

Notes on the Systematics, Distribution and Natural History of the South American Lungfishes in the genus *Lepidosiren* Fitzinger 1837 (Dipnoi: Lepidosirenidae)

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Abstract

Lungfishes (Dipnoi) remain central to interpreting broad patterns of vertebrate evolution because members of this group exhibit an array of fish-like and tetrapod-like characters. The living South American Lungfish, *Lepidosiren paradoxa*, is one of only six extant species of this ancient group. Together with its sister genus *Protopterus*, which includes four species from Africa, *Lepidosiren* belongs to the family Lepidosirenidae, which is strongly demarcated in cranial and postcranial features from the third living genus, *Neoceratodus*. In the last fifty years, research attention on living lungfishes has focused disproportionately on the Australian and African species. There has never been a comprehensive revision of Lepidosirenidae, nor has there been any modern effort to characterize its species or to discover anatomical characters for examining intrafamilial relationships. Although it is widely distributed in South America, few details about the biology of *Lepidosiren paradoxa* – including basic range and distribution data – are available. Most accounts date from the 19th or early 20th century. The time is right to review the history of investigations on this genus as a prelude to future research.

Introduction

Since the first descriptions of fossil and living lungfishes in the 1820's and 1830's, members of this group have proved exceptionally interesting to paleontologists, systematists, morphologists, embryologists and physiologists (e.g., Bemis et al., 1987a; Schultze & Cloutier, 1996; Graham, 1997; Liem et al., 2001). By the 20th century, three living genera and six living species of lungfishes were known (Figure 1; see Eschmeyer, 1998). Now at the beginning of the 21st century, ichthyologists and paleontologists recognize more than 200 species of living and fossil lungfishes in more than 60 genera (Marshall, 1987; Schultze & Cloutier, 1996; Martin, 1997; Kemp, 1997) yet many basic details about the biology of the living species remain unknown. This is particularly true for the genus *Lepidosiren*, a characteristic species of the South American ichthyofauna (Figure 2). *Lepidosiren paradoxa* was not only the first living species of lungfish formally named but also the stimulus for a lively scientific debate about the placement of lungfishes relative to other bony fishes and land vertebrates (Bemis et al., 1987b). Now more than 165 years after its discovery, we still lack broadly based revisionary studies of *Lepidosiren*, have incomplete knowledge of its range in South America, and know few details about its anatomy, natural history or development beyond those published more than 50 years ago. Much of the information about *Lepidosiren* is scattered in older accounts, not linked to maps or other tools for understanding the range of this species, and unknown to contemporary ichthyologists. For all of these reasons, we considered that it would be useful to review available information as a precursor to framing a new collaborative research program on this most interesting genus.

The history of discoveries and issues concerning *Lepidosiren* is summarized in a time-line in Figure 3 (also see Conant, 1987). Soon after Fitzinger's (1837) description of specimens from the Madeira River in central Amazônia, *Lepidosiren* went unreported from the Amazon basin for nearly fifty years until it was "rediscovered" by Emil Goeldi in the 1890's (Goeldi came to South America from Switzerland in 1880; his first name is

transliterated to Emílio in Brazil). Goeldi (1896) showed that the genus occurs from Peru to the mouth of the Amazon near Belém. Bridge (1898) provided a detailed description of skeletal anatomy. Kerr's detailed embryological studies of *Lepidosiren* began at the turn of the 20th century, originally to parallel Semon's research on development of *Neoceratodus* (Semon, 1901) and Budget's research on *Protopterus* (Budget, 1900, 1901, 1903; also see Shipley et al., 1907 and Hall, 2001). The last field investigations of ecology and behavior were conducted in the 1930's. Since then, most research on *Lepidosiren* has examined physiological questions (e.g., McMahon, 1969; Bemis & Lauder, 1986, Bemis 1987), captive breeding (Parsons, 1935), development (Pehrson, 1949) and higher relationships of lungfishes as a group (Bemis et al., 1987b).

