ON THE MONO- OR POLYPHYLETIC ORIGIN OF TETRAPODS

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The problem of the origin of terrestrial tetrapods is one of the controversial questions of biology. Many investigations have been devoted to it in the field of paleontology, comparative anatomy and embryology. In the past decade, interest in this problem has increased especially in connection with new discoveries of fossil forms which are more or less close to the ancestors of the tetrapods.

As long as the links which connect fishes with tetrapods are not conclusively established, there is room for hypotheses and propositions about the peculiarities of the structure, taxonomic position, singleness and multiplicity of initial forms, the time and places of the appearance of the first tetrapods and the causes for their appearance.

At the end of the 19th century, terrestrial amphibians were linked with dipnoan fishes. Paleontology rejected this proposition, based on the great specialization in the Dipnoi and the impossibility of the homology of their bones with the bones of tetrapods. In the 20th century, only a few investigators consider that the origin of some tetrapods, namely tailed amphibians (Urodela), is possible from the Dipnoi (Wintrebert, 1910; Holmgren, 1933; Save-Soderbergh, 1934; Lehman, 1956). At the present time, one can consider it generally accepted that tetrapods derived from lung fishes of the order[1] Rhipidistia which unites two suborders, i.e., Holoptychioidei and Osteolepidoidei, which correspond to the groups Porolepiformes and Osteolepiformes of Jarvik (E. Jarvik, 1942).

The opinion of investigators is divided as to the actual representatives of the Rhipidistia which served as starting points for the tetrapods. The most widespread hypothesis is that of polyphyletic derivation. Its basic source was the detailed survey of the anatomy of the ethmoid region of the skull of lower Gnathostomata by Jarvik (1942). As a result of the comparison of the structure of the snout of <u>Eusthenopteron</u> (Osteolepiformes) and <u>Porolepis</u> (Porolepiformes) and their comparison with the skull structure of amphibians, primarily <u>Rana</u> (Anura) and <u>Salamandra</u> (Urodela), Jarvik came to the following conclusions: 1) The Rhipidistia represent two separate groupings, i.e., Porolepiformes and Osteolepiformes; 2) modern tailless and tailed amphibians are sharply distinguished from one another by the structure of the ethmoid, which indicates their derivation from various fishlike ancestors; 3) the distinctions between Anura and Urodela correspond

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to the differences in the structure of the snout of Rhipidistia and in connection with this the former should be considered to issue from Osteolepiformes and the latter from Porolepiformes. Osteolepiformes served as the beginning for all remaining tetrapods (Eutetrapoda). Lepospondylous amphibians (Lepospondyli) which are brought into question with Urodela just as are Apoda are not examined by Jarvik (fig. 1).

In recent years, Jarvik has published a series of works devoted to the questions of the origin of the tetrapods, with an analysis of the structure of separate components of the skeleton and espec-

--fig. 1--

ially of the skull. The hypotheses of diphyly in his later works has developed into full polyphyly (Jarvik, 1955). Thus, one of his graphs (Jarvik, 1960, figs. 18n and 30) shows that not only Anura and Urodela but also Labyrinthodontia, Sauromorpha and Theromorpha arise independently from Osteolepiformes. The time of the appearance of tetrapods moves to the lower Silurian or even Ordovician (Jarvik, 1964).

The investigations of Jarvik created lively discussion among biologists. They present a pattern of detailed study of the skeleton of fossil vertebrates. However, a whole group of scholars are not in agreement with the conclusions of these studies. Many zoologists (Shmal'gauzen, 1959, 1964; Eator, 1959; Szarski, 1962; Parsons and Williams, 1962, 1963) consider this contrasting of Anura and Urodela untenable and reject the hypotheses of their diphyletic derivation. The studies of I. I. Shmal'gauzen in this regard deserve special attention. He has dealt for many years with questions of the origin of terrestrial vertebrates. A series of experimental investigations was conducted under his direction on the development of amphibians with the aim of clarifying the succession in evolution of the structure of fishes and tetrapods and the degree of similarity and difference in their beginnings in Anura and Urodela. The investigations, which dealt with the development of many elements of the skeleton and sensory organs in amphibians, in no way support their polyphyletic origin. On the other hand, data from embryology indicating the homology of many organs of Anura and Urodela along with their possession of a complex of tetrapod characteristics which hardly could have appeared in a parallel way in various evolutionary lines and along with the

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[1] The taxonomy of lungfishes (superorder Crossopterygii) is according to "Usnovy paleontologii" (1964).

