Notes on Triassic Fishes from Madagascar.

By

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I

Errolichthys mirabilis LEHMAN.

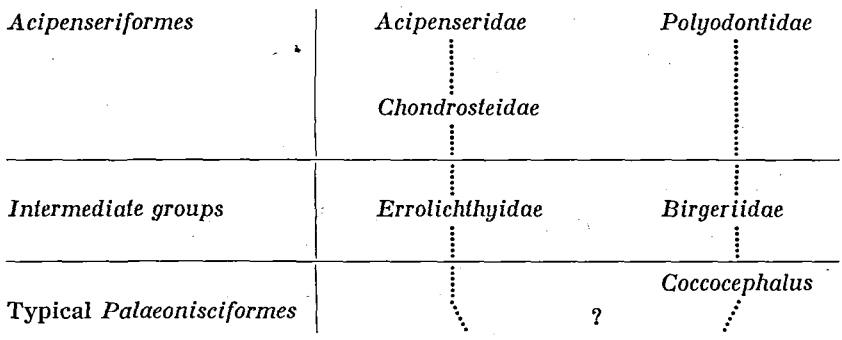
During a visit to Madagascar in 1953, made possible by a grant from the Danish State Research Foundation, I succeeded in securing a very large collection of fishes and some fine stegocephalians from the classical exposures of early Triassic marine deposits in the northern part of the island. The material of fishes will be dealt with mainly in connection with my studies on the closely related Eotriassic fish faunas from East Greenland, but I think it useful to publish observations on specially interesting forms as independent notes, of which the present paper appears as the first.

Based on a single specimen belonging to the British Museum of Natural History and collected by Dr. ERROL I. WHITE, Dr. J.-P. LEHMAN in his great work on the Triassic fishes from Madagascar (LEHMAN 1952) erected the highly interesting genus *Errolichthys* with the only species *E. mirabilis* and representing a family of its own: the *Errolichthyidae*.

LEHMAN pointed out that the new family showed close affinities to the *Acipenseriformes* (= *Chondrosteidae* + *Acipenseridae* + *Polyodontidae*), but still possessed a number of original *Palaeonisciform* characters, and accordingly he placed the *Errolichthyidae* in an intermediate position between the *Palaeonisciformes* and the *Acipenseriformes* instead of including it in the last-mentioned of these groups.

The family *Birgeriidae* has by several authors (i. a. WATSON 1928, ALDINGER 1937, E. NIELSEN 1949) been supposed to occupy a somewhat similar intermediate position between the *Acipenseriformes* and the typical *Palaeonisciformes*, but while *Birgeria* is placed on or near the evolutionary line leading towards the *Polyodontidae*, *Errolichthys* shows closer affinities to the *Chondrosteidae* and must accordingly be placed near the evolutionary line leading towards the *Acipenseridae*.

Roughly the positions of the two families *Errolichthyidae* and *Birgeriidae* can be sketched as follows:



With the discovery of *Errolichthys* we have thus gained new evidence for considering ALDINGER's order *Sturiomorpha* (ALDINGER 1937, pp. 377–379) an artificial group (cf. LEHMAN 1952, pp. 195–196), and as shown in the above scheme even the term *Acipenseriformes* must be abandoned unless, which is by no way certain, the *Acipenser* line and the *Polyodon* line issue from a not too remote common ancestral form within the *Palaeonisciformes*, and this form as well as the intermediate groups *Errolichthyidae* and *Birgeriidae* are included in the *Acipenseriformes*.

LEHMAN's only specimen of *Errolichthys* comprised the head and a very short foremost part of the trunk with parts of the shoulder-girdle and the pectoral fin. The head was strongly compressed, but in spite of this LEHMAN succeeded in restoring the main features of the dermal head skeleton in dorsal as well as lateral view (LEHMAN 1953, text-figs. 80, 82).

The material at my disposal comprises the following specimens of *Errolichthys mirabilis*:

Specimen M T 1, collected north of the village of Ambarakaraka, and comprising a compressed but well preserved head and a short adjoining part of the trunk. Length of the head (measured as in the following specimens from the anterior end of the lower jaw to the posterior end of the boundary between the operculum and the suboperculum) 80 mm.

Specimen M T 2, collected south of the village of Bobatomendry, and comprising a slightly compressed head and a short anterior part of the trunk. Length of the head about 97 mm.

Specimen M T 3, collected from the same locality as specimen M T 2, and comprising a number of isolated structures from a single head, i. a. an operculum, a suboperculum, a series of branchiostegal rays, the two mandibles, and the big unpaired ventral dental plate.

Specimen M T 4, collected north of Ambarakaraka, and comprising an impression of the posterior part of the left side of a fairly large head.

Specimen M T 5, collected east of Bobatomendry, and comprising a small compressed head with the foremost and hindmost parts missing. Estimated length of the head between 60 and 70 mm.

Specimen M T 6, bought by a native in the village of Iraro, and comprising a much compressed head and the shoulder-girdle. The head, which shows many interesting details, measures about 94 mm in length.

Specimen M T 7, bought by a native in the village of Iraro, and comprising a compressed head with a very well preserved shoulder-girdle. Length of head about 90 mm.

As could be expected this new material adds considerably to our knowledge of *Errolichthys mirabilis* in showing not only certain skeleton structures which are missing in LEHMAN's single specimen, but also the range of variability in outline and number of the more or less reduced elements of the dermal skeleton.

According to LEHMAN the neural endocranium was well ossified, and as far as could be ascertained it formed a continuous structure much as in the *Saurichthyidae* and certain *Palaeoniscoidea*; owing to the state of preservation very little information could, however, be given of its structural details.

In the specimens now at hand the head region is also more or less compressed, and the neural endocranium therefore severely damaged. As far as I can see, this indicates that the degree of ossification of this structure was much less than in *Pteronisculus, Boreosomus, Saurichthys,* and several other forms found in the same deposits, for in these forms the neural endocrania of a relatively high percentage of the specimens are in a perfect condition even if, as is sometimes the case, they have been displaced, and are now lying separated from their protecting dermal bones.

