四足动物起源假说的回顾与现状

H.-P. 舒尔茨

(德国柏林自然博物馆，古生物研究所)

摘要 研究历史表明，导致四足动物亲缘关系的假说发生变化是现生或化石种类的发现，而不是新学说的出现。目前，四足动物与希望螈类 (elpistostegids)，以及这两个类群与骨鳞鱼类的姊妹群关系已被接受。通过比较肉鳍鱼类相互关系的最新假说，可以看出其中三种假说可能性最大，概率几乎相同，即肺鱼不是四足动物的近亲而与不同的肉鳍鱼类可能有亲缘关系。具新性状的基位肉鳍鱼类的发现或者性状状态极向的重新解释会有助于解决肺鱼类在支序图中的位置。

关键词 肺鱼，骨鳞鱼类，四足动物，系统发育

历 史 回 顾

人们期待一个新学说会改变或改进对系统发育关系问题的认识。然而，具体到四足动物起源问题，则并不尽然。譬如，1859 年达尔文《物种起源》的发表并未对这一起源问题的认识产生影响 (Rosen 等，1981)。相形之下，四足动物起源假说的发展历史表明，现生或化石种类的发现 (表 1) 却左右着我们关于四足动物与鱼类关系的认识。

第一种现生肺鱼是 1836 年在南美发现的 (Fitzinger，1837; Natherer，1837)，并被解释为一种四足动物。Bischoff (1840) 将南美肺鱼置于两栖类之中，而 Owen (1839) 则认为它是鱼类 (关于 1840 — 1860 年间肺鱼的归属见 Rosen 等，1981，和 Conant，1987)。1859 年达尔文《物种起源》出版之后，Haeckel (1866) 是第一位将肺鱼置于系统树 ("Stammbaum") 中的学者。在他的树中，肺鱼的位置靠近两栖类。这反映出关于同源的解释 (Bischoff，1840) 在没有任何新的分析的情况下被转化成系统树 (Haeckel，1866)。另一种现生肺鱼 (澳洲肺鱼，Krefft，1870) 的发现没有使得肺鱼亲缘关系的讨论发生变化。

骨鳞鱼类真掌鳍鱼 (*Eustenopteron*) 采自加拿大魁北克东部 Miguasha 的上泥盆统沉积中，它的描述 (Whiteaves，1881，1883) 掀开了关于四足动物亲缘关系讨论的新篇章。Cope (1892) 认为真掌鳍鱼是四足动物的祖先。很多年来，许多研究人员为这一观点进行了辩护。尤其是 Jarvik 为真四足动物 (Eutetrapoda) 起源所进行的辩护 (进一步查询资料，见 Jarvik，1980)。Cope (1892) 提到了一些真掌鳍鱼与四足动物的相似特征，如偶鳍的内部结构，奇鳍的退化，具上颌骨，舌接型颌弓与脑颅联结方式。

Holmgren (1933) 根据偶鳍的个体发育研究，提出了一个四足动物的双系起源

说。他将有尾两栖类的四肢骨骼与肺鱼偶鳍的原鳍型骨骼进行比较,而将所有其它四足动物的四肢骨骼与扇鳍鱼类 (尤其是真掌鳍鱼和 *Sauripterus*) 偶鳍的双歧式内骨骼进行比较。瑞典学派也主张四足动物双系起源说。Jarvik (1942) 仅对有尾两栖类的祖先类群作了变动。他认为有尾两栖类起源于孔鳞鱼类,而真四足动物起源于骨鳞鱼类。他基于鼻囊结构的不同将肺鱼排除在外,同时他指出鼻囊结构在其它类群间是相似的。

东格陵兰上泥盆统最顶部岩层中鱼石螈 (*Ichthyostega*) 的发现没有改变四足动物起源的讨论。鱼石螈被当作一种原始四足动物 (Säve-Söderbergh, 1932),它仍保留着一些鱼类特征 (Jarvik, 1952)。1938 年,现生空棘鱼类拉蒂迈鱼 (*Latimeria*) 在南非的发现未对系统发育系统学讨论产生影响,这或许是因为从化石空棘鱼类已经知道其结构及系统位置同四足动物有相当差距。然而在通俗的文章中,拉蒂迈鱼仍经常被当作四足动物的“姊妹”。