presence of traits characteristic only of amphibians, rather bear witness in favor of a monophylatic origin of modern amphibians (Shmal'gauzen, 1959). Special interest is created by the ascertainment of the homology of "doubtful structures", i.e., structures casting doubt on the generality of their origin among various forms of amphibians. Their number includes, in part, the lepospondylous type of vertebrae and the structure of the limbs of Urodela. The wholly cylindrical vertebrae of Lepospondyli are similar to the vertebrae of Urodela. As the studies of I. I. Shmal'gauzen (1959, 1964) have shown, in the latter, the vertebrae are formed by the same elements as in other amphibians. They could easily have

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issued from a rachitomous type basic for all tetrapods, i.e., the representation of the isolated situation of Lepospondyli is without foundation.

The difference in the embryonic development of the limbs of the modern Urodela and Anura served as one of the bases for their diphyleticism. At one time Holmgren (1933) presented a diagram of the limbs of the Urodela and Anura on the basis of embryological investigations and generalizations. The first diagram was notable for the presence of the jointed skeletal axis testifying, as it were, to the origin of the limbs of Urodela from biserial archipterygium of lungfishes or the Dipnoi. The basis for the formation of such an axis was the presence of a skin formation between the first two digits in the larvae of Hynobius at early stages of development. This formation in the opinion of I. I. Shmal'gauzen (1959) is coenogenetic. This diagram does not correspond to the formation of the limbs of a single representative of tetrapods including mature Urodela. The composition of the limbs of the latter is very similar to that of the remaining tetrapods especially the labyrinthodonts, e.g., Eryops and Trematops (Shmal'gauzen, 1915). The diagram given by Holmgren for Anura reflects the general structure of a pentadactyl limb with the exception of mature Anura whose limbs are highly specialized.

The difference in the embryonic development of the limbs of Urodela and Anura were examined even before Holmgren by A. N. Sewertzoff (Sewertzoff, 1908) as has been noted by Jarvik (1964). The latter, citing these differences as one of the arguments for the diphyleticism of amphibians, used a partial quotation from the work of A. N. Sewertzoff, "Must we therefore accept that the limbs of the reptiles Anura, on the one hand, and Urodela on the other developed phylogenetically in complete independence from one another?" However, A. N. Sewertzoff strongly upheld the idea of the monophyletic origin of ter-restrial amphibians as the continuation of this quotation omitted by Jarvik indicates: "But in what way should we explain in this case the unquestionable similarity in the position of skeletal elements of the limbs in these forms? I will not develop these conclusions further. They lead to such improbable results, that it is clear to anyone who does not have a preconceived opinion, that they derived from an incorrect precondition, i.e., that the heterochromy in the development of the digits is an expression of the primary line of development of the limbs of the ancestors of terrestrial vertebrates. We see, however, that for this phenomenon there is another, more probable explanation, and we have come to the conclusion that the phenomenon of heterochromy in the development of elements of autopodium does not provide a basis for the proposition that the limbs of Urodela developed from a form with a small radius" (Sewertzoff, 1950, p. 214).

The conclusions of Jarvik produced critical response even from some paleoichthyologists. (Vorob'eva, 1962; Kulczycki, 1960; Romer, 1962; Thomson, 1962, 1964; Gross, 1964). As was shown by the study of a series of lungfishes (Porolepis, Panderichthys, Platycephalichthys, Ectosteorhachis), the characteristic types of snout in Porolepiformes and Osteolepiformes presented by Jarvik as a basic argument for polyphyleticism did not find confirmation in many points. It became clear that these types of snout embraced far from all Rhipidistia. According to a series of traits, the two types overlap because of the presence of intermediate forms. In addition doubts were expressed about the viability of the interpretation of separate structures, and also of the possibility of their being homologous with the structures of the ethmoid of modern amphibians.

Jarvik considers (Jarvik, 1942)[2] the character of the internasal wall one of the basic differences of the osteolepiform and porolepiform types of snout. In Eusthenopteron (fig. 2, 1) the nasal cavities are close together and separated

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by a fine, continuous partition (septum nasi). In Porolepis (fig. 2, 2) on the other hand, they are widely separated, and between them is situated the ethmoidal section of the cranial cavity in front of which lies the paired internasal pit (cavum internasals), which, according to Jarvik, contains the

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[2]For the subsequent survey of the peculiarities of of formation of osteolepiform and porolepiform types of snout we have in mind this particular work of Jarvik and therefore no citations to it will be given.

paired intermaxillary gland, which is homologous to that of amphibians and opens ventrally into the oral cavity. A similar gland also was in Eusthenopteron according to Jarvik but was significantly smaller and was located in a small depression (fossa apicalis, see fig. 5) which occupied the
--fig. 2--
extreme anterior part of the ventral surface of the ethmoid and opened into the posterior part of the oral cavity by a canal crossing the vertical toothed plate of the vomers (iv. p). Jarvik granted great phylogenetic significance to the latter canal in comparing it with the canals of labyrinthodonts and Anura. Starting from the presence of the ethmoidal section of the cranial cavity in Porolepis, the conclusion was made that the structure of the ethmoidal part of the brain differs in Porolepiformes and Osteolepiformes.

