A NEW VERTEBRATE LOCALITY IN THE EIFELIAN OF THE KHUSH-YEILAGH FORMATION, EASTERN ALBORZ, IRAN.

by

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CONTENTS

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RESUME

Un nouveau gisement de Vertébrés a été découvert en 1976 dans la partie inférieure de la coupe-type de la formation de Khush-Yeilagh, dans l'Alborz oriental (Iran). Il s'agit d'une faune très riche et très diverse, concentrée en une couche centimétrique accessible en plusieurs endroits. L'étude préliminaire de cette faune a donné la composition suivante : Placodermes (Phlyctaenilda indet., Groenlandaspididae indet., Coccosteidae indet., *Holonema* sp., Ptyctodontida indet., Antiarcha indet., *Bothriolepis* cf. *kwangtungensis*), Elasmobranchii (Ctenacanthidae indet.), Acanthodii (*Gyracanthus* sp., « *Onchus* » *overathensis*, Ischnacanthiforme indet.), Dipnoi (? Dipteridae indet.), « Crossopterygii » (*Onychodus* cf. *sigmoides*, Holoptychiidae indet., Osteolepididae indet.). Cette faune est sûrement antérieure au Givétien moyen et très probablement d'âge Eifélien moyen ou inférieur. Compte tenu de sa diversité, elle pourra probablement servir de faune de référence pour l'étude des Vertébrés dévoniens en Asie centrale et au Moyen-Orient.

ABSTRACT

A new Devonian vertebrate locality has been discovered in 1976 in the basal part of the Khush-Yeilagh Formation in the eastern Alborz Mountains of Iran. The fossils occur in a band one centimeter thick which is identifiable at other outcrops in the area. A preliminary study of the remains has yielded the following faunal list : Placodermata (Phlyctaenilda indet., Groenlandaspididae indet., Coccosteidae indet., *Holonema* sp., Ptyctodontida indet., Antiarcha indet., *Bothriolepis* cf. *kwangtungensis*), Elasmobranchii (Ctenacanthidae indet.), Acanthodii (*Gyracanthus* sp., « *Onchus* » *overathensis*, Ischnacanthiforme indet.), Dipnoi (? Dipteridae indet.), « Crossopterygii » (*Onychodus* cf. *sigmoides*, Holoptychiidae indet., Osteolepididae indet.). This fauna is older than the Middle Givetian and probably of Middle or Lower Eifelian age. Owing to its diversity, it may prove possible to use it in the future as a reference fauna for the study of the Devonian vertebrates in Central Asia and the Middle East.

INTRODUCTION

The new Devonian fish locality described herein was discovered in May 1976 by four of us (F.G., A.H., P.J. and M.M.) during an exploratory field trip in the Palaeozoic series of the Khush-Yeilagh area of Iran. The 1976 field trip was sponsored by the Geological Survey of Iran and the Centre National de la Recherche Scientifique of France. In May 1977, excavations were made at this locality (by A.B. and P.J.) thanks to the sponsorship and the technical assistance provided by the Department of the Environment of Iran. All specimens collected during this last field trip will, after study, be deposited in the Iran National Museum of Natural History.

Abbreviations : M.G.S.I., Museum of the Geological Survey of Iran, Mehrabad, Tehran, Iran.
M.M.T.T., Muzé-ye Melli-ye Tarikh-e Tabi'i (Iran National Museum of Natural History), Shah Abbas 21, Tehran, Iran.

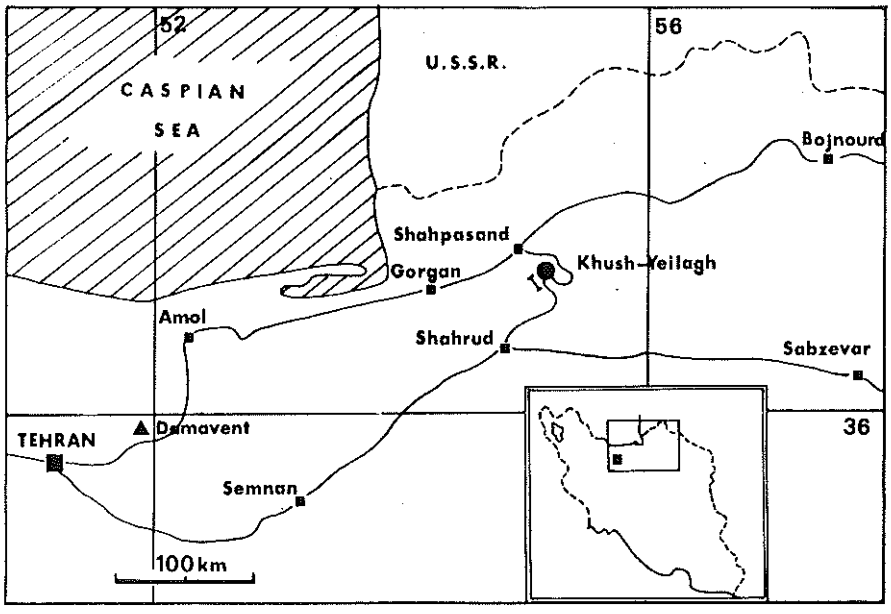

Fig. 1. — Locality map. The type section of the Khush-Yeilagh Formation is indicated southwest of Khush-Yeilagh village.

GEOLOGICAL SETTING

The Khush-Yeilagh area is situated at the boundary between the Central and Eastern Alborz Mountains and between the Mazenderan and Khorassan provinces. The Palaeozoic rocks recorded from this area have been studied in detail by Bozorgnia (1973) and Stampfli (1978) ; the reader is referred to these authors for information concerning tectonics and palaeogeography. In the Khush-Yeilagh area the Middle Palaeozoic is subdivided into three of four formations the age of which is not always perfectly known. The lowermost of them, the Soltan Maidan Formation, is referred to the Silurian. It is followed by the Padeha Formation, referred with doubt to the Lower Devonian. It is overlain by the relatively well-dated Khush-Yeilagh Formation which represents the Middle and Upper Devonian and possibly includes the Tournaisian. The Khush-Yeilagh Formation is, in its turn, overlain by a succession of formations (Mobarak, Bagherabad, Gheselghaleh, Dorud, Ruteh, Gheshlagh, and others) which all belong to the Carboniferous and Permian.

The Vertebrate locality described here lies in the basal part of the Khush-Yeilagh Formation and is particularly well developed in the type section of the formation, on the ridge called Tiré-Gadj-Khopar-Than, about 2 km southwest of Khush-Yeilagh village (fig. 1). Stampfli (1978) recently subdivided the Khush-Yeilagh Formation into seven lithostratigraphic units, the lower three (members 1-3) representing the Middle Devonian. Member 1 rests conformably on the Upper Member of the Padeha Formation. In the Khush-Yeilagh most of the fish remains occur in Member 1 referred by Stampfli (1978) to the Eifelian and Lower Givetian on the basis of the invertebrate fauna. Some very poorly preserved remains of large placoderms have also been collected in Member 5, about 400 meters North of the type section and are suggestive of the Frasnian.