希望螈 (*Elpistostege*) 最初被记述为一种原始四足动物,当作骨鳞鱼类与四足动物之间的一种过渡类型 (Westoll, 1938)。Worobjewa (1973) 和 Schultze & Arsenault (1985) 指出希望螈与当时被认为是骨鳞鱼类的 *Panderichthys* 关系密切。Schultze (1969) 根据牙齿结构认为 Panderichthys 是四足动物的姊妹群。希望螈类 (= panderichthyids) 是扇鳍鱼类中唯一像四足动物那样具有三对颅顶骨片的类群 (Schultze 和 Arsenault, 1985);它们从骨鳞鱼类中划分出来,并被定义为一个单系类群,作为四足动物的姊妹群 (Vorobyeva 和 Schultze, 1991)。Jarvik (1952) 描述了采自东格陵兰上泥盆统最顶部地层中的另一种原始四足动物——棘螈 (*Acanthostega*)。Lebedev (1984)、Ahlberg (1991a, 1995) 和 Ahlberg 等 (1994) 又从俄罗斯、苏格兰和拉脱维亚的上泥盆统地层中补充了一些零碎的早期四足动物化石。这些发现缩短了早期四足动物与希望螈类之间的距离,但是由于它们像鱼石螈那样被归属于四足动物,因此并未改变希望螈类与四足动物的姊妹群关系 (Ahlberg 和 Milner, 1994)。

Miles (1977) 描述了晚泥盆世肺鱼 *Griphognathus* 的腭。Gardiner 和 Rosen 各自独立地解释它类似四足动物的腭,并重新建立了肺鱼与四足动物具最密切亲缘关系的假说 (Gardiner, 1980; Rosen 等, 1981)。该假说没有赢得支持 (见 Ahlberg 和 Milner, 1994)。支撑这一假说的性状不能经受同源性的检验。随着一种具有肺鱼和基位孔鳞鱼类离征的基位肉鳍鱼类—奇异鱼 (*Diabolepis*, Chang 和 Yu, 1984) 的发现,肺鱼作为四足动物姊妹群的位置很快就被置疑。在高阶类元比较时,基位类元 (basal taxa) 较之于现生或“典型”类元能提供更多信息 (Schultze, 1987, 55 页; Huelsenbeck, 1991)。分子生物学家仅仅根据对现生种类的调查提出了肺鱼与四足动物的亲缘关系 (参考 Meyer, 1995)。分子生物学家局限于少数容易获得的现生类元 [Lecointre (1994) 的分类学取样水平 A],而形态学家将他们的研究扩展到一个更广的类元范围 [Lecointre (1994) 的水平 B],古生物学家更是扩展到化石类元 [Lecointre (1994) 的水平 C]。换句话说,古生物学家将一个类群在整个演化历史中的类元都包括进来。尽管化石类元保存的性状不全,但是,基位类元能够澄清性状的序列和类群的亲缘关系 (Arratia, 1995)。基位类元载有一套未受到数百万年演化影响的性状 (Marshall 和 Schultze, 1992)。相形之下,现生类元的一套性状甚至都不能支持亲缘关系相当密切的类元的单

系性 (Meyer 和 Dolven, 1992: 只有 27% 的概率支持三个现生肺鱼属的单系性)。正如 Bergström (1994) 在谈论后生动物分子生物学研究时所建议的那样，只有去除"背景噪音"才能获得可靠结果。

综上所述，第一种现生肺鱼的发现引发了关于肺鱼 – 四足动物亲缘关系的讨论。随着真掌鳍鱼的发现，四足动物被认为与骨鳞鱼类关系密切。这两个类群间更密切的关系是基于 *Panderichthys* 的结构。而 *Griphognathus* 的腭导致肺鱼 – 四足动物亲缘关系的重新建立。随着奇异鱼的发现，肺鱼被认为与孔鳞鱼类关系密切。在过去的 155 年中，使得四足动物在肉鳍鱼类中的姊妹群越来越明确的是基位化石种类的发现，而不是一个新的演化理论或者分析系统学资料的新方法的出现。