Recent investigations have shown that a broad internasal wall is characteristic even of some Osteolepiformes: Platycephalichthys (Vorob'eva, 1959), Panderichthys (Vorob'eva, 1960, 1962), Ectosteorhachis (Thomson, 1964), and apparently Glyptopomus (Jarvik, 1950). For the first two genera, the presence of the ethmoidal cranial cavity has also been established (fig. 3, 2). Its existence in Porolepis, on the other hand, is doubted by Kulczycki (1960) who assumes that the cranial cavity in this fish begins behind the level of the anterior walls of the eye sockets (fig. 4, 3, 4). The functional significance of the ethmoidal cavity of lungfishes is still unclear. However, Jarvik's assumption that the anterior portion of the brain (fig. 4, 3, hem) is located in it is not justified. Judging by the narrow aperture of the cranial cavity in the posterior section of the sphenethmoid of Panderichthys and Platycephalichthys, only olfactory canals could pass in the interorbital area of these fishes, i.e., the ethmoidal cavity could not include the hemispheres of the brain. It is possible that the ethmoidal cavity is analogous to the rostral cavity of Latimeria and served as an organ of balance supplementing the canals of the lateral line (Vorob'eva, 1962, p. 20).

As far as the cavum internasale and fossa apicalis are concerned, Kulczycki and Thomson are inclined to consider them homologous and the only receptacle of the large front teeth of the lower jaw. This possibly does not diminish the significance of these pits since the teeth or toothed spiral is not developed at the anterior end of the lower jaw in all Rhipidistia.

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The structure of the nasal cavities also is suggested as a means of distinguishing two types of snout in Rhipidistia: the character of the walls, the presence or absence of branches and projections subdividing them, the number and position of openings of blood and neural canals, the position and size of notches and openings joining the nasal cavities with the external environment, with the eye socket and with the oral cavity and in particular the position of the nares and the size of the choanal notches. This presentation of the great phylogenetic significance of the details of the structure of
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the nasal cavity into sections can distinguish even close forms: Panderichthys, Eustenopteron, Platycephalichthys (Vorob'eva, 1962) and, conversely, can coincide in representatives of both groups (Porolepis, Panderichthys). Thomson considers it generally impossible on the basis of paleortological evidence to compare the sections of the nasal capsule with the divisions of the nasal sac. Therefore, although a ventro-lateral depression for example is found even in Eusthenopteron and Ectosteorhachis, it is impossible to decide whether it corresponds to the outgrowth of the olfactory sac and whether this outgrowth contains Jacobson's organ.

The position of crests and processes in the nasal cavity can also coincide in representatives of both groups. In particular, the processus intermedius or its homolog is as much pronounced in Porolepis (Kulczycki, 1960) as in Eusthenopteron (fig. 2, 1, pr. im), is somewhat altered in Ectosteorhachis (Thomson, 1964) and is lacking in Panderichthys (Vorob'eva, 1962). Therefore, the assumption by Jarvik that the rostrale laterale in Osteolepiformes always has this process in distinction from Porolepiformes is without confirmation. At the same time, in Panderichthys there is a similarity of the rostro-caudal crest characteristic of Porolepis (fig. 2, 2, ri. w. al) and a small lateral depression re. l, corresponding in position to recessus lateralis.

The interpretation of the processes of the nasal cavity and the homologizing of them with processes in amphibians has been the object of doubt. Kulczycki opposes the homology of the rostro-caudal process of Porolepis (crista subnarina according to Kulczycki) with the processus rostrocaudalis of Urodela and considers that its appearance is connected with the passage of the suborbital sensory and postnasal canals. He does not agree with the presence in Porolepis of Seydel's process (fig. 2, 2, pr. S) and points to the fact that if the crista subnarina is homologous to the processus rostrocaudalis, then the small choanal process, appearing as its continuation, occupies a different position from that

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of Seydel's process in Urodela. According to Kulczycki, there is also no recessus lateralis for Jacobson's organ in <u>Porolepis</u>.

