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Large Upper Devonian Arthrodires from Iran

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ABSTRACT

From the Upper Devonian of East Iran, fossil remains of three genera of brachythoracid arthrodires are described: *Eastmanosteus* sp., *Holonema rugosum* (Claypole), and *Aspidichthys ingens* (Koenen). This occurrence extends the range of distribution of the three genera, but like all others known is situated within the "tropics" of the Devonian. In *Eastmanosteus*, the levator capitis muscle attaches on both sides of the posteromedian cusp of the nuchal plate. The double sockets on the ventral surface of the nuchal plate run upward and backward so that they are interpreted as grooves for the craniospinal process of the neural endocranium in accordance with Stetson (1930). On the posterior dorsolateral plate of *Aspidichthys* the main lateral line canal turns postero-ventrally and no canal passes onto the median dorsal plate.

From Iran, Devonian fish remains were recorded first by Rieben (1935) from SSE of Zonuz, Azerbeidjan (p. 82: "*Holoptychius* cf. *flemingi* AG., *Bothriolepis* and *Dinichthys*": The remains are a scale of *Holoptychius* sp.; a dendrodont tooth belonging to a genus of the Holoptychiidae having osteodentine with a canal system like that of *Laccognathus* in the pulp cavity; a piece bearing an imprint of a plate from a bothriolepid and other fragments of arthrodiran plates; and a fragment of a plate from a brachythoracid smaller than the members of the Dinichthyidae). Later, fossil Devonian fishes were found near Kerman, East Iran, by members of the German Geological Mission Iran in 1959/1960 (Huckriede *et al.*, 1962) and by Professor Dr. O.H. Walliser during a collecting party in the Tabas area, East Iran, in 1965. All collected remains of arthrodires are fragments; only the remains found by Professor Walliser are complete enough to warrant their description.

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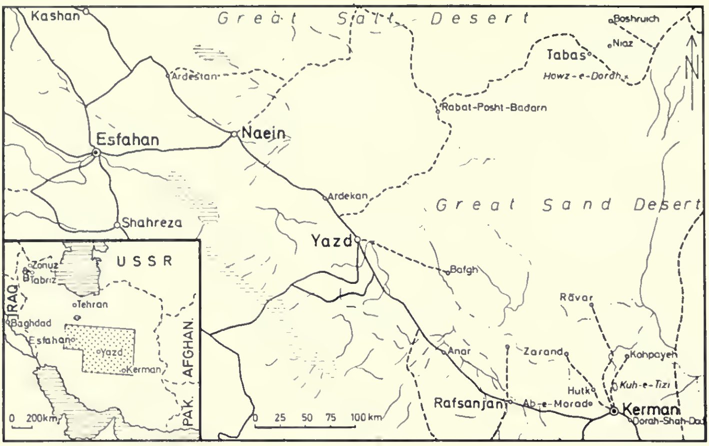

FIG. 1. Map of Central and East Iran with the localities of arthrodires: Niaz near Tabas; and Hutk, Ab-e-Morad, Dorah-Shah-Dad, and the mountain Kuh-e-Tizi near Kermān.

All arthrodires known from Iran are Upper Devonian in age (the remains of arthrodires cited by Huckriede *et al.* (1962, pp. 56, 57, 60, 69) as Givetian in age apparently are Lower Upper Devonian in age, to judge from the cited conodonts and brachiopods (Walliser, *pers. comm.*). The fragments found in East Iran belong to large specimens well known from Devonian deposits in North America, but rare outside North America.

The classification of the arthrodires is in a state of flux. Here, the classification of Miles (1969, p. 125) is adopted for the specimens described:

Class Placodermi

- A. Order Arthrodira
  - I. Suborder Dolichothoraci
  - II. Suborder Brachythoraci
    - 10. Fam. Holonematidae: *Holonema* and ? *Aspidichthys*
    - 15. Fam. Dinichthyidae (+ Dunkleosteidae): *Eastmanosteus*

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SYSTEMATIC DESCRIPTION

Family Dinichthyidae Newberry, 1888

Genus **Eastmanosteus** Obruchev, 1964. Figures 2, 3; Plate 1.

Material.—Fragment of the posterior part of the head shield (GPIGö 655-165-2a), fragment with parts of the marginal and postorbital plate (GPIGö 655-165-2b), two fragments of the suborbital plate (GPIGö 655-165-2c, d), and further fragments of the same specimen (GPIGö 655-165-2).

Horizon/locality.—Lower Upper Devonian (do I, Adorf, Frasne) /1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran.

Description.—The best preserved specimen of arthrodires from the Upper Devonian of East Iran belongs to *Eastmanosteus*, a genus of the Dinichthyidae (see below). The remains of the specimen were not found in association but were scattered in a gully on a slope over a distance of 150 m. The posterior part (nuchal plate and articulation area) of piece GPIGö 655-165-2a of the head shield was taken directly from the outcrop; the anterior part (parts of the right central plate) was taken a few meters away; the other parts of head shield (GPIGö 655-165-2b, c, d and 2) were collected in the same gully, at a still greater distance. To judge from the colouring, weathering, surrounding rock, and matching of the remains of epizoans across the edges all these pieces may belong to one specimen.


a
b
c

Dorsal surface (fig. 2A; pl. 1b): Except for parts of the left posterior process, the nuchal plate **(Nu)** is completely preserved. The Nu has an overall trapeziform to deltoid outline. The anterior suture is tripartite: in the median line one broad-based short wedge runs in between the central plates, the two other lateral wedges are more pronounced and are directed toward the centers of ossification of the central plates. From the lateral wedges the suture runs posterolaterally toward the glenoid fossa with a wide lateral excursion of the suture in the area between central and paranuchal plates. Anterior to the glenoid fossa the lateral margin of the Nu turns in an acute angle to form the posterior margin of the Nu. The posterior margin of the Nu is slightly concave with a posteromedian cusp **(mc.Nu)** projecting prominently. Above the posteromedian cusp a shallow depression is developed. Only fragments of the other plates have been found. Parts in sutural connection with the Nu are preserved of the paranuchal plate **(PNu)**, so that the glenoid fossa **(f.gl)**, the opening of the ductus endolymphaticus **(d.end)**, and parts of the sensory canals can be seen. The main lateral line canal **(lc)** is evident superficially as a deep groove extending anteriorly from the glenoid fossa. The surface course of the groove is interrupted in this area, and two pores are found there. The posterior pore is deeper than the groove; after passing this pore the main lateral line becomes completely bone-enclosed and runs below the second shallow pore to the groove continuing again superficially. The completely bone-enclosed canal and the pores are an apparent individual variation (cf. Schultze, 1969, text-fig. 8). We have here a mixture of the lateral line canal types of the classification of Ørvig (1971, p. 12). A "superficial lateral line canal . . . in deep groove" (type 2a) is transformed into a "deep, closed lateral line canal" (type 1) which underpasses a "superficial lateral line canal . . . in shallow groove" (type 2b—the second shallow pore). The two pores are larger than the pores figured by Ørvig (1971, text-fig. 2G); they contained a part of the lateral line and are not openings of nerve branches. Anterior to the glenoid fossa, a groove for the posterior pit line **(pp)** branches off from the main lateral line and extends a short distance medially. The posterior pit line groove terminates bulbously at its median end. Two grooves **(csc, soc)** of the sensory-line system are preserved on

PLATE 1. *Eastmanosteus* sp., posterior part of the head shield (GPIGö 655-165-2a + b). Lower Upper Devonian (do I)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. × ⅓. **a.** Ventral surface. **b.** Dorsal surface. **c.** View from behind.