当 前 的 讨 论

有现生种类的四足动物可以回溯到早石炭世 (图 1)。这与四足动物在晚泥盆世的初次出现之间存在着两千五百万年的间断 (Carroll, 1994)。图 1 晚泥盆世中的短实线代表晚泥盆世的四足动物 (*Acanthostega*, *Ichthyostega*, *Tulerpeton*, *Ventastega*)。

Schultze (1969) 和 Worobjewa (1973) 认为中泥盆世 – 晚泥盆世早期的希望螈类 *Panderichthys* 与四足动物的关系密切，而 Rosen 等 (1981) 认为晚泥盆世早期的肺鱼 *Griphognathus* 与四足动物的关系密切。Rosen 等 (1981) 将 *Griphognathus* 作为肺鱼的一个原始分子，因此他们有理由认为肺鱼与四足动物有密切亲缘关系。自 Rosen 等 (1981) 出版以后，一系列的论文指出了 Rosen 等对性状的错误解释。这些研究，除 Chang (1991) 的之外，都赞同将骨鳞鱼类作为四足动物的姊妹群，但在肺鱼的系统位置上存在分歧。Schultze (1994) 建立了一个具 216 个性状的数据集合，在此基础上对这些假说进行比较，获得不同假说的概率估量。Chang (1991) 的假说概率最低 (比最短树多 27 步)，随后是 Rosen 等 (1981) 的假说 (多 22 步) 和支持 Rosen 等 (1981) 的假说 (多 16 或 22 步)。有三种肺鱼不同系统位置的假说可能性最大。最短树指示肺鱼与空棘鱼类的姊妹群关系 (图1: b; Northcutt, 1987)。随后两种假说只有一步之差。一种将肺鱼作为所有其它肉鳍鱼类的姊妹群 (图 1: c; Schultze, 1987)，另一种将肺鱼作为孔鳞鱼类的姊妹群 (图 1: a; Maisey, 1986; Ahlberg, 1991b)。

今天，希望螈类已被普遍接受为四足动物的姊妹群，骨鳞鱼类是这两个类群的姊妹群 (Ahlberg 和 Milner 1994)。希望螈类与四足动物至少共有 12 个独有性状和 2 个逆转性状 (图 1 中的 1; Schultze, 1994): 与鱼类弓形颅顶相对照的扁平颅顶; 具成对额骨; 顶孔位于眶孔之后; 具鳞骨凹; 眶孔背位; 前鳃盖管即使有，也已退化成凹线; 缺失背鳍; 索上鳍条比索下鳍条发育; 骨化程度高的肋骨; 大的肩胛片; 眼睛以及两块主要骨片的联结部位处于同一水平线; 膜质颅间关节之前有两对大的骨片; 膜质骨缺失整列层; 缺失真正的珐琅质。后两个性状与原始肉鳍鱼类相比为逆转性状。

骨鳞鱼类与希望螈类 + 四足动物也至少共有 12 个独有性状和 2 个逆转性状 (图 1 中的 2; Schultze, 1994): 多环齿型褶齿质 (polyplocodont plicidentine); 每侧具一个外鼻孔; 只有前外鼻孔开口在侧吻片上; 腭部的鼻孔 (= 内鼻孔) 为前上颌骨、上颌

骨、锄骨和腭骨所围；肩带附肢关节的近端隆起；两块近相等的骨骼构成偶鳍的第二轴节；肩胛关节窝为一坎穴；肱骨具外表头（和其它肱骨特征）；奇鳍辐状骨未分节；腹侧窗在出水鼻孔的背面；颊部由颧骨、眶后骨、鳞骨、方颧骨和前鳃盖骨组成；膜质前入水鼻孔具膜质间突（＝隔颌骨）；仅有两块眶上骨；胸鳍未伸长。后两者为逆转性状。

