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First assemblage of Acanthodian scales and spines from the Famennian (Upper Devonian) of Durnal (Belgium), palaeobiogeographical and palaeoenvironmental implications

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ABSTRACT. The vertebrate microremains assemblage from the Famennian (Upper Devonian) of the Belgian locality of Durnal is compared with those of the Famennian of Strud, Latvia and Gondwanan Frasnian localities.

These faunal comparisons allow palaeoenvironmental and palaeobiogeographical considerations on the faunal interchanges between Gondwana and Euramerica during the Middle-Late Devonian. Isolated acanthodian spines and scales, usually relatively scarce in the Famennian deposits in Belgium, constitute the major part of the Famennian microremains assemblage from Durnal, together with actinopterygian scales and sarcopterygian teeth and scales. This acanthodian fauna from Durnal is the first known association of spines and scales in Northern France and Belgium.

KEYWORDS. Vertebrates, Acanthodians, Actinopterygians, Sarcopterygians, Microremains, Famennian, Belgium.

RÉSUMÉ. Aiguillons et écailles d'acanthodiens dans le Famennien (Dévonien supérieur) de Durnal (Belgique), données sur la paléobiogéographie et le paléoenvironnement. Des microrestes de vertébrés ont été extraits de grès fins plus ou moins carbonatés du Famennien (Dévonien supérieur) de Durnal (Province de Namur, Belgique). Les restes d'acanthodiens, relativement rares dans le Famennien de Belgique, ont été trouvés en abondance avec des dents et des écailles de sarcoptérygiens ainsi qu'avec des éléments dermiques d'actinoptérygiens. Cet assemblage, représentant la première association d'aiguillons et d'écailles d'acanthodiens de la Belgique a été comparé aux assemblages du Famennien de Strud, de Lettonie et du Frasnien du Gondwana. Ils renforcent les données paléobiogéographiques concernant les échanges entre l'Est du Gondwana et le Sud de l'Euramerica au cours du Dévonien.

MOTS-CLÉS. Vertébrés, Acanthodiens, Actinoptérygiens, Sarcoptérygiens, Microrestes, Famennien, Belgique.

1. Introduction & geological context

The Durnal locality has yielded a microfauna consisting of associated acanthodian scales and spines, actinopterygian scales and sarcopterygian teeth and cosmine-covered scales. This locality (Fig. 1) is situated in the eastern allochthonous part (Dinant synclinorium) that is separated from the parautochthonous (Namur synclinorium) by the Midi Fault, the latter northernly overthrusting the Brabant Massif (Khatir et al., 1992).

The Langlier quarry of the Durnal locality, along the Bocq Valley, shows the Evieux Formation, upper Famennian in age. It belongs to the Condroz sandstone sequence (Paproth et al., 1986). The sediments of the Condroz Group result from an important progradation of deltaic complexes (Thorez et al., 2006).

1.1 Lithostratigraphical and biostratigraphical context

Famennian deposits from Belgium correspond to a regressive megasequence with short transgressive pulses (Bultynck & Dejonghe, 2001). The Evieux Formation, in the prograding lithofacies context, consists of an alternation of sandstones, silstones, dolostones, and carbonate sandstones. In Durnal, the Evieux Formation is considered as an autochthonous carbonate deposit of the Dinant Allochthonous, and is dated from the Lower-Middle *expansa* zone (Thorez et al., 2006, fig. 4).

The Strud locality (Namur Province, Belgium, Fig. 1) has provided an *Ichthyostega*-like lower jaw (Clément et al., 2004). This specimen is the first occurrence of a Devonian tetrapod in western continental Europe. This locality, close to Durnal and also in the Dinant Allochthonous, is attributed by Prestianni et al. (2007) to the Famennian biozone number 7 of Edwards et al. (2000) corresponding to *rhomboidea* to *expansa* (Streel, pers. comm.).

A study of the Famennian vertebrate microremains of Belgium has been carried out in order to contribute to the evaluation of the fauna associated with early tetrapods and to specify their palaeoenvironment.

1.2 Palaeogeographical & palaeoenvironmental context

During Famennian times, the Condroz shelf was a relatively shallow epicontinental sea. The Durnal and Strud localities were situated in the south of Laurussia in a context of regression and shortening, bordering the southern side of the Old Red Continent. The uppermost part is interrupted by a short transgressive event: the restricted marine or peritidal Fontin Member with dolomite. Durnal was in a lagoonal context behind the sand barrier (Thorez et al., 2006, fig. 6) and the climate was considered as arid to semi arid in the tropical belt (palaeolatitude 10° and 20° south) (Thorez et al., 2006).