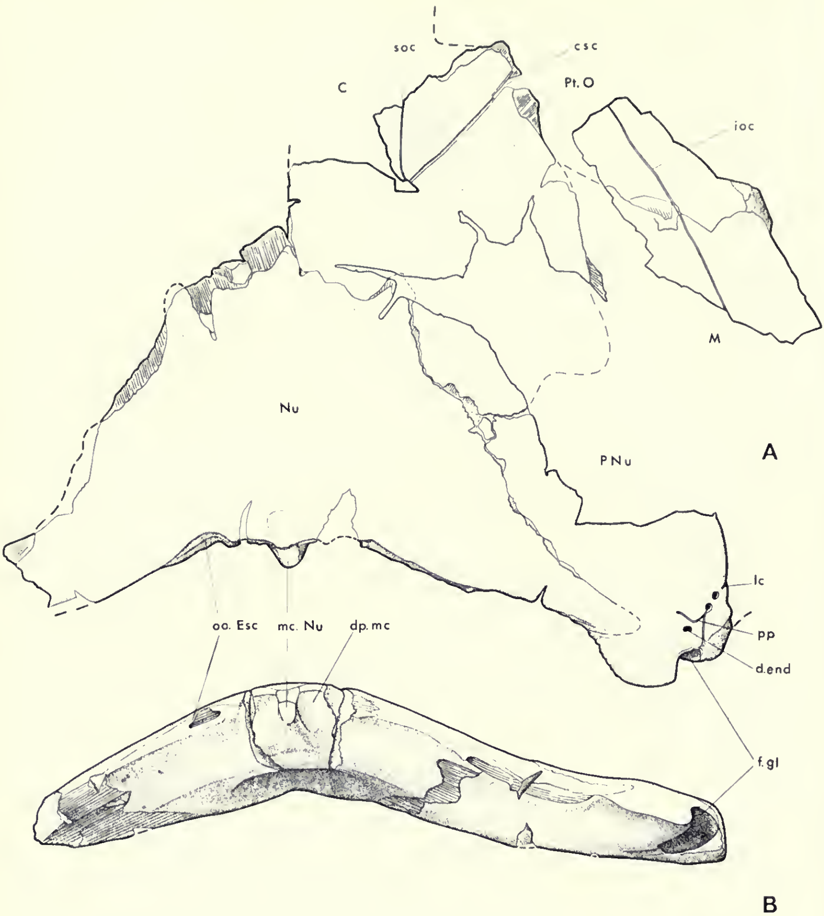


FIG. 2. *Eastmanosteus* sp., posterior part of the head shield (GPIGö 655-165-2 a + b). Lower Upper Devonian (do I) / 1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. × ⅓. A. Dorsal view. B. View from behind.

C central plate, **M** marginal plate, **Nu** nuchal plate, **P** pineal plate, **PM** postmarginal plate, **PNu** paranuchal plate, **Pr.O** praeorbital plate, **Pt.O** postorbital plate, **ch.pr.sv** channel for dorsal aspect of supravagal process of neural endocranium, **csc** central sensory canal, **d.end** external opening of ductus endolymphaticus, **dp.la** depression for labyrinth part of the neural endocranium, **dp.mc** depression on both sides of the posteromedian cusp of Nu, **f.gl** glenoid fossa, **ioc** infraorbital sensory canal, **la.orb** descending, orbital exoskeletal bone lamina, **lc** main lateral line canal, **mc.Nu** posteromedian cusp of Nu, **oa.ESc** overlap area for extrascapular plate, **pp** posterior pit-line groove, **p.pts.Nu** paired pits in ventral surface of Nu (double sockets), **soc** supraorbital sensory canal.

the right central plate **(C)**. The wavy suture between the C and the Nu and parts of the suture between the C and the postorbital plate **(Pt.O)**, between the C and the marginal plate **(M)** are preserved. The center of the C is the only place where an ornamentation of minute (0.3 mm. in diameter) tubercles exist (cf., ornamentation of *E. licharevi*, Obrutcheva, 1962, pl. 3, fig. 2). Only two small fragments of the left C lie on the overlapping area of the Nu. Piece GPIGö 655-165-1b, which bears the suture between the Pt.O and the M and the infraorbital sensory canal **(ioc)**, has been oriented by comparison with *Dunkleosteus* as described by Heintz (1932). The infraorbital sensory canal crosses the suture between the Pt.O and the M in a pronounced, anteriorly directed wedge, and the suture on the ventral surface between the Pt.O and the M is drawn out to form a postero-laterad process of the Pt.O.

View from behind (fig. 2B; pl. 1c): The extrascapular plates were not found, but the dorsal surface of the posterior margin of the Nu shows two depressed areas **(o.a.Esc)** into which the anterio-median extremities of the Esc probably fit. These structures have some of the characteristics of sutures. Lateral to the posteromedian cusp of the Nu is the area of insertion **(dp.mc)** of the dorsal part of the levator capitis muscles. The head shield has been flattened during fossilization. To restore original conditions in *Dunkleosteus* Heintz (1932, fig. 35) has rotated the axes of the glenoid fossae. In bringing the axes of the glenoid fossae to a horizontal position, as Heintz (1932) has done, it is necessary to move the right lateral part of our specimen so that the crack in the middle of the right side and the separation along the overlap area on the ventral surface of the Nu become closed by rotating the PNu ventromediad. By such a rotation the lateral part which is now more horizontal becomes more arched than the middle part. The middle part, in its present condition, conforms more closely to the original condition than do the lateral parts.

Ventral surface (fig. 3; pl. 1a): The insertion **(dp.mc)** of the dorsal part of the levator capitis muscle can be seen on the ventral surface of the Nu, on either side of the posteromedian cusp. The insertion is separated by a strong ridge from two deep pits **(p.pts.Nu)**—the "double sockets" of Heintz (1932). The long axes of these pits are directed posterodorsad, and end above the ridge which separates them from the areas of insertion on either side of the posteromedian cusp. It seems improbable that a muscle directed posteroventrad (e.g., the levator capitis muscle) could insert in the