目前只有肺鱼在肉鳍鱼类中的位置尚有疑问。肺鱼或者是孔鳞鱼类（图1中的a），或者是所有其它肉鳍鱼类（图1中的c）或者是空棘鱼类（图1中的b）的姊妹群。只有当化石种类被排除在外，肺鱼作为四足动物姊妹群的位置才能从肺鱼与孔鳞鱼类的姊妹群关系中推演出来。将问题的讨论局限于现生种类是片面的。同样，早期的讨论也是片面的，因为当时只有现生肉鳍鱼类（南美肺鱼和非洲肺鱼）被充分认识。从鱼到四足动物的过渡，器官的创新只能在希望螈类和骨鳞鱼类中寻找。与Meyer（1995）的观点相反，这些创新（如内鼻孔，双歧式偶鳍内骨骼）并不能从现生种类的分析中回溯到肺鱼和四足动物的共同祖先。这两个类群的共同祖先有两个外鼻孔，原鳍型偶鳍内骨骼和典型的肉鳍鱼类特征。接受三种可能假说中的任何一种都不会影响到这些特征的分布。典型的四足动物特征最早出现是在骨鳞鱼类和四足动物的共同祖先中。另有一些四足动物特征同样也是四足动物和希望螈类，或者四足动物和骨鳞鱼类的离征，而非肺鱼和四足动物的离征。

只有通过增加新的基位类元（Schultze，1987；Huelsenbeck，1991），或者增加新的性状，或者重新评价性状状态，才能解决肺鱼在肉鳍鱼类中的位置。新的基位类元能够改变性状状态序列并且增加新的性状，因此我期待通过增加新的基位类元能够在这三个假说中作出一个决定。所以，中国早泥盆世的肉鳍鱼类（Chang，1982；Chang和Yu，1984；Yu，1990）是非常重要的。对这些基位肉鳍鱼类的专门研究能够补充我们对这些种类的认识，从而使三个假说中的这个或那个得到支持或者被抛弃。

（朱敏译，张弥曼校）

THE ORIGIN OF TETRAPODS-PAST AND
PRESENT HYPOTHESES

Hans-Peter Schultze

(Institut für Paläontologie, Museum für Naturkunde, Invalidenstr. 43, D-10115 Berlin, Germany)

Abstract　Discoveries of new extant or fossil forms have historically changed the hypotheses of relationship of tetrapods, not the appearance of new theories. At present a sister group relationship between tetrapods and elpistostegids and that of these two groups to osteolepiforms is accepted. A comparison of recent hypotheses on the interrelationships of sarcopterygians demonstrates that three hypotheses of the relationship of lungfishes to different sarcopterygians except close to tetrapods nearly have the same probability. New basal sarcopterygians with new characters or new interpretations of the polarization of character states may solve the placement of lungfishes.

Key words　Lungfishes, Osteolepiformes, Tetrapoda, Phylogeny

Historical review

One should expect that a new theory changes or improves the understanding of phylogenetic questions. That does not seem to be true of the origin of tetrapods as Rosen et al. (1981) have already shown in the case of the appearance of Darwin's "On the origin of species" in 1859. In contrast, the history of the development of hypotheses on the origin of tetrapods demonstrates that discovery of new extant or fossil forms (Tab. 1) shapes our understanding of the relationship of tetrapods to fishes.

The first extant lungfish was discovered in 1836 in South America (Fitzinger, 1837; Natterer, 1837) and interpreted as a tetrapod. Bischoff (1840) placed the lepidosirenid lungfishes within the amphibians, whereas Owen (1839) attributed them to fishes (for the assignment of lungfishes between 1840 and 1860 see Rosen et al., 1981, and Conant, 1987). After publication of Darwin's "On the origin of species" in 1859, Haeckel (1866) was the first to place lungfishes in a phylogenetic tree ("Stammbaum"), he placed them close to amphibians. That shows that the interpretation of homologies (Bischoff, 1840) was transfered into a phylogenetic tree (Haeckel, 1866) without any new analysis. The discovery of an additional extant lungfish (*Neoceratodus* in Australia; Krefft, 1870) did not change the discussion of the relationship of lungfishes neither with fish nor with tetrapods.