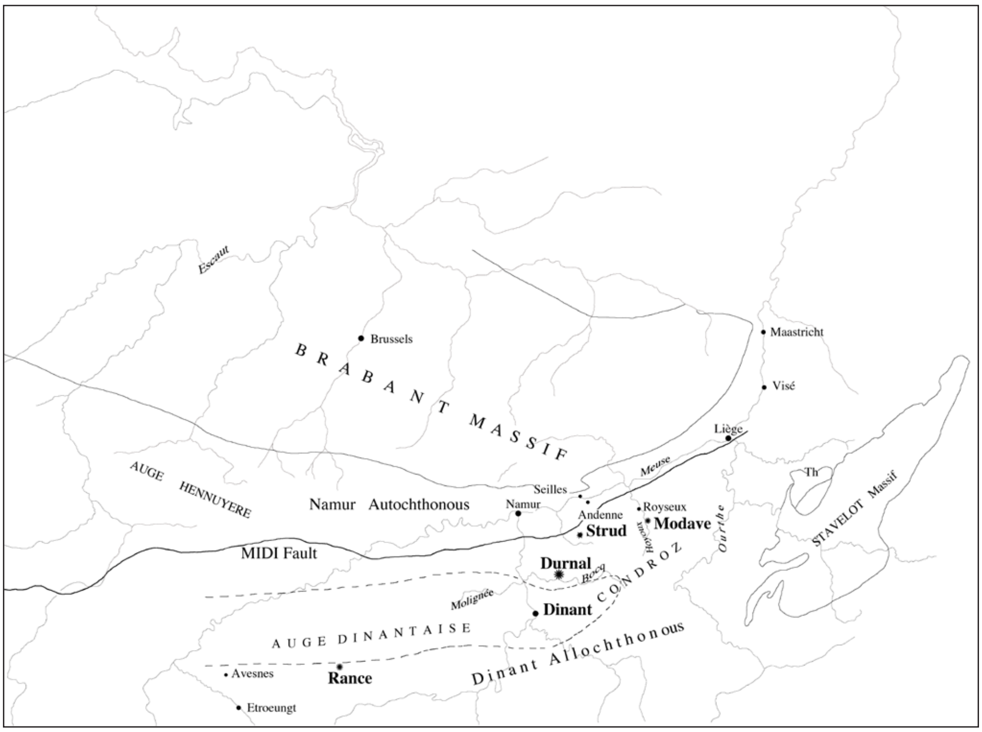
2. Material and method

Sample n°4, level 2, was collected in the Langlier quarry, Durnal locality in 1999. The sample, a psammite (micaceous sandstone) with clay and carbonate levels, was treated with 8% solution of formic acid. Three different sieves were used: 250µm, 100µm, and 50µm.
SEM : FEI, quanta 200 ESEM (Environmental scanning electronic microprobe).
Location: Langlier Quarry, Durnal, Namur Province, Belgium.
Age: Upper Famennian (Fa2c), early-middle *expansa* Zone.
N° DU corresponds to the plot number of SEM photomicrographs.
N°CVUL is the vertebrate collection number of the University of Lille.

3. Mineralogy and marine indexes (Plate 1)

Under SEM observations, all microremains appear covered by mineral ghosts (Plate 1A-B). An electronic dispersal probe has been used in order to determine their composition. Measurements on very scarce minerals found (Plate 1F), give the following composition: iron FeO almost 34 %, oxygen 21% and aluminium 11%. It suggests a kind of Al-substituted goethite, sometimes bipyramidal (Cornell & Schwertmann, 2003). However, some tiny raspberry-like pyrite elements, i.e. framboids, are present in cavities (Plate 1C). They usually indicate a rapid mineralization early in diagenesis, in a confined environment within the first

Figure 1. Localities with geological main structures after Paproth et al., 1983.



centimeter of the sediments, but can also appear long after, during the fossilization process (Cornell & Schwertmann, 2003).

The Durnal locality presents various marine markers such as echinoderm (Plate 1G-K) and conodont (Plate 1L-O) microremains, but also brachiopods and nautiloids. In contrast, no marine influence is recorded in the Strud locality so far and it is considered as more proximal than Durnal.

4. Previously described ichthyofauna

Complete or partly articulated vertebrate specimens are rare in the Devonian-Carboniferous levels of Belgium with the few exceptions being the chondrichthyan *Denaea* and the actinopterygians *Osorioichthys* and *Benedenius* (Fournier & Pruvost, 1928; Taverne, 1997; De Koninck, 1878). Previous studies on Famennian vertebrate microremains of Northern France and Belgium mainly dealt with faunas found in a more carbonate context, with the description of different assemblages: chondrichthyans with crushing teeth, acanthodians, actinopterygians and sarcopterygians (Derycke et al., 1995a,b; Derycke-Khatir, 2005). In Northern France and Belgium, Devonian sarcopterygian remains were previously limited to dipnomorph occurrences, with the porolepiform *Holoptychius* and the lungfish *Dipterus*, respectively known by isolated scales and tooth plates (Lohest, 1888; Leriche, 1931; Cloutier & Candilier, 1995). Isolated dermal elements of Sarcopterygii indet. have also been found in the lower Famennian of Rance (Belgium) (Derycke-Khatir, 2005, pl. 33: 1-3, pl. 34: 3-7, pl. 35: 1, 5-7; Fig. 2). Two large tetrapodomorph fishes, the tristichopterids *Eusthenodon wangsjoi* and *Langlieria socqueti*, were described from the Langlier quarry, Durnal locality (Clément, 2002; Clément et al., 2009).