Interest in lungfishes stems in part from their peculiar mosaic of anatomical, physiological and developmental characteristics – a mosaic that caused leading 19th century scientists to debate for decades whether they should be considered fishes or amphibians (e.g., beginning with Fitzinger, 1837, Natterer, 1837; Owen, 1839, 1841; Weigman, 1839; Müller, 1844; see review by Bemis et al., 1987b). The 19th century debates presaged a series of publications in the 1980's and 1990's about the phylogenetic relationships of tetrapods, lungfishes, and coelacanths (Rosen et al., 1980; Jarvik, 1981, Forey, 1987; Schultze, 1987). Most analyses now indicate that lungfishes (and not coelacanths) are the living sister group of tetrapods (e.g., Forey et al., 1991; Forey, 1998; Meyer & Wilson, 1990; Schultze, 1991; Zardoya & Meyer, 1997; but see Northcutt & Bemis, 1993). Some Devonian lungfishes come from environments regarded as fully marine (e.g., the Gogo Formation of Western Australia; see Miles, 1977). In contrast, living lungfishes occur only in freshwater rivers, swamps or lakes, and they are physiologically incapable of crossing large expanses of saltwater (i.e., they are primary freshwater fishes). The three living genera of lungfishes also are known as fragmentary fossils in many freshwater deposits (unlike their distinctive toothplates, the cartilaginous endoskeleton of post-Paleozoic lungfishes is not prone to fossilization). For example, the Australian lungfish, *Neoceratodus forsteri* Krefft 1870 lives

today in three relatively small coastal rivers in Queensland (Kemp, 1987). Closely related fossil forms are widely distributed in Australia, and fossils assigned to *Neoceratodus* occur on other continents, including South America and Africa (add refs here). A comparatively large amount of recent research effort has concentrated on *Neoceratodus* (e.g., Bartsch, 1994; Arratia et al. 2001; Brooks & Kind, 2002), but this is not the case for the other two extant genera, *Lepidosiren* and *Protopterus*.

General Systematics of Lepidosirenidae

Specimens available to Fitzinger (1837) came from the Rio Madeira, a tributary of the Amazon in central Amazônia. Since the 1830's, the species has been reported from many other localities in South America, but surprisingly few details about its distribution and ecology are available. The fossil record of *Lepidosiren* extends from the Late Cretaceous of South America to the Recent (Stirton, 1953). Four living species and several fossils in the genus *Protopterus* are known from Africa (Figure 1; *P. annectens* Owen 1839; *P. aethiopicus* Heckel 1851; *P. dolloi* Boulenger 1900; and *P. amphibius* Peters 1845; Trewavas 1954 resurrected *P. amphibius* by showing that it can be distinguished from other species of *Protopterus* by vertebral counts and fin proportions also see Greenwood, 1987). Poll (1961) recognized subspecies of *P. annectens* and *P. aethiopicus* (also see Gosse 1984; Figure 1). Together, *Lepidosiren* and *Protopterus* form the monophyletic family Lepidosirenidae, on the basis of shared derived characters of the toothplates, axial skeleton, and paired and median fins (Figure 1; also see Miles, 1977; Bemis, 1984b; note that Nelson, 1994 retained the genera in separate mono-generic families).

Lepidosirenids exhibit a clear vicariance pattern that is linked to the separation of Africa and South America in the Cretaceous (Fernández et al., 1973; Novacek & Marshall, 1976; Keast, 1977; Lundberg, 1993). *Protopterus* occurs from the West African coast to Ethiopia, as far north as the Nile River, in great lakes of central Africa, the Zaire River

system to west, as well as short rivers of the southeastern coast as far south as South Africa (Boulenger, 1909; Trewavas, 1954; Bemis, 1983). *Protopterus dolloi* from the Zaire River basin, which was continuous with the proto-Amazon basin during the Mesozoic, is strikingly similar in external anatomy to Amazonian *Lepidosiren* (Trewavas, 1954). Its internal anatomy has not been closely compared to that of *Lepidosiren*.