In Member 1, the main fish horizon (Kh1, fig. 2) is a 1-3 centimeter thick bonebed situated within a massive arkosic sandstone layer, about 1.5 meters above the purple conglomerate forming the basal layer of the Khush-Yeilagh Formation. This fish horizon may be followed to the south, where it seems to split into three or four separate horizons, while the arkosic sandstone layer becomes considerably thicker. South of the Yarghli Chechmeh ridge the fish remains of this horizon are more scattered, but of larger size than in the Tiré-Gadj-Ghopar-Than locality. This difference may be due to environmental conditions.

Above the arkosic sandstone layer, there is a series of alternating limestone, marl and calcareous sandstone layers which yielded some fish remains. The green calcareous sandstone overlying the arkosic sandstone yielded oogones of characae, actinopterygian and thelodont scales associated with some badly preserved conodonts which are suggestive of an Emsian-Eifelian age (A.H.). This second fish bearing layer is named here Kh2 (fig. 2).

Finally, the rich brachiopod and trilobite-bearing marly limestone beds of the top part of Member 1 have also yielded remains of acanthodians, elasmobranchs, placo-

derms, actinopterygians and struniiforms (Kh3, fig. 2). They are referred to the Middle Givetian (Brice *et al.*, 1973 ; see also Stampfli, 1978, p. 40, for the complete invertebrate list).

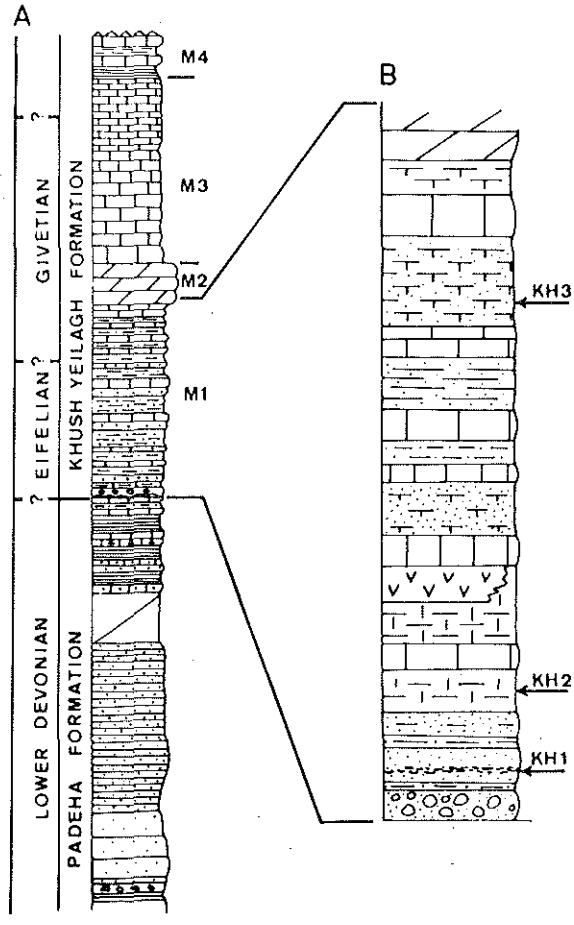

Fig. 2. — Type section of the Padeha and Khush-Yeilagh Formations. A, from Stampfli, 1978. B, more detailed section of Member 1 at the Tiré-Gadj-Ghopar-Than ridge.
Kh1, main fish horizon (bone-bed) in the arkosic sandstone ; Kh2, green marly sandstone containing *Amaltheolepis*-like thelodont scales and Emsian-Eifelian conodonts ; Kh3, marl and marly sandstone containing a rich invertebrate fauna of Middle Givetian age and some fish remains ; M/1-M/4, lithostratigraphical units of the Khush-Yeilagh Formation (Members 1, 2, 3, 4).

The age of the main fish horizon (Kh1) is pre-Givetian : it lies below an invertebrate fauna referred to the Middle Givetian (Stampfli, 1978, p. 40) and the conodonts found beneath it and above the arkosic sandstone may either be referred to the Uppermost Emsian or to the Eifelian (A.H.). The thelodont scales associated with these conodonts are quite similar to those of *Amaltheolepis* from the Eifelian of Spitsbergen (Ørvig, 1969 ; Karatajute-Talimaa, 1978). Considering these facts, the main fish horizon, which is just below the conodont-thelodont assemblage, may reasonably be referred to the Eifelian.

SYSTEMATIC STUDY

1/ PLACODERMATA

ORDER ARTHRODIRA WOODWARD, 1891
SUBORDER PHLYCTAENIOIDEI MILES, 1973 (D.G.)
INFRAORDER PHLYCTAENII MILES, 1973 (Pl. 1, fig. 1 & text fig. 3)

We can ascribe to dolichothoracid arthrodires some tens of isolated plates, all of them being referred to the Phlyctaenii. Many of them, although having a typical phlyctaeniid pattern, cannot be assigned to any particular genus or species. This is the case for the anterolateral, the anterior dorsolateral and the posterior ventrolateral plates. The median dorsal plates, however, indicate the presence of at least two different forms among the Phlyctaenii in this locality.

The first one belongs to the Groenlandaspididae (text fig. 3 E), characterized by its peculiar median dorsal plate with a high and pointed dorsal crest. In lateral view, the dorsal angle of this crest is relatively open and its top is not very high (when compared to forms like *Groenlandaspis seni* Janvier et Ritchie, 1977). Ritchie (1975) suggested that, among the Groenlandaspididae, the median dorsal plate possessed a high crest in early forms — as examplified by *Tiaraspis* (Gross, 1962) — and a low crest in later forms. The median dorsals from Khush-Yeilagh show that relatively low-crested forms existed as early as the Eifelian.

The posterior dorsolateral corresponding to these median dorsal plates have also been recognized (Janvier et Ritchie, 1977, fig. 1 E). They possess the typical high dorsal expansions and the wide angle drawn by the lateral line groove, which bends ventrally behind the radiation center of the plate.

Among the Groenlandaspididae, the earlier forms (e.g. *Tiaraspis*) differ from the latest ones (*Groenlandaspis*) in many details of the trunk armour. An important difference concerns the shape and proportions of the anterolateral plate. In *Tiaraspis*, this plate is quadrangular and does not differ markedly from the same plate of the Phlyctaeniidae (White, 1969). In *Groenlandaspis*, this plate is much lower and more elongate with a shallow pectoral embayment.

Among the Khush-Yeilagh material, all the anterolateral plates referred to Phlyctaenii have the typical shape found in that group and do not show any particular elongation as seen in *Groenlandaspis* (Ritchie, 1975, fig. 2). Consequently, it may be suggested that either none of these plates belong to the groenlandaspidid mentioned above, or that this groenlandaspidid has retained, like *Tiaraspis* the common phlyctaeniid design of the anterolateral plate. In this respect, the groenlandaspidid from Khush-Yeilagh could be a primitive form within that group.

