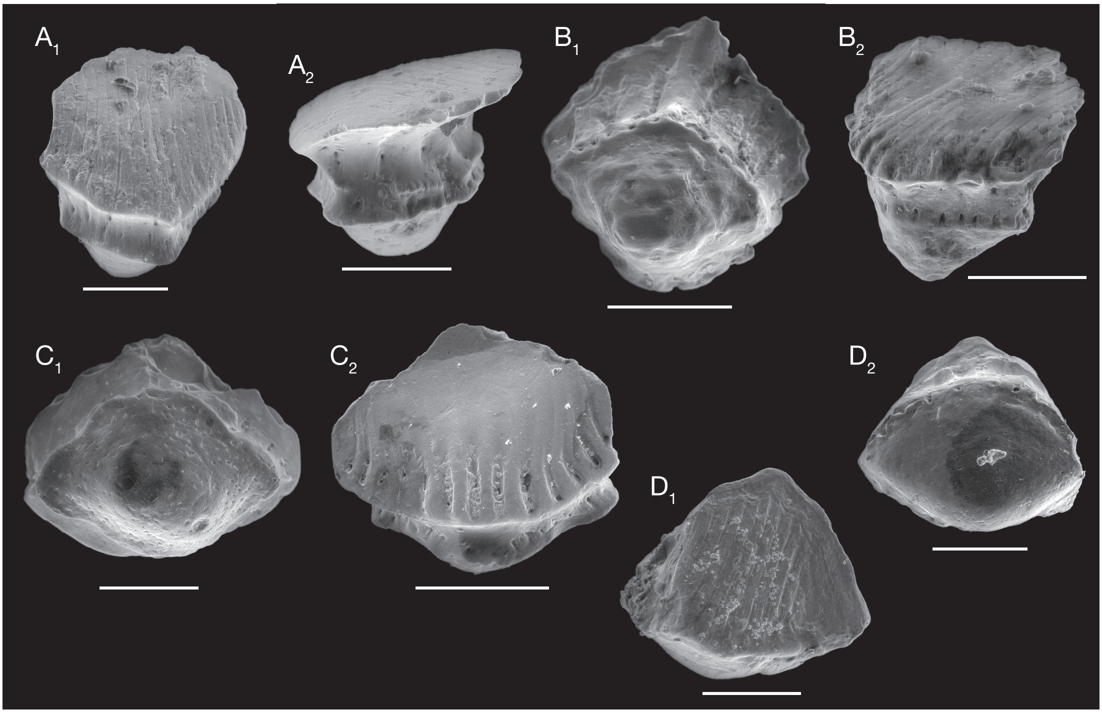

FIG. 8. — Acanthodian scales of *Milesacanthus* cf. *ancestralis* from the Emsian (Devonian) of southern Algeria: **A**, MNHN.F.ALD-36; **A_1**, crown view; **A_2**, lateral view; **B**, MNHN.F.ALD-37; **B_1**, basal view; **B_2**, front view; **C**, MNHN.F.ALD-38; **C_1**, basal view; **C_2**, front view; **D**, MNHN.F.ALD-39; **D_1**, crown view; **D_2**, basal view. Scale bars: A-B, C2, 400 µm; C1, D, 300 µm.

have also been assigned to *Antarctilamna*. The case of *Machaeracanthus*, considered here as ambiguous, will not be dealt with because it concerns spines and scales. In Spain (Mader 1986; Wang 1993) as in Brittany (Viré-en-Champagne, DG pers. obs.) *Leonodus* teeth occur with *Machaeracanthus* scales and/or spines. In the Poyales Escalombreras section (Wang 1993: 100, 141), *Leonodus*-type teeth and *Machaeracanthus*-type scales are statistically the most abundant microremains. This observation and the fact that *Machaeracanthus* scales have a growth style that is at odds with that observed in characteristic acanthodian scales, lead to question the "acanthodian" status of such scales. It might be suggested that *Machaeracanthus* scales and *Leonodus* teeth could belong to the same animal. But only the discovery of an articulated (even partially) specimen would test this hypothesis.

