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# Migration and speciation of the South American Iniidae (Cetacea, Mammalia)

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## Abstract

The South American Iniidae immigrated from the Pacific coastal regions to the lake system of the sub-Anden molasse[1] troughs in the Miocene some 15 million years ago. Here, following the disappearance of the link with the Pacific sea as a consequence of the Anden orogenesis in the Pliocene (5 to 1.8 million years ago), they had to adapt to the sub-Anden lakes of the freshwater molasse. These lakes were very turbid owing to the huge load of sediment delivered from the geologically rapidly rising cordilleras. The Iniidae reacted to this with a reduction of their visual capacity. The prototype *Inia boliviensis* ensued in the Bolivian sub-Anden troughs. They migrated via the Iquitos gate to the larger Amazon – Orinoco river system during the Pleistocene (1.8 million to 10 000 years ago). Here they developed into the "modern" *Inia geoffrensis* (larger brain, reduced dental count). At the beginning of the Holocene some 10 000 years ago the surrounding landscape changed from the previous semiarid savanna to the rainforest with its black water. This water separated the, upto that time, united turbid water regions of the Amazon – Orinoco and formed, in the region of the present Rio Negro, and acid black water barrier, avoided by the *Inia geoffrensis* and thus causing the development of subspecies, the *Inia geoffrensis geoffrensis* and the *Inia geoffrensis humboldtiana*. The former of these subspecies is bound to the Amazon and the latter to the Orinoco river system (Trebbau and Van Bree 1974).

[1] Molasse (trough) is a term of the French-Swiss Alpine geology and means sinking troughs neighboured to young orogens (e. g. the Alpes or the Anden), filled up by coarse rubble caused by the uplifting mountains.

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## Introduction

Of the South American Odontoceti only the Iniidae are definite freshwater dwellers and – in contrast to other species – therefore don't occur in brackish coastal waters. Perhaps this is because the Iniidae – a unique exception? – traversed the continent from the Pacific almost to the Atlantic. Among the Iniidae there are three species or subspecies: *Inia boliviensis* limited to the Bolivian sub-Anden, and *Inia geoffrensis* which with the subspecies *Inia geoffrensis geoffrensis* settled in the Amazon district and *Inia geoffrensis humboldtiana* settled in the Orinoco river system (Van Bree and Robineau 1973; Pilleri and Gihr 1977; Pilleri et al. 1982; Trebbau and Van Bree 1974).

*Inia boliviensis* is said to be the original species and this assumption is based (among other things) on the fact that reduction in dental count and the increased cerebralisation are looked upon as a progressive development.

The distribution of the *Inia boliviensis* is identical with the area of the geologically extinct Lake Beni. This lake was the Pleistocene remnant of a bigger Pliocene lake system known as the sub-Anden freshwater molasse. This itself developed from the Miocene marine molasse and had, even during the beginnings of the Anden orogenesis, a connection with the Pacific. The oldest species of Iniidae, *Proinia patagonica* True, have for this reason been traced and proved in marine layers of the Lower Miocene in Patagonia (True 1909, 1910).

Barnes in a recent letter to the author (Aug 29, 1984) pointed out that *Proinia patagonica* is not a species of Iniidae, but is probably some kind of large Squalodontidae. Also the North American genera *Lophocetus* and *Kampholophos* have been called Iniidae, but in his paper (Barnes 1978) he re-assigned them to Kentriodontidae.

## Results and discussion

The Iniidae as ordered to the Platanistoidea (Pilleri et al. 1982) (Barnes in his letter: The evolutionary history of all Platanistoidea is very poorly understood, and most reputed fossil taxa need serious re-examination) developed, at the turn of the Miocene to the Pliocene, perhaps 22 million years ago, out of the Squalodontoidea from Burdigal (Miocene) later extinct (see fig. 3 in Rothausen 1968). The Squalodontoidea were, from the most part, closely tied to the shallow waters in the immediate coastal region where the water was relatively warm. It is also true of the early Iniidae that they were coastal dwellers (Oelschläger 1978). Their primeval structure allows this supposition.

The early Iniidae inhabitated the Pacific coastal region and in the Middle Miocene, some 20 million years ago, when the Anden orogenesis began (Zeil 1979), thrust into the newly forming molasse lakes. Here they suffered a similar fate to many former coastal dwellers which, after the loss of the link with the Pacific, had to adapt to the isolated and freshening molasse lakes. It is not wonder that in the contemporary sub-Anden – that is the east side of the Andean Cordilleras, many forms of life exist that show a relationship to the Pacific: horned pike, sardine, shrimps, sole, ray . . .