The second type of median dorsal plate (text fig. 3 D) shows no marked difference with that of *Phlyctaenius* (Heintz, 1933) and other Phlyctaeniidae like *Cartieraspis* (Pageau, 1969, pl. 36, fig. 11, 13). It is elongate in shape, rather narrow, and ends posteriorly with a pointed angle. The front end of the plate is truncated and forms a

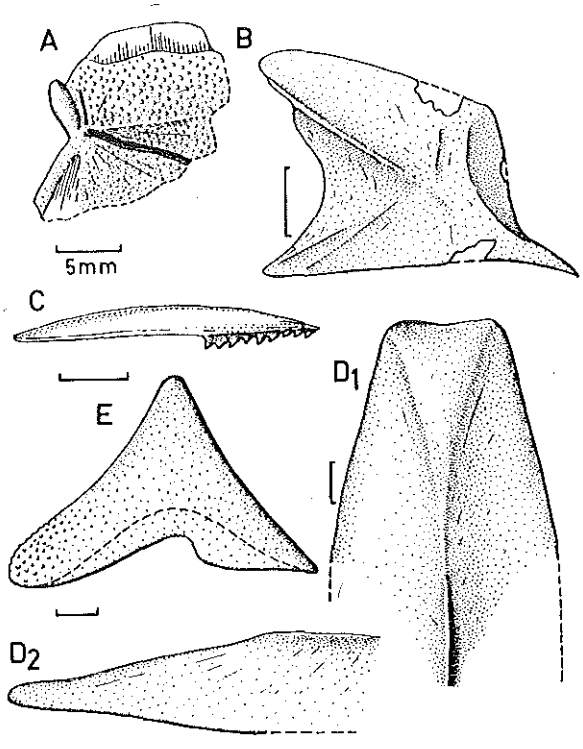

Fig. 3. — Phlyctaenioidei indet., Eifelian, Khush-Yeilagh, Iran. A-D, Phlyctaenii indet. ; A, anterior dorsolateral plate (D.F.Kh1, 0072, M.M.T.T.) ; B, anterolateral plate (D.F.Kh1, 0074, M.M.T.T.); C, spinal plate (D.F.Kh1, 0073, M.M.T.T.) ; D, incomplete median dorsal plate in dorsal (1) and lateral view (2) (D.F.Kh1, 0075, M.M.T.T.) ; E, Groenlandaspididae indet., median dorsal plate, lateral view (D.F.Kh1, 0076, M.M.T.T.), the interrupted line indicates the dorsal limit of the internal cavity.

relatively wide edge when compared to the Spitsbergen phlyctaeniids as examplified by *Dicksonosteus* (Goujet, 1975, fig. 5 A). As in the latter, the radiation center is situated in the posterior third of the plate. The ornamentation is poorly preserved but consists of very small tubercles.

The latter type of median dorsal probably belongs to the same kind of animal as the anterior dorsolateral plate (text fig. 3 A and pl. I, Fig. 1). The plates are similar in size, proportions and ornamentation. On the anterior dorsolateral plate, the groove for the lateral line is wide and converges anteriorly with a crest (« Dorsolateralkante », Gross, 1962), which crosses the plate anteroposteriorly. The front part is badly preserved but shows an articular condyle which seems to be rather flat and slender, like that of *Dicksonosteus* (Goujet, 1975, fig. 5 A ; pl. 3, Fig. 2).

Isolated spinal plates (fig. 3 C) are quite abundant in the Khush-Yeilagh material. They are variable in size but all of them have the same general design and proportions. They are relatively short, when compared to those of e.g. *Arctolepis* (Heintz, 1929 ;

Goujet, 1978), and their free part represents less than half of their total length. They bear mesial hooks like those of *Dicksonosteus*, *Tiaraspis* or *Aggeraspis*.

Among the anterolateral plates (text fig. 3 B), the most common design is suggestive of that found in *Arctolepis*, *Neophlyctaenius* (White, 1969, fig. 2, 18) and the Canadian forms : *Batteraspis*, *Gaspeaspis*, *Cartieraspis* and *Quebecaspis* (Pageau, 1969, pl. 33, Fig. 7-11 ; fig. 22 E, I, L-O). In some of these plates the ridges which divide their surface into quadrants are particularly well marked and a double posterolateral ridge may be observed, as is commonly the case in *Aggeraspis heintzi* (Gross, 1962, fig. 9 Q-T). Some other anterolateral plates are very small (about 1 cm2) and differ from the larger ones by their proportions. It is, for the time being, impossible to decide whether they belong to young individuals or represent a different taxon. Pageau (1969), however, has clearly shown that considerable variations in size and shape occur in the anterolateral of the Phlyctaeniidae.

INFRAORDER BRACHYTHORACI STENSIO, 1944
FAMILY HOLONEMATIDAE OBRUCHEV, 1932 (E.M.K.)

Genus *HOLONEMA* Newberry, 1889

Holonema sp.

(Pl. 1, fig. 10, 13, 16, 21, & text fig. 4)

This new Iranian material of *Holonema* is represented by the imprints of several isolated plates of the head shield and the trunk shield (central, marginal, postmarginal, nuchal, paranuchal, suborbital, posterior superognathal, anterior dorsolateral, anterolateral and spinal plates), and a number of fragments. Two *Holonema* species can be used for comparison : the most completely known Frasnian *H. westolli* Miles, from the Gogo Formation in Australia (Miles, 1971), and the Eifelian *Holonema* n. sp. from the Narva (Narova) Formation of Estonia and Leningrad district. The latter species (studied by E. Mark-Kurik, in preparation) is closest in age to the Khush-Yeilagh *Holonema* species. Most of the other *Holonema* species are geologically younger and are poorly known or mainly described on the basis of the plates of the trunk armour.

When compared to *H. westolli*, the central plates from Khush-Yeilagh (text fig. 4 A, B) possess a shorter posterior division and a shorter median contact with the contralateral central plate. In the marginal plate (text fig. 4 E), all the edges are occupied by overlap areas ; here is no space left for the spiracular opening (cf. Miles, 1971). That part of the anterior division between the infraorbital (*i.o.c.*) and the postmarginal (*p.m.c.*) canals is much shorter ; the posterior division extends deeper into the paranuchal plate and the postmarginal canal is more anteriorly directed. In the postmarginal plate (text fig. 4 G), the lateral edges form an almost right angle ; consequently, the posterolateral angles of the skull roof were well-pronounced and situated more ante-