The description of the osteolepiform crossopterygian *Eusthenopteron* from Upper Devonian deposits of Miguasha in eastern Quebec, Canada (Whiteaves, 1881, 1883), started a new chapter in the discussion of the relationship of tetrapods. Cope (1892) placed *Eusthenopteron* as the ancestor of tetrapods, a position which was defended over

Table 1 Discovery of new forms and their impact on hypotheses of tetrapod relationship

表 1 新种类的发现以及它们对四足动物相互关系假说的影响

discovered form	year	hypotheses
Diabolepis	**1984**	Chang & Yu: lungfish-porolepiforms
	1981	Rosen et al.: lungfish-tetrapods
	1980	Gardiner: lungfish-tetrapods
Griphognathus (palate)	*1977*	
	1969	Schultze: *Panderichthys*-tetrapods
Panderichthys	*1941*	
Elpistostege	*1938*	Westoll: *Elpistostege* = tetrapod
	1942	Jarvik: diphyly rhipidistia-tetrapods
Latimeria	*1938*	
Ichthyostega	*1932*	
	1933	Holmgran: diphyly lungfish-tetrapods
		osteolepiforms-tetrapods
	1892	Cope: *Eusthenopteron*-tetrapods
Eusthenopteron	*1881*	
	1871	Günther: Ceratodontids = lungfish
Neoceratodus	*1870*	
	1840	Bischoff: lungfish = tetrapod
	1839	Owen: lungfish = fish
Protopterus	*1837*	Fitzinger: lungfish = tetrapod
Lepidosiren	*1836*	

Explanations: Sequence arranged from latest to the earliest date; *1836* = year of discovery; **1840** = year of new hypothesis.

years by many researchers, especially by Jarvik for the origin of the Eutetrapoda (see Jarvik, 1980, for further references). Cope (1892) mentioned the internal structure of the paired fins, the reduction of unpaired fins, the presence of a maxilla, and hyostyly as similarities of *Eusthenopteron* with tetrapods.

Holmgren (1933) proposed a diphyletic origin of tetrapods based on ontogenetic investigations of paired appendages. He compared the extremity of urodeles with the archipterygial skeleton of the paired fin of lungfish and the extremity of all other tetrapods with the dichotomous internal skeleton of paired fins of rhipidistians especially *Eusthenopteron* and *Sauripterus*. The Swedish school held on to the hypothesis of diphyletic origin of tetrapods. Jarvik (1942) only changed the group of origin for the urodeles. He derived the urodeles from porolepiform rhipidistians and the Eutetrapoda from osteolepiform rhipidistians. He excluded the lungfish based on differences in nasal structures, where he demonstrated similarities between the other groups.

The discovery of *Ichthyostega* in uppermost Upper Devonian rocks of East Greenland did not change the discussion of the origin of tetrapods. *Ichthyostega* was recognized as a primitive tetrapod (Säve-Söderbergh, 1932) which has still preserved some fish characters (Jarvik, 1952). The discovery of the extant coelacanth *Latimeria*

in South Africa in 1938 had no impact on phylogenetic discussions either because the structure and the position of coelacanths were known from fossil representatives being very different from that of tetrapods. Nevertheless *Latimeria* was often represented as the "sister" of tetrapods in popular accounts.

Elpistostege was described as a primitive tetrapod and placed as an intermediate between osteolepiforms and tetrapods (Westoll, 1938). Worobjewa (1973) and Schultze and Arsenault (1985) have shown that *Elpistostege* is closely related to *Panderichthys*, a genus assigned to osteolepiforms at the time. *Panderichthys* was considered the sister group of tetrapods based on tooth structure by Schultze (1969). The elpistostegids (= panderichthyids) are the only rhipidistian fishes with three pairs of skull roof bones like tetrapods (Schultze and Arsenault, 1985); they can be defined as a monophyletic group separate from osteolepiforms and as the sister group of tetrapods (Vorobyeva and Schultze, 1991). Jarvik (1952) described a new primitive tetrapod, *Acanthostega*, from the uppermost Upper Devonian of East Greenland. Lebedev (1984), Ahlberg (1991a, 1995) and Ahlberg et al. (1994) added further fragmentary early tetrapod remains from the Upper Devonian of Russia, Scotland, and Latvia. These finds closed the distance between early tetrapods and elpistostegids, but they did not change the sister group relationship between elpistostegids and tetrapods (Ahlberg and Milner, 1994) because they are assigned to the latter as *Ichthyostega* was.