The concurrence between the marine and freshwater forms is often so great that – e. g. – "the slender, little, elliptical sole *Achiropsis natteri* looks, indeed, like a true sole from the sea – one that is stunted in growth" (Lüling 1969). And "the freshwater sardine *Lycengraulis batesii* which grows to length of over 14 cm and is common in the Rio Ucayali and Rio Huallaga below Yurimagua looks very like the related *Engraulis ringens* – that sardine which composes the enormous fish swarms of the Humboldt current in front of the North Chilean and Peruvian coast" (Lüling 1969).

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It was in this sub-Andean molasse lake district that the original species of *Inia boliviensis* developed out of the *Proinia* species.

The new environment of these molasse lakes caused further adaption. Surrounded by savanna and arid regions (Klammer 1982) and bounded by the rapidly growing cordilleras the molasse lakes and their tributaries were very rich in sediment which led to a considerable and permanent turbidity of the waters. The *Inia* had, in addition to adapt to this turbidity, a reduction of their visual capactiy (Pilleri and Pilleri 1982). The river dolphin *Inia* has been microphthalmic since this time (see also Gewalt 1978). The Pliocene molasse lakes filled the whole of the northern sub-Anden. From there it was possible for *Inia* to penetrate via existing or newly forming lakes into the river system of the Amazon and the Orinoco. Such links existed relatively early and are particularly to be supposed where, for a geologically long period, a zone of subsidence has existed. The Amazon Graben traverses the South American continent from Guayaquil to the mouth of the Amazon (see fig. 1), passed the region of the later sub-Anden. The Amazon Graben is older than the Anden Cordilleras and even older than the Atlantic ocean which formed some 110 million years ago. Thus the Graben finds an appropriate continuation on the African side in the Bénoué Graben which can be followed to Lake Chad (Grabert 1983).

How early this passage may have existed, when a connection between the sub-Anden and the mouth of the Amazon can be proved for the first time follows from the examination of sediments from the Amazon delta cone (Damuth and Kumar 1975). This cone shows fine-grained laminated deposits in its oldest part (Cretaceous to Lower Miocene). These deposits demonstrate a calm and slight sedimentation. However, in the Middle Miocene the deposit picture changes. This indicates a stronger transporting power (more volume of water) and an increased catchment area (newly tapped sub-Anden) (Supco and Perch-Nielsen et al. 1977).

It is possible to take the bay of Guayaquil – at the Pacific end of the Amazon Graben – as entrance for the Iniidae into the sub-Anden instead of the district round of Arica. However the fossil precursor *Proinia patagonica* (from the marine Miocene of Patagonia, see True 1910) makes it clear that the Iniidae (or their marine precursors) extended far to the south.

The Pacific Iniidae must have made their way via the Bolivian sub-Anden to the freshwater system of the Amazon and the Orinoco and did this using the Purús – (Grabert 1967), ore probably the Iquitos-gate (see Fig.). Their penetration of this system is placed at the turn of the Pliocene to the Pleistocene and from this time on a differentiation between the *Inia boliviensis* and *Inia geoffrensis* is to be reckoned with.

In spite of this very old and repeatedly reactivated subsidence zone of the Amazon Graben a continous sea connection has never existed, although at both ends marine Upper Cretaceous layers are deposited (Kehrer and Kehrer 1969; Katzer 1903). The Amazon Graben was, particularly in the Upper Miocene and the Pliocene, a fluvially, limnally marked system similar to that in the recent East African Graben.

It is precisely in the region of this passage that the first fossil freshwater dolphin, *Plicodontinia,* were proved in the Plio-Pleistocence Pebas layers in the upper Amazon region (Miranda Ribeiro 1938). Although, today, these passages are no longer clearly visible that is because just there a very considerable coverage with very young Anden material is present. This Amazon Graben (De Loczy 1968, 1970; Grabert 1983) demonstrates even today with its minor and medium earthquakes its active subsidence tendency (Berrocal and Assumpção 1982). This is particularly so in the region of the northern peripheral fault of the Amazon Graben (see Fig.).