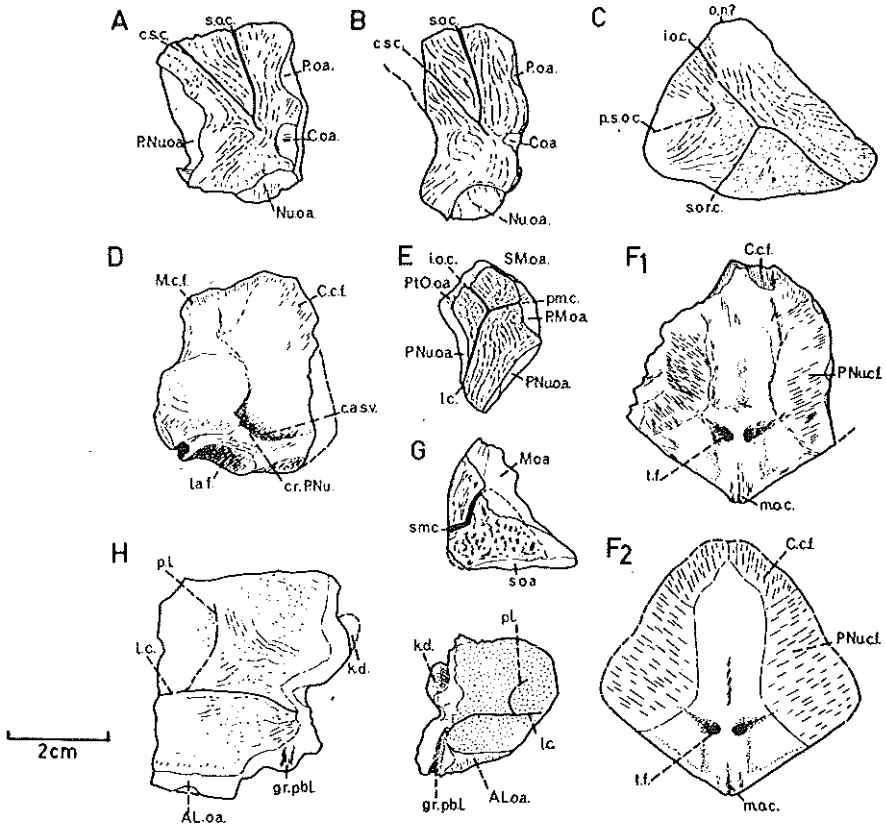

Fig. 4. — *Holonema* sp., Eifelian, Khush-Yeilagh, Iran. A, B, left central plates (D.F.Kh1, 0078, M.M. T.T.) ; C, right suborbital plate (D.F.Kh1, 0079, M.M.T.T.) ; D, right paranuchal plate, ventral view, juvenile individual (D.F.Kh1, 0080, M.M.T.T.) ; E, left marginal plate (D.F.Kh1, 0081, M.M.T.T.) ; F, nuchal plate, ventral view, (F1, D.F.Kh1, 46, M.G.S.I. ; F2, attempted reconstruction of the whole plate) ; G, left post-marginal plate (D.F.Kh1, 47, M.G.S.I.) ; H, right anterior dorsolateral plate (D.F.Kh1, 48, M.G.S.I.) ; I, left anterior dorsolateral plate, juvenile individual (D.F.Kh1, 0082, M.M.T.T.).

AL. o.a., overlap area for the anterolateral plate ; *ca.s.v.*, cavity for the supravagal process ; *C.c.f.*, contact face for the central plate ; *C.o.a.*, overlap area for the central plate ; *c.s.c.*, central sensory canal ; *cr. PNu*, paranuchal crista ; *gr.pbl.*, groove for postbranchial lamina of anterior lateral plate ; *i.o.c.*, infraorbital sensory canal ; *kd.*, condyle ; *l.a.f.*, lateral articular fossa ; *l.c.*, main lateral line ; *M.c.f.*, contact face for the marginal plate ; *m.o.c.*, median occipital crest ; *M.o.a.*, overlap area for the marginal plate ; *Nu.o.a.*, overlap area for the nuchal plate ; *o.n.* ?, presumed orbital notch ; *p.l.*, anterior dorsolateral sensory-line ; *p.m.c.*, postmarginal canal ; *PM.o.a.*, overlap area for the postmarginal plate ; *PNu.c.f.*, contact field for the paranuchal plate ; *Pnu.o.a.*, overlap area for the paranuchal plate ; *P.o.a.*, overlap area for the pineal plate ; *p.s.o.c.*, postsuborbital canal ; *PtO.o.a.*, overlap area for the postorbital plate ; *SM.c.* submarginal canal ; *SM.o.a.*, overlap area for the submarginal plate ; *so.a.*, subobstantic area ; *s.o.c.*, supraorbital canal ; *s.o.r.c.*, supraoral canal ; *t.f.*, transverse fossa.

riorly than in *H. westolli*. The largest nuchal plate (text fig. 4 F) indicates that the contact faces for the paranuchal plates are wider (*P.Nuc.f.*), the plate itself shorter, and its posterior division more prominent. The structure of the visceral surface of the paranuchal plate resembles closely that of *H. westolli*. This is also true for the suborbital plate (text fig. 4 C), and the posterior superognathals (pl. I, fig. 10-12). The largest fragment of anterior dorsolateral plate (text fig. 4 H) has a higher ventral portion than that of *H. westolli*. The second specimen (text fig. 4 I ; pl. I, fig. 16) probably belongs to a younger and smaller individual of the same species. Its ornamentation consists of tubercles. A fragment of the anterior lateral plate (pl. I, fig. 13) suggests that this plate was slender anteriorly, and that the postbranchial notch of the anterior edge was deeper. Judging from two poorly preserved fragments, the spinal plate seems to have been long and slender, as is the case in *H. westolli* and in the Eifelian *H.* n. sp.

The Khush-Yeilagh Holonematid resembles the Eifelian *H.* n. sp. from the U.S.S.R. by the shape of the central plates, by the comparatively short anterior portion of the marginal plate, by the more widely diverging postsuborbital and supraoral canals of the suborbital plate, and by the higher ventral division of the anterior dorsolateral plate. The ornamentation is typical for *Holonema*, consisting of tuberculated ridges and rows of tubercles. Tuberculate ornamentation prevails in smaller individuals ; it becomes more ridged in larger and older specimens.

The *Holonema* species from Khush-Yeilagh has a comparatively short skull roof with pronounced posterolateral angles, and probably represents a new species. It differs from *H. westolli* and seems to be different from the other new species mentionel here from the Eifelian of Estonia and Leningrad district, although it shares with the latter a certain number of characteristics.

FAMILY COCCOSTEIDAE TRAQUAIR, 1888 (D.G.)

Coccosteidae gen. et sp. indet.

(Pl. 1, fig. 2, 3, 6, 7 & text fig. 5)

Various isolated plates can be assigned to coccosteid arthrodires, but, to date, it is still impossible to decide whether they have to be referred to one single form or to several different genera and species. For this reason, this material is summarily presented here without any precise assignment. Because the plates of coccosteids have a relatively wide range of variation (as shown by *Coccosteus cuspidatus*, Miles et Westoll, 1968), the minor differences observed between isolated plates from Khush-Yeilagh are probably not taxonomically valuable.

As for the other arthrodires, the plates of the trunk armour are most abundant in this locality. The median dorsal plate (text fig. 5 A ; pl. I, fig. 3) is fairly common and quite characteristic. Its proportions are somewhat similar to those of the median dorsal of *Coccosteus cuspidatus* Miles et Westoll, 1968, fig. 28), but the median posterior process is lacking. This process is present in the majority of the coccosteidae (*sensu*