Regular investigations of the Strud quarry, near Gesves, Namur Province, since 2004 allowed the collect of numerous isolated remains of placoderms (bothriolepids, phyllolepids, groenlandaspids), holoptychiid porolepiforms, "dipterid" and rhynchodipterid lungfishes (Clément & Boisvert, 2006), tetrapodomorph fishes (tristichopterids, osteolepids, and possibly rhizodontids), rare tetrapods (Clément et al., 2004), an undetermined actinopterygian, and acanthodian spines and scales.

5. Systematic Paleontology

Class ACANTHODII Owen, 1846
Order DIPLACANTHIFORMES Berg, 1940
Genus *Devononchus* Gross, 1940

TYPE SPECIES.– *Devononchus concinnus* (Gross), 1930 [Onchus]

Devononchus cf *D. tenuispinus* Gross, 1933

Spines Plate 2 J, M, N, P

Description: smooth broken spines (N, P), rounded in section. The broken spine elements do not exceed 2 mm in length. They are comparable with similar Upper Devonian spines from Ketleri in Latvia (Gross, 1933, p. 21, pl. II: fig. 2), such as *Devononchus tenuispinus* described in the Famennian of Latvia. Except "*Onchus*" *peracutus* (renamed *Bryantonchus* by Burrow, 2007) from the Emsian of USA, it is considered as the only taxon with smooth rounded spines. Two broken ridged spine pieces (J, M), laterally compressed, around 4 mm long each, show smooth longitudinal ridges (almost 20 per side) slightly decreasing in width posteriorly. These fragments also from *Devononchus* correspond to the insertion area of all diplacanthiform spines with parallel ridged structure (C. Burrow, pers. comm.)

Diplacanthidae have long, slender fin spines strongly ornamented with smooth longitudinal ridges parallel to the leading edge of the spine (revised diagnosis, Young & Burrow, 2004: 25), and narrow, closely spaced parallel ridges on the spine insertion (Burrow, 2007).

Leriche (1931) described two spines of *Onchus* from the Upper Devonian of Belgium (Macignos d'Ouffet). The element that he assigned to *Onchus* cf *rectus* (Leriche, 1931, pl. V: fig. 3) is not an acanthodian spine but rather a large isolated sarcopterygian tooth. *Onchus latus* (Leriche, 1931, pl. V: fig. 4), 4 cm long, is much larger than the material presented.

Diplacanthid scales are usually ornamented with longitudinal converging or transverse ridges. None of this type of scale has been recorded in our material. They are dated from the Lower Devonian to Upper Devonian from Canada, Scotland, the Baltic (Denison, 1979), Byelorussia, Main Devonian Field, Timan Pechora (Valiukevičius & Kruchek, 2000), Severnaya Zemlya (Valiukevičius, 2003), South America (Burrow et al., 2003), Saudi Arabia (Burrow et al., 2006), Iran (Hairapetian et al., 2006), Antarctica (Young & Burrow, 2004), and possibly Western Australia (Gross, 1971).

Family MESACANTHIDAE Moy-Thomas, 1939
Teneracanthus Burrow & Young, 2005

TYPE SPECIES.– *Teneracanthus toombaensis* Burrow & Young, 2005

Teneracanthus cf *T. toombaensis*

SCALES Plate 2A-I

Some isolated smooth scales were found in the same rock sample as fin spines described above. Their size is about 0,2-0,3 mm. They show a nipped-in waist neck (Plate 2A, G), a posteriorly turned up elongated crown (Plate 2A, C, H) and a base slightly displaced forward (Plate 2B-D, F, I). The base of scale has an inverted pyramid shape but is more (Plate 2A) or less (Plate 2E) pointed and not so narrow than *Teneracanthus* (Burrow & Young, 2005, fig. 5A, B, D). They also figured scales with a more flattened base considered as caudal scales (Burrow & Young, 2005, fig. 5F, G, H).

Smooth scales are also present in Acanthodiformes such as Mesacanthidae and Acanthodidae but the scales from Durnal are here putatively attributed to Mesacanthidae due to the presence of corresponding spines.

SPINES Plate 2K, L

Description: A fragment of smooth spine, 2 mm long, with rounded pores irregularly spaced on the posterior side. The spine is slightly laterally compressed.

Burrow & Young (2005, figs 4E-G) figured fragments of spines from the Early-Middle Devonian of Australia, laterally flattened with “irregularly-spaced rounded pores” located on the trailing edge of the spine. In contrast to our specimens, this Australian material shows a leading edge separated by grooves.

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1871
ACTINOPTERYGII indet.

Plate 3A-B

An almost complete flank scale shows well preserved sides. The external surface is covered by well-marked ridges on which characteristic ganoine tubercles are identifiable (Derycke & Chancogne-Weber, 1995). This isolated scale cannot be further determined than Actinopterygii indet.

Subclass SARCOPTERYGII Romer, 1955
SARCOPTERYGII? indet.

Plate 3C-K

Two scales are fringed by a groove (Plate 3C, G) and show a very smooth surface punctuated by small pores. They are more densely grouped near the margin (Plate 3D, F). This pattern corresponds to a cosmine cover also identifiable in section (enamel-like cover, pore, dentine and trabecular bone (Plate 3E, H-I)).