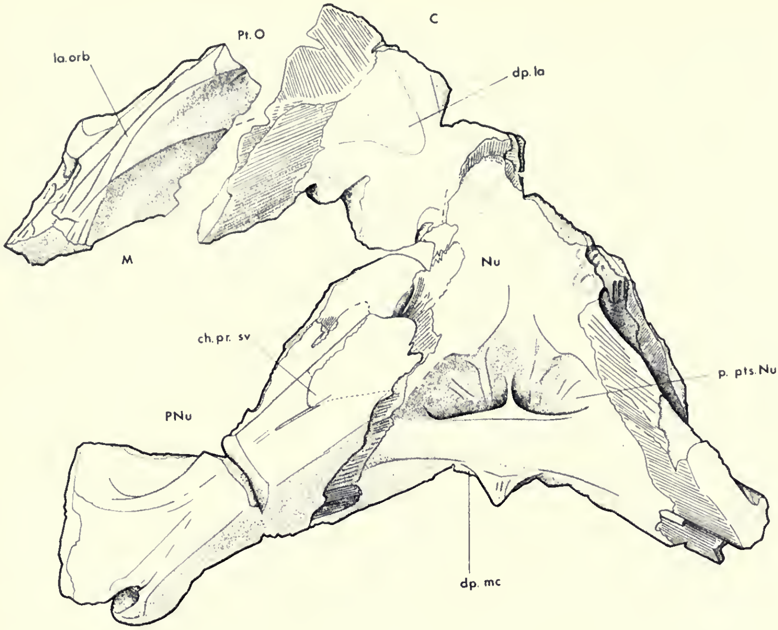


FIG. 3. *Eastmanosteus* sp., posterior part of the head shield in ventral view (GPIGö 655-165-2a + b). Lower Upper Devonian (do I) 1.8 km. NW Niaz, on the Sardar river, 21 km. ENE Tabas, East Iran. × ⅓. See Figure 2 for abbreviations.

pits as it would have to bend around the ridge behind the pits, a tortuous course for a muscle. Thus, as suggested by Stetson (1930, pp. 30, 31; compare Miles and Westoll, 1968, p. 400), the pits may have accommodated craniospinal processes of the neural endocranium. Beside the pits, a slight channel **(ch.pr.sv)** on the ventral surface of the right PNu might be an area of attachment of the neural endocranium to the ventral surface of the head shield (cf. Miles and Westoll, 1968, text-fig. 2a). The posterior boundary of attachment of the neural endocranium to the exocranium is not marked between this slight channel and the double sockets. Anterolateral to this channel, into which may fit the supravagal process of the neural endocranium, the bone is partly broken away so that the opening of the ductus endolymphaticus cannot be seen on the ventral surface.

The right PNu was moved laterally during fossilization so that the overlap area of the Nu is exposed. On the left side of the Nu the overlap area is free, and only a fragment of the left PNu has been preserved. This fragment is found on the inner side of the cranial shield where the suture between Nu and PNu turns up to the posterior margin. The PNu overlaps the Nu on the dorsal and ventral surfaces and fits into the deep notch formed in the Nu between the surface layer and the "nuchal thickening" ("hind consolidated arch of the roof" or "hind thickening" of Heintz, 1932). This deep notch (seen on the left side of the Nu in fig. 3) is filled up by bone of the PNu. In this region the PNu extends from the nuchal thickening to the flattened area (the cucullaris depression) of the ventral surface of the PNu. Beginning at the glenoid fossa a slight depression extends anteromediad on the nuchal thickening. The depression is a little deeper posteriorly, near the glenoid fossa, where a small pore of a vessel can be seen.

The central plate (C) overlaps the Nu, the postorbital **(Pt.O)**, and the marginal plates (M). The C fits into a channel of the Pt.O and the M, where these plates both underlie the C by a wide lamina (see the overlap area on the ventral surface of the C, fig. 3), and overlie the C at the same place by a narrow lamina (see overlap area on the dorsal surface of the C, fig. 2A). On the midventral surface of the C is situated a wide depression (the "top impression on bridges" of Heintz, 1932, text-fig. 13) which has a position like that of "the two shallow channels for the semicircular canal ridges on the endocranium" (Miles and Westoll, 1968, p. 386, text-fig. 2A). According to Heintz (1932, p. 196), "the impression . . . was occupied by the otic capsules". In this region, too, the neural endocranium is similar to the reconstructed endocranium of *Coccosteus* (Miles and Westoll, 1968, text-figs. 15, 16), and a "preendolymphatic depression" (Stensiö 1963, fig. 89A: *Dunkleosteus intermedius*) seems to be absent.

On the ventral surface of piece GPIGö 655-165-2b (fig. 3: left side up), the suture between the Pt.O and the M extends posteriorly to the edge of the descending, postorbital bone lamina (**la.orb**), and then turns anteriorly.

Other remains: Many small pieces (all without ornamentation) of the specimen have been collected (some belonging to gnathal elements and all with no. GPIGö 655-165-2). But only two pieces (GPIGö 655-165-2c + d) could be identified precisely, as parts of the left suborbital plate, because of the course of the sensory canals and the form of the inner (visceral) surface (see also, Heintz, 1932, text-figs. 21, 22). On piece GPIGö 655-165-2c, the suborbital branch of the infraorbital canal ends anteriorly directly below the dorsal edge of the suborbital lamina (= "the handle" of Heintz, 1932), not farther anteriorly as in *Dunkleosteus*. The anterior part of a ridge R_2 of Heintz, 1932, text-fig. 22) is preserved on the inner side. Piece GPIGö 655-165-2d, showing the posterior part of the suborbital branch of the infraorbital canal and the anterior part of the supraoral sensory canal, is broken just below the branching of the two canals. On the inner side, the dividing of the four ridges (R_1–R_4 of Heintz, 1932, text-fig. 22) can be seen, but the more elevated crests of R_2 and R_4 are broken away. Four pores (diameter about 1 mm.) are situated in an antero-posterior row in the deepened part above the ridge R_2. Continuing this row, two smaller pores penetrate the rostral part of the suborbital plate. These pores could be the openings for the branches of nerves leading to the neuromasts in the sensory canal.

Comparison.—The genera of Dinichthyidae are not well defined. The old genus "*Dinichthys*" has been divided by Lehman (1956) and Obruchev (1964) into three genera (*Dinichthys, Dunkleosteus,* and *Eastmanosteus*), such that the genus *Dinichthys* itself is the most poorly known. A reinvestigation of the holotype of *Dinichthys* is needed. To permit determination of the specimen described above, the characters of the posterior head shield of *Eastmanosteus* and *Dunkleosteus* have been combined (fig. 4).

Dinichthys Newberry, 1873. The type species (*Din. herzeri*) of the genus has been based on an infragnathal plate. A head shield belonging to this species with certainty is unknown; therefore the genus cannot be taken into consideration here.

SPECIES: *Dinichthys herzeri* Newberry, 1873.

Dunkleosteus Lehman, 1956 (fig. 4E). Posterior margin of the head shield concave; Nu short and broad, triangular to pentagonal; PNu extending far backwards from the posterior boundary of Nu; prominent glenoid process; C leaf shaped, the point of intersection of the sutures between P (pineal plate), C, and Pr.O (preorbital plate) as far anterior as the point of intersection of the sutures between Pt.O, C, and Pr.O; suture between M and Pt.O runs anterolaterally from the point where it meets C.

SPECIES: *Dunkleosteus intermedius* (Newberry, 1889), *D. terrelli* (Newberry, 1873), *D. curtus* (Newberry, 1888).

Eastmanosteus Obruchev, 1964 (fig. 4A). Posterior margin of head shield not or only a little concave; Nu trapeziform with a tripartite anterior suture (a median wedge extends between the central plates, and the two lateral wedges are directed toward the center of C),[1] a postero-lateral process of Nu is projected over the PNu; PNu not extending far backward from the posterior boundary of Nu; glenoid process not prominent; C very irregularly bounded (lobed), the anterior suture, extending medially from the point of intersection of Pt.O, C, and Pr.O, turns anteriorly at about a right angle approximately half-way to the median line, then turns mediad again to reach the median line behind P (the pineal plate should intercalate between the frontal parts of the C of *E. pustulosus* as in *E. magnificus, E. marsaisi,* and *Dunkleosteus intermedius* in contrast to figure 4A = reconstruction by Eastman, 1898); the suture between M and Pt.O runs postero-laterally so that the suture reaches the lateral margin at a point more posteriorly located than is its junction with C.