The Amazon – Orinoco river system, during the Pleistocene in the main united, was surrounded by savanna as were the sub-Anden molasse lakes. This led to large sediment transport which made the water turbid, – the rainforest so typical today didn't exist as yet –, at least not to the present extend. Besides this the seawater level lay here, as all over the

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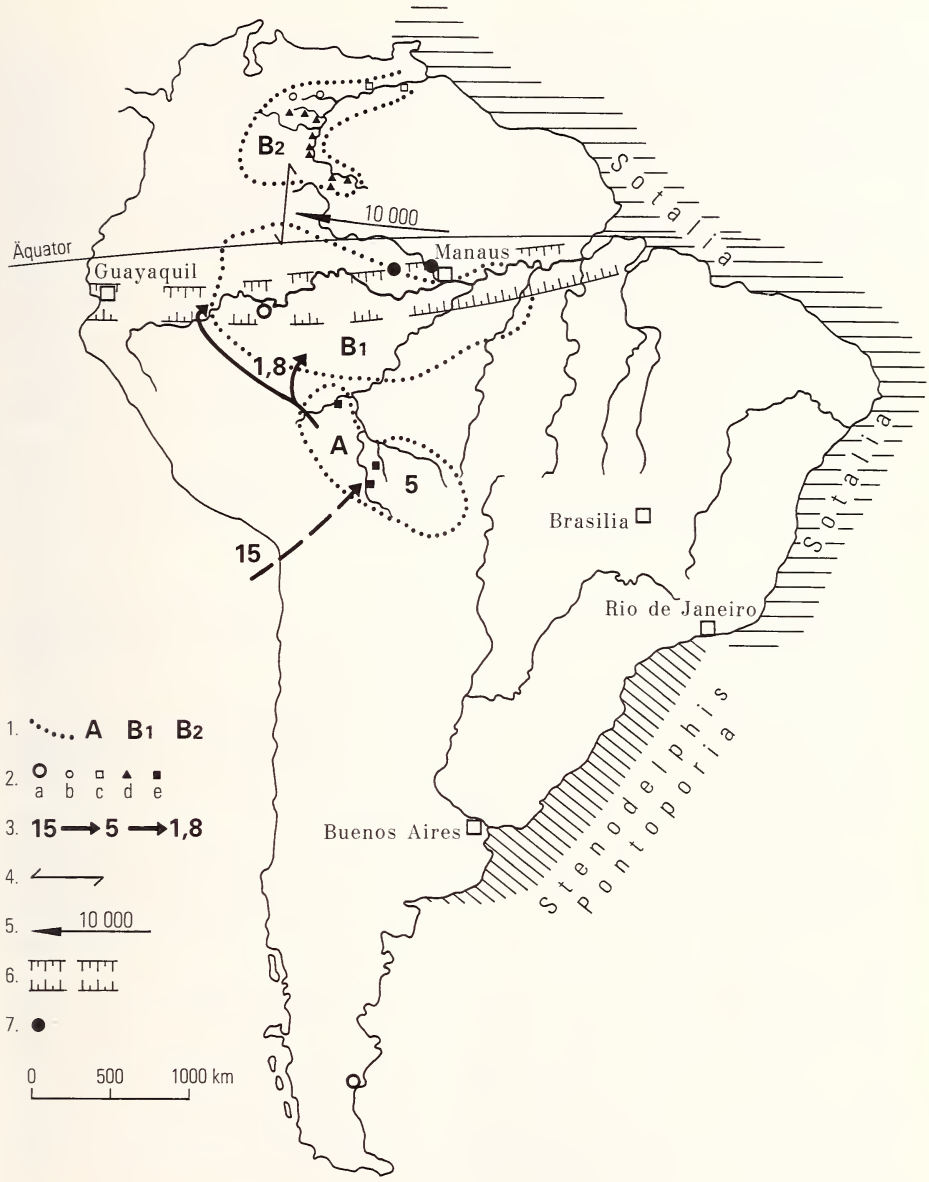


1: Range of the Iniidae. A = *Inia boliviensis*; B1 = *Inia geoffrensis geoffrensis*; B2 = *Inia geoffrensis humboldtiana*. – 2a: fossil Iniidae: *Proinia patagonica, Plicodontinia*; recent Iniidae: b = *Inia geoffrensis humboldtiana* (see GEWALT 1978); c = *I. geoffrensis humboldtiana* (see TREBBAU and VAN BREE 1974); d = *I. humboldtiana* (see PILLERI and PILLERI 1982); e = *I. boliviensis* (see PILLERI 1977). – 3: Migration of the Proiniidae from the Miocene coastalregions (15 million years ago) to the Bolivien sub-Anden; development of the *Inia boliviensis* through adaptation to the freshwater environment (5 million years ago); immigration to the Amazon – Orinoco system and further development to *Inia geoffrensis* (1.8 million years ago). – 4: The formerly united Amazon-Orinoco river system. – 5: Separation of the once united systems through the formation of a blackwater barrier some 10 000 years ago. – 6: The Amazon Graben. – 7: Seismic events about the northern edge of the Amazon Graben in the last decades