Cosmine tissue occurs in Palaeozoic dipnomorphs (lungfishes and porolepidids) (Sire et al., 2009) and tetrapodomorph ‘osteolepidids’. According to the shape of the scale and the high pore density on the exposed surface, we assume that this material could belong to an osteolepidid.

An isolated tooth (Plate 3J, K) is densely covered by mineral ghosts. The crown is too abraded to assure the presence of longitudinal ridges and the broken base of this tooth shows no trace of dentine organization. It is then impossible to provide a further determination.

6. Conclusion

6.1 Palaeobiodiversity

The vertebrate macrofauna of Strud differs from that of the Famennian Castkill Formation of Pennsylvania, USA, where occurs the oldest association of the acanthodian *Gyracanthus* (or gyracanthids), chondrichthyans (*Ageleodus*) and early tetrapods in the Northern Hemisphere (Turner et al., 2005). In Strud and Durnal, there are neither chondrichthyans nor gyracanthid acanthodians. Acanthodian material from Strud is composed of tiny elongate ridged spines, smooth spines, and rare patches of squamations.

%		Rance	Dinant	Durnal	Modave
chondrichthyan	1	18,2	80	0	33,3
acanthodian	2	27,3	2,5	75	52,4
actinopterygian	3	36,3	15	6	9,5
sarcopterygian	4	18,2	2,5	19	4,8
		22 specimens	41 specimens	16 specimens	21 specimens

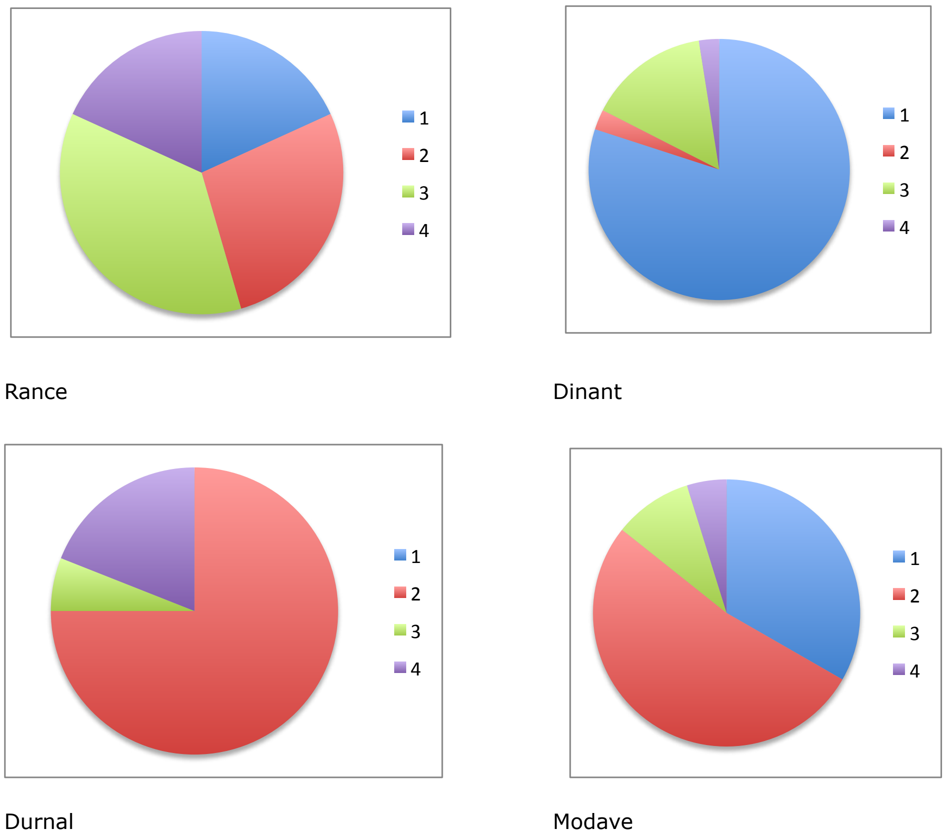


Figure 2. Quantitative distribution of fish microremains in the Famennian localities (Rance, Dinant, Durnal and Modave) of the Dinant Allochthonous.

The nearby Durnal locality, younger in age than the Strud locality (late Famennian *versus* upper middle Famennian), has provided a microfauna consisting of acanthodian scales and fin spines, and less abundant actinopterygian scales and sarcopterygian cosmine-covered scales.

Isolated fin spine fragments from Durnal correspond to different acanthodian diplacanthiforms such as *Devononchus* sp., and the mesacanthid *Teneracanthus* sp. (Derycke & Clément, 2006). "Typical" Middle Devonian assemblages are dominated by diplacanthiforms and acanthodiforms (Valiukevicius & Kruchek, 2000 in Burrow 2007), but only diplacanthiforms are present in our material in younger (Upper Devonian) levels.

Famennian acanthodians were previously mainly described from the Belgian Ardennes (Modave, Rance and Dinant) on the basis of isolated scales and spines (Leriche, 1931; Derycke & Chancogne-Weber, 1995; Derycke-Khatir, 2005).