The teeth from southern Ahaggar (Fig. 4) represent one of the oldest evidence of multicuspidate teeth. Derycke (2007) proposed that the asymmetry in the number of cusplets reflects a kind of budding. It is not related to the position in the mouth, which is characterized by a twisted crown or base more than by the number of cusplets, as considered in *Thrinacodus* St. John &Worthen, 1875 (Duncan 2003), even though *Thrinacoselache* Grogan & Lund, 2008 finally displays a single tooth morphology: asymmetrically curved teeth with twisted lingual bases (Grogan & Lund 2008: 973).

Regarding the scales (Figs 5-7), their histology is unique, with a network of wide canals opening out anywhere on the scale surface, and a kind of box-in-box pattern with only two growth stages, not continued in the base (Fig. 7A-E, H). The combination of an unusual high neck and short Sharpey's fibers suggests that the scales were inserted deep in the skin and grew inside the skin. Furthermore the morphology, the size but also the density of the cells may depend on the location of the scales on the body and their maturation. The type of scale growth does not correspond to any of the types defined by Karatajute-Talimaa (1998: 48). Usually, the growth of the skin is compensated by addition of odontodes in front of, or around their primordium – resulting in a growth in breadth – and/or addition of new larger scales. Here, the scales were growing in height. We are unable to explain this growth or relate it to a particular kind of squamation.

Comparisons were made with other scales, including those of *Wetteldorfia*, which is considered as an acanthodian (Emsian, Eifel, Vieth-Schreiner 1983; Emsian, Saudi Arabia, Burrow *et al.* 2006), "*Nogueralepis* sp." (Emsian, Saudi Arabia, Burrow *et al.* 2006) and *Elegestolepis* Karatajute-Talimaa, 1973 (Silurian, Tuva, Karatajute-Talimaa 1973), but the material is considered to be in fact the squamation of *Tassiliodus lessardi* n. gen., n. sp.

This material raises questions concerning the limits of histological data in the problem of relationships between chondrichthyans and acanthodians: some characters are chondrichthyan ones (pallial dentine, foramina emerging in the neck and in the base), whereas others are more acanthodian-like (box-in-box pattern or "onion-like structure", mesodentine, also foramina in the neck). The relationships between chondrichthyans and acanthodians are already debated and possibly explained by mosaic evolution (Brazeau 2009).

The chondrichthyan material (Figs 4-6) comprises scales and teeth from one small sample (around 5 × 10 cm). How can we interpret this assemblage? Does it belong to the same organism? Chondrichthyan teeth (Fig. 4) have been found along with chondrichthyan scales (93%) (Figs 5, 6) and acanthodian scales (6%) (Fig. 8). Furthermore, the presence of tentaculites on the same sample suggests that it rather represents a thanatocoenosis with maybe reworking.

Stratigraphy

The association with a petalichthyid placoderm and the presence of *Arduspirifer*, suggests that the sample can be dated as Emsian. This dating is supported by comparisons of the scales with those of *Milesacanthus*, of "*Nogueralepis* sp." (Saudi Arabia) and of *Wetteldorfia* (Eifel & Saudi Arabia) (Emsian; Vieth-Schreiner 1983; Burrow *et al.* 2006).

Palaeogeographic incidence

Emsian levels in all the Sahara correspond to a transgression (Fabre 1976: 125) and are marine. The early chondrichthyans *Pucapumpella* and possibly *Antarctilamna* are known from Gondwana, but *Doliodus* and *Protodus* are from Laurussia (Turner & Miller 2005: 245). The new taxon *Tassiliodus* n. gen. fills a biogeographic gap (Turner & Miller 2005: figs 3; 6). It is one of the earliest multicuspidate chondrichthyan teeth, and the first evidence for an Emsian chondrichthyan taxon in North-West Gondwana.

The assemblage with Gondwanan affinities (*sensu* Young 1987 *in* Forey *et al.* 1992) found in south Algeria comprises acanthodians, placoderms and chondrichthyans and is comparable to the Saudi Arabian assemblage, sharing an absence of thelodonts, heterostracans, osteostracans and galeaspids (Forey *et al.* 1992). Some scales confirmed the Gondwanan affinities by comparison to *Milesacanthus*, *Wetteldorfia* and the new taxon (previously compared to "*Nogueralepis* sp.") (Emsian, Saudi Arabia; Burrow *et al.* 2006).

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