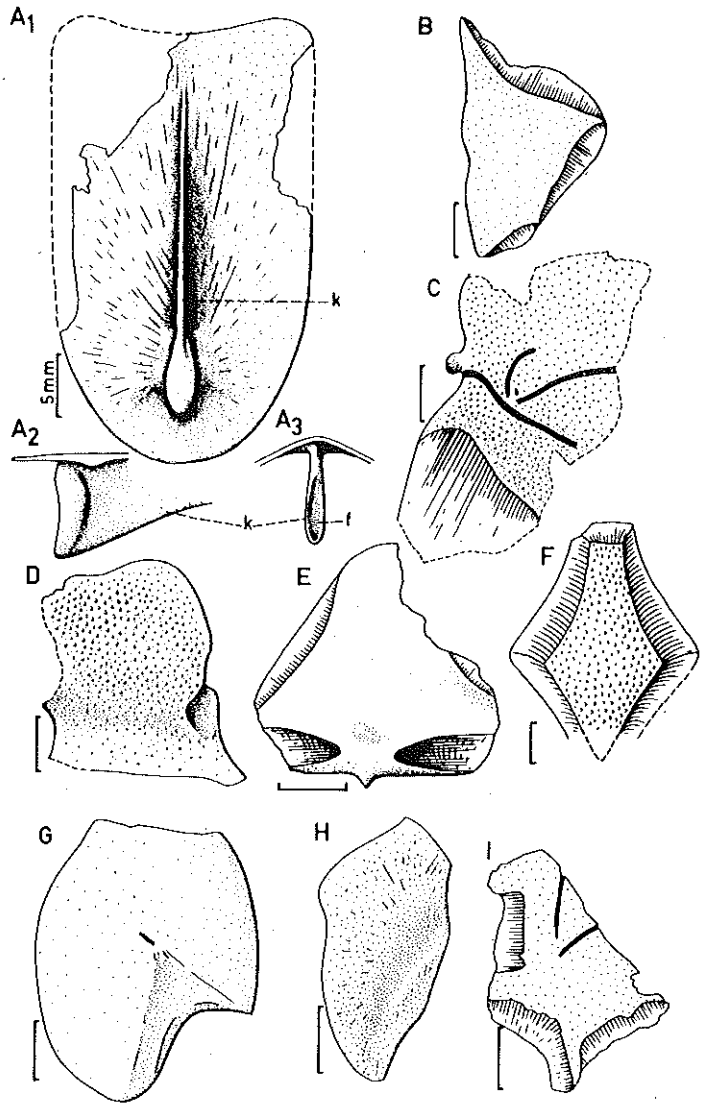

Fig. 5. — Coccosteidae indet., Eifelian, Khush-Yeilagh, Iran. A, median dorsal plate in ventral (1), lateral (2) and posterior (3) view (2, 3, posterior part only) (D.F.Kh1, 0083, M.M.T.T.) ; B, right posterior dorsolateral plate (D.F.Kh1, 0084, M.M.T.T.) ; C, left anterior dorsolateral plate (D.F. Kh1, 0085a, M.M.T.T.) ; D, right anterolateral plate (D.F.Kh1, 0086, M.M.T.T.) ; E, nuchal plate, ventral view (D.F.Kh1, 0087, M.M.T.T.) ; F, posterior median ventral plate (D.F.Kh1, 0102, M.M.T.T.) ; G, left anterior ventrolateral plate (D.F.Kh1, 0089, M.M.T.T.) ; H, left posterior ventrolateral plate (D.F.Kh1, 0090, M.M.T.T.) ; I, right central plate (D.F.Kh1, 0091, M.M.T.T.).

f., fossa on the posterior edge of the keel ; *k.*, ventral keel of the median dorsal plate.

Obruchev, 1967, p. 202). The median dorsals from Khush-Yeilagh have a rounded posterior end, like that of *Watsonosteus fletti* (Miles et Westoll, 1968, fig. 7 C). On the visceral surface, the keel (*k.*, text fig. 5 A1-3) is well developed but not as high as in the reference species *C. cuspidatus*. On one of the best preserved plates, the carinal process is rather low but there is a well-marked posterior fossa (*f.*, text fig. 5 A 3), as in other coccosteids.

The other plates are less taxonomically significant, as is often the case in coccosteids. The anterior dorsolateral plate (text fig. 5 C ; pl. I, fig. 2) is known from a relatively well preserved specimen. Its external surface is, as usual in coccosteids, evenly tuberculated. It shows the forked groove for the main lateral line of the body ; the ventral line runs obliquely across the surface of the bone from the condylar region to the lower third of the posterior margin. The dorsal groove branches off from this main line in the midpart of its course and reaches the upper third of the posterior margin. A supernumerary groove exists : it is more superficially marked on the surface of the bone ; it branches off from the same point as the main lateral line groove, and has a curved course.

A posterior lateral plate (text fig. 5 B) does not show any particular difference with that of *C. cuspidatus* (Miles et Westoll, 1968, fig. 31 H), but differs markedly from that of the other coccosteids (Miles, 1966, fig. 13).

The anterior lateral plate (text fig. 5 D) differs from that of *C. cuspidatus* to a higher degree. Its ventral margin, which comes into contact with the spinal plate, is long and the general morphology of the plate is close to that of *Millerosteus minor* (Miles, 1964, fig. 8 C). The same long spinal edge is present on the anterior ventrolateral (text fig. 5 G) which resembles that of *Eldenosteus* and *Millerosteus* (Miles, 1964, fig. 2 A-B ; fig. 8 D).

The posterior median ventral plate (text fig. 5 F) and the posterior ventrolateral plate (text fig. 5 H) have the general coccosteid design. However, the posterior ventrolateral does not possess the spine produced by the lateral edge of its ventral lamina, which exists in both *Coccosteus* and *Millerosteus* (Miles, 1964, fig. 8). In this respect, it has the same morphology as that of *Eldenosteus* (Miles, 1964, fig. 2) or *Plourdosteus*.

The plates of the skull roof are represented by complete nuchals (text fig. 5 E), a fragmentary central, and part of the lateral margin of a skull-roof with connected postorbital and marginal plates (pl. I, fig. 6). All these plates are so similar to corresponding ones of *C. cuspidatus* that one would have recognized a specific identity if the trunk plates were unknown.

A complete suborbital plate in internal aspect (pl. I, fig. 7) differs markedly from the known suborbital plates of other Coccosteidae by the wide orbital embayment, the narrow anterior « handle », and a high and short posterior « blade ». These features could lead us to separate this specimen from the other coccosteid skull elements found at Khush-Yeilagh, and place it in a different taxon.

The extensive study of all the material collected from Khush-Yeilagh will probably reveal the presence of several coccosteid taxa.

ORDER PTYCTODONTIDA GROSS, 1932 (P.J.)

Ptyctodontida indet.

(Pl. 1, fig. 15)

Isolated tooth plates of relatively large ptyctodontids (pl. I, fig. 15) are fairly abundant among this material, but no other dermal bones of the head or the trunk have been identified with certainty. Therefore, it would be hazardous to assign a generic name to these specimens, since tooth plates of ptyctodontids are known to be taxonomically rather atypical (Miles et Young, 1977). In our material, the upper tooth plates generally have an acute anterior end. In general, they have no shearing edge (except in the region of the beak) and show relatively broad tritorial surfaces. In this respect, they more closely resemble the tooth plates of *Ptyctodus*.

ORDER ANTIARCHA COPE, 1885 (P.J.)
FAMILY ? BOTHRIOLEPIDIDAE COPE, 1886

Genus *BOTHRIOLEPIS* Eichwald, 1840

Bothriolepis cf. *kwangtungensis* P'an, 1964

(Pl. 1, fig. 4 & text fig. 6)

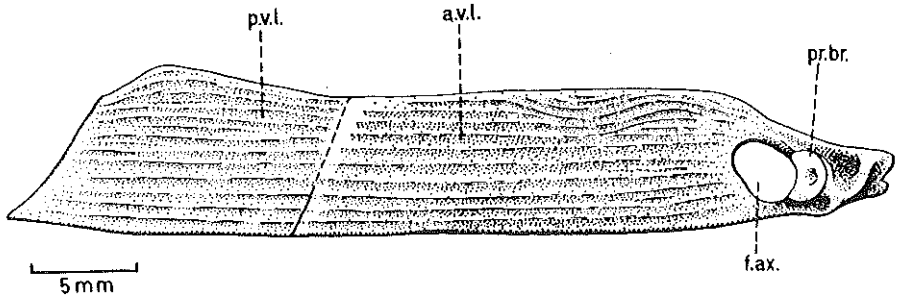

Fig. 6. — *Bothriolepis* cf. *kwantungensis* P'an, Eifelian, Khush-Yeilagh, Iran. Right anterior and posterior ventrolateral plates, lateral view (reconstruction based on the specimens D.F.Kh1, 0093 and 0094, M.M.T.T.).
avl, pvl, anterior and posterior ventrolateral plates respectively ; *f.ax.*, axillar foramen ; *pr.br.*, brachial process.