I therefore suspect that the endocranium of *Errolichthys* was mainly cartilaginous although with a rather thin lining of perichondral bone. As to its detailed structure the specimens at hand are not sufficient for a satisfactory restoration, even if further preparation of some of my specimens would probably add to our at present extremely scanty knowledge.

The parasphenoid (*Psph*) as shown by LEHMAN extends backwards below the occipital region as in *Birgeria, Saurichthys, Polyodon, Acipenser,* and several other *Palaeonisciform* derivatives. The foremost end of the parasphenoid is not pointed but gently rounded, the antero-lateral margins of the bone being convex instead of concave as in LEHMAN's restoration (LEHMAN 1952, text-fig. 79). The tooth-bearing area on the oral face of the parasphenoid extends backwards behind the centre of radiation, probably almost to the posterior margin of the bone, and at least the pars anterior of the parasphenoid is relatively broader than in LEHMAN's figure. Anterior to the parasphenoid some of the new specimens show a mosaic of smaller dermal bones, the oral faces of which are completely covered with densely set teeth of about the same size as those on the parasphenoid itself. These small plates (*Dp. d*) might have arisen by fragmentation either of a paired or unpaired vomer or of the foremost end of the parasphenoid itself.

The bones of the dermal cranial roof are as shown by LEHMAN strongly reduced, especially anteriorly. Some of them have disappeared completely, others are represented mainly by a tube surrounding part of the sensory canal system, others again have undergone fragmentation or have strongly fringed margins. All of them are also greatly reduced in thickness, and their outer face show a system of ramifying fine grooves which must have lodged small vessels formerly enclosed in the bones. It is not amazing that under such conditions the pattern of the dermal cranial roof varies from specimen to specimen.

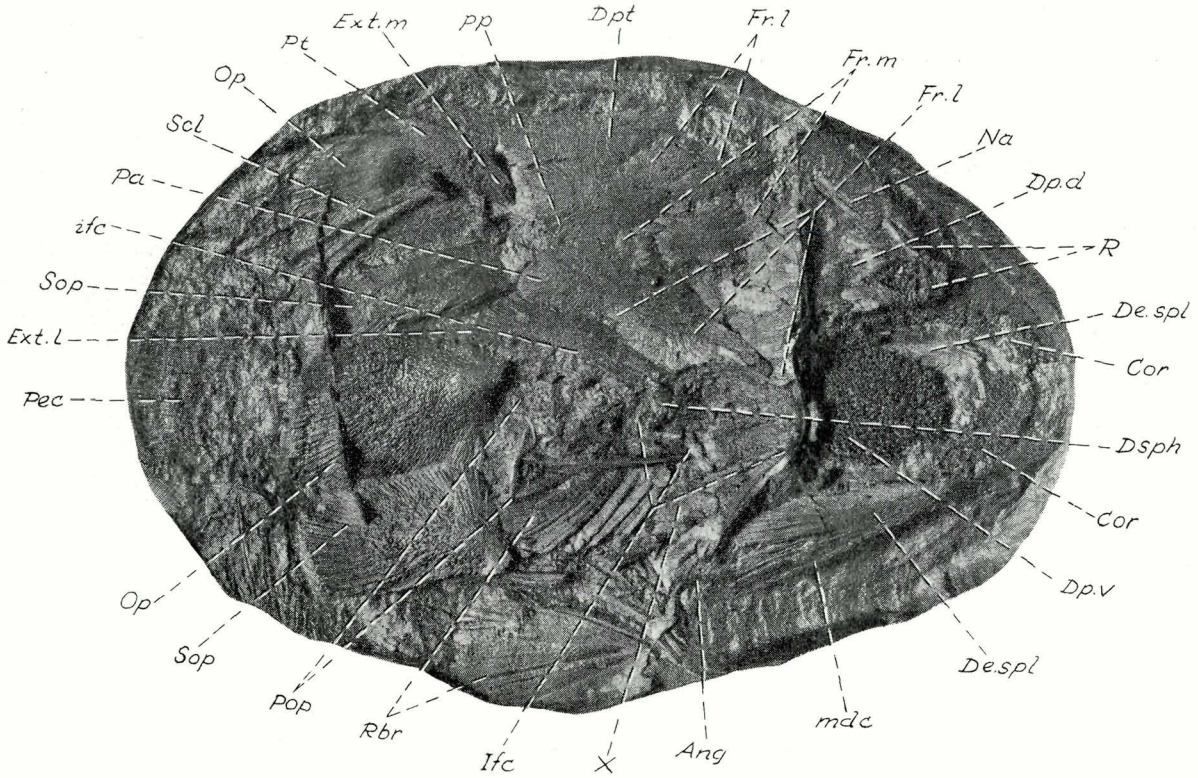


Fig. 1. *Errolichthys mirabilis* LEHMAN. Head and anterior part of trunk region (cast). Specimen M T 1. Ca. 1.2×. *Ang*, angular; *Cor*, coronoid series; *De. spl*, dentalo-splenial; *Dp. d*, dorsal dental plate; *Dpt*, dermopterotic; *Dp. v*, ventral dental plate; *Dsph*, dermophenotic; *Ext. l*, lateral extrascapular; *Ext. m*, medial extrascapular; *Fr. l*, lateral frontal series; *Fr. m.*, median frontals; *Ifc*, infraorbital series; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pec*, pectoral fin; *Pop*, preopercular series; *Pt*, posttemporal; *R*, rostral series; *Rbr*, branchiostegal rays; *Scl*, supracleithrum; *Sop*, suboperculum; *X*, unidentified dental plate; *ifc*, infraorbital sensory canal; *mdc*, mandibular sensory canal; *pp*, posterior pit-line.