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*Table*

**Immigration and speciation of the South American Iniidae in time and space**

| | | |
|---|---|---|
| Holocene | formation of blackwater and development of subspecies of *Inia geoffrensis geoffrensis* (= Amazon) and of *Inia geoffrensis humboldtiana* (= Orinoco). | |
| —10.000 years— | | |
| Pleistocene | Immigration to the larger ecosystem of the amazon and Orinoco.<br>Development to the modern *Inia geoffrensis* with greater cerebralisation and reduced dental count. | Persistence in original region of the Bolivian sub-Anden of the primeval forms of *Inia boliviensis* until today. |
| | *Plicodontinia,* a fossil form from the limnal fluvial Pebas layers of the upper Amazon region. | |
| —1.8 m.y.— | | |
| Pliocene | Formation of freshwater molasse with turbid waters as a result of larger sediment transport from the rising cordilleras.<br>Adaption of the Iniidae to the turbid water environment e.g. by a reduction in visual capacity (microphthalmic). | |
| —5 m.y.— | | |
| Miocene | Immigration of the marine Proiniidae (e.g. *Proinia patagonica* True) from the Pacific to the marine molasse troughs east of the rising Andes.<br>Some 15 million years ago the beginning of the proper Andes orogenesis. | |

world, about 100 m lower since the freshwater was bound as ice in the polar regions during the Pleistocene ice age. In consequence heavy erosion was possible. At this time wide expanses of the formerly to the Pacific orientated sub-Anden were connecting to the Atlantic via the old pre-Andean watershed (prior to the Andean orogenesis).

Indications are supplied by examining the heavy-minerals in the Pleistocene sands of the Amazon mouth (Schnitzer and Faria 1981). The many waterfalls and rapids particularly on these stretches are evidence of the geological immaturity of the river beds and thus of the relatively young age of these passages (Grabert 1971, 1982).

The immigrant *Inia* in this river system extended as it was through this tapping developed into the "more modern" *Inia geoffrensis.* The broader region and in addition the many-sided biotope posed greater demands so that *Inia* reacted with a higher cerebralisation (the reduction in dental count can be attributed to a greater availability of fish and food). These environmental conditions, however, changed at the beginning of the Pleistocene.

The Pleistocence inland ice began to melt causing the seawater level to rise by some 100 m to the present mark. This rise can be observed all over the world and is valid for the Amazon mouth region as well. Examination for the Amazon terraces supplied clear evidence of this (Klammer 1971). The delta cone supplied until then with sediments was flooded and "drowned". The damning back of waters and delayed drainage in Central Amazonia caused the formation of such typical river-lake landscapes as "várzea" in which by far the largest part of the sediment load was caught up and not carried further to the delta (Sioli 1966; Irion 1976, 1982; Absy 1979). The huge river estuary of the Amazon came into beeing. However the amount of water flowing from the unchanged catchment area remained constant so that the phenomenon of the fresh barrier extending far out into the Atlantic came about.

As simply as the climatic story of the Quaternary Amazon is described just as differentiated is it when observed more closely. It is, in fact, marked by frequent changes from arid to humid phases of varying length in which the rainforest shrank or extended. Tropical rainforest has always been present in the Amazon region if only as a gallery forest at least since the time during which the region has been traversed by the equator and tropical zones. This is proved by the few climatic witnesses for the time since the decay of

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Gondwana, approximately since the Jurassic – Cretaceous boundary some 110 million years ago. Large scale and long-termed climatic changes were however influenced by two geological main events: by just that decay of Gondwana which caused the formation of the expanse of water of the Atlantic to the east of South America, and by the Andean orogenesis which formed mountains out of the Pacific coastal region. These, lying across the mainwind direction parallel to the equator, have governed the meterological conditions in the Amazon region lying to the east.

Thus it is assumed that during the maximum glaciation the annual mean temperature was 4 to 5 centigrades (4–5 °C) lower than today, less precipitation occurred and thus the climate was drier (Van der Hammen 1972). Apart from this, major climatic events can have caused a displacement of the climatic belts so that desert latitudes may well have been pushed considerably north towards the equator. Klammer (1982) shows e. g. for the Pliocene of the Pantanal an arid condition with dune sedimentation.