Several trunk plates of a very small antiarch from Khush-Yeilagh are strikingly similar to the corresponding plates of *Bothriolepis kwangtungensis* P'an (1964, pl. 6-7) from the Middle Devonian of the Mangzixia series, Taihepo, Kwangtung province of China. This species differs from all other known antiarchs by the considerable elongation of the anterior plates of the trunk armour, whereas the posterior ones remain

relatively short. The presence of this derived characteristic in both forms may suggest that they are, at least, more closely related to each other than to any other species of this genus. In the Khush-Yeilagh form, like in *B. kwangtungensis*, the ornamentation of the plates consists of thin, sinuous, more or less parallel ridges sometimes turning into elongate tubercles.

All the plates recorded from our material seem to belong to individuals of nearly the same size. The reconstruction of the two ventrolateral plates (text fig. 6) is based on two plates found on the same block (see the anterior ventrolateral, pl. I, fig. 4) and about 5 cm from each other. It shows clearly that the anterior ventrolateral plate (AVL) is more than twice as long as the posterior ventrolateral one (PVL). The plates of the pectoral appendages, however, differ somewhat from those of *B. kwangtungensis*. The central dorsal plate of the proximal division of the pectoral appendage is narrower proximally in the Khush-Yeilagh form than in the Chinese one. Unfortunately, no plate of the skull roof of this small antiarch has been found in Khush-Yeilagh.

Antiarcha indet.

(Pl. 1, fig. 9)

Some other trunk plates (pl. I, fig. 9) belong to a different antiarch taxon. It is much larger than *B.* cf. *kwangtungensis* and shows the typical antiarch vermiculate ornamentation. A well preserved posterior ventrolateral plate shows a pronounced angulation between the lateral and ventral laminae (about 80° in the midpart) and a serrated ventrolateral edge. It is more suggestive of the corresponding plate in *Gerdalepis rhenana* (Gross, 1941) than of that in typical *Bothriolepis* species. There again, the specimens available are not sufficient for a more precise determination.

2/ ELASMOBRANCHII (P.J.)

Some spines having an ornamentation of the *Ctenacanthus* type have been found in the Khush-Yeilagh fauna (pl. I, fig. 20). They differ from most of the Upper Devonian *Ctenacanthus* spines by their rounded anterior edge.

3/ ACANTHODII (P.J.)

ORDER INDET.

Genus *GYRACANTHUS* Agassiz, 1837

***Gyracanthus* sp.**

(Pl. 1, fig. 5 & text fig. C & D)

We refer to this genus a great number of flattened and more or less curved spines, ornamented with thin parallel ridges which form chevrons on the anterior edge. These spines have a large internal cavity ending in their distal part (pl. I, fig. 5). Some of them have a straight anterior edge (text fig. 7 C) and may have been situated in front of the

median fins, whereas others have a strongly curved anterior edge (fig. 7 D) and were probably attached to the shoulder girdles in front of the pectoral fins. The spines of the former type possess a narrow groove in the middle of their posterior face (text fig. 7 C2). Again, the taxonomic value of the spines referred to the genus *Gyracanthus* is uncertain. These spines are mainly known from the Upper Devonian and Lower Carboniferous, but may also occur in the Lower Devonian.

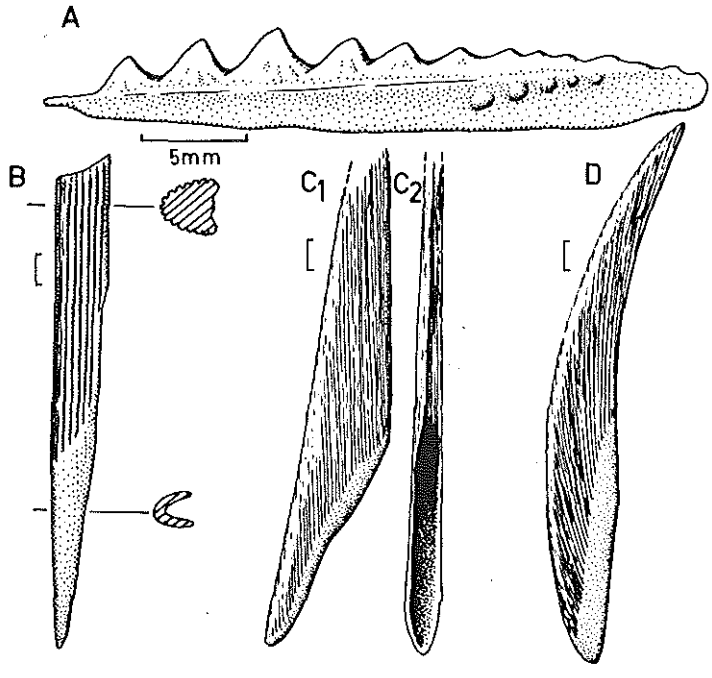

Fig. 7. — Acanthodii, Eifelian, Khush-Yeilagh, Iran. A, Ischnacanthiforme indet., right jaw bone in medial view (D.F.Kh1, 0097, M.M.T.T.) ; B, *« Onchus » overathensis* Gross, median spine, lateral view an horizontal sections (D.F.Kh1, 0098, M.M.T.T.) ; C, D, *Gyracanthus* sp. ; C, median spine in lateral (1) and posterior (2) view (D.F.Kh1, 0099, M.M.T.T.) ; D, lateral spine in lateral view (D.F.Kh1, 0100, M.M.T.T.).

Genus *« ONCHUS »* Agassiz, 1837

« Onchus » overathensis Gross, 1937

(Text fig. B)

An incomplete large spine (text fig. 7 B) is strikingly similar to that described by Gross (1937, pl. 8, fig. 8) from the Emsian of Overath under the name *Onchus overathensis*. Without discussing the value of the generic name *« Onchus »*, we may reasonably assume that the specimen from Khush-Yeilagh belongs to a species which is very close — if not the same — to the German one. This spine is probably a median

fin spine. It is hollowed by a canal and its posterior face is slightly concave, with a median ridge. The ornamentation consists of rounded, parallel ridges.

ORDER ISCHNACANTHIFORMES BERG, 1940

Ischnacanthiformes indet.

(Text fig. A)

A badly preserved jaw bone (text fig. 7 A) may be referred to an indetermined Ischnacanthiform. It bears triangular teeth and a row of blunt tubercles on the posterior part of its medial surface. It recalls *Acanthodopsis* but also resembles somewhat *Atopacanthus* (Ørvig, 1957) and *Persacanthus* (Janvier, 1976).

Finally some dermal shoulder girdles (pl. I, fig. 8) with a spine ornamented with convergent ridges, may belong to a climatiid acanthodian. Their mesial aspect clearly shows the cavity which housed the endoskeletal shoulder girdle.