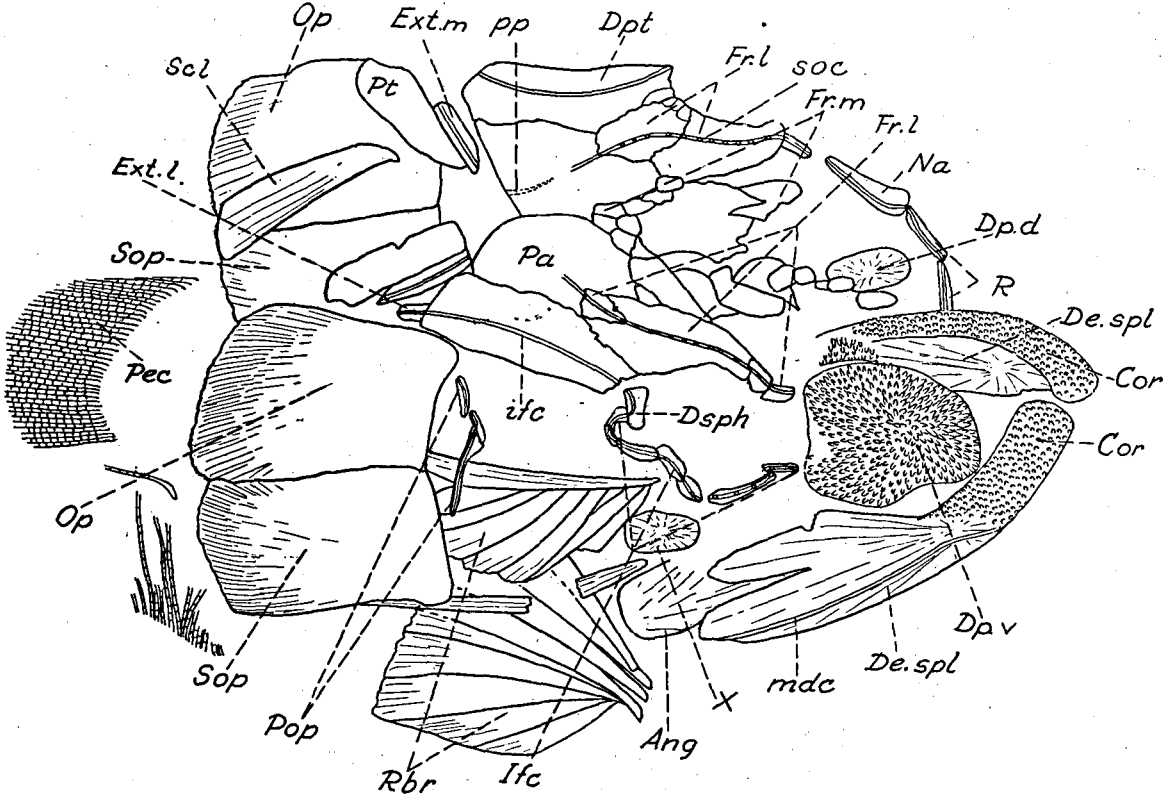


Fig. 2. *Errolichthys mirabilis* LEHMAN. Sketch of specimen M T 1 (fig. 1). Ca. 1.6x. *soc*, supraorbital sensory canal. Other letters as in fig. 1.

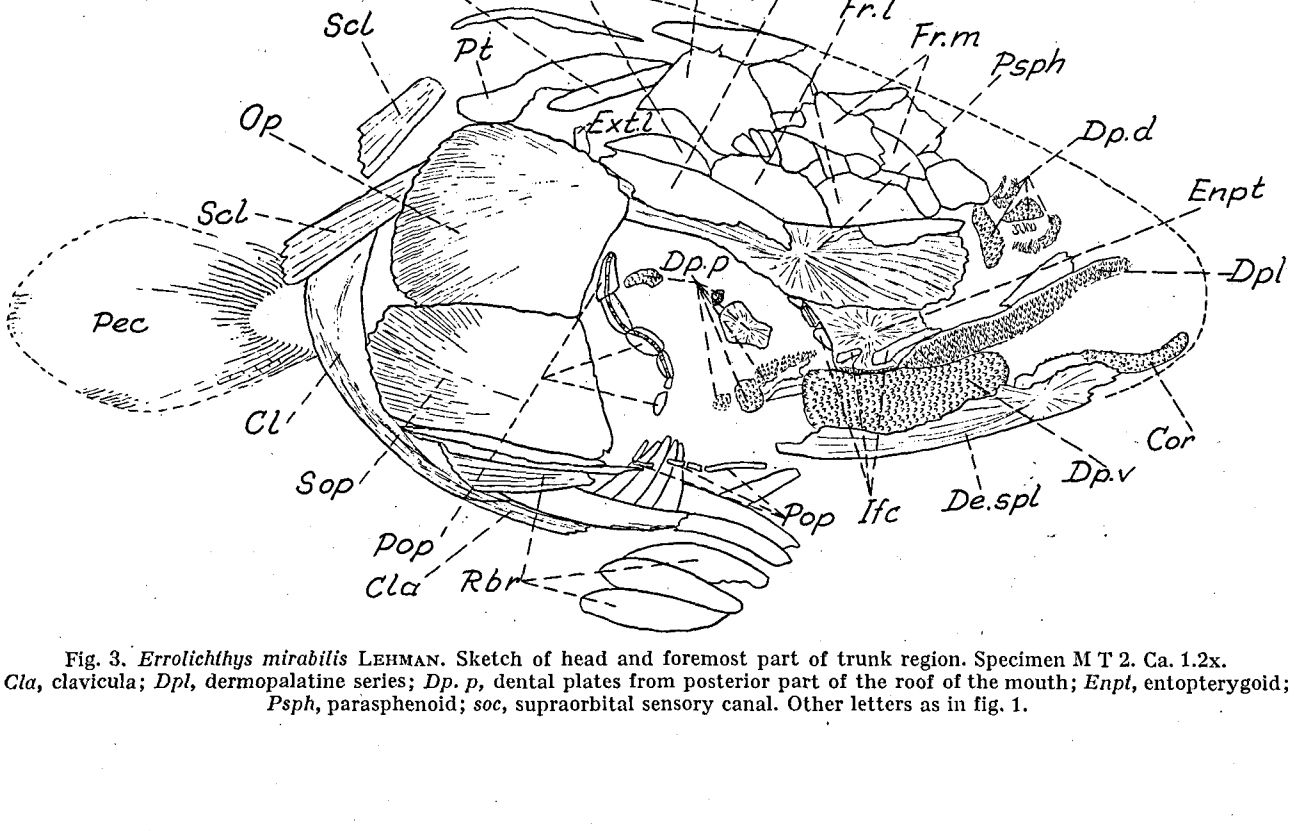


Fig. 3. *Errolichthys mirabilis* LEHMAN. Sketch of head and foremost part of trunk region. Specimen M T 2. Ca. 1.2x. *Cla*, clavicula; *Dpl*, dermopalatine series; *Dp. p*, dental plates from posterior part of the roof of the mouth; *Enpl*, entopterygoid; *Psph*, parasphenoid; *soc*, supraorbital sensory canal. Other letters as in fig. 1.