Levels of the same age (Middle *expansa* zone) from a borehole in the Rheno-Hercynian Massif in Germany show a higher diversity of vertebrate microremains including a high content of chondrichthyans (Hampe & Schindler, 2004). Peaks of abundance of chondrichthyans in *expansa* zone have also been observed in the Ardenne (Derycke-Khatir, 2005), in the Carnic Alps (Randon et al., 2007) and in the Tafilalt (Derycke, in progress) related to the early *expansa* transgression (Ginter et al., 2002). In contrast, acanthodians dominate the vertebrate assemblage in the *expansa* zone of Durnal (Fig. 2). The toothless acanthodiform and diplacanthiform acanthodians are usually placed at the lower level in terms of trophic relationships, with sarcopterygian (porolepiforms and tetrapodomorphs) considered as top predators (Luksevics, 1992). The other peaks of abundance of acanthodians in the Devonian are registered in the *varcus* zone (Givetian) at least in Mauritania and in the Boulonnais (Racheboeuf et al., 2001; Derycke et al., 1995a; Derycke-Khatir, 2005).

6.2 Palaeobiogeography-Palaeoenvironment

The richness of microremains in a single locality is not necessarily directly linked to the real biota diversity and disparity present in that local area during the Devonian times. This non-correlation is partly due to taphonomic biases, different fossilization processes, and potential post-mortem transport. Their studies (determination, tendencies, comparisons, etc.) however provide geographic and environmental information, as evidenced by the Belgian Famennian localities of Rance, Dinant, and Modave (Fig. 1) (Derycke-Khatir, 2005). From these localities, two chondrichthyan genera (*Ctenacanthus*? sp. scales, *Protacrodus* sp.) are both only found in Modave, Liège Province (*rhomboidea-marginifera* conodont-zones) and in Dinant, Namur Province (*postera-expansa-praesulcata* conodont-zones).

Rance (Hainaut Province), the oldest locality considered (*Palmatolepis triangularis* conodont-zone) is the richest in actinopterygian remains (around 40%, Fig. 2). Dinant and Durnal localities dated respectively from *postera-expansa-praesulcata* zones and from *expansa* zone of the Famennian. They both yielded smooth-crowned acanthodian scales. Dinant-Viaduc, south of Durnal, is very rich in chondrichthyan remains (80%), so could be rather distal whereas Durnal, without any chondrichthyan remains but with the highest acanthodian content (75%) (Fig. 2), may be more proximal. According to the palaeogeography, Dinant is in the, so called "Auge Dinantaise" (Fig. 1) or Dinant Trough, a deeper zone than Durnal in the northern part (Khatir, 1990; Averbuch, person. comm.), in a global context of synsedimentary tectonics (Thorez & Dreesen, 1986; Paproth et al., 1986).

The Ketleri Formation in Latvia, late Famennian in age (*expansa* zone, Lebedev et al., 2010), contains some vertebrate elements similar to those of Famennian localities in Belgium. It yields tetrapods, porolepiforms, tristichopterids and diplacanthiform acanthodian spines (e.g., *Devononchus* also found in Durnal and characteristic of Baltica since the middle Givetian, Lebedev et al., 2010). Deposition of the Ketleri Formation corresponds to almost the same conditions as those known in Belgium, that is a shallow basin under brackish conditions (Luksevics & Zupins, 2004). The Ketleri Formation, included in the Porolepiform Realm sensu Lebedev & Zakharenko, shows many endemic taxa (Lebedev & Zakharenko, 2010; table 6: 117).

The acanthodian Mesacanthidae (*Teneracanthus*) is younger in Belgium (Derycke & Clément, 2006) than in east Gondwana (Australia: Young & Burrow, 2004; Burrow & Young, 2005; and Saudi Arabia: Burrow et al., 2006). They could have dispersed following the west boundary current (WBC) (Paproth et al., 1986; Thorez et al., 2006) and contributed to the faunal interchange between East Gondwana and Euramerica at the end of the early Devonian and then during the Late Devonian (Long, 1986; Young et al., 2010; Janvier & Clément, 2005).

Our knowledge of the abundance and diversity of Famennian acanthodians in Eurasia and Gondwana is highly restricted compared to our knowledge of the chondrichthyans fauna (e.g., Derycke, 1992; Ginter et al., 2002; Ivanov, 1999; Ivanov & Rodina, 2004; Randon et al., 2007; Derycke et al., 2008), thus strongly limiting large faunal comparisons.

Famennian acanthodians are recorded in North America (Gross, 1973), Europe (Valiukevicius, 2000; Esin et al., 2000), China (Zhu et al., 2000), Turkey (Janvier et al., 1984), South Africa, Australia (Long et al., 2004), Morocco (Derycke, 1992; Derycke-Khatir, 2005; Derycke et al., 2008; Ginter et al., 2002) and Iran (Young et al., 2010; Ginter et al., 2010).