4/ DIPNOI (M.M.)

ORDER ? DIPTERIFORMES LEHMAN, 1966

? Dipteriformes indet.

(Pl. 1, fig. 18-19)

Several lungfish tooth plates have been found among the Khush-Yeilagh specimens. Some of them are very large (about 5 cm long) and others are medium sized (about 1 cm long), but all are typical tooth plates with ridges formed by fusion of tubercle rows. In this respect, these lungfishes have reached the level of specialization of e.g. *Dipterus valenciennesi*. In the largest specimens (pl. I, fig. 18-19), there are 7 or 8 rows of blunt denticles which fade away in the worn part of the tooth plate. On the contrary, the smaller tooth plates show distinct rows of cusp-like denticles which remain visible even in the posterior part. In the large upper tooth plates, the outermost and the innermost rows of denticles subtend an angle of about 35°. In a relatively small lower tooth plate, these rows subtend an angle of about 95° and the ridges are worn out in the mesial part of the specimen.

These tooth plates, although being quite variable in shape and size, probably belong to the same species. The difference between the wear of the small and the large ones may be due to a change in the diet of the fish during growth.

At first glance, the upper tooth plates from Khush-Yeilagh are strikingly similar to those of *Stomiahykus thlaodus* Bernacsek (1977, pl. 2) from the Eifelian of the Yukon Territory, Canada. The number of ridges is approximately the same (7 in *S. thlaodus*) and in both cases, these ridges turn distally into rows of blunt denticles. They also somewhat recal the tooth plates of *Chirodipterus australis* Miles (1977) but are much more elongate in shape.

5/ « CROSSOPTERYGII » (P.J.)

ORDER OSTEOLEPIFORMES JARVIK, 1942
FAMILY OSTEOLEPIDIDAE COPE, 1889 (Pl. 1, fig. 14)

The osteolepids are represented by a few skeletal elements e.g. a shoulder girdle (pl. I, fig. 14), a snout, a lower jaw and a gular plate. The characteristics observed on the snout, especially the position of the pineal foramen, the size of the orbital notch and of the prenasal fossa, are suggestive of *Thursius* (Jarvik, 1948 ; Vorobjeva, 1977). The cleithrum resembles that of the Middle Devonian osteolepids from Scotland, namely *Osteolepis* and *Thursius*.

ORDER POROLEPIFORMES JARVIK, 1942
FAMILY HOLOPTYCHIIDAE OWEN, 1860 (Pl. 1, fig. 17)

Dermal bones of large holoptychiids are fairly abundant in this fish horizon. One of the most characteristic specimens is a well preserved cleithrum (pl. I, fig. 17) which resembles very much that of *Glyptolepis baltica* Gross (1936, fig. 3, 8). Some cycloid scales ornamented with ridges are also referred to a holoptychiid.

ORDER STRUNIIFORMES JESSEN, 1966
FAMILY ONYCHODONTIDAE NEWBERRY, 1857

Genus *ONYCHODUS* Newberry, 1857
Onychodus cf. *sigmoides* Newberry, 1857

A parasymphysial tooth whorl and several tooth-bearing dermal bones are referred to as *O.* cf. *sigmoides*, a species known mainly from the Middle Devonian of the eastern United States. As in this species, the teeth of the dentary and of the maxillary are numerous, slender and straight. The parasymphysial teeth are normaly pointed, without any harpoon-like tip. They are strikingly similar, in shape and size, to those of *O. sigmoides.*

CONCLUSIONS

This vertebrate faunal assemblage is composed of two previously distinct groups. One group is characteristic of wholly marine facies, and the other is characteristic of the « Old Red Sandstone » facies. The latter facies has traditionnaly been considered both continental and fresh water in origin, but it seems to be a marine tidal flat facies in many cases (Goujet, 1978).

This preliminary study already leads to the following conclusions :

1/ The presence of typical coccosteid arthrodires of relatively small size is suggestive of an early Middle Devonian age (the Coccosteidae are to date unknown in the Lower Devonian), but the abundant phlyctaeniids recall the early Devonian fish faunas of Europe and North America. Phlyctaeniids, however, occur in the Middle Devonian and even in the Frasnian in a restricted number of localities. The coccosteids from Khush-Yeilagh seem to be quite similar to those of the Upper Eifelian localities of Scotland. The phlyctaeniids, although difficult to determine on the basis of detached plates, are suggestive of those described from the Upper Emsian or Lower Eifelian of the Gaspé Sandstone of Québec. The groenlandaspid resembles more the Lower Devonian *Tiaraspis* than the Upper Devonian groenlandaspids. Finally, the holonematid, probably belonging to the genus *Holonema* itself, resembles more closely an undescribed Eifelian form from Estonia than the Upper Devonian forms.

2/ The antiarchs from Khush-Yeilagh are also more suggestive of Middle Devonian forms than of Upper Devonian ones. The genus *Gerdalepis*, if correctly determined among the material, would rather indicate an Eifelian or Givetian age. The small *Bothriolepis* cf. *kwangtungensis* would also indicate a Middle Devonian age.

3/ The elasmobranch and acanthodian remains give comparatively poor information, with the exception of « *Onchus* » *overathensis* which may indicate an Emsian or Eifelian age.

4/ The dipnoan tooth plates are surprisingly large for an early Middle Devonian age. However, Eifelian forms such as *Stomiahykus thlaodus* may reach nearly the same size and show quite a similar tooth plate pattern.

5/ The onychodontid struniiform from Khush-Yeilagh is more suggestive of *O. sigmoides*, from the Middle Devonian of the United States, than of the Upper Devonian *Onychodus* species from Europe and Asia. The specimens referred to an holoptychiid porolepiform can hardly be used for stratigraphical purposes. However, they strongly resemble the corresponding bones of the Middle Devonian *Glyptolepis baltica*. Finally, the few fragments of osteolepid recorded from this locality may possibly be referred to the genus *Thursius*, known in the Baltic area as early as the Middle Eifelian.

6/ Most of the groups represented in this fish horizon are usually considered as having a world-wide distribution, since they are found in North America, Europe, Western Asia and Australia. However, this distribution seems to follow the Tethyan (or paleo-Tethyan) margin of the proto-Gondwanian land mass. The more and more precise data we receive now on the Middle Devonian of China, for instance, do not fully confirm the supposed world-wide distribution of the Devonian fish groups. The holonematids and the coccosteids seem to be lacking in the rich Devonian localities of China, whereas the antiarchs seem to be more abundant and more diversified throughout the Devonian series, than in any of the North America, European and Australian localities. A species-to-species comparison of the Khush-Yeilagh fauna with other Middle Devonian faunal assemblages of Asia and Europe will probably permit in the future a better

understanding of the provincial affinities of the Oriental Alborz region. For the time being, the only remarkable form of this fauna, from a palaeobiogeographical point of view, is the small antiarch resembling *B. kwangtungensis*. In fact, it shows a specialization (the lenghtened anterior and shortened posterior plates of the thorax) which has never been encountered elsewhere than in *B. kwangtungensis* itself, restricted to a locality of the Kwangtung region in China. If these two antiarchs are more closely related to each other than to any other antiarch, and if they represent, as it seems, a group of bothriolepids having a restricted geographical distribution, it may be concluded that a close relation existed between China and Northeastern Iran in the Middle Devonian. This fits relatively well the conclusions reached by Stampfli (1978, p. 278, fig. 98). In fact, Iran and Central Cina may have represented two closely set points of the Tethyan margin. However, the great similarity between the other fishes of Khush-Yeilagh and the forms known from the Middle Devonian of Eastern Europe must be kept in mind.