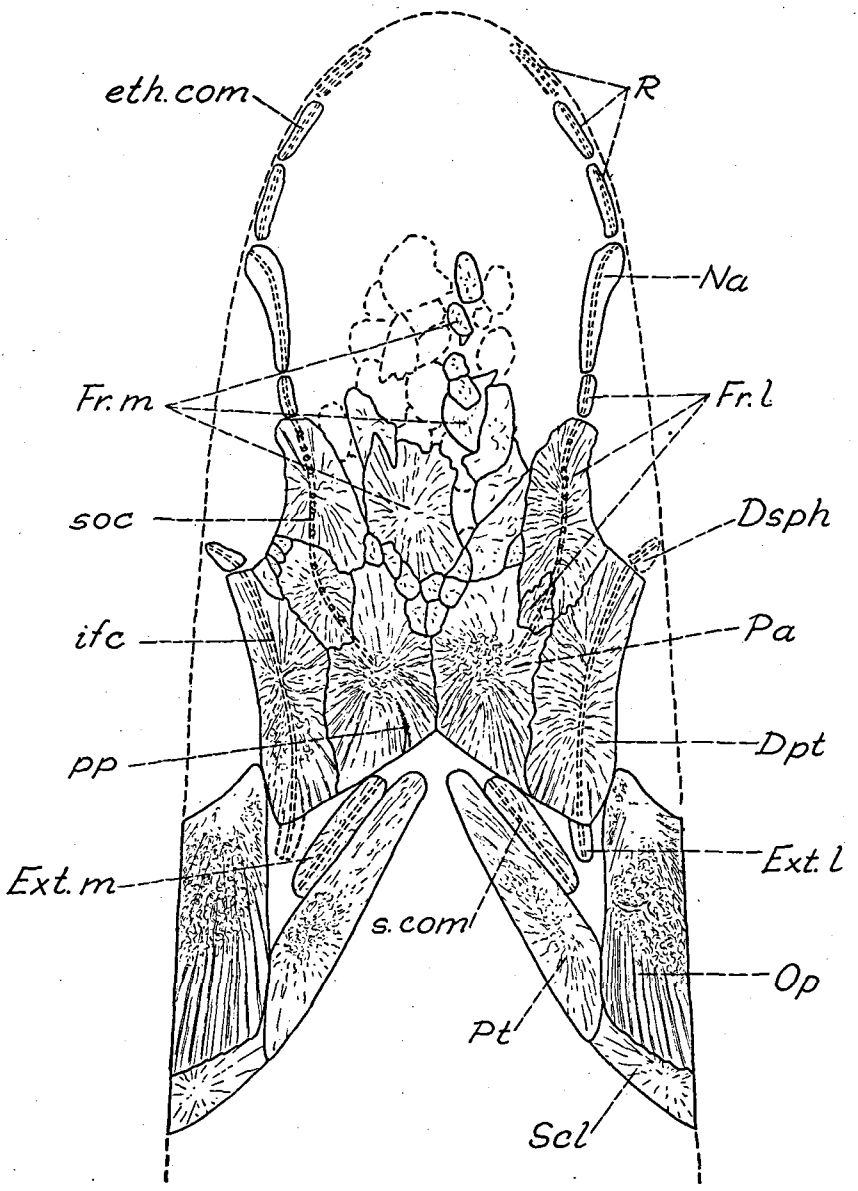


Fig. 4. *Errolichthys mirabilis* LEHMAN. Attempted restoration of the head and shoulder-girdle in dorsal view. Mainly based on specimen M T 1. Ca. 1.9x. *eth. com*, ethmoidal commisure; *s. com*, supratemporal commisure. Other letters as in fig. 1.

According to LEHMAN the extrascapular bones, in addition to the series containing the supratemporal commisure (*c. com*) and part of the cephalic division of the main lateral line (*l. c*), comprises an anterior series of (4?) anamestic bones. The existence of these anamestic bones cannot be verified on my material, and I am inclined to believe that LEHMAN's anterior extrascapular series is the dorsal surface of the occipital region of the neural endocranium exposed behind the posterior margins of the parietals and dermopterotics. Of LEHMAN's 3 pair of extrascapulars connected with the sensory canal system I have only observed two, viz. a long and narrow medial (*Ext. m*) and a much shorter lateral (*Ext. l*) element. It is however not impossible that a third element once occupied the area behind the small lateral extrascapular, but has been lost in the specimens investigated by me.

The dermopterotics (*Dpt*) i.e. the supratemporo-intertemporals in the terminology used in my previous papers (but see STENSIÖ 1947, p. 93, LEHMAN 1952, pp. 18, 128) and the parietals in my specimens agree rather closely with LEHMAN's restoration, but the supraorbital sensory canal (*soc*) can be followed backwards from the lateral frontal series into the parietal almost as far back as to the centre of radiation, and the left parietal in specimen M T 1 shows a distinct groove extending from a point just behind the centre of radiation backwards to the hind margin of the bone. I am inclined to believe that this groove (*pp*) represents the posterior pit-line of the cranial roof. A lateral parietal (*Pa. l*) corresponding to that described by LEHMAN is found on the right half of the cranial roof in specimen M T 2.

The dermosphenotic (*Dsph*), which in LEHMAN's specimen has much the same shape as the postorbito-dermosphenotic in *Acipenser sturio*, is in my specimens a much smaller bone. Probably LEHMAN's dermosphenotic contains the homologue of one or more of the hindmost elements in the postorbital part of the infraorbital series.

As restored from my material, the infraorbital series contains 9 separate bones (*Ifc*, *Ant*) of which all but the foremost one, which corresponds to the antorbital in typical *Palaeonisciformes*, are reduced almost to tubular structures around the sensory canal. The same number of separate infraorbitals is found in LEHMAN's restoration, but the relative length of the different infraorbitals is not the same as in my restoration.