SPECIES: *Eastmanosteus pustulosus* (Eastman, 1897), *E. magnificus* (Hussakof and Bryant, 1918), *E. licharevi* (Obrutcheva, 1956), *E. marsaisi* (Lehman, 1956).

The above-mentioned features argue for a closer relationship between *Eastmanosteus* (especially the older species *E. pustulosus*) and the Coccosteidae (Miles, 1969, p. 163) than between *Dunkleosteus* and the Coccosteidae. *Eastmanosteus* and the Coccosteidae (see Miles and Westoll, 1968) resemble each other in that the posterior margin of the head shield is straight or only slightly concave, in that the Nu has a trapeziform shape and projects in the PNu with a postero-lateral process, in that PNu extends not or only for a short distance behind the Nu, in that the glenoid process is small, and in that the suture between the C and the Pr.O has the same courses (at least the course of the suture between the M and the Pt.O seems to correspond).

As regards the specimen from East Iran, most of its features can be compared only with those of *Eastmanosteus,* but comparison with the various species of *Eastmanosteus* is difficult. In *E. pustulosus* (fig. 4A; Eastman, 1898, 1907, pl. 12 = 1908, pl. IV; Kulczycki, 1957, text-figs. 8, 9, pl. 4) the Nu has a nearly mathematical form of a trapezoid. In the anterior suture the middle wedge is not pronounced, as in the specimen from East Iran; the middle wedge extends a little forward only from the deep posteriorly running suture between the prominent lateral wedges. The outer surface of the plates in *E. pustulosus* is tuberculated. No photograph is given of

[1] According to Mr. J. Boylan, the tripartite anterior suture has little significance, even in one specimen of *Eastmanosteus* the suture is not tripartite. He argues that the posterior prolongation of C in between Nu and PNu is more important, but this region is not preserved well enough for use in the described specimen.

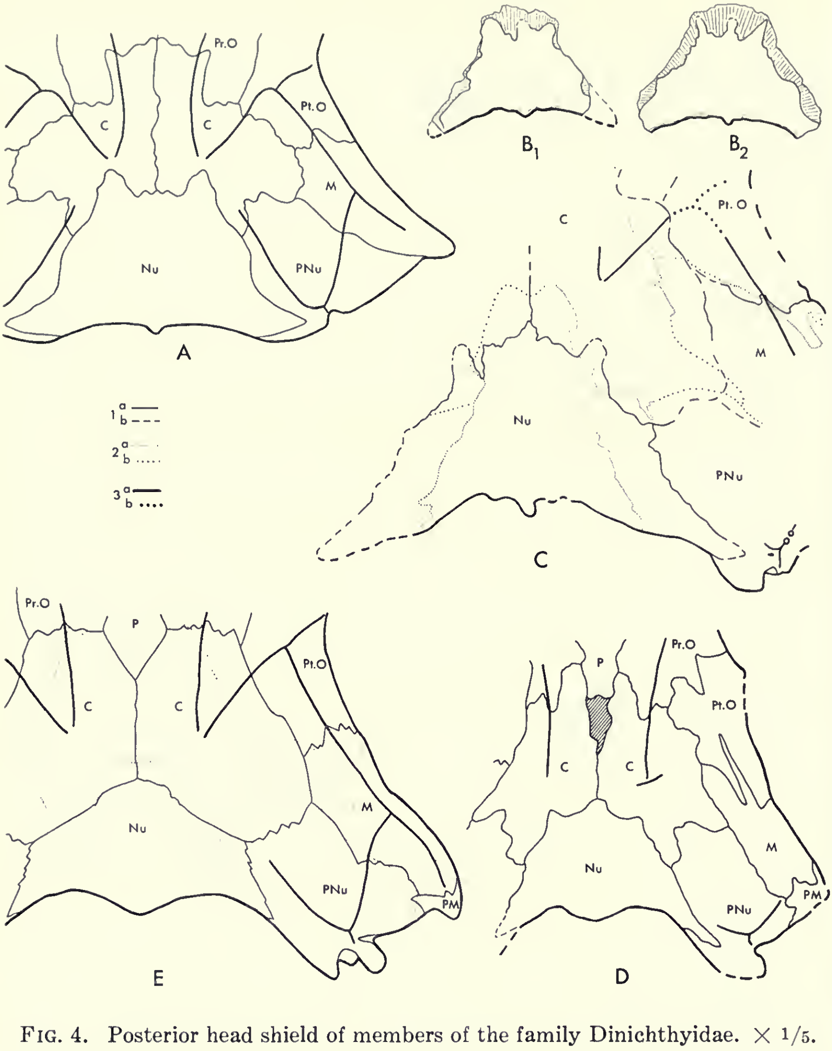


FIG. 4. Posterior head shield of members of the family Dinichthyidae. × 1/5.

Key: **A.–D.** *Eastmanosteus* Obruchev. A. *E. pustulosus* (Eastman), Middle—Upper Devonian, USA. After Eastman (1898, fig. 2). B. Nuchal plate of *E. licharevi* (Obrutcheva), Upper Devonian, USSR. B_1. Holotype. After Obrutcheva (1962, fig. 42a). B_2. "*Dinichthys* sp. 2". After Obrutcheva (1962, fig. 42b). C. *E.* sp., Upper Devonian, Iran. D. *E. marsaisi* (Lehman), Upper Devonian, Morocco. After Lehman (1956, pl. 4 = counterpart and pl. 3 = part of the holotype combined). **E.** *Dunkleosteus intermedius* (Newberry), Upper Devonian, USA. After Heintz (1932, figs. 12 and 13 combined).

1. Sutures on the dorsal surface (*a.* seen, *b.* restored); 2. sutures on the ventral surface (*a.* seen, *b.* restored); 3. sensory canals (*a.* seen, *b.* restored).

See Figure 2 for abbreviations.