There is no doubt about the homology of the upper internal postnasal opening (fig. 3, 1. f.e. enp.) with the external posterior naris (fig. 2, 2, fe. exp.) and also about Jarvik's assumption that the lacrimonasal canal (ductus nasolacrimalis) passed through this opening parallel with a branch of the upper maxillary nerve (ramus maxillaris). This homology makes the absence of a similar opening in some Rhipidistia which do not have an external posterior naris (<u>Platycephalichthys</u>, Vorob'eva, 1962) completely inexplicable. As investigations in the area of the embryology of tailed amphibians have shown (Medvedeva, 1960), the lacrimonasal canal is developed in them primarily at the expense of a section of the suborbital sensory canal of fishes which section is connected with the bones of the infraorbitale anterior and rostrale later'le and partly of the olfactory sac. According to I. I. Shmal'gauzen (1964), the external part of the posterior naris plays a part in the formation of the canal. Thomson (1964) considers that most probably blood vessels and nerves passed across the interior postnasal opening into the nasal cavity. The existence of an external posterior naris in Rhipidistia is somewhat doubtful. This doubt is produced by a new discovery of the skull of <u>Panderichthys</u>. Although, the posterior external naris was noted in this genus (Vorob'eva, 1962), it is none the less possible that because of inadequate preservation of the described skull after its excavation (fig. 3, 2, fe. exp. ?) a piece of the suborbital sensory canal was admitted in the rear corner of the ethmoid. Judging by the position of the posterior naris in <u>Porolepis</u> (Jarvik, 1942, pl. 4, fig. 2) which is very similar to that in <u>Panderichthys</u>, doubt arises as to its existence even in the first genus.

The size of the anterior naris and the choanal notches apparently does not have great taxonomic significance. Small choanal notches as in <u>Porolepis</u> are known for several Osteolepiformes (<u>Panderichthys</u>, <u>Platycephalichthys</u>). It is possible that small internal nares are a mark of primitiveness (Kulczycki, 1960). The internal nares of Rhipidistia and terrestrial vertebrates represent [in agreement with Jarvik] an independent formation having nothing in common with the external posterior naris, in contrast to the "false" nares of the Dipnoi which were formed by it. A contrasting opinion was expressed by A. N. Sewertzoff (Sewertzoff, 1926) who considered the internal nares of tetrapods a derivative of one of the external nares of bony fishes, which moved into the oral cavity. Later, I. I. Shmal'gauzen (1958) came to the conclusion that the internal nares of terrestrial vertebrates were homologous with the medial part of the posterior naris of fishes. He observed preserved traces of the movement of the naris in the oral cavity in the embryos of tailless amphibians. The detailed investigations of I. I. Medvedeva (1960a, 1961, 1965) on the development of internasal nares in the embryos of Anura and Urodela which affirm their complete homology with the internal nares of the other vertebrates showed that at the very early stages of development of tailed amphibians the beginnings of the naris and of its canal is situated next to the beginnings of the choanal canal or is even common with it. This can serve to some degree as a proof of the derivation of the choanal canal from the canal of the posterior naris of bony fishes.

As was noted above, the interpretation of some canals (blood vessels and neural branches) in the nasal cavity of Rhipidistia is debated. Jarvik considers that the nasobasal canal giving off the branch n. profundus across the anterior nasal wall of fossa apicalis (fig. 4, 1, c. hb) is character-istic of the Osteolepiformes group only. However, this canal was also found by Kulcycki in <u>Porolepis</u>. On the other hand, the orbital-rostral passage is not surrounded by it which, according to Jarvik, is characteristic of <u>Porolepis</u>. The canal conducting the lateral branch n. profundus (fig. 4, 4, r. prl) across the lateral part of the postnasal wall of <u>Porolepis</u> would, according to Thomson, more likely conduct blood vessels into the nasal cavity.

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Jarvik also considers that in Osteolepiformes there is a single neural canal leading from the nasal cavity upward to the dorsal surface of the ethmoid, but in <u>Porolepis</u> a multitude of such canals penetrate the dorsal part of the medial wall, the neighboring parts of the prenasal wall and the medial part of the testum nasi. In addition, the nervus profundus which is weakly developed in <u>Eusthenopteron</u> is well developed in <u>Porolepis</u> (fig. 4: 1, 3, n. pr). In <u>Porolepis</u> the medial nasal branch (fig. 4: 3, r. prm) in the nasal cavity divides into many
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dorsal branches. At the same time, Thomson finds that n. profundus is developed approximately identically in <u>Porolepis</u>, <u>Eusthenopteron</u> and <u>Ectosteorhachis</u> (fig. 4: 2). However, the canal trans-versing the dorsal wall of the nasal capsule of <u>Porolepis</u> relates more closely to the nervus opthalmicus superfacialis VII than to the nervus profundus V.

