Migration history of air-breathing fishes reveals Neogene atmospheric circulation patterns

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ABSTRACT

The migration history of an air-breathing fish group (Channidae; snakehead fishes) is used for reconstructing Neogene Eurasian precipitation and atmospheric circulation patterns. The study shows that snakeheads are sensitive indicators of summer precipitation maxima in subtropical and temperate regions, and are present regularly if the wettest month exceeds 150 mm precipitation and 20 °C mean temperature. The analysis of 515 fossil freshwater fish deposits of the past 50 m.y. from Africa and Eurasia shows two continental-scale migration events from the snakeheads' center of origin in the south Himalayan region, events that can be related to changes in the Northern Hemisphere circulation pattern. The first migration, ca. 17.5 Ma, into western and central Eurasia may have been caused by a northward shift of the Intertropical Convergence Zone that brought western Eurasia under the influence of trade winds that produced a zonal and meridional precipitation gradient in Europe. During the second migration, between 8 and 4 Ma, into Africa and East Asia, snakeheads reached their present-day distribution. This migration could have been related to the intensification of the Asian monsoon that brought summer precipitation to their migratory pathways in East Africa–Arabia and East Asia.

Keywords: paleoclimate, paleobiogeography, fishes, Neogene.

INTRODUCTION

Snakeheads (Channidae) are the only air-breathing fishes with a wide geographic distribution during the Cenozoic and are used here as a climate proxy. I demonstrate that channids are sensitive indicators of summer precipitation maxima in extratropical regions and that their long-term migration history can be related to changes in large-scale Northern Hemisphere precipitation patterns reflecting changes in the general atmospheric circulation.

Snakehead fishes are a group of highly predatory freshwater fishes with a partly amphibious lifestyle; they have an excellent fossil record in the Eurasian Neogene (Böhme, 2003; Reichenbacher, 1993; see Data Repository, Appendices DR1 and DR2[1]). The recent distribution of snakeheads shows a remarkable disjunction and is restricted to tropical African and tropical to temperate Asian regions, both having a monsoonal rainfall pattern (Fig. DR1; see footnote 1). Two genera are known, the African *Parachanna* and the Asian *Channa*, with 27 extant species (Musikasinthorn and Taki, 2001).

Because of a labyrinth-like suprabranchial organ in the upper gill chamber, snakeheads breathe atmospheric oxygen (Munshi, 1985), and are able to survive very low oxygen conditions. They can live outside of water for a considerable time (Munshi and Hughes, 1992) and travel overland (Lee and Ng, 1994). Some species are good jumpers (Sterba, 1959). Burmese fishermen call snakeheads ''torpedo fish'' and report that they can jump up to 4 m high, enabling these fishes to migrate uphill at the beginning of the rainy season (my personal observation). Because of this ability, snakeheads have an excellent migratory potential, and shallow watersheds present no serious obstacle to them. Because their overland motion starts in the tropics with the rainy season, I conclude that it depends on regional precipitation, hydrology, and the atmospheric water vapor content.

The large size (0.3–1.8 m) and heavy bones and teeth of channids make them excellent potential fossils. Their fossil records in various types of aquatic and terrestrial environments (see following and Table DR1; see footnote 1) indicate an amphibious lifestyle in the past similar to that of today.

MATERIAL AND METHODS

This study is based on a data set from my ''lower vertebrate'' database (Böhme and Ilg, 2003). I extracted all Eurasian and African freshwater fish–bearing localities from the latest early Eocene to early Pliocene (50–4 Ma; $n = 515$), containing 184 channid records (Table DR1; see footnote 1). From the present-day distribution of snakehead fishes, 96 representative climate stations (Appendix DR3; Table DR2; see footnote 1) were selected in order to examine the influence of climate on their extant distributions. I compiled current climate data from M.J. Müller and D. Hennings (Global Climate Data Atlas, 2004).