Of the much reduced rostrals (*R*) I have only observed three on each side, while LEHMAN's specimen shows about six. Probably the rostrals and the infraorbitals vary in extent and number from specimen to specimen, but it must be borne in mind, too, that the elements of these two series are of small size, and as they are not mutually connected by suture, some of them may have been lost or displaced before the final burial of the specimens.

As shown by LEHMAN the frontals are represented by a right and left series of canal bones, the lateral frontals (*Fr. l*), and between these series by a group of numerous small anamestic plates, the medial frontals (*Fr. m*).

Quite possibly the central group of anamestic plates, in addition to medial frontal components, also contains parietal and postrostral compo-

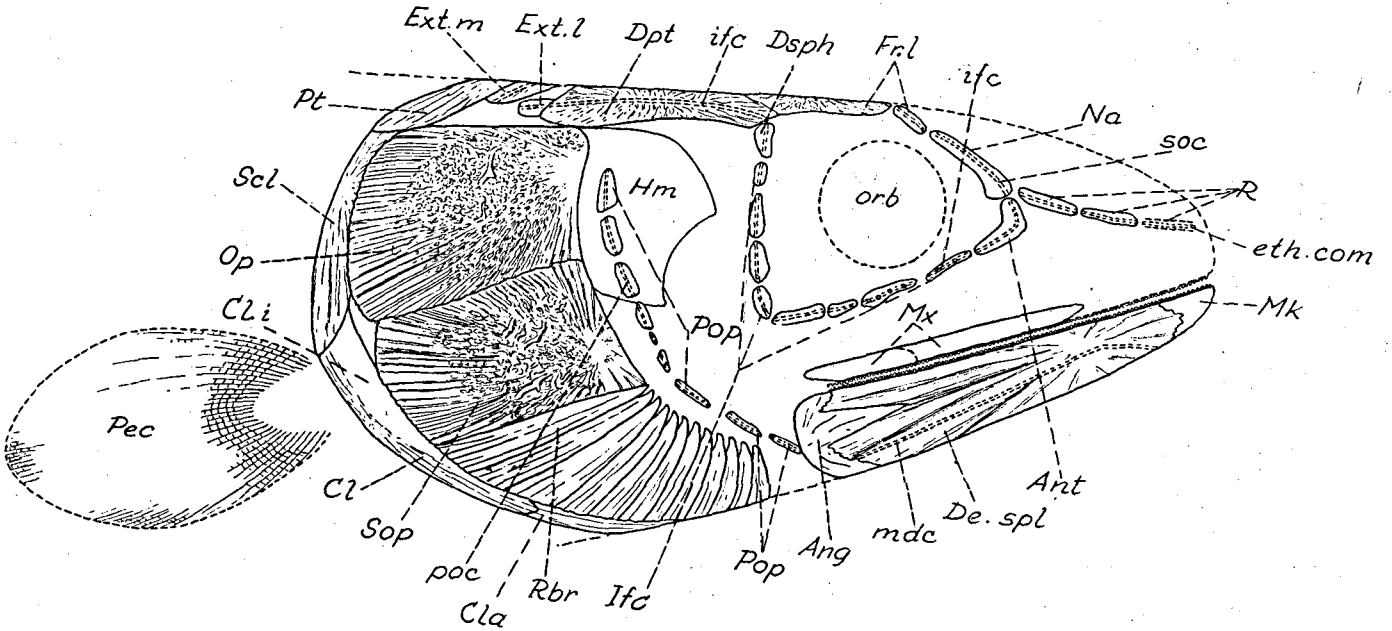


Fig. 5. *Errolichthys mirabilis* LEHMAN. Attempted restoration of the head and shoulder-girdle in lateral view. Mainly based on specimen M T 1. Ca. 1.6x.

Ant, antorbital; *Cl*, cleithrum; *Cla*, clavicula; *Cl. i*, internal lamina of cleithrum; *Hm*, hyomandibula; *Mk*, Meckelian cartilage; *Mx*, maxillary; *eth. com*, ethmoidal commisure; *orb*, orbital opening with presumed position of eye; *soc*, supraorbital sensory canal. Other letters as in fig. 1.

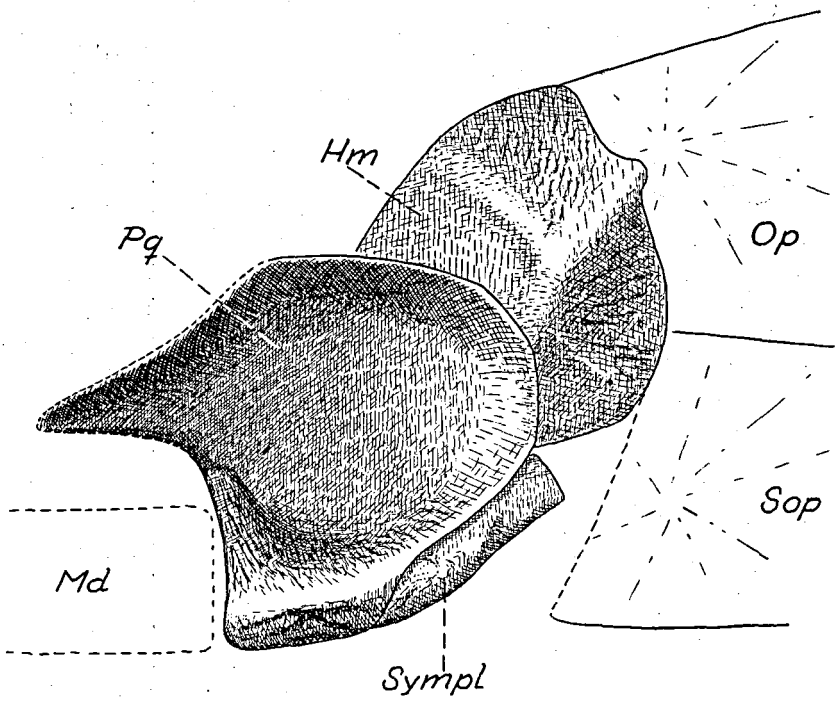


Fig. 6. *Errolichthys mirabilis* LEHMAN. Sketch of hyomandibula, symplectic, posterior part of palatoquadrate and mandible, and part of operculum and suboperculum, in mainly lateral view. (owing to distortion of the specimen the mandible and the pars quadrata are shown in dorsal view). Specimen M T 6. 2x.
Hm, hyomandibula; *Md*, mandible; *Op*, operculum; *Pq*, palatoquadrate; *So*, suboperculum; *Sympl*, symplectic.

nents, and there can be no doubt that this mosaic of small bones extends farther forward than in the restoration given by LEHMAN.