There has never been a comprehensive revision of Lepidosirenidae, nor has there been any modern effort to characterize its species or to discover anatomical characters for examining intrafamilial relationships. Bemis (1983, 1984b) collected in Kenya, prepared and studied the skulls and toothplates of 23 adult specimens of *Protopterus aethiopicus* and 10 adult specimens of *P. annectens* and compared them to the few skeletal materials of *Lepidosiren* then held in collections. This allowed him to describe several putative generic-level differences between the skulls and toothplates of *Lepidosiren* and *Protopterus* (Figure 4; Bemis, 1984a; also see Kemp, 1998). Still, on the basis of these materials he could not closely examine skeletal differences among species within the genus *Protopterus*, nor could he examine whether *L. paradoxa* nests within *Protopterus* as its external similarities to *P. dolloi* suggest. Moreover, inadequate early developmental material prevented Bemis from making in the 1980's the detailed analyses now standard for comparative studies in fish systematics and osteology (e.g., Grande & Bemis, 1991, 1996, 1998; Bemis & Grande, 1992, 1999; Hilton, 2002b, 2003). The limited osteological material studied to date also hampers interpretation of fossils, although it is clear that some fossil lepidosirenids are invalidly named because they are indistinguishable from living species.

DISTRIBUTION

Although *Lepidosiren paradoxa* was described in 1837, its distribution within South America remains poorly known. More than 196 specimens of *Lepidosiren* are held in systematic collections but almost half of these (89 specimens) lack detailed locality data. From available collection records, published localities and personal communications we

know that *Lepidosiren* has a very broad range in South America (Figure 5). Details, however, are difficult to establish because so many museum specimens lack good locality data. The type locality for *L. paradoxa* Fitzinger 1837 is the Madeira River, a tributary of the Amazon (the types are in Vienna). Castlenau (1855) described *L. dissimilis* from a single specimen from the Ucayali River (the type is in Paris). His 19th century contemporaries (e.g., Gunther, 1870: 323) regarded *L. dissimilis* as synonymous with *L. paradoxa*, but no one has closely reexamined this. As already noted, for much of the 19th century few specimens were taken from the Amazon or its tributaries. It was not until Goeldi (1896, 1897a, b, 1898a, b) that *Lepidosiren* was “rediscovered” in the Amazon, and shown to occur from the Ucayali River to the mouth of the Amazon near Belém.

Holmberg (1887) reported *Lepidosiren* in the Gran Chaco of Paraguay (Rio Paraná drainage). Soon, Ehlers (1894a, b) secured 30 Paraguayan specimens collected by Bohls (1894) and described them as *L. articulata* based on differences in head shape, narial openings, scales and fins relative to published descriptions of *L. paradoxa* from the Amazon. These differences are summarized in Table 1. Lankester (1894, 1896, 1897) dismissed Ehlers’ (1894a) new species after examining specimens in European collections. He corrected a mistake in the description of *L. paradoxa* concerning segmentation of the skeletal axis of the paired fins (it is segmented in *Lepidosiren* from both Amazonia and the Rio Paraná, but Ehlers had interpreted this as a species-level difference). Lankester noted (1896: 24) coloration differences in Amazonian and Paraguayan specimens, which he attributed to preservation artifacts. It is remarkable to us that no one reinvestigated Ehlers’ interpretation, especially because Lankester studied only external features and measurements of the eight specimens available to him. Yet we know that such external features cannot reliably distinguish all species in the family Lepidosirenidae. For example, vertebral counts (typically from x-rays) are needed to distinguish specimens of *P. amphibius* from *P. annectens* (e.g., Trewavas, 1954; Bemis, 1983).

The range of *Lepidosiren* in the Amazon and Paraná river systems is easily reconciled with the fossil record of the genus, the geologic history of South America, and also with the biogeography of other South American fresh water fishes (e.g., Fernández et al. 1973; Lundberg et al., 1998). Its range in Caribbean and Atlantic drainage basins also may be understood in the context of other groups of freshwater fishes, but much more work needs to be done. For example, specimens from Guyana (e.g., AMNH 97664), French Guyana (e.g., MNHN 1999/1610; MNHN 2002/0504; MNHN 2001/1559) and Colombia (NRM 16681; AMNH 38137SW; FMNH 92661) have yet to be closely compared to specimens of *Lepidosiren* from the Amazon and Paraná systems.