The palate of the Late Devonian lungfish *Griphognathus* was described by Miles (1977). Gardiner and Rosen interpreted it independently from each other as tetrapod-like and re-established the hypothesis that the lungfishes are the closest relatives of tetrapods (Gardiner, 1980; Rosen et al., 1981). The hypothesis has not found support (see Ahlberg and Milner, 1994). The characters forwarded for the hypothesis did not stand the test of homology. The placement of lungfishes as a sister group of tetrapods was soon put in doubt with the discovery of *Diabolepis* (Chang and Yu, 1984), a basal sarcopterygian with synapomorphies of lungfishes and basal porolepiforms. Basal taxa (Schultze, 1987, p. 55; Huelsenbeck, 1991) are more informative for comparison of higher taxa than extant or "typical" taxa. Nevertheless, the relationship between lungfish and tetrapods has been proposed by molecular biologists on the basis of investigation of extant forms alone (see Meyer, 1995, for references). Molecular biologists are restricted to few easy available extant taxa (taxonomic sampling level A of Lecointre, 1994), whereas morphologists expand their investigations to a broader spectrum of taxa (level B of Lecointre, 1994) and paleontologists to fossil taxa (level C of Lecointre, 1994). In other words, paleontologists include taxa throughout the history of the evolution of a group. Basal taxa can clarify sequence of characters and relationship of groups despite the limitation of characters in fossil taxa (Arratia, 1995). Basal taxa carry a set of characters which is not affected by the million of years of evolution to the present level (Marshall and Schultze, 1992). In

contrast, a set of characters of extant taxa may not even support monophyly of closely related taxa (Meyer and Dolven, 1992: only 27÷ probability for monophyly of the three extant lungfish genera). One may have to exclude "background noise" to get reliable results as suggested by Bergström (1994) for molecular investigations of metazoan phyla.

In conclusion, the discovery of the first extant lungfish initiated the discussion of lungfish-tetrapod relationship. The tetrapods were placed close to the osteolepiform rhipidistians with the discovery of *Eusthenopteron*. A closer sister group relationship was based on structures of *Panderichthys*, whereas the palate of *Griphognathus* led to a re-establishment of lungfish-tetrapod relationship. The lungfish were placed close to the porolepiforms with the discovery of *Diabolepis*. The discovery of basal fossil forms narrowed the sister group of tetrapods within sarcopterygians during the last 155 years and not the appearance of new theories on evolution or new methods of evaluation of phylogenetic data.

Actual discussions

Extant tetrapods can be traced back to the early Carboniferous (Fig.1). A gap of 25 million years separates the earliest appearance of tetrapods in the Carboniferous from their appearance in the Late Devonian (Carroll, 1994). The short solid line in the Late Devonian of figure 1 represents the Late Devonian tetrapods (*Acanthostega*, *Ichthyostega*, *Tulerpeton*, *Ventastega*).

Schultze (1969) and Worobjewa (1973) placed the Middle to early Late Devonian elpistostegid *Panderichthys*, Rosen et al. (1981) the early Late Devonian lungfish *Griphognathus* close to the tetrapods. Rosen et al. (1981) considered *Griphognathus* as a primitive member of the lungfishes, so that they could justify a close lungfish-tetrapod relationship. The publication of Rosen et al. (1981) started a series of publications which demonstrated misinterpretation of characters, etc. These analyses, except that of Chang (1991), agree in the placement of osteolepiforms as the sister group of tetrapods, but differ in the placement of lungfishes. A comparison of these hypotheses on the base of a data set of 216 characters (Schultze, 1994) gives a probability estimate of the different hypotheses. Chang's (1991) hypothesis is the least probable one (27 steps more than the shortest tree), followed by Rosen et al.'s (1981) hypothesis (22 steps more) and hypotheses (22 or 16 steps more) supporting Rosen et al. (1981). Three hypotheses with three possible placements of lungfishes appear as the most probable ones. The lungfish - coelacanth sister group relationship (Fig. 1: *b*; Northcutt, 1987) appears in the shortest tree, followed with one step difference by two hypotheses, one placing the lungfishes as sister group of all other sarcopterygians (Fig. 1: *c*; Schultze, 1987) and the other with lungfishes as sister group of porolepiforms (Fig.1: *a*; Maisey, 1986; Ahlberg, 1991b).