In regard to quantity of apertures on the posterior nasal wall for n. profundus, there can be several variants. In particular, in Osteolepiformes there is one large (<u>Platycephalichthys</u>) or relatively narrow (<u>Eusthenopteron</u>, <u>Eusthenodon</u>) aperture (fig. 3: 1, c. pr), but it can also be

lacking (Panderichthys). In the latter case, n. profundus possibly entered the nasal cavity together with n. olfactorius, as Kulczycki noted for one of the forms of Porolepis.

Kulczycki considers that Porolepis and Eusthenopteron have an identical arrangement of the following nerves: n. opthalmicus profundus, n. maxillaris, r. palatinus VII, r. buccalis VII (fig. 4) and accompanying blood vessels. Thomson partly supports him in this. Thus, according to Jarvik, the lateral parts of the snout in Osteolepiformes are supplied chiefly

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by r. maxillaris V, but in Porolepis by n. profundus, which causes doubt on the part of Thomson. The latter considers that Jarvik was influenced here only by modern Urodela in which r. maxillaris V terminates in an orbit. Meanwhile, in some aquatic, tailed amphibians, where a system of a lateral line and corresponding buccalis lateralis VII was retained, the latter passes into an orbital-rostral passage (truncus infraorbitales) together with r. maxillaris V and this mixed trunk stretches ahead farther than in terrestrial amphibians. And as far as traces can be found of buccalis lateris VII in Porolepis, the possibility of the presence in them even of r. maxillaris V (fig. 4: 4, max plus buc) cannot be excluded. Further, in agreement with Jarvik, in Eusthenopteron r. buccalis lateris passes forward to the top of the snout laterally to the internal nares giving off small branches to the anterior parts of the infra-orbital sensory canal. In Porolepis, on the other hand, it is divided into several branches in the orbit and only one of them goes forward across the orbital-rostral passage medially from the internal nares supplying the forward part of the infra-orbital canal (fig. 4: 3, r. buc). According to Thomson, in Ectosteorhachis the nerves passed across the dermal bones rather than between these bones and the nasal capsule as in Eusthenopteron. Information about the arrangement of r. buccalis lateralis in Rhipidistia is insufficient in his opinion.

R. palatinus VII in Eusthenopteron passes across the antero-lateral part of the vomer and passing it divides into three branches. In Porolepis the nerve passes across the medial part of the vomer and does not divide at this juncture. Thomson observed an analogous picture in Ectosteorhachis.

Jarvik affirms that traces of fusion of a palato-quadrate complex and ethmoid are present in Eusthenopteron and absent in Porolepis. A contradictory opinion is held by Kulczycki who points to the traces of a synchondralic articulation between processus apicalis palato-quadratum and the olfactory tract of the sphenethmoid in Porolepis. It is possible that the merging of the palato-quadrate complex with the ethmoid was characteristic of all Rhipidistia. In any case, the groove for the palato-quadratum, which is not covered by the periosteal bone, is present also on the ethmoid of Ectosteorhachis, Panderichthys and Platecephalichthys. In connection with this, the observations on the development of the endocranium of tailed amphibians (Hynobiidae) put forth by N. S. Lebedkina (1963) are interesting. They showed that in the larvae there is a close connection of the palatal arch with the ethmoid.

It is considered that one of the differences between Osteolepiformes and the Porolepiformes is the formation of the parasphenoid and the vomers. In Eustenopteron (fig. 5) the parasphenoid is narrow and stretches under the ethmoidal tract to the prenasal area of the endocranium; the vomers with a vertical toothed plate and a long, posterior branch are met ahead along the suture on which are located a pit and the openings of the inter-vomerine canal (inter-vomerine pit, lv. p) which connects the fracta fossa apicalis with the posterior part of the oral cavity. In Porolepis the parasphenoid is wide and barely reaches to the ethmoidal tract; the vomers without posterior branches are widely separated and lack a vertical plate of the inter-vomerine canal. In agreement with the description of Ectosteorhachis (Romer, 1937), the parasphenoid of Rhipidistia can be of a dual formation, consisting of a base and a shagreen plate resting on it. The parasphenoid in Eusthenopteron and Eusthenodon also has a similar formation (Jarvik, 1937). In connection with this, observing the formation of the parasphenoid should obviously lead to examining the level of development of both its parts. The width of the interorbital septum, which has possibly vital significance in the taxonomy of Rhipidistia in particular as a distinguishing characteristic of suborders of Osteolepidoidei and Holoptychioidei (Vorob'eva, 1962). The length of it is apparently connected with the length of the