Concerning the palaeoenvironment, acanthodians are present in both marine and non-marine facies from the late Ordovician to the Permian (Dineley & Loeffler, 1993). The Late Devonian is a period of radiation for vertebrates and of terrestrialisation for tetrapods. As for actinopterygians (Friedman & Blom, 2006), the acanthodian radiation in more proximal areas might be by iterative invasion.

Levels rich in acanthodian remains are known for example in the Givetian of France (Boulonnais) (Derycke et al., 1995a; Derycke-Khatir, 2005) and of Mauritania (Adrar) (Racheboeuf et al., 2001). In the Boulonnais, the material has been extracted from nodules in grey marls in the upper part of Blacourt Formation. This level corresponds to shelf deposits in the infratidal zone (Pelhate & Poncet, 1988) under a hot and humid continental climate (Chamley, 1988). In the Adrar (Mauritania), the conodont fauna is indicative of shallow environmental conditions and the ostracod fauna indicates a euryhaline warm, and poorly oxygenated environment (Racheboeuf et al., 2001).

The acanthodians of Durnal have been collected in the Evieux Formation considered as a proximal restricted marine or lagoonal environment behind a sand barrier under an arid climate (Thorez et al., 2006) comparable with Ketleri environment considered as a shallow basin under brackish conditions (Luksevics & Zupins, 2004).

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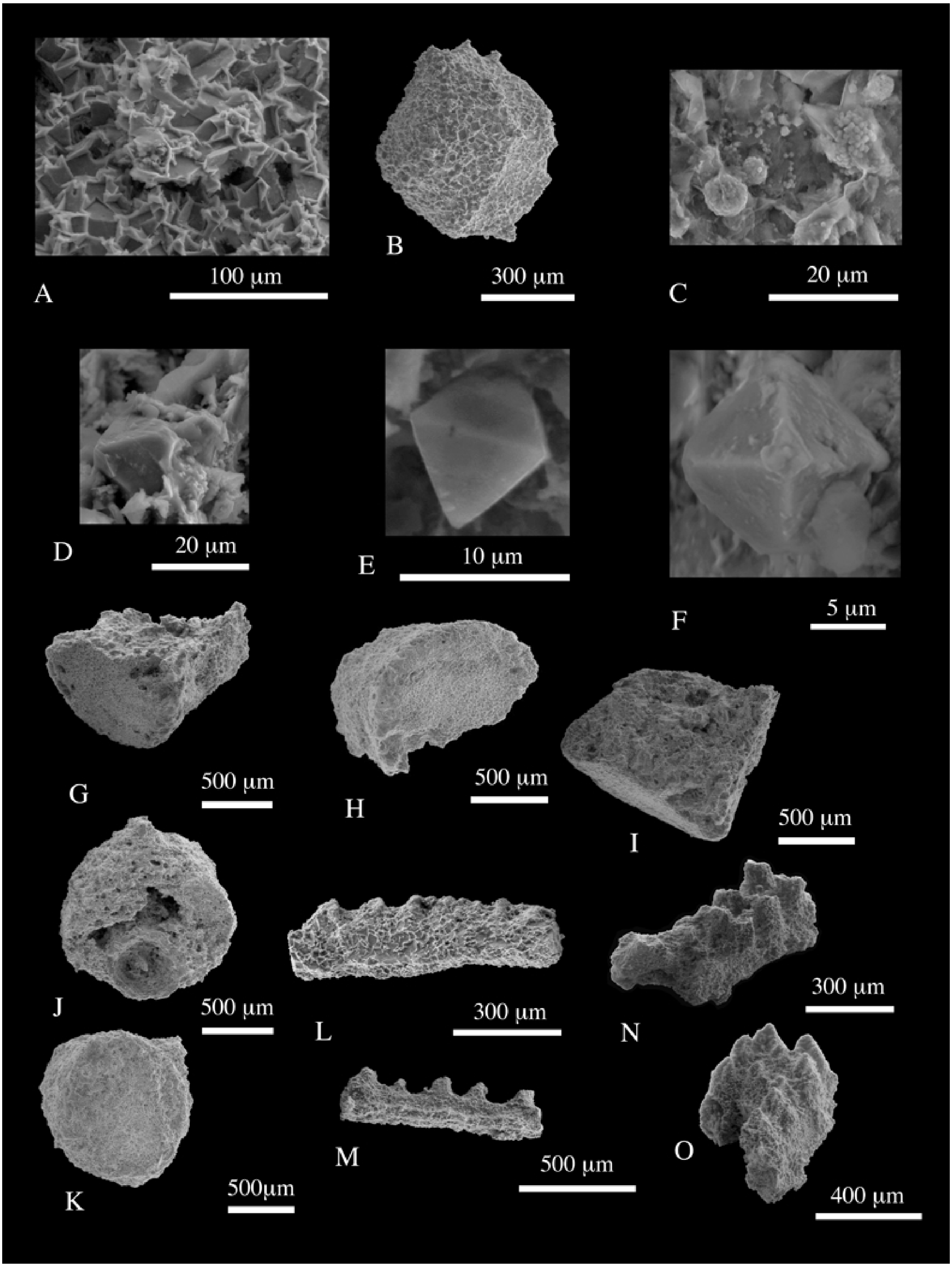