the head shield of "*Dinichthys*" *magnificus*, but from the reconstruction of the head shield (Hussakof and Bryant, 1918, text-figs. 8, 9) the species has to be placed within the genus *Eastmanosteus* because it agrees in all above-mentioned features. In this largest species of *Eastmanosteus*, the anterior suture of the Nu has three pronounced wedges, the median one pointed and short-based like the lateral ones (compare fig. $4B_2$), in contrast to the specimen from East Iran. The postero-lateral processes of the Nu extend far laterad as in the specimen from East Iran, so that both forms have a Nu of similar shape (except for the caudal margin, which is straight in *E. magnificus*, and the middle wedge in the anterior suture). Both forms differ in ornamentation (*E. magnificus* with "closely-crowded, non-stellate tubercles," Hussakof and Bryant, 1918, p. 36). The third species cited above is *E. licharevi*, based on an isolated Nu (fig. $4B_1$, here including "*Din.* sp. 2", Obrutcheva, 1956, text-fig. 42b—fig. $4B_2$ in this paper). In shape, the Nu resembles that of *E. magnificus* especially in the tripartite nature of the anterior margin of the Nu, of "*Din.* sp. 2." In addition to the great difference in size, the concave posterior margin of the Nu in *E. licharevi* differs from the straight posterior margin of the Nu in *E. magnificus*. The outer surface of the plates of both species are tuberculated. Thus, the specimen from East Iran differs from *E. licharevi* in the same way as it does from *E. magnificus*. *E. licharevi* resembles *E. magnificus* in the same manner as *E. marsaisi* resembles *E. pustulosus*. On the basis of this resemblance, *E. marsaisi* (fig. 4D: the reconstruction is based on the counterpart mainly = Lehman, 1956, pl. 4; the holotype is broken in the middle of the bone and the counterpart shows the sutures nearer to the surface) is placed in the genus *Eastmanosteus* contrary to Lehman (1956). The generic characters are: the tripartite anterior suture, the overall shape, and the posterolateral processes of the Nu; the shape and the course of the anterior suture of the C (cf. Lehman, 1956, pl. 6: spec. B and *E. pustulosus*); and the course of the suture between the Pt.O. and the M. In contrast to the other species of *Eastmanosteus* and the specimen from East Iran, the posterior margin of the head shield is clearly concave as in *Dunkleosteus*. *E. marsaisi* differs from the specimen from East Iran in the form of the wedges on the anterior suture of the Nu and in the clearly concave posterior border of the head shield. The pronounced wedges on the suture between the Pt.O and the M seem to be a very distinctive feature of *E. marsaisi*.

In summary, the specimen from East Iran differs clearly from *E. pustulosus* and *E. marsaisi*, but resembles *E. magnificus* and *E. licharevi*. In contrast to the last mentioned species, the outer surface of the plates of the East Iran specimen is not tuberculated (except for a few minute tubercles on the center of the C), and the wedges on the anterior suture of the Nu are shaped differently. But these characters are insufficient to erect a new species. The specimen from East Iran is therefore described as *Eastmanosteus* sp.

Arthrodires indet. Plate 3f.

Material.—Left interolateral plate (GPIGö 655-164-1) and different fragments (Huckriede *et al.*, 1962, pp. 55–57, 59, 60, 67, 69).

Horizon/locality.—GPIGö 655-164-1: float from Lower Upper Devonian (do I, Adorf, Frasne)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. Fragments in BfB: Upper Devonian/different localities around Kerman, East Iran.

Description.—Small fragments of large arthrodires have been collected from different localities NW of Niaz and around Kerman (15 km. SW Ab-e-Morad, near Hutk, near Dorah-Shah-Dad and in the mountain Kuh-e-Tizi) and have been recorded by Prof. Walliser from a section at Howz-e-Dorah (46 km. SE Tabas; see Stöcklin *et al.*, 1965, p. 12: horizon 18). But the only piece complete enough to be identified is a left interolateral plate **(IL)** of a large, indeterminate arthrodire. The ventral surface (pl. 3f) is smooth and with out any groove similar to those of other arthrodires (see Miles and Westoll, 1968, text-figs. 38a, 42c and cited literature p. 440). The medial margin runs postero-medially and dorsally, forming an acute angle and continues as the dorsal border of the ascending lamina. Only a part of the ascending lamina is preserved, but it could not extend so far dorsad as in *Dunkleosteus* (Heintz, 1932, text-fig. 62A, pl. 8, fig. 20) or *Coccosteus* (Miles and Westoll, 1968, text-figs. 38b, 42a). The dorsal margin seems to extend downward medio-laterad as in *Plourdosteus* (Gross, 1933a, pl. 2, fig. 25). Laterally, the dorsal margin of the ascending lamina splits into two; between them a flat triangular surface is formed (the overlap area for the anterior venterolateral plate). The lateral part of IL is broken away.

Family Holonematidae Obruchev, 1933

Genus **Holonema** Newberry, 1889. Plate 3d, e.

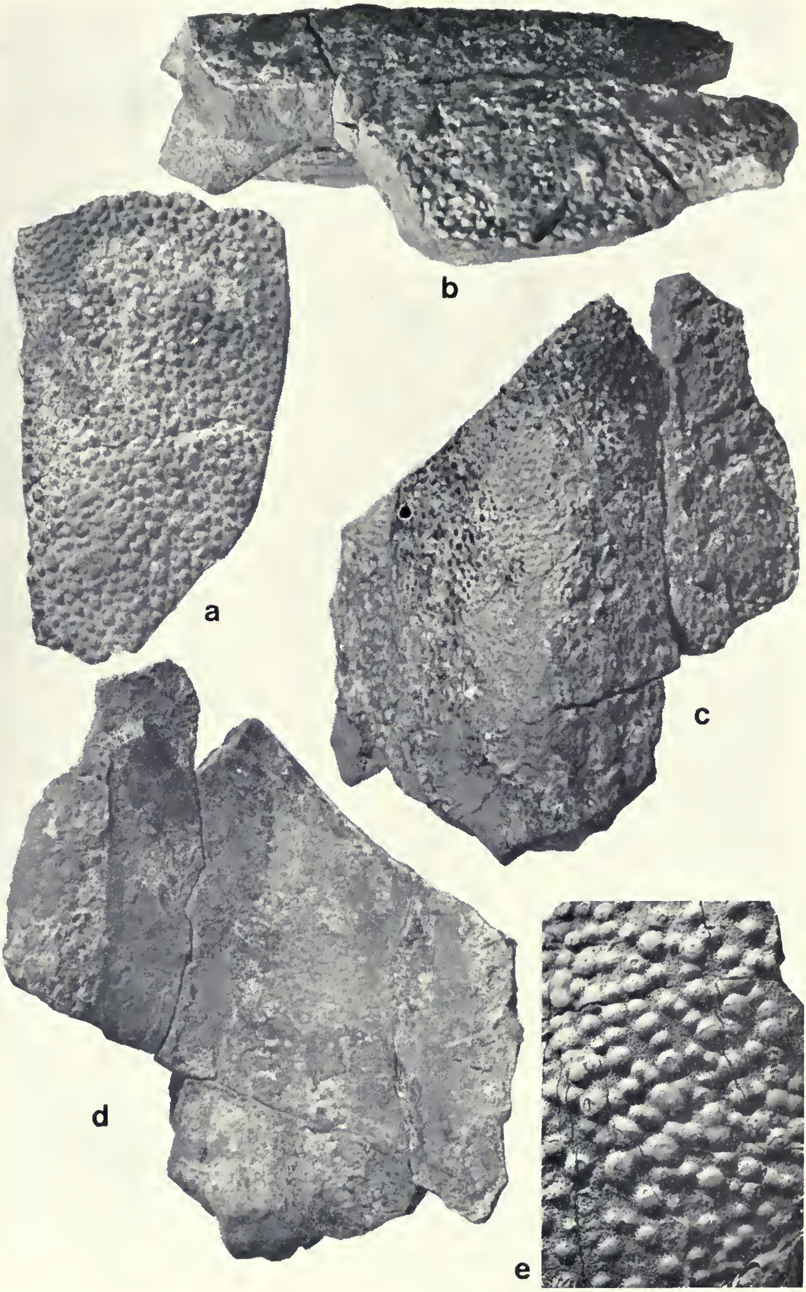
Material.—Fragment of the left anterior dorsolateral plate (GPI-Gö 655-165-1) and fragment BfB 91.