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anterior palatal recess (fossa apicalis, cavum internasale). The length of the shagreen plate indicates various stages of evolutionary development, according to the opinion of Thomson. In particular, the gradual transition from the stage of Eusthenopteron to that of Porolepis can be

seen among osteolepids in the series <u>Osteolepis</u>, <u>Megalichthys</u>, <u>Ectosteorhachis</u>, in which the toothed medial plate is progressively shortened. As far as
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the degree of dissociation of the vomers is concerned, there is apparently a correlation with the length of the parasphenoid. The degree of development of the posterior branch, like the presence of a vertical toothed plate, is apparently a characteristic of genera or families. The majority of osteolepids (<u>Ectosteorhachis</u>, <u>Osteolepis</u>, <u>Clyptomus</u>, <u>Megalichthys</u>, <u>Thursius</u>) have a short posterior branch which, on the other hand, is well developed in <u>Platycephalichthys</u>, <u>Panderichthys</u>, <u>Eusthenopteron</u>, <u>Eusthenodon</u>. The vertical plate is lacking in <u>Megalichthys</u>. According to the theory of Kulczycki, the latter characteristic in conjunction with the short posterior branch of the vomers testifies to the primitiveness of the form.

Since in <u>Ectosteorhachis</u> as well as in <u>Porolepis</u> the vomers are not encountered along the medial suture, it is difficult to judge if they had an intervomerine canal which was able to pass even in soft tissues. (Thomson, 1964)

As is evident from the analysis presented of data on the formation of the snout of Rhipidistia, there still remain many unclear and debatable points about this problem. Apparently, however, the series of peculiarities in the formation of the ethmoid taken by Jarvik as a basis for the division of two phylogenetic trunks of Rhipidistia is not justified. They have obviously much less significance in taxonomy being characteristic of genera or at best, families.

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Comparative anatomy of the snout of Rhipidistia thus still does not present proof for the resolution of the question about the origin of amphibians from one or from several groups of lungfishes. Also, available data indicate that the Rhipidistia are much more diverse than was assumed earlier, and it is completely possible that further study of this group will lead to significant altera- tions in its taxonomy. However, all known Rhipidistia reveal an obvious similarity in the chief features of the formation of the ethmoid (in nervous and circulatory systems, in the internasal wall, in the nasal cavities) which testifies to the utility of considering them one.

There remain (besides questionable facts) only a few peculiarities of the formation of the snout of Rhipidistia which support the hypotheses of Jarvik, in particular, the differences in the position of the canals of some blood vessels and the quantity of neural branches and their passages (the different position of ramus opthalmicus superficialis VII, vena cerebralis anterior). To these small differences one should add also the later data of Jarvik about the structure of the branchial apparatus of <u>Eusthenopteron</u> and <u>Glyptolepis</u> and the formation of the tongue of amphibians (Jarvik, 1964). Unfortunately, however, the branchial apparatus is unknown for other Rhipidistia, and therefore making any such broad generalizations is clearly premature. Besides, Jarvik (1964) affirms that the confirmation of his hypothesis lies in the differences in the microstructure of the scales of Osteolepiformes and Porolepiformes presented by Orvig (T. Orvig, 1957). Such an assertion is without foundation since in most primitive representatives of this group (<u>Porolepis</u> and <u>Osteolepis</u>) the scales have an almost identical formation (Orvig, 1957, table to page 406). The difference between them basically comes down to the methods of formation (cyclomorial or synchronomorial) of the later layers of dentin. These methods obviously bear witness to different evolutionary stages of development. As Orvig himself affirms, in the ancestral forms of Porolepiformes and Osteolepiformes the scales were apparently covered by cyclomorial layers of dentin (Orvig, 1957, pg. 420), i.e., they had a single means of formation. In addition, <u>Porolepis</u> and <u>Osteolepis</u> had a very similar construction of the teeth differing in the simple plication of the walls and in the presence of a broad pulp cavity. This also brings these forms together.