The rainforest reduced during the dry periods served as refuges for the forest fauna. New forms developed out of the isolated and reduced populations. These came into secondary contact with one another when the forests extended again as the result of an increasing humidity of the climate; this is particulary true of birds indigenous to forest (Haffer 1969, 1977). Their differenciation and probably that of other vertebrates (P. Müller 1973) is thus geologically young and took place relatively rapidly (see also Tricart 1975).

The Iniidae living in the waters of the Amazon will have been only slightly affected by these events. That changed, however, when as the seawater level rose following the melting of the inland ice and growth of the continous rainforest the black water rich in humus appeared.

The flooded forest, the "igapó" (see Irmler 1977), developed with the rising water level and increased quantities of humus material conditioned by the vegetation entered the water, coloured it brown and gave it the high degree of acidity (Sioli 1968). The already nutritionally poor soils were almost leached by the nearly sterile rainwater: the Podzol soils of the Amazon lowland developed (Klinge 1967, 1969). The length of the descent for the waters having been reduced by the rising of the seawater level together with the capacity of the vegetation for retaining meant that hardly any sediment was transported and the turbid water changed to black water. The present blackwaters are of Holocene age and is geologically really young, too.

Blackwaters formed particulary there where the flooded forest, together with its river-lakes and a low height above sea level, found optimal conditions for developing – in the region of the Rio Negro. This region thrusts like a barrier of blackwater in the formerly united turbid water regions of the Amazon and Orinoco and separates these into a northern (= Orinoco) and a southern (= Amazon) region.

In this the formerly uniform population of *Inia geoffrensis* was split up and the differentiation of the subspecies into *Inia geoffrensis geoffrensis* (= Amazon) and *Inia geoffrensis humboldtiana* (= Orinoco) began. Although it is reported that *Inia* have been seen in blackwater, if very rarely (Pilleri and Pilleri 1982), they do not appear to feel comfortable there. That may depend on a lack of fish as food and on the high acidity of the riverwater, up to 3.8 $p_H$ (according to Sioli 1968).

## Zusammenfassung

*Migration und Artbildung der südamerikanischen Iniidae (Cetacea, Mammalia)*

Die südamerikanischen Iniidae sind im Miozän, vor rund 15 Mio. J., aus pazifischen Küstengewässern in die subandinen Molasseseen eingewandert, wo sie sich dann nach Verlust der Verbindung zum Meer infolge der Anden-Orogenese im Pliozän (5 bis 1.8 Mio. J.) in den Seen der Süßwassermolasse anpassen mußten. Diese Seen waren durch die angelieferte hohe Sedimentfracht aus den geologisch

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rasch emporwachsenden Cordilleren sehr trübe, worauf die Iniidae durch eine Reduktion des Sehapparates reagierten; sie sind microphthalm.

Im bolivianischen Subandin entstand die Urform von *Inia boliviensis.* Diese wanderte im Pleistozän (1.8 Mio. J. bis 10 000 J.) über die Iquitos-Pforte in das Amazonas-Orinoco-Flußsystem ein und bildete sich dort zur „modernen" *Inia geoffrensis* um (höhere Cerebralisation, Zahnzahl-Reduzierung). Mit Beginn des Holozäns vor rund 10 000 J. wandelte sich die bisherige Steppen- und Savannen-Landschaft in den Regenwald mit seinen Schwarzwässern um. Diese spalteten das bisher einheitliche Trübwasser-Gebiet von Orinoco und Amazonas auf und bildete – im Bereich des heutigen Rio Negro – einen Schwarzwasser-Riegel mit hohen Säuregraden, der von *Inia geoffrensis* gemieden wird und der dadurch zur Unterarten-Bildung von *Inia geoffrensis geoffrensis* und *Inia geoffrensis humboldtiana* führte; erstere Unterart ist auf das Amazonas-, letztere auf das Orinoco-Flußsystem beschränkt (Trebau und Van Bree 1974).

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# The adrenal gland weights of the African elephant, *Loxodonta africana*

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## Abstract

Adrenal glands were collected from 71 male and 172 female elephants shot in Western Uganda in the period 1973 to 1974. This took place in Murchison Falls and Queen Elizabeth National Parks and included both the dry and wet seasons. The analysis of the material collected, revealed a variety of facts. The right adrenal gland is consistently heavier than the left one. There is very little sex difference in adrenal weights of coeval specimens. Adrenal weights generally increase pari passu with age in the young animals. The female elephants exhibit adrenal weight changes with the reproductive states but this is not significant. There is no evidence of seasonal or geographical variation in the adrenal gland weights of elephants of the same age and/or sex. Suggestions are put forward to try and account for the observations made.

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