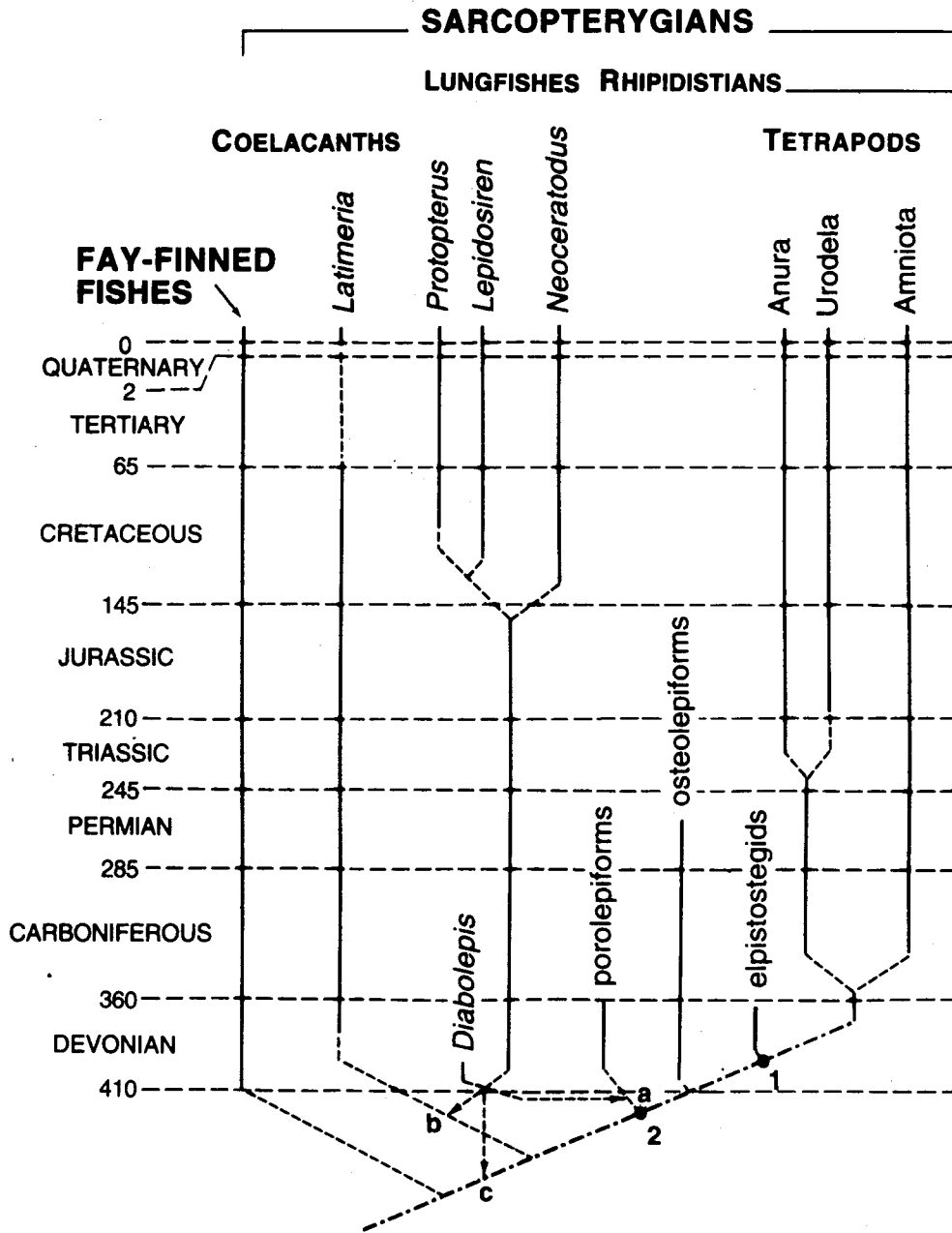Today the elpistostegids have generally been accepted as the sister group of

Fig. 1　Distribution through time and interrelationships of sarcopterygians. Solid lines = fossil occurences; broken lines = hypothesized relationships; a, b, c = three discussed relationship schemes of lungfish, a = sistergroup of porolepiforms, b = sister group of coelacanths, c = sister group of all other sarcopterygians; 1 and 2, see text.