Horizon/locality.—GPIGö 655-165-1: float from Lower Upper Devonian (do I, Adorf, Frasne)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. BfB 91: Upper Devonian (horizon 9–12 in Huckriede *et al.*, 1962, p. 60)/core of anticline of Hutk, N Kerman, East Iran.

Description.—Fragments of *Holonema* are easily identifiable because of the characteristic ornamentation of radiating ridges on the outer surface of the plates. The two fragments found in East Iran show these ridges, which anastomose to form a network (especially pl. 3d). The preservation is poor, and the small tubercles (see Wells, 1942, pl. 97, fig. 4) composing the ridges can be seen on only a few ridges in the left part of piece BfB 91.

Piece GPIGö 655-165-1 (pl. 3d) is a small fragment of the left anterior dorsolateral plate **(ADL)**. Only the basal part of the condyle is preserved; the elongated narrower, anterior-medial end (compare Kulczycki, 1957, pl. X, fig. 2) is broken away. Lateral to the condyle a groove is formed, but the "condylus subglenoidalis" (Obruchev, 1933) following this groove laterally, is lost. The left broken margin follows for some distance the course of the lateral line (*lc.a* of Ørvig, 1969). Fragment BfB 91 (pl. 3e) is very poorly preserved and is without any significant feature to place it in a part of any plate; therefore, the orientation given in Plate 1a is arbitrary. The inner side is weathered strongly so that the original surface can not be seen.

Comparison.—From the similar ornamentation, both fragments may belong to the same species, despite the distance of 350 km. between the two localities (in contrast to Huckriede *et al.*, 1962, p. 60, the horizon of fragment BfB 91 is here considered as Lower Upper Devonian; see p. 54). In addition to the fact that the ornamentation is different on different plates, Miles (1971, pp. 174–175) has shown that the ornamentation in *H. westolli* was changing during growth. Ridges such as in the described fragments are characteristic for adult specimens. The ornamentation of the described fragments is similar to that of the species *H. rugosum* (Claypole, 1883, text-fig. on p. 667), *H. radiatum* (Obruchev, 1933, pl. V, VI), *H. ornatum* (Traquair, 1909, pl. XLVI), and partly *H. westolli* (Miles, 1971, figs. 14, 20, 73). There are few differences in the ornamentation between the first three species. The interspaces between the ridges seem to be broader in *H. rugosum* than in the others, and the described fragments agree with *H. rugosum* in this respect. Therefore they are tentatively referred to *H. rugosum*.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Family ? Holonematidae Obruchev, 1933

Genus **Aspidichthys** Newberry, 1873. Figure 5; Plate 2; Plate 3a-c.

Material.—Part of the median dorsal plate (GPIGö 655-154-1a) with a fragment of the counterpart (GPIGö 655-154-1b); posterior dorsolateral plate (GPIGö 655-159).

Horizon/locality.—GPIGö 655-154-1a, b: float from Lower Upper Devonian (do I, Adorf, Frasne)/0.7 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. GPIGö 655-159: float from Upper Devonian (Frasne, possible Famenne, too)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran.

Description.—The genus *Aspidichthys* was based by Newberry (1873) on a median dorsal plate **(MD)** of very large size with an ornamentation "of knobs, or bosses of smooth, shining enamel, of the size and form of split peas" (Newberry, 1889, p. 73). But the typical structure of the genus is the form of the carinal process on the posterior inner surface of the MD (shown for the type species *A. clavatus* by Sinclair and Walker, 1956, fig. 1–3). With this structure the MD (GPIGö 655-154-1a) can be identified as belonging to the genus *Aspidichthys*. In ornamentation, size, and thickness of the bone, the posterior dorsolateral plate **(PDL;** GPIGö 655-159) fits together with the MD, and it probably belongs to the same species.

In GPIGö 655-154-1a, the posterior part of the MD is preserved without any natural boundary; only the right periphery seems not to be far from the natural boundary (pl. 2c). The MD is strongly arched—enclosing an angle of ca. 110°, but the median part is rounded. If any longitudinal median ridge existed it could be formed only in the most posterior part, which is not preserved. The ornamentation consists of rounded, smooth tubercles, 2–4 mm. in diameter, with a stellate-looking base (pl. 2e). In some places, the tubercles are arranged in rows. In the lateral and posterior parts they are larger, and sometimes confluent. The inner surface (pl. 2 d) is smooth and arched like the outer surface and is without a median longitudinal keel. Only in the posterior part, a thick, rounded carinal process slopes gently posteroventrad (pl. 2b), but

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PLATE 2. *Aspidichthys* cf. *ingens* Koenen. Upper Devonian/0.7 km. (fig. a) and 1.8 km. (fig. b) NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran.

a. Posterior dorsolateral plate (GPIGö 655-159). × 0.4.

b–e. Median dorsal plate (GPIGö 655-165-1a). b. view at the right side. c. dorsal view. d. ventral view, × 0.4. e. detail of figure c (near the anterior = above border). × 1.2.

the ventral part of the process is missing. From behind (fig. 5; pl. 3 c) two grooves **(gr)** can be seen on the top of the carinal process, directly below the highest point of the arched plate. Near the broken

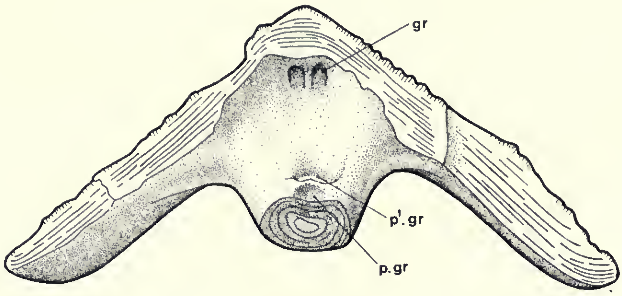

FIG. 5. *Aspidichthys* cf. *ingens* Koenen, median dorsal plate from behind (GPIGö 655-154-1a). Lower Upper Devonian (do I)/0.7 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. × ½.

Key: **gr** paired groove on carinal process, **p.gr** posterior groove on carinal process, **p'.gr** preceding stage of the posterior groove. The lines in the broken parts indicate the internal structure simplified.

ventral end of the process, a very short part of the posterior, unpaired groove **(p.gr)** is preserved. Dorsally, the bone is broken away so that a preceding stage of the posterior, unpaired groove **(p'.gr)** appears on a deeper level.