The lateral frontal series in specimen M T 1, on which specimen my restoration of the dermal cranial roof is mainly based, comprises three canal bones of which the two hindmost correspond to the large posterior lateral frontal in LEHMAN's restoration, while the foremost one is much shorter than the anterior part of the lateral frontal series in LEHMAN's specimen. On the other hand, the nasal (*Na*) in specimen M T 1 is considerably longer than in LEHMAN's restoration, and it therefore seems likely that its posterior part corresponds to the foremost one of his small lateral frontals. A number of small anamestic bones is found along the orbital margin of the left posterior lateral frontal of specimen M T 1. These bones have evidently arisen by beginning fragmentation of the posterior lateral frontal and of an adjoining part of the dermopterotic (*cf.* figs. 2 and 4).

The preopercular series (*Pop*) is much longer than restored by LEHMAN, extending from near the antero-dorsal corner of the operculum to the posterior end of the mandible and comprising about 9 small bones, the

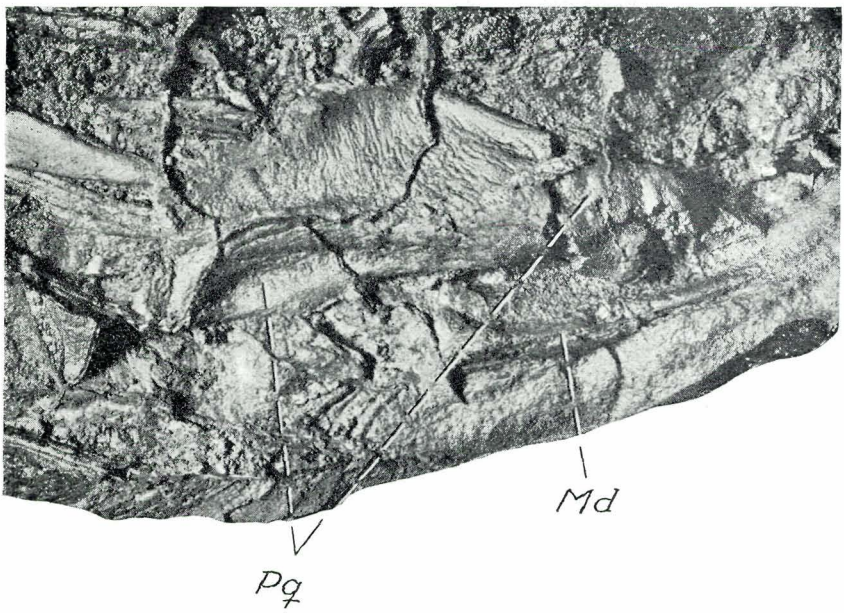


Fig. 7. *Errolichthys mirabilis* LEHMAN. Detail of cast of specimen M T 6, showing ora face of left palatoquadrate and posterior part of mandible. Ca. 1.5x.

most reduced of which appear merely as slender tubes around the prepercular sensory canal (*poc*).

The maxillary (*Mx*), which according to LEHMAN probably has completely disappeared, is present in specimen M T 5 as a long and narrow plate placed as shown in the restoration (fig. 5). As a matter of fact the maxillary in specimen M T 5, as also indicated in my restoration, consists of two pieces, but I am rather certain that this is due to post mortem damage of the specimen and not to fragmentation connected with the considerable reduction of the bone. If the maxillary carried teeth cannot be decided at present. On the external face of the long mandible I have observed only two dermal bones, viz. a large dentalo-splenial (*De. spl*) and a rather small posterior bone (*Ang*), which I have interpreted as an angular. Very likely better preserved specimens than those at my disposal will, however, show the existence also of a small supraangular, but I consider it highly improbable that an independent splenial, as shown in LEHMAN's restoration, exists.

The dentalo-splenial, which does not extend forward to the symphysis, in addition to the greater part of the lateral face of the mandible, to some extent also covers the mandible dorsally, its dorsal marginal zone extending inwards as a horizontal lamina as in many normal *Palaeonisciformes*. The whole upper face of the mandible is covered by densely set teeth of the same type as those found on the parasphenoid and the smaller dermal bones anterior to the parasphenoid. As far as can be seen these teeth are situated

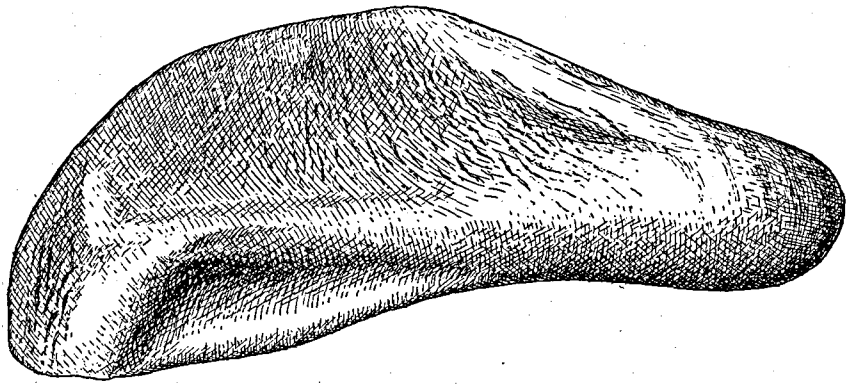


Fig. 8. *Errolichthys mirabilis* LEHMAN. Sketch of the oral face of left palatoquadrate shown in fig. 7. Ca. 2.2x.

partly on the horizontal lamina of the dentalo-splenial and partly on a series of small coronoids (*Cor*) and eventually also on a somewhat larger prearticular. The exact boundaries of the coronoids and the prearticular could, however, not be traced on any of my specimens owing to the density of their teeth-covering. The Meckelian cartilage (*Mk*) is ossified in one piece from the pars articularis to the symphysis, and its foremost