Lungfish toothplates are so distinctive that they tend to be quickly recognized in any fossil deposit that yields them. Fossil toothplates of *Lepidosiren* have been found only in South America, at localities ranging from Upper Cretaceous to Miocene in age (Sige, 1968; Fernández et al., 1973; Santos, 1987; Schultze, 1992; Arratia & Cione, 1996; Lundberg, 1997, Gayet & Meunier, 1998, Gayet et al., 2001; Table 2). The presence of *Lepidosiren* in the El Molino Formation, Upper Cretaceous of Bolivia, is biogeographically interesting. The locality is Middle Maastrichtian, making this one of the earliest records of *Lepidosiren*, and the deposit has yielded taxa of fishes found living today only in Africa (e.g., bichirs, Polypteridae) and North America (e.g., gars, Lepisosteidae). As yet no whole-body fossil of *Lepidosiren* has been found.

Natural history and development

Adult *Lepidosiren* live as solitary individuals in burrows that they construct in swamps or shallow lakes (Kerr, 1950; Figure 6). Because they are obligate air-breathers (i.e., they drown if prevented from accessing air; see Burggren & Johansen 1987), relatively shallow water is essential. The water surface often is covered with floating plants. Although South American lungfish do not aestivate, as do African lungfishes (Carter & Beadle, 1930; Johnels & Svensson, 1954; Liem, 1987; Graham, 1997, 1999), they can withstand seasonal

drying of their habitats as long as some moisture remains in their burrows. Reproduction occurs during the rainy months, when adults move into flooded areas and build elongated burrows as nests. Males develop filaments known as “pelvic gills” on their pelvic fins and exhibit parental care, protecting eggs and young in the nest. The pelvic gills can be induced to form by injections of testosterone (Urist, 1973) and are believed to release oxygen into the water of the nest to raise its oxygen content (Cunningham, 1932; Cunningham & Reid, 1932; Graham, 1997). Kerr (e.g., Kerr, 1900, 1901a, 1901b, 1902, 1909; also see review in Kerr 1919) closely studied larval *Lepidosiren*. External gills are prominent throughout the yolk-sac larval period and are retained into the free-living larval and juvenile stages (Figure 7). These gills are usually resorbed in older juveniles and adults (unlike some species of *Protopterus*, which retain small external gills throughout life). Juvenile specimens of *Lepidosiren* typically have a pattern of bright yellow spots; these spots are lost as the individual grows, with adults achieving a black or slate-grey color.

The most recent reports on the habits of *Lepidosiren* were written 50 to 100 years ago (Kerr, 1898a, b, c, d; also see his expedition memoir, Kerr, 1950; Carter & Beadle, 1930, 1931), but all of these were based on specimens studied at sites in the Gran Chaco of Paraguay. Lungfish habitats in Amazonia differ from those in Paraguay. For example, where *Lepidosiren* lives in the Gran Chaco, its habitat dries out almost completely during the dry season. In Amazonia, however, the water retreats following seasonal flooding so that the fish can move with the water level from seasonally flooded forests back into permanent channels (Cox Fernandes, 1997).

(Pantanal – FM please write something here) Harder et al. (1999) reported physical parameters for water-filled clay pits near the Rio Cuiabá in the Pantanal of Brazil, where they collected *Lepidosiren* for physiological research.

(Amazônia – JZ and GMS please write something here)

(Belem – write something here)

(Paraná-Paraguay – RCC and LM please write something here)

Conclusions

Although *Lepidosiren paradoxa* was described in 1837, its range within South America remains poorly known. No one has closely compared anatomical, genetic or other types of variation across the range of *Lepidosiren*. A discounted 19th century interpretation that *Lepidosiren* from the Gran Chaco are differentiated at the species level from *Lepidosiren* in Amazônia remains intriguing because we lack such comparative studies. Additionally, basic biological facts such as breeding season, habitat quantification, abundance, growth rates etc., remain unknown across South America. Lungfishes are central to interpreting broad patterns of vertebrate evolution, such as questions about the origin of tetrapods. Thus, gaps in our knowledge of *Lepidosiren* are important to fill, for this genus is one of only three extant genera of lungfishes.