Plate 1. Mineralogy (A-F), Al-substituted goethite/echinoderms (G-K)/conodonts (L-O). A. magnification on Sarcopterygian? tooth 1, photo du-002, plot DU1; B. acanthodian scale, CVUL photo du-104, plot DU3; C-E. enlargement on undetermined & not figured tooth-plate 2, C. framboids of pyrite, photo du-129, D-E. Al-substituted goethite, D. photo du-131, E. photo du-130, plot DU1; F. enlargement on tooth 4, photo du-021, plot DU1; G-I. echinoderm element 1, photos du-061, du-120, du-37, plot DU1; J-K. echinoderm element 2, photo du-038, du-119, plot DU1; L-O. conodont fragment, plot DU3, L. photo du-100; M. photo du-102; N. du-108; O. du-113.

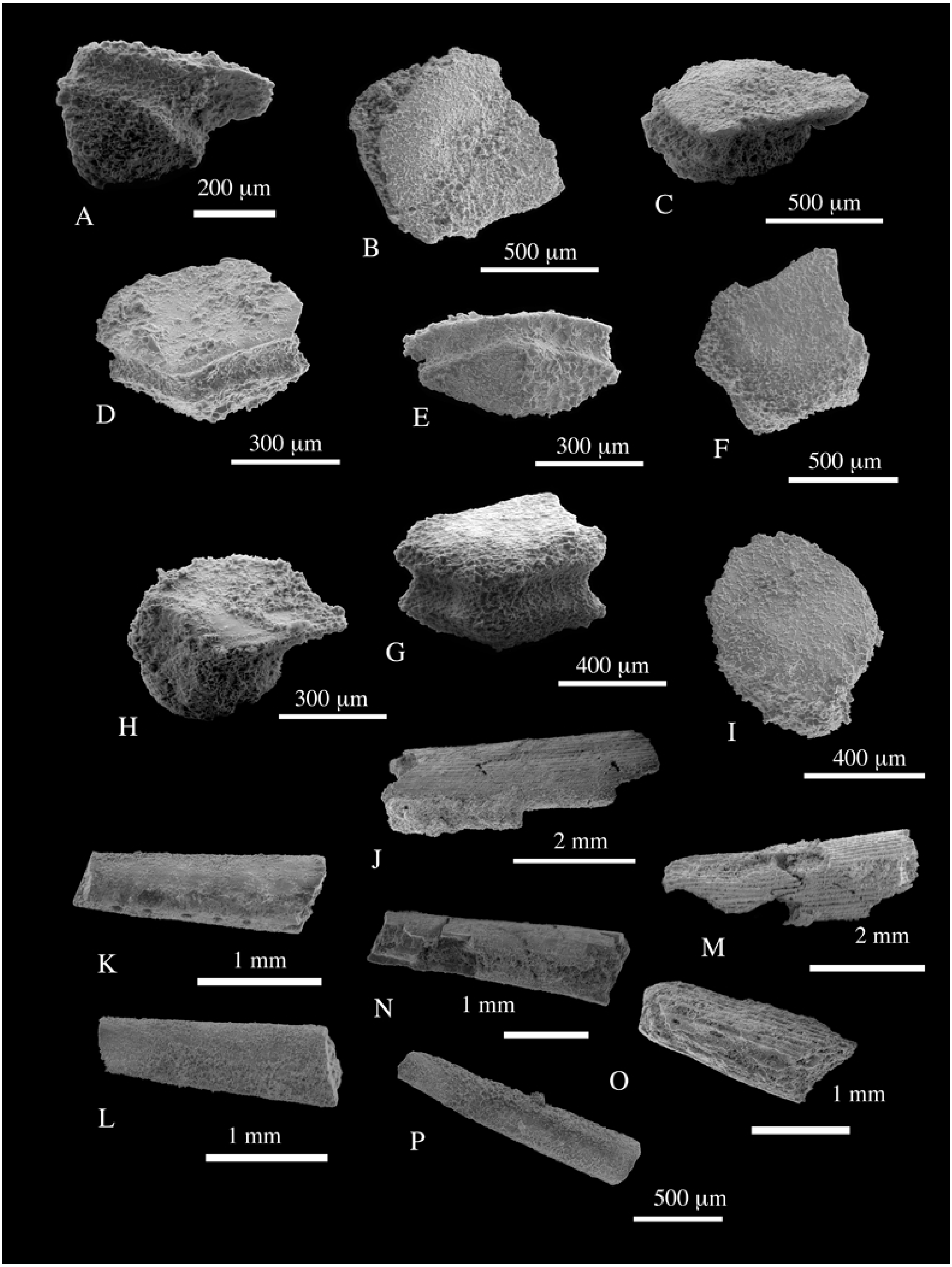

Plate 2. Acanthodian scales (A-I) and spines (J-P). Scales A-I of *Teneracanthus* cf *T. toombaensis*, plot DU3 A. CVUL 116 photo du-109, lateral view; B-C. CVUL 117 photos du-94 and 110; D-E. CVUL 118 photos du-97 and 112; F-G. CVUL 119 photos du-103 and 114; H. CVUL 120 photo du-115; I. CVUL 121 du-107.
Spines J-P, J, M, N, P, *Devononchus* cf *D. tenuispinus*, J. CVUL 122, plot DU2, photo du-73, lateral view; K-L. *Teneracanthus* cf *T. toombaensis* CVUL 123, plot DU 4, photos du-172 et 155, postero-lateral and lateral views; M. CVUL 124, plot DU2, photo 79; N. CVUL 125, plot DU4, photo du-152; O. CVUL 126, plot DU2, photo du-72; P. CVUL 127, plot DU4, photo du-151.