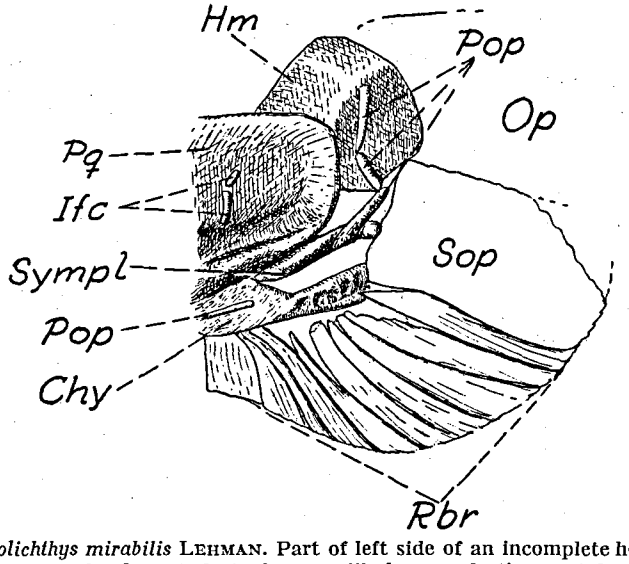


Fig. 9. *Errolichthys mirabilis* LEHMAN. Part of left side of an incomplete head showing posterior part of palatoquadrate, hyomandibula, symplectic, ceratohyal, dermal bones of the opercular fold and parts of the infraorbital and preopercular series. Specimen M T 4. Nat. size.

Chy, ceratohyal; *Hm*, hyomandibular; *Ifc*, infraorbital series; *Op*, operculum; *Pop*, preopercular series; *Pq*, palatoquadrate; *Rbr*, branchiostegal rays; *Sop*, subopercu-lum; *Sympl*, sympletic.

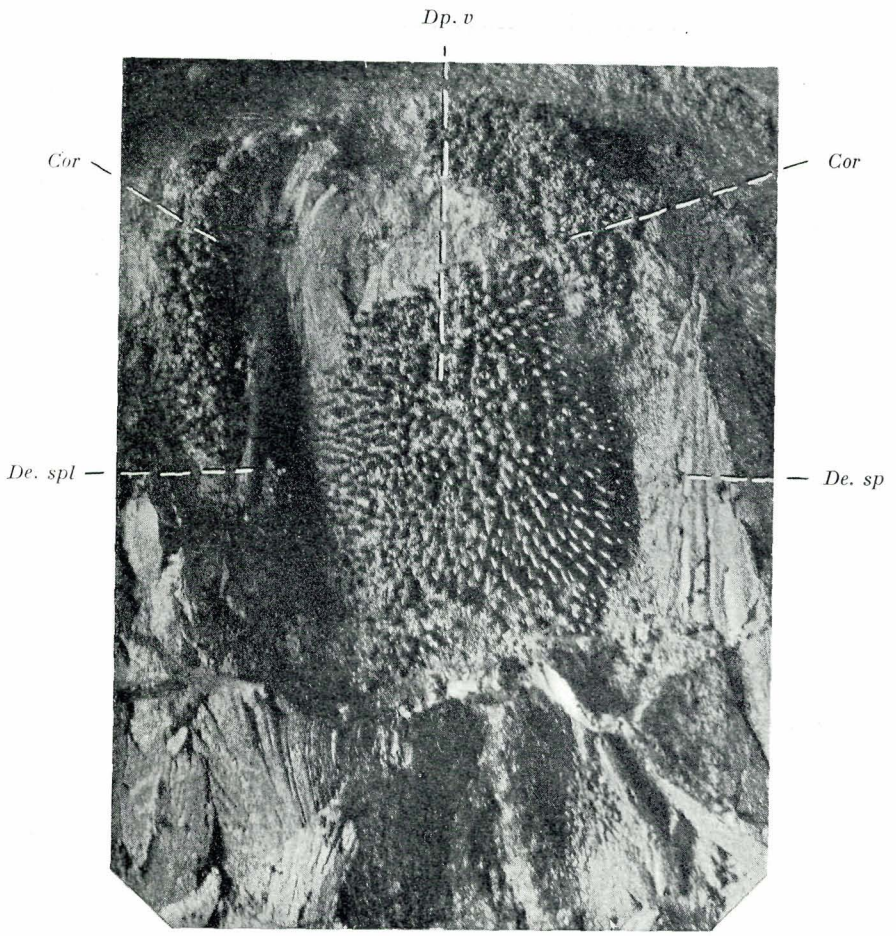


Fig. 10. *Errolichthys mirabilis* LEHMAN. Ventral dental plate and anterior part of right and left mandibles in dorsal view. Detail of the cast of specimen M T 1 shown in fig. 1. 3x.

part is strongly medially curved. Between the two mandibles we find in the floor of the mouth a large oval unpaired plate (*Dp. v*), the oral face of which is closely set with teeth of the usual type. This dental plate had probably the same relations to the visceral endoskeleton as the ventral dental plate in *Bobasatrania* (cf. E. NIELSEN, 1952).

The floor of the mouth is thus extremely well equipped with teeth, and the same is the case with its roof. We have already mentioned that the dermal bones on the ventral face of the neural endocranium are equipped with numerous closely set teeth, and the same is the case with the dermal bones of the palatoquadrate, the outlines of which are therefore very difficult to trace. A large entopterygoid (*Enpt*) is present in some of my

specimens, while the ectopterygoid and eventually a dermometapterygoid seem to be dissolved in numerous smaller plates (*Dp. p*). Another group of small tooth-bearing plates, arranged in a single row, probably represents the dermopalatine series.