The preserved posterior part of the right posterior dorsolateral plate **(PDL;** pl. 2a) has the natural boundary along the right side, but the anterior part and a short posterior part of the PDL are missing. On the left side, a notch is preserved where the ventral lateral margin of the MD fits between overlying and underlying laminae of

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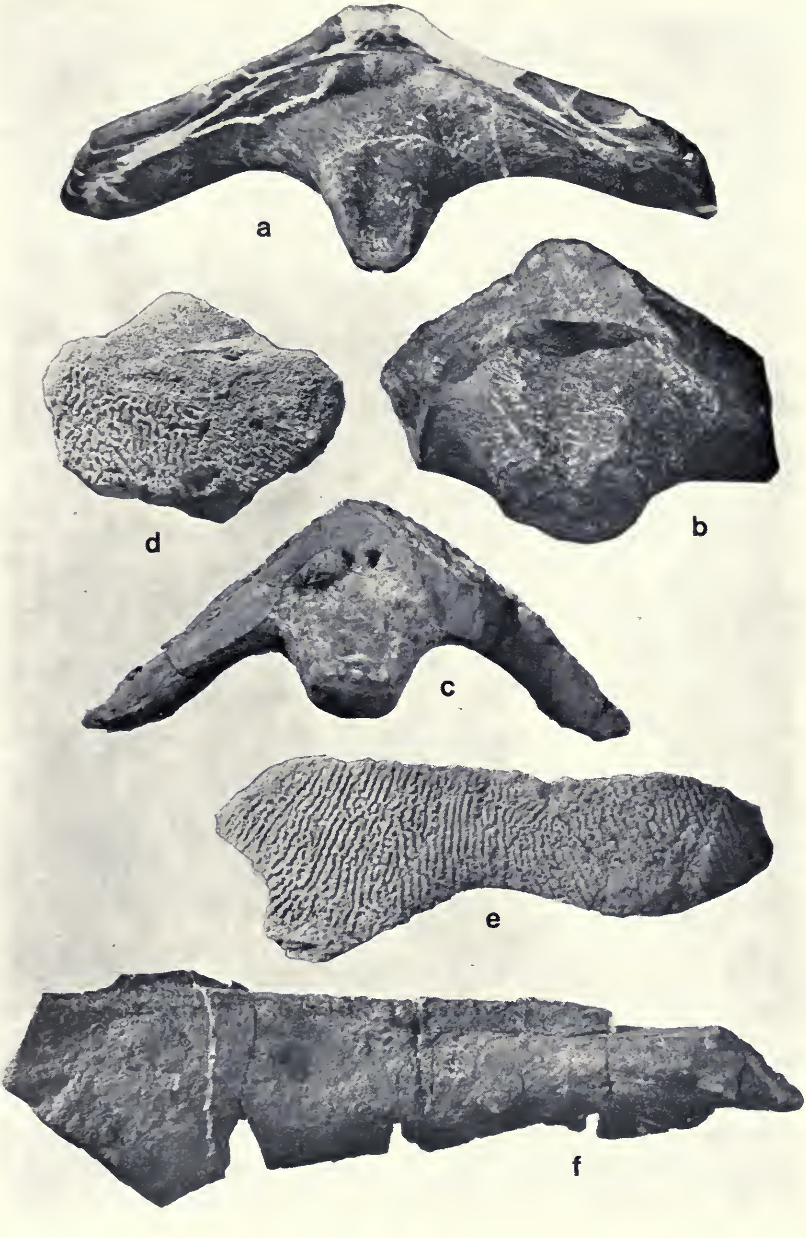
PLATE 3. **a.** *Aspidichthys clavatus* Newberry, median dorsal plate (PF 1863, Field Museum of Natural History, Chicago), view from behind. × 0.5. Hanover shale, Upper Devonian/Chautauqua County, New York State, USA.

b. *Aspidichthys* cf. *ingens* Koenen, median dorsal plate (UF 101, Field Museum of Natural History, Chicago), view from behind. × 0.5. Chadakoin formation, Upper Devonian/Chautauqua, Chautauqua County, New York State, USA.

c. *Aspidichthys* cf. *ingens* Koenen, median dorsal plate (GPIGö 655-154-1a), view from behind. × 0.5. Lower Upper Devonian (do I)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran.

d, e, *Holonema* cf. *rugosum* (Claypole). **d.** Part of the left anterior dorsolateral plate (GPIGö 655-165-1). × 1. Lower Upper Devonian (do I)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran. **e.** Part of an undetermined plate (BfB 91). × 1. Upper Devonian/anticline of Hutk, N of Kerman, East Iran.

f. Left interolateral plate of an arthrodire indet., ventral surface (rostral margin below. GPIGö 655-164-1). × 0.5. Lower Upper Devonian (do I)/1.8 km. NW Niaz on the Sardar river, 21 km. ENE Tabas, East Iran.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the PDL. From the left anterior corner of the PDL, the lateral line groove (appearing as a light line in pl. 2a) extends posteriorly along the left edge for one-fourth of its length, then turns to the middle of the plate, and ends after 1½ cm. The lateral line may continue over the bone, for it can be followed farther, 2½ cm. in the same direction, through the tubercles to near the middle of the PDL. The tubercles have the same size as the tubercles in the lateral and posterior part of the MD (3–4 mm. in diameter). They are arranged in rows, but only over short distances. The inner surface is smooth and flat, but is curved ventrad near the left margin.

Comparison.—Two species of the genus *Aspidichthys* are known: *A. clavatus* Newberry, 1873, the type species, and *A. ingens* Koenen, 1883. According to Miles (1965, p. 548), *A. notabilis* Whiteaves, 1892 should not be included in this genus. The typical carinal process of the MD, the MD itself, is not known in *A. notabilis.* Sinclair and Walker (1956), in contrast, are convinced that *A. notabilis* belongs to the genus *Aspidichthys* because of the similar ornamentation. However, the tubercles on plates of *A. notabilis* are smaller (max. 2 mm. in diameter, Whiteaves, 1892, p. 355), irregularly arranged, and more widely removed from each other than in the other species. In *A. clavatus* and *A. ingens* the size of the tubercles is nearly the same (up to 4 mm. in diameter), the tubercles are arranged in rows over long distances (especially in the lateral parts of the MD; cf. Koenen, 1895, pl. 3, fig. 1; Sinclair and Walker, 1956, fig. 1). "The only obvious differences between the median dorsal plates of *A. ?ingens* and *A. clavatus* are that in the latter this plate is less steeply folded down the mid-line, and that posteriorly the median longitudinal ridge rises to form a low crest" (Miles, 1965, p. 548). The angle between the left and right outer surfaces of the MD amounts in *A. clavatus* to 150° (after Sinclair and Walker, 1956, fig. 3), but 130° in the Field Museum specimen PF 1863 (pl. 3a) and in *A. ingens* to 130° (in the posterior part of GPIGö 476-6—Koenen, 1895, his pl. 3, fig. 1) or 120° (Miles, 1965) or 110° (Kulczycki, 1957). Even though these few measurements overlap, the angle of the above described MD from East Iran is situated in the other end of the variation range of *A. ingens* from *A. clavatus,* so that it seems reasonable that the specimen from East Iran belongs to the former species. The small difference in ornamentation (the tubercles are not arranged in rows over long distances) may be considered as local geographic or individual variation.

The new structure in the MD from East Iran is the occurrence of two grooves on the top of the posterior side of the carinal process. Comparison with published figures is not possible because this region is not prepared in most of the described specimens. By preparation a very deep but single groove has been discovered in this region in the Field Museum specimen UF 101 of *A.* cf. *ingens* (pl. 3b; compare Miles, 1965, pl. 1, fig. 4). In contrast, in the Field Museum specimen PF 1863 of *A. clavatus* (pl. 3a), the posterior side of the carinal process forms a plain ending with shallow depressions along the connection with the arched plate. Aside from the division into two grooves the feature in the specimen from East Iran is similar to *A. ingens*.