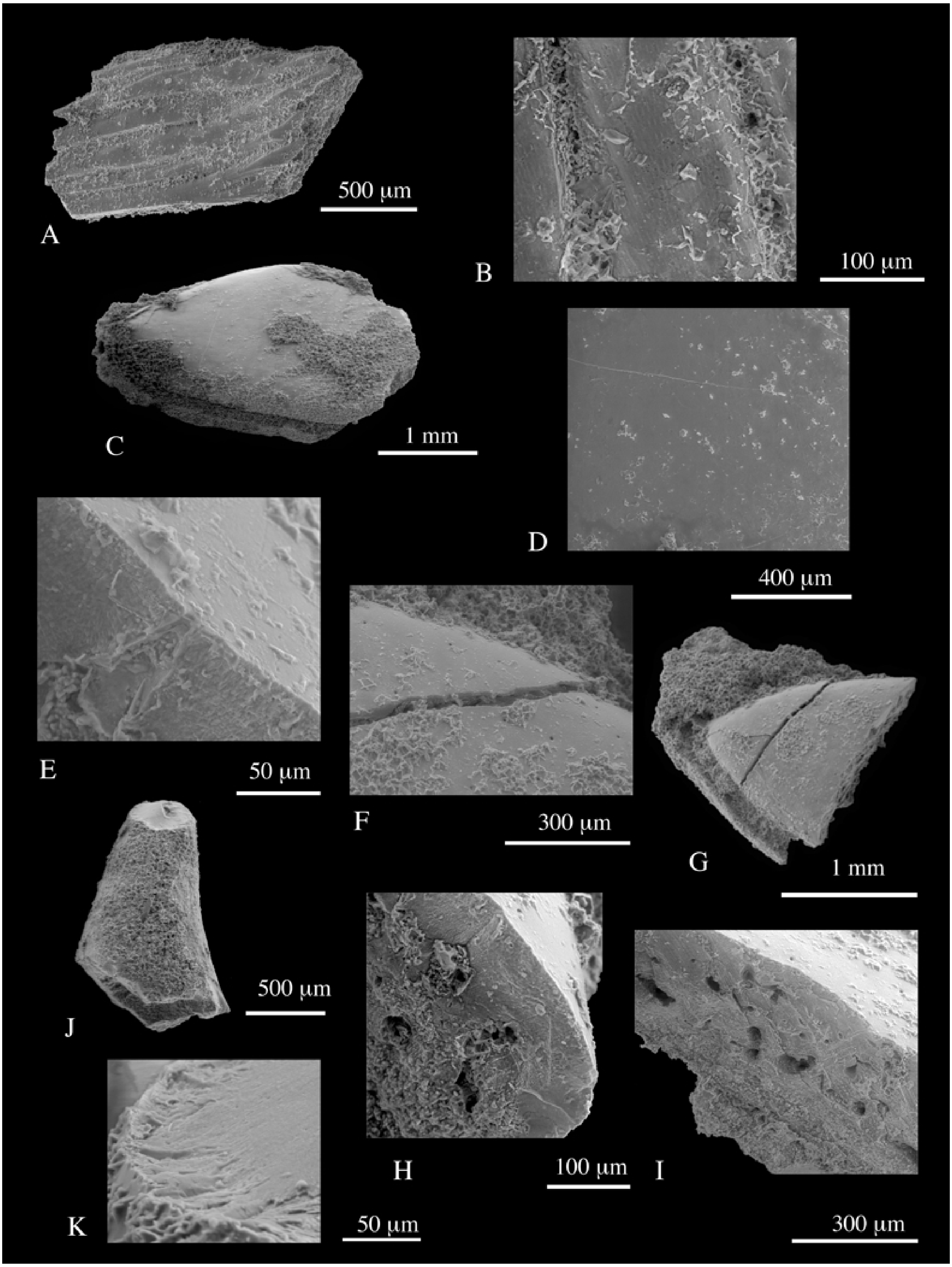

Plate 3. Actinopterygians, Sarcopterygians.
A-B. Actinopterygian scale 3, external view and magnification of the surface, CVUL 128, plot DU1, photos du 51-52.
C-D. Sarcopterygian scale 5, external view and magnification of the surface, CVUL 129, plot DU2, photos du-85 & 78; E-I. Sarcopterygian scale 6, E, H & I magnifications on the broken side, F, G external views, CVUL 130, plot DU2, photos du-88, 84, 83, 90, 86.
J-K. Sarcopterygian? tooth 1, lateral and magnified views, CVUL 131, plot DU1, photo du-1 & 3.