RESULTS

Climatic Significance of Snakehead Fishes

To document the influence of temperature and precipitation on snakehead fish distribution, I analyzed the mean precipitation during the wettest month (P_{wm}) and the mean temperature of the wettest month (T_{wm}) (Fig. 1; Appendix DR4 and Fig. DR2 [see footnote 1]). The extant distribution of snakehead fishes appears limited by both temperature and precipitation and is best characterized by high precipitation during a warm season (Fig. 1). The analysis of climate data reveals that snakeheads occur if the wettest month has a mean temperature >20 °C, pointing toward a summer precipitation maximum in subtropical and temperate regions. In the tropics their distribution seems to be limited only by P_{wm}, which varies between 50 mm and 1400 mm (95% confidence interval: 84–1000 mm). If climate stations are near the dryer limit of the P_{wm} versus T_{wm} climate space occupied

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[1]GSA Data Repository item 2004066, supplementary information to material, methods, channid biology and data used in constructing figures, is available online at www.geosociety.org/pubs/ft2004.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301-9140, USA.

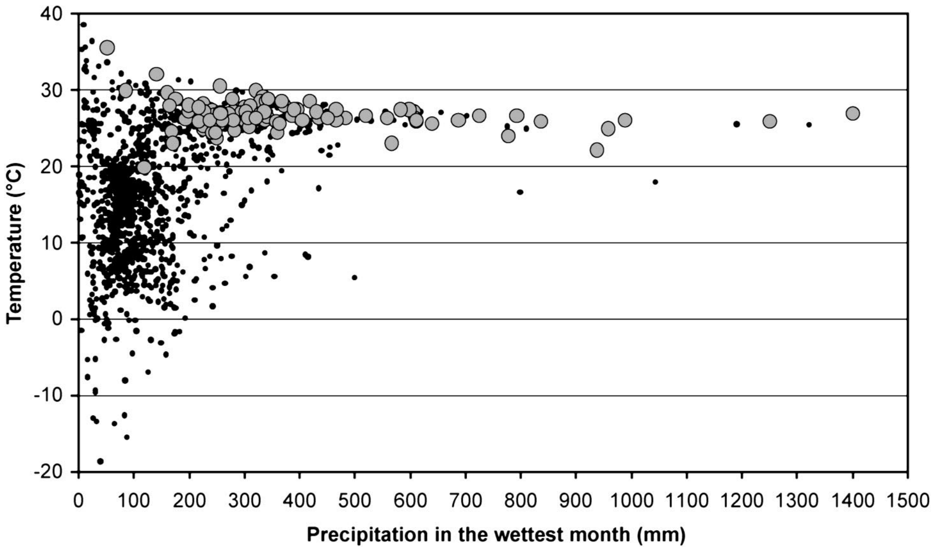

Figure 1. Distribution of extant snakeheads in P_{wm} vs. T_{wm} climate space (P_{wm} = precipitation during wettest month, T_{wm} = mean temperature of wettest month) in which data from 1266 climate stations are plotted. Climate data are from M.J. Müller and D. Hennings (Global Climate Data Atlas, 2004). Small black dots—climate stations without snakeheads (n = 1170); large gray dots—climate stations with snakeheads (n = 96).

by snakeheads, the proportion of snakehead-bearing stations diminishes. Such climate stations are situated in Pakistan near the border between summer-wet (monsoonal) and winter-wet areas (Iranian plateau). I conclude that the present-day extratropical distribution of snakeheads is limited by the amount of summer precipitation, because the channids are commonly present if the rainfall exceeds 150 mm. They are absent in arid regions when the wettest month has <50 mm precipitation. The P_{wm} versus T_{wm} correlation suggests that as the extratropical summer precipitation decreases, the conditions become increasingly unfavorable for snakeheads, and their survival becomes progressively dependent on other parameters, such as the local hydrological cycle. It is hypothesized here that a decrease in summer precipitation due to a decrease in air humidity reduces the ability of snakeheads to live outside water bodies and therefore lessens their migration potential. These limitations would imply that the distribution history of snakeheads is strongly related to changes in the atmospheric circulation pattern and that past migrations and extinctions are associated with climate shifts.