Table 1 . Differences between *Lepidosiren paradoxa* and *L. articulata* noted by Ehlers (1894a).

<p><i>Lepidosiren paradoxa</i>, Fitzinger 1837. Type Locality: Madeira River (tributary to the Amazon River). Coat of scales distinct; snout conical; nasal apertures transversely oval; limbs with unsegmented cartilaginous axis.</p>
<p><i>Lepidosiren articulata</i>, Ehlers 1894a. Type Locality: Gran Chaco (tributary to the Paraná River system). Coat of scales more or less concealed by thick epidermis; head and snout longer than in <i>L. paradoxa</i>, bluntly rounded off in front; nasal apertures circular, with conical papilla; limbs with segmented cartilaginous axis.</p>

Table 2. Fossil *Lepidosiren*. Modified from Arratia & Cione, 1996.

Species	Country	Locality	Formation	Stratigraphic Assignment	References
† <i>Lepidosiren</i> cf. <i>L. paradoxa</i>	Perú	Laguna Umayo	Vilquechico	Late Cretaceous	Sigé, 1968 Marshall et al., 1985
† <i>Lepidosiren</i> cf. <i>L. paradoxa</i>	Bolivia	Pajcha Pata & Vila Vila	El Molino	Late Cretaceous (Middle Maastrichtian)	Schultze, 1992 Gayet et al., 2001
† <i>Lepidosiren</i> cf. <i>L. paradoxa</i>	Bolivia	Tiupampa	Santa Lucía	Early Late Paleocene	Schultze, 1992 Gayet et al., 2001
† <i>Lepidosiren</i> <i>paradoxa</i>	Argentina	Jujuy Province	Lumbrera	Eocene	Fernández et al. 1973 Cione 1978, 1986a
† <i>Lepidosiren</i>	Colombia	Rio Magdalena	La Venta	Late Miocene	Stirton, 1953 Lundberg, 1997
† <i>Lepidosiren</i> <i>megalos</i>	Brazil	Estado- Do- Acre		Tertiary	Santos, 1987

Figure Captions

Figure 1. Relationships of living species of Lepidosirenidae. Characters at Node A (modified slightly from Miles, 1977) are: (1) Frontal bone (interpreted as homologous to bone B of fossil dipnoans by Miles 1977) is situated below the adductor muscles and has spread over the dorsal surface of the neurocranium; (2) the posterior part of the internasal septum is reduced, in association with the development of large pterygopalatine toothplates; (3) the pterygopalatine and prearticular tooth-plates have columns of "petrodentine" surrounded by trabecular dentine; (4) the subnasal cartilage is attached to the nasal capsule; (5) the vomer is reduced to small, conical tooth and (6) the outer dermal series of the lower jaw is reduced to a single bone (angular) and there is extensive development of Meckel's cartilage on the lateral and mesial faces of the prearticular. Characters at Node B include: (7) extreme reduction of fin rays and web of the pectoral and pelvic fins; (8) body extremely elongate; Characters at Node C include: (9) presence of six gill arches with five gill clefts (Nelson, 1994); (10) reduction in size of frontal bone to only partially cover the neurocranium (Bemis, 1983; also see Figure 4).

Figure 2. Photograph of a captive specimen of *Lepidosiren paradoxa* from Amazônia.

Figure 3. Timeline for discoveries related to the study of *Lepidosiren*.

Figure 4. Comparison of cranial features of *Lepidosiren paradoxa* and *Protopterus a. aethiopicus*. Note differences in the shape of the frontal bone (fr).

Figure 5. Map showing localities for fossil and Recent *Lepidosiren* based on museum records and literature. Three major drainage basins are color-coded (Orinoco in pink; Amazon in blue; Paraná in yellow). As yet, *Lepidosiren* is unreported from the Orinoco basin.

Figure 6. A locality for *Lepidosiren paradoxa* on Careiro Island near Manaus, Amazônia, Brazil.

Figure 7. Juvenile specimen of *Lepidosiren paradoxa* showing external gills.

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