The most interesting feature in the PDL is the course of the lateral line groove, which bends postero-ventrad and does not pass over to the MD. In the more complete PDL of *A. ingens* (Gross, 1937, pl. 5, fig. 4), the lateral line groove begins its course from nearly the middle of the anterior margin, and extends posteriorly to the left (dorsal) margin, and then follows the left margin posteriorly without passing over to the MD. According to the terminology of Stensiö (1969), this is the "ligne latérale principale" **(lc)**, which may or may not be continued posteriorly (in soft tissue) to the unarmoured body. The groove for the "ligne dorsale latérale antérieure" **(ld)**, which extends to the radiation center of the MD, does not occur in *Aspidichthys*.

Concerning the sensory lines on the thoracic armour, the terminology used by Stensiö (1969) is useful (see also Miles, 1971, pp. 191–193). The postero-ventrally directed line on the anterior dorsolateral plate **(ADL)** is the "venterolateral line" or "ventral branch of the main lateral line" (in accordance with Ørvig, 1969); the more or less horizontal line on ADL and PDL is the "main lateral line"; the line extending onto the MD is the "dorsolateral line" or "dorsal branch of main lateral line" (often branching off from the main lateral line of the PDL). In this connection the course of the main lateral line in PDL of *Aspidichthys* shows that a lateral line directed dorsad on ADL does not necessarily have to be the dorsolateral line. Here the main lateral line takes the course high up close to the suture to MD. That could be the case in some species or specimens of *Holonema,* too. Even Miles (1971) reconstructed the course of the lateral lines on the trunk shield of *H. westolli* in accordance with the hypothetical scheme of Ørvig (1969). The grooves of the lateral line system vary so much on the trunk shield of arthrodires that it seems to me doubtful that one can fit them into a strict scheme.

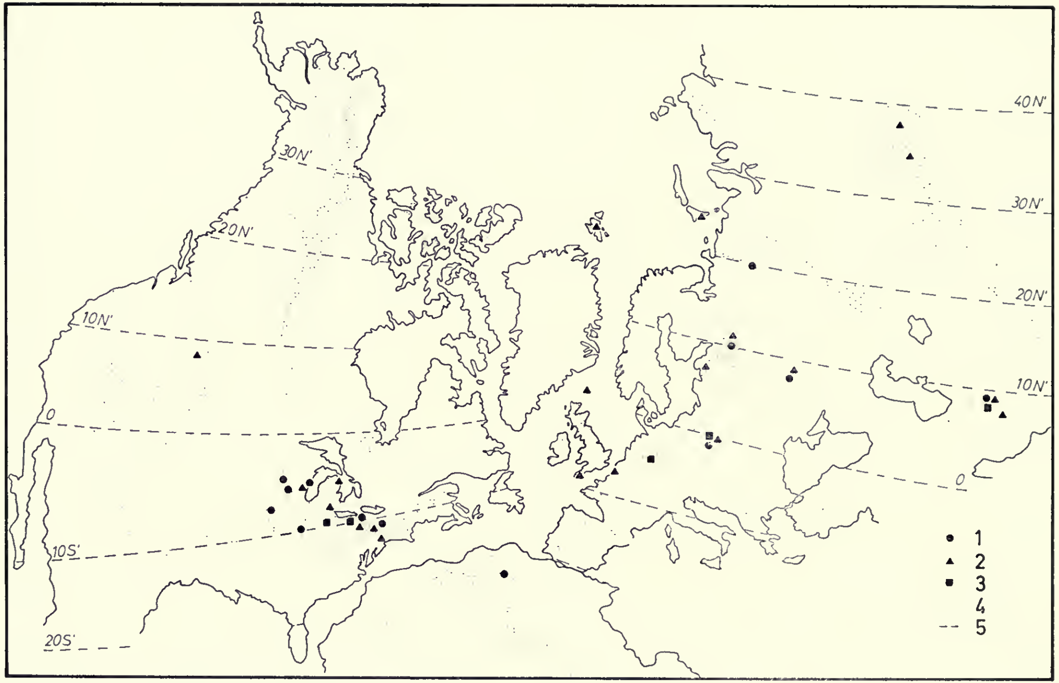

FIG. 6. Occurrence of the three large arthrodire-genera *Eastmanosteus* (= 1), *Holonema* (= 2), and *Aspidichthys* (= 3). 4 = Devonian outcrops. 5 = palaeomagnetic latitudes of Devonian, after Khramov (1967: Eurasia) and after Irving (1964: America, text-fig. 9.29 = Carboniferous and text-fig. 9.30 = Silurian combined). Map from Bullard *et al.* (1965, text-fig. 8).

The relationships of the genus *Aspidichthys* are problematical. *Aspidichthys* has been placed in the Holonematidae by Gross (1937), Schmidt (1938), and Kulczycki (1957), a placement questioned by Miles (1964, 1971) because of the difference in the ornamentation and in the form of the carinal process. Besides *Aspidichthys*, the two genera *Deveonema* (Kulczycki, 1957) and *Arctonema* (Ørvig, 1969) of the Holonematidae have an ornamentation consisting of isolated tubercles comparable to those of *Aspidichthys*, but differences in form of the carinal process exist. No general review of the genus *Aspidichthys* can be made here, and the genus is put questionably within the family Holonematidae.

PALAEOGEOGRAPHIC DISTRIBUTION

As mentioned above, large arthrodires, well known from the Devonian rocks of USA, have been found less often in other parts of the northern hemisphere. Of the three genera for which fragments are described above, *Holonema* has the widest distribution (fig. 6:*2*), a circumstance perhaps explainable by the peculiar ornamentation by which even small fragments can be easily recognized. *Holonema* is known from Middle and Upper Devonian rocks in North America and Eurasia. The genus *Eastmanosteus* (fig. 6: *1*) is known for the same period, but apparently has a smaller distribution than *Holonema*. Very few pieces of *Aspidichthys* (fig. 6: *3*) have been found and these have all been of Upper Devonian age. *Eastmanosteus* and *Aspidichthys* (including even "*A.*" *notabilis* from Middle Devonian) have a distribution apparently equatorial, as reconstructed for Devonian time by palaeomagnetic and lithologic data (occurrence of evaporites, reefs, etc.). All three genera occurred in apparently tropical to subtropical climate. Farther to the north *Holonema* occurs in the Minusinsk depression and in the Altai mountains, but also with evaporites (there is some discrepancy in Eastern Sibiria, where lithology and fossils indicate warm climate, too, see Chlupáč *et al.*, 1967, pp. 875, 876).

Not only do the same genera occur in North America and in Eurasia, but also the same or closely related species. The resemblance between *Eastmanosteus pustulosus* of North America and Poland (Kulczycki 1957), and *Aspidichthys ingens* in North America (Miles 1965), Poland, and Iran is very striking. In *Holonema* the three species *H. rugosum* (North America and Iran), *H. radiatum* (USSR and Poland), and *H. ornatum* (Shetland Isles and England) are very similar. According to Miles (1969, p. 129), these genera have a "broad adaptive zone." Thus these large forms may have been ecologically suited for easy dispersal. In any case, these genera probably were marine forms. Their widespread distribution in the Devonian may perhaps also be interpretable in the context of the hypothesis of continental drift.

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ADDENDUM

In 1972, a group of French geologists has collected in the region of Iran reported on here. They also found a rich fish fauna including *Eastmanosteus* and *Holonema*.

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