7/ The most striking feature of the taphonomy of the Khush-Yeilagh fish horizon is that it contains representatives of practically all the groups of Devonian gnathostomes (except the actinopterygians, but this may be due to the small size of their bones and scales, which are difficult to trace in this relatively coarse sandstone). Usually, the Devonian detritic facies contain more antiarch, groenlandaspidid and osteolepid remains than coccosteid, holonematid or dipnoan remains which are often restricted to more typically marine facies. Of course, exceptions may occur. Consequently, this assemblage of fishes belonging to different ecosystems suggests that the remains have been accumulated, after a short transportation, by currents or waves.

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PLATE I

All the specimens come from the main fish horizon (Kh1) of the Tiré-Gadj-Ghopar-Than ridge, Khush-Yeilagh, Iran.

Fig. 1 - Phlyctaeniida indet., right anterior dorsolateral plate (D.F.Kh1, 007, M.M.T. T.). x 3/2.

Fig. 2 - Coccosteidae indet., right anterior dorsolateral plate (D.F.Kh1, 0085b, M.M. T.T.). x 2.

Fig. 3 - Coccosteidae indet., median dorsal plate, (D.F.Kh1, o101, M.M.T.T.) ventral view. x 1.

Fig. 4 - *Bothriolepis* cf. *kwangtungensis* P'an, right anterior ventrolateral plate (D.F. Kh1, 0093, M.M.T.T.) ventrolateral view. x 2.

Fig. 5 - *Gyracanthus* sp., lateral spine (D.F.Kh1, 0103, M.M.T.T.), lateral view. x 1.

Fig. 6 - Coccosteidae indet., right lateral part of the skull-roof (D.F.Kh1, 0104, M.M. T.T.), ventral (6) and dorsal (6') view. x 3/2.

Fig. 7 - Coccosteidae indet., right suborbital plate (D.F.Kh1, 0105, M.M.T.T.), medial view. x 3/2.

Fig. 8 - Acanthodii indet. (? climatiiform), right dermal shoulder girdle (D.F.Kh1, 0106, M.M.T.T.), medial view. x 1.

Fig. 9 - Antiarcha indet., left posterior ventrolateral plate (D.F.Kh1, 0106, M.M.T.T.), ventrolateral view. x 2/3.

Fig. 10 - *Holonema* sp., right posterior superognathal (D.F.Kh1, 0107, M.M.T.T.), lateral view. x 1.

Fig. 11 - *Holonema* sp., left posterior superognathal (D.F.Kh1, 0108, M.M.T.T.), medial view. x 1.

Fig. 12 - *Holonema* sp., right posterior superognathal (D.F.Kh1, 0109, M.M.T.T.), lateral view. x 2.

Fig. 13 - *Holonema* sp., anterior part of a right anterolateral plate (D.F.Kh1, 0110, M.M.T.T.), lateral view. x 1.

Fig. 14 - Osteolepididae indet., left cleithrum and scapulocoracoid (D.F.Kh1, 0088, M.M.T.T.), medial (14) and lateral (14') view. x 1.

Fig. 15 - Ptyctodontida indet., upper tooth plate (D.F.Kh1, 0111, M.M.T.T.), lateral view. x 1.

Fig. 16 - *Holonema* sp., left anterior dorsolateral plate (D.F.Kh1, 0082, M.M.T.T.), juvenile individual, lateral view. x 3/2.

Fig. 17 - Holoptychiidae indet., left cleithrum (D.F.Kh1, 0112, M.M.T.T.), lateral view. x 4/5.

Fig. 18 - Dipnoi indet., right entopterygoid tooth plate (D.F.Kh1, 0113, M.M.T.T.), ventral view. x 4/5.

Fig. 19 - Dipnoi indet., left entopterygoid tooth plate (D.F.Kh1, 0114, M.M.T.T.), ventral view. x 4/5.

Fig. 20 - Ctenacanthidae indet. median spine (D.F.Kh1, 0115, M.M.T.T.), anterior view. x 4/5.

Fig. 21 - *Holonema* sp., right paranuchal plate (D.F.Kh1, 0080, M.M.T.T.), juvenile individual, ventral view. x 1.


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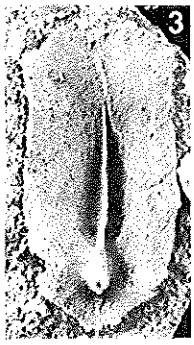
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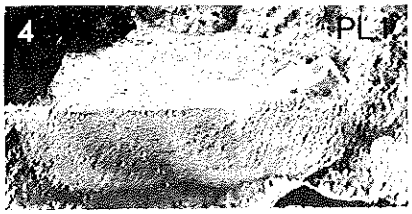
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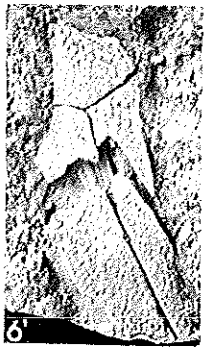
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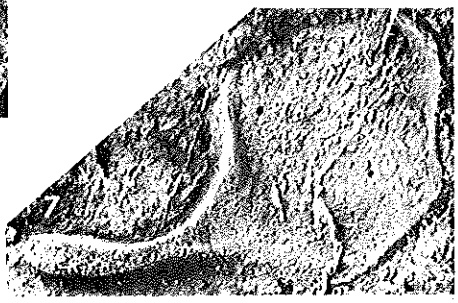
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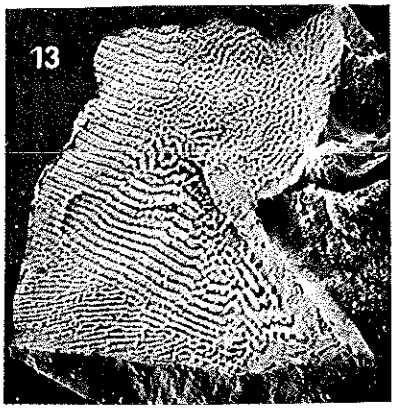
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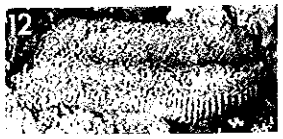
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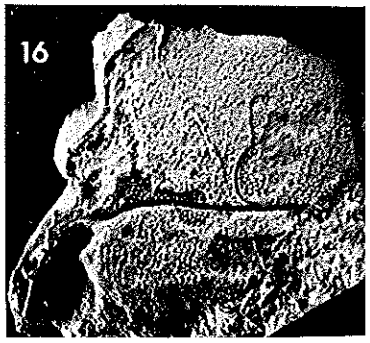
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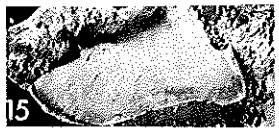
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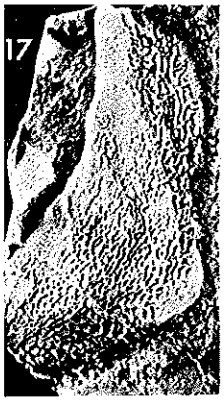
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