In our view, the microstructure of the integumentary bones, scales and teeth of Rhipidistia provides the possibility not only more clearly to present the stages of their evolutionary develop- ment and the phylogenetic links between separate groups but also in some degree to clarify the closeness of one or another representatives to the ancestral forms of tetrapods. Data on the microstructure of integumentary bones and teeth of ancient tetrapods, e.g., Stegecephalia, testify in particular to the greatest closeness to them of one of the representatives of Osteolepiformes, i.e., <u>Panderichthys</u> (Vorob'eva, 1960, 1962).

The methods of Jarvik which served as the foundation for the hypothesis of the polyphyletic origin of terrestrial vertebrates have been justly criticized by several paleontologists (Thomson, 1962; Gross, 1964). The basic defects are the limitation of the scope of investigation (e.g., the snout of Rhipidistia) and the small number of forms analyzed. At the outset, the fact that primarily two representatives of lungfishes (<u>Porolepis</u> and <u>Eusthenopteron</u>) are considered as initial forms for amphibians which are also distant in taxonomic position and geological age, predetermines

the presentation of tetrapods as diphyletic. The comparison of details of the formation of the ethmoid of these Rhipidistia is made basically with presently existing amphibians including very specialized ones (for example, the frog) which creates great discrepancies in the interpretation of these details. At the same time, Jarvik's statements on the polyphyletic origin of tetrapods, which in a series of cases are based on questionable facts are too categorical.

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While there are no indisputable proofs in paleontology of the monophyletic origin of amphibians, a group of facts does support it: 1. As indirect proofs one should include the great similarity in basic features of the formation of the ethmoid of Rhipidistia in spite of the seeming differences in individual representatives. 2. Among Rhipidistia only Osteolepiformes (Eusthopteron, Sauripterus?)

--fig. 6--

have the formation of fins similar to the formation of a pentadactyl limb (fig. 6). Fins with a biserial archipterygium (judging from the long-lobed fins of Holoptychus and Glyptolepis) could hardly have been transformed into such a highly differentiated organ. In addition, the limbs of mature Urodela and Eusthenopteron have an almost identical formation; this similarity extends even to separate bones of the hand and foot. 3. Some support in favor of monophyleticism can also be given by the absence among known Rhipidistia of groups which could be recognized as standing closely to the ancestors of the tetrapods. The closest to the latter, apparently only Osteolepiformes of the type Eusthenopteron and especially Panderichthys (Vorob'eva, 1962) unfortunately have been little studied. 4. At the same time, known finds of fossil amphibians testify in favor rather of a dichotomous than a parallel development of separate branches. In particular, Urodela, which according to Jarvik appear to the side of the main line of evolution of terrestrial vertebrates and have an origin independent from fish-like ancestors of the Silurian period, are unknown until the lower Cretaceous or Jurassic period (fig. 7). In addition, they are apparently very close to Lepospondyli which already flourished in the Carboniferous period. It is more logical to suppose that Urodela branched off precisely from them. The Lepospondyli in turn apparently derived from the same branch as labyrinthodents. On the basis of ancient finds, the origin of Anura is well known, and they are encountered beginning from the Triassic period. From the comparison of Anura with labyrinthodents one can come to a conclusion about their origin from the latter. Apoda are not known in a fossil condition. The appearance of the first tetrapods has been indicated as seemingly by the end of the middle (Vorob'eva, 1962) or upper (Gross, 1964) Devonian Period since in the Silurian Period bony fish are still unknown and in the early Devonian Period only one genus of lungfishes has been found, i.e., Porolepis, but at the end of the upper Devonian Period the first Stegocephalia are encountered, i.e., the ichthyostegids.

The ideal condition for the solution of the problem of the origin of tetrapods would be discoveries of intermediate forms between different groups of vertebrates. The ecological divergence which has existed since the very beginning of the emergence of tetrapods and which has been accompanied by significant morphological differences greatly hampers the clarification of phylogenetic

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links. For an understanding of the peculiarities and paths of the formation of the structures of tetrapods much could be gained through a study of lungfishes and especially of ancient Rhipidistia. However, since using paleontological discoveries as a base rarely permits a complete restoration of the history of the origin of a group, one must consider the data

--fig. 7--

of related disciplines. In particular, the study of contemporary amphibians and especially embryological investigations of the most primitive Urodela can be of considerable use for the solution of this problem.