图 1　肉鳍鱼类的年代分布与相互关系。实线: 化石记录; 虚线: 假设的关系; a, b, c: 肺鱼在谱系树上三个可能的位置, a− 与孔鳞鱼类构成姊妹群, b− 与空棘鱼类构成姊妹群, c− 与所有其它的肉鳍鱼类构成姊妹群。

tetrapods, and the osteolepiforms as the sister group of both (Ahlberg and Milner, 1994). Elpistostegids share at least 12 unique characters and two reversals (1 in Fig. 1) with tetrapods (Schultze, 1994): flat skull as contrast to the arched skull of fishes; presence of paired frontals; position of parietal opening posterior to orbits; presence of squamosal embayment; dorsal position of orbits; preopercular canal reduced to pit line if present; absence of dorsal fins; epichordal lepidotrichia more developed than hypochordal lepidotrichia; well-ossified ribs; large scapular blade; eyes at level of junction between two principal bones; two large pairs of bones anterior to dermal intracranial joint; and absence of cosmine and of true enamel on dermal bones as reversals in comparison to primitive sarcopterygians.

Osteolepiforms also share at least 12 unique characters and two reversals (2 in Fig. 1) with elpistostegids and tetrapods (Schultze, 1994): polyplocodont plicidentine; one external nasal opening on each side; only anterior narial opening opens at lateral rostral; palatal narial opening surrounded by premaxilla, maxilla, vomer, and palatine (=choana); convex proximal part of pectoral appendage joint; two subequal elements as second axial segment of paired fins; screw-shaped, concave scapula glenoid; ectepicondyle on humerus (and other humeral features); unjointed radials in median fins; fenestra ventrolateralis dorsal to excurrent nostril; cheek composed of jugal, postorbital, squamosal, quadratojugal, and preoperculum; dermal anterior incurrent naris with internal dermintermedius process (=septomaxilla); and only two supraorbitals and a not-elongated pectoral fin as reversals.

At present only the position of lungfishes within sarcopterygians is in question. The lungfishes form either the sister group of porolepiforms (a in Fig.1), or that of all other sarcopterygians (c in Fig.1), or that of coelacanths (b in Fig.1). A position of lungfishes as sister group of tetrapods can be deduced from a sister group relationship of lungfish and porolepiforms only if fossil forms are excluded. It is a limited view reduced to extant forms. The same was the case at the beginning of the discussion of the problem when only extant sarcopterygians (*Lepidosiren* and *Protopterus*) were known sufficiently. Innovations in the transition from fish to tetrapods can only be found in elpistostegids and osteolepiforms. Contrary to Meyer (1995), these innovations (e. g., choana, dichotomous internal paired fin skeleton) cannot be traced back from an analysis of extant forms to the common ancestor of lungfishes and tetrapods. The common ancestor of both groups had two external nasal openings and an archipterygial internal paired fin skeleton, typical sarcopterygian fish features. That is independent of acceptance of any of the three possible hypotheses. These typical tetrapod features appear first in the common ancestor of osteolepiforms and tetrapods. That is also the case with other tetrapod features which are synapomorphies of tetrapods and elpistostegids or of tetrapods and osteolepiforms, but not of lungfishes and tetrapods.

The placement of lungfishes within sarcopterygians can only be solved by addition of new basal taxa (Schultze, 1987; Huelsenbeck, 1991) or by addition of new charac-

ters or of re-evaluation of character states. New basal taxa can change the sequence of character states and add new characters so that I expect a decision between the three hypotheses from addition of new basal taxa. The Early Devonian sarcopterygian taxa of China (Chang, 1982; Chang and Yu, 1984; Yu, 1990) are therefore very important. Specific search for these basal forms could supplement our knowledge of these forms so that one or the other of the three hypotheses may be supported or discarded.

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