In specimen M T 6 the oral and the posterior part of the aboral face of the left palatoquadrate are seen as very clear impressions, and there can be no doubt that the palatoquadrate was ossified in one piece from its hindmost to its foremost end as is the case in several other primitive Actinopterygians. The aboral face of the posterior part of the palatoquadrate is concave both in a dorso-ventral and a rostro-caudal direction, the dorsal, posterior, ventral, and to some extent also anterior marginal zones of the ossification being bent outwards as shown in fig. 6. The bend is most pronounced farthest ventrally, where the pars quadrata extends laterally as an almost horizontal plate, the anterior margin of which forms the condyle for the articulation with the lower jaw. The oral face of the same palatoquadrate is seen in figs. 7 and 8, which figures do not agree very well in outlines with fig. 6 showing the same structure in aboral view. The disagreement must be due to the fact that the oral impression is not quite complete posteriorly where it has been hidden beneath other structures.

As shown in figs. 7 and 8 the visible part of the oral face of the palatoquadrate is divided by very prominent broad ridges in three areas, a large dorsal, a smaller ventral, and a still smaller posterior one, all of which appear as shallow concavities, ornamented with very fine grooves, probably for small vessels. In the dorsal area we find a small rounded elevation which might be interpreted as a not very conspicuous basal process.

The hyomandibula (*Hm*) is preserved as more or less complete impressions of its lateral face in specimens M T 4, 5, and 6. It is a very broad, laterally compressed structure with a rather small processus opercularis, and placed in close contact with the postero-dorsal part of the palato-

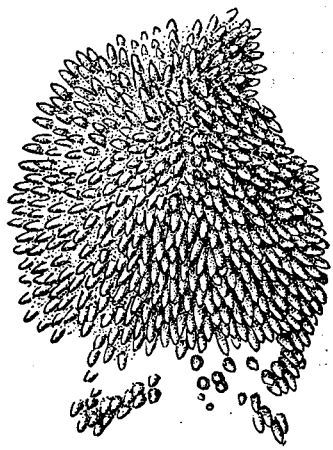


Fig. 11. *Errolichthys mirabilis* LEHMAN. Sketch of the ventral dental plate shown in the preceding figure. 3x.

quadrate as shown in fig. 6. Distally to the hyomandibula and in close contact with the postero-ventral part of the palatoquadrate a long and fairly massive symplectic (*Sympl*) is found, and specimen M T 4 furthermore shows part of a strong ceratohyal ossification (*Chy*). The hyoid arch is thus well ossified as was also the case with the mandibular arch, but no remnants at all have been observed of the branchial arches which accordingly were probably cartilaginous.

As described by LEHMAN the dermal bones of the opercular fold show much less sign of reduction than most of the other dermal bones of the head. The operculum (*Op*) is larger than the suboperculum (*Sop*) while the opposite is the case in *Chondrosteus*. The number of branchiostegal rays (*Rbr*) is about 12.

The dermal bones of the shoulder-girdle are as described by LEHMAN very narrow. The series comprises a posttemporal (*Pt*), a supracleithrum (*Scl*), a cleithrum (*Cl*), and a clavicle (*Cla*). The cleithrum has a rather broad, smooth internal lamina (*Cl. i*), while its external sculptured face is extremely narrow. The clavicle, which was not found by LEHMAN, is rather small, and as the cleithrum it is equipped with an internal lamina. As to the ossified endoskeleton of the shoulder-girdle mentioned by LEHMAN the new material gives no further details, nor can the number of ossified radials in the endoskeleton of the pectoral fin be stated with certainty. The pectoral fin itself is vertical and provided with a small lobe. The number of lepidotrichia is about 35.

LEHMAN mentions the presence of some rather large cycloid scales from the region just behind the head. Although the corresponding region is also present in some of my specimens, I have not been able to discover the slightest remnants of scales, and if I should judge from my material only, my conclusion must be that *Errolichthys* was naked.

The new contributions to our knowledge of the structure of *Errolichthys* gives no reason for doubting LEHMAN's assumption that this interesting genus occupies an intermediate position between the *Palaeonisciformes* and the *Acipenseroidea*. On one hand, the not reduced dentition, the many branchiostegal rays, the presence of a maxillary, the structure of the mandible, and the course of the supraorbital sensory canal from the lateral frontal series into the parietal speaks about a closer relationship with the *Palaeonisciformes* than assumed by LEHMAN, on the other hand the presumed slight ossification of the neural endocranium, the relationship between the hyoid and the mandibular arch with the vertical or forwardly inclined suspensorium, and the eventual lack of scales rather strengthens the assumed relationship with the *Acipenser* line.

At present it seems impossible to point out a probable ancestral form to *Errolichthys* among the known *Palaeonisciformes*. In my extensive material of Eotriassic fishes from East Greenland I have, however, discovered a single specimen of an *Errolichthys* or a form closely related to *Errolichthys* which differs mainly from the species from Madagascar in the less progressed state of reduction of the dermal bones of the head.

A study of this interesting specimen might throw a new light on the ancestry of *Errolichthys mirabilis*.

DANSK RESUMÉ

I 1952 beskrev J.-P. LEHMAN en overordentlig interessant ny Fisketype, *Errolichthys mirabilis* LEHMAN, fra Nordmadagascars marine Triasaflejringer. LEHMAN's Materiale omfattede kun et enkelt ufuldstændigt Eksemplar, paa Basis af hvilket han opstillede ikke blot en ny Art og Slægt, men ogsaa den ny Familie, *Errolichthyidae*, som han mente at kunne placere som en intermediær Gruppe mellem *Palaeonisciformes* og *Acipenseriformes*. Under mit Ophold paa Madagascar i 1953 lykkedes det mig at tilvejebringe yderligere 7 Eksemplarer af *E. mirabilis*, paa Basis af hvilke det er muligt paa en lang Række Punkter at komplettere den af LEHMAN givne Beskrivelse. De nye Iagttagelser bekræfter LEHMAN's Opfattelse af Familien *Errolichthyidaes* systematiske Stilling, og sammenholdt med de Iagttagelser, der væsentligt paa Basis af Materiale fra Østgrønland er gjort over *Birgeria* systematiske Stilling, synes det klart, at *Acipenseriformes* ikke kan betragtes som en naturlig Enhed, idet *Polyodon* og *Acipenser* Linierne er adskilte helt fra deres Udspring fra Stamgruppen *Palaeonisciformes*.

Til Slut nævnes at *Errolichthys* eller en *Errolichthys* meget nærstaaende Slægt ogsaa findes i de marine Eotriasaflejringer i Nordøstgrønland.

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