A correct solution of the problem of the origin of terrestrial vertebrates is of great importance for their taxonomy. The problem concerns not only by what kind of roots lungfishes are connected with tetrapods, but also whether the existing system reflects phylogenetic links between groups or whether it is based on the principles of similarity. The attempt to introduce the concept of polyphyly into the existing system inevitably leads to the destruction of the boundaries between taxonomic categories. In particular, if discussion concerns the polyphyletic origin of amphibians, the continued existence of their independent phyletic branches destroys the boundary between classes of fishes and amphibians. The diagnostics of the old classes loses its value, and the dialectical representation of them as a new quality representing a complicated complex

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of characteristics is rejected. Instead of such classes, degrees and stages of development of separate, parallel characteristics are offered. A passion for separate characteristics leads investigators to polyphyly. At the same time, if separate traits of structure can indeed develop in parallel fashion in various groups, then the parallel development of very complex combinations of characteristics like those of families, orders and classes is very doubtful. According to the opinion of Gross (1964), which the author shares, if polyphyly of species and genera can be considered fully plausible, polyphyly of larger categories raises doubts, since it has no factual verification. Thus, as long as there are no discoveries proving transfer from class to class and, in particular, from fishes to amphibians in several independent branches, it is apparent that the polyphyletic origin of tetrapods must be rejected.

LEGENDS FOR FIGURES

Figure 1. Diagram of the polyphyletic origin of tetrapods according to Jarvik (E. Jarvik, 1964, fig. 28)

Figure 2. Restoration of the anterior part of the ethmoid, rear view.

1 - Eusthenopteron, 2 - Porolepis; magnification: 2X (Jarvik, 1942, fig. 52 A, 46 A); Vo - vomer; cav. in - internasal cavity (cavum internasale), c. ext - canal for ramus externus narium n. profundus, c. nb - nasobasal canal, fe. ch - choanal notch, fe. ona, fe. exp - notches for anterior and posterior nares; pr. im - processus intermedius, pr. S - palatal process (processus Seydol's), re. 1 - lateral depression of nasal cavity (recessus lateralis), ri. in - internal crest, ri. w. al. - rostro-caudal crest (crista rostrocaudalis), sn - internasal septum (septum nasi).

Figure 3. Rear view of ethmoid.

1 - Eusthenodon, magnification: X 3/2 (Jarvik, 1937, fig. 13), 2 - Panderichthys, magnification: X 1 (Vorob'eva, 1962, drawing - 3; Psph - parasphenoid, Vo - vomer, art. aup - medial surface for articulation of palatoquadrate complex, c. olf - olfactory canal, c. pr - aperture of canal for nervus profundus, etch. cr. - ethmoid skull cavity, fe. ch. - notch internal nares, fe. enp and fe. n.p.c. - innter postnasal aperture, fe. exp.? - notch of external posterior naris.

Figure 4. Top view of ethmoid.

1 - Eusthenopteron (Jarvik, 1964, fig. 20), 2 - Ectosteorhachis (Thomson, 1964, fig. 1 and fig. 6 combined, 3 - Porolepis (Jarvik, 1964, fig. 20c), 4 - Porolepis (Kulczycki, 1960, fig. 5); a. ci - artery carotis interna, an - anterior external naris, a. pn - artery palato-nasalis, b. olt - bulbus olfactorius, cav. in - internasal cavity (cavum internasale), c. nb - nasobasal canal, c. pr. - canal for nervus profundus, c. prm. - canal for ramus terminalis n. profundus, dnl - lacrimonasal duct (ductus naso-lacrimalis), hem - hemisphere of anterior brain: max plus buc - n. maxillaris plus r. buccalis lateralis VII (truncus infraorbitalis), ntr - posterior nasal tube or proximal part of lacrimonasal duct, n. pr - nervus profundus, pi - pineal organ, r. bac - ramus buccalis, r. mn, r. ln - ramus medialis and ramus lateralis narium n. profundus, r. mx - ramus maxillaris V, r. o. lat - ramus opthalmicus superfacialis VII, r. pal - ramus palatinus VII: r. prl, r. prm - ramus terminalis lateralis and medialis n. profundus; sac. n - olfactory sac; I - n. olfactorious; II - n. opticus.

Figure 5. Ethmoid of Eusthenopon from below; magnification: X 3/2 (Jarvik, 1937, fig. 16)

Psph - parasphenoid, Vo - vomer, art. aup - surface for articulation of palatoquadrate bone, fe. ch - notch of internal nares, fossa ap - apical pit, f. ap - apical aperture, iv. p - pit of intervomerine canal.

Figure 6. Diagram of the transformation of the fin of Rhipidistia into a pentadactyl limb.

1 - Eusthenopteron, 2 - transitional stage, 3 - primitive tetrapod stage (Jarvik, 1964, fig. 27); see text for discussion.

Figure 7. Diagram of the origin of tetrapods according to Gross (W. Gross, 1964, Abb. 3)