Fossil Distribution of Snakehead Fishes

Fossil snakeheads are known from the early Eocene (ca. 50 Ma) of Pakistan (Roe, 1991). They were restricted to tropical south Himalayan freshwater deposits (Baluchistan, Pakistan, India, Nepal) until the end of the early Miocene, ca. 17.5 Ma (Fig. 2A), when they expanded rapidly into subtropical western Eurasia (Böhme, 2003). In deposits formed during a remarkably short time interval between ca. 17.5 and 13 Ma, these fishes are recorded from many localities in this area; high fossil abundances occur in all kinds of freshwater ecosystems, paleosols, and karstic environments (Appendix DR3; Table DR1; see footnote 1), indicating the group's high migration potential and an amphibious lifestyle outside water bodies similar to today.

The analysis of African and Eurasian sites with fossil freshwater fishes reveals three main areas of distribution of snakehead fishes outside the south Himalayan basins during the middle Miocene (Fig. 2B): (1) west and central Europe (north of the Pyrenean and Alpine Ranges), (2) western and eastern Kazakhstan (between the Paratethys Sea in the west and the Tienshan Range in the south), and (3) southern Siberia (Lake Baikal). Snakeheads are lacking in the southern parts of western Eurasia (Mediterranean region, eastern Europe, Arabia), eastern Eurasia (Mongolia, China, Japan), and Africa.

The distribution of snakeheads in the late middle to late Miocene (13–8 Ma) is quite different from that in the middle Miocene (Fig. 2C). As the fossil record shows, they disappear from western Eurasia during the late middle Miocene (ca. 13 Ma) and are restricted to an area west of central Asia (eastern Kazakhstan) and South Asia.

The next remarkable shift in the distribution of snakeheads occurred during the Messinian and early Pliocene (8–4 Ma), when they established their present-day distribution (Fig. 2D). For the first time, their fossils are recorded from the African continent (East African rift valley in Uganda—Van Neer, 1994) and from East Asia (Yüshe Basin in China—Liu and Su, 1962).

DISCUSSION

One of the most remarkable features of the past snakehead fish distribution is the migration into western Eurasia during the end of the early Miocene (ca. 17.5 Ma). The areas of settlement—west and central Europe, Kazakhstan, and southern Siberia—belong to the midlatitudes (38°–45°N paleolatitude), and the geologic evidence confirms a subtropical climate during the early and middle Miocene (Mai, 1995). This type of climate allows monthly average temperatures over 20 °C only during the summer, suggesting a summer precipitation maximum in these areas. This expansion of snakehead fishes coincides with the beginning of the Miocene climatic optimum between 18 and 17 Ma (Zachos et al., 2001). This interval is characterized by a remarkable shift in European mean annual temperatures and a strong increase of winter temperatures and decrease of the annual range of temperature (Böhme, 2003; Utescher et al., 2000). The data presented here suggest, furthermore, an increase of summer precipitation in western Eurasia.

An increase of summer precipitation would lead to more favorable growing conditions for vegetation, which is consistent with a more frequent occurrence of evergreen elements in central Europe and of plant species showing tropical affinities (Mai, 1995). High precipitation is also indicated by clay minerals and hydrogen isotopes (Gilg, 2000). A high seasonal rainfall in central Europe is indicated by laterite and bauxite occurrences dated between 16.2 and 15.5 Ma (Schwarz, 1997), implying mean annual precipitation of >1200 mm and as many as 6 dry months with precipitation of <60 mm (Price et al., 1997). The data presented here suggest that the dry season must fall within the cooler winter months.

These summer-wet areas between 17.5 and 13 Ma are in contrast to the probably dryer climate of the Mediterranean region, eastern Europe, and Arabia (western Eurasia), as well as Mongolia, China, and Japan (eastern Eurasia), where snakeheads are lacking (Fig. 2B). This pattern points either to arid to semiarid climate conditions (P_{wm} < 50 mm) in these areas or to a climate with dryer summers where precipitation falls mainly in the cooler winter months.

For the time of the Miocene climatic optimum, these data suggest a zonal summer precipitation gradient in western Eurasia with summer-wet areas north of 38°N paleolatitude and dry areas between 30°N and 38°N paleolatitude. This zonality seems to have been interrupted in the central and eastern Paratethys region, where a drier climate persisted, producing an additional meridional summer precipitation gradient in the European midlatitudes, with a wet western and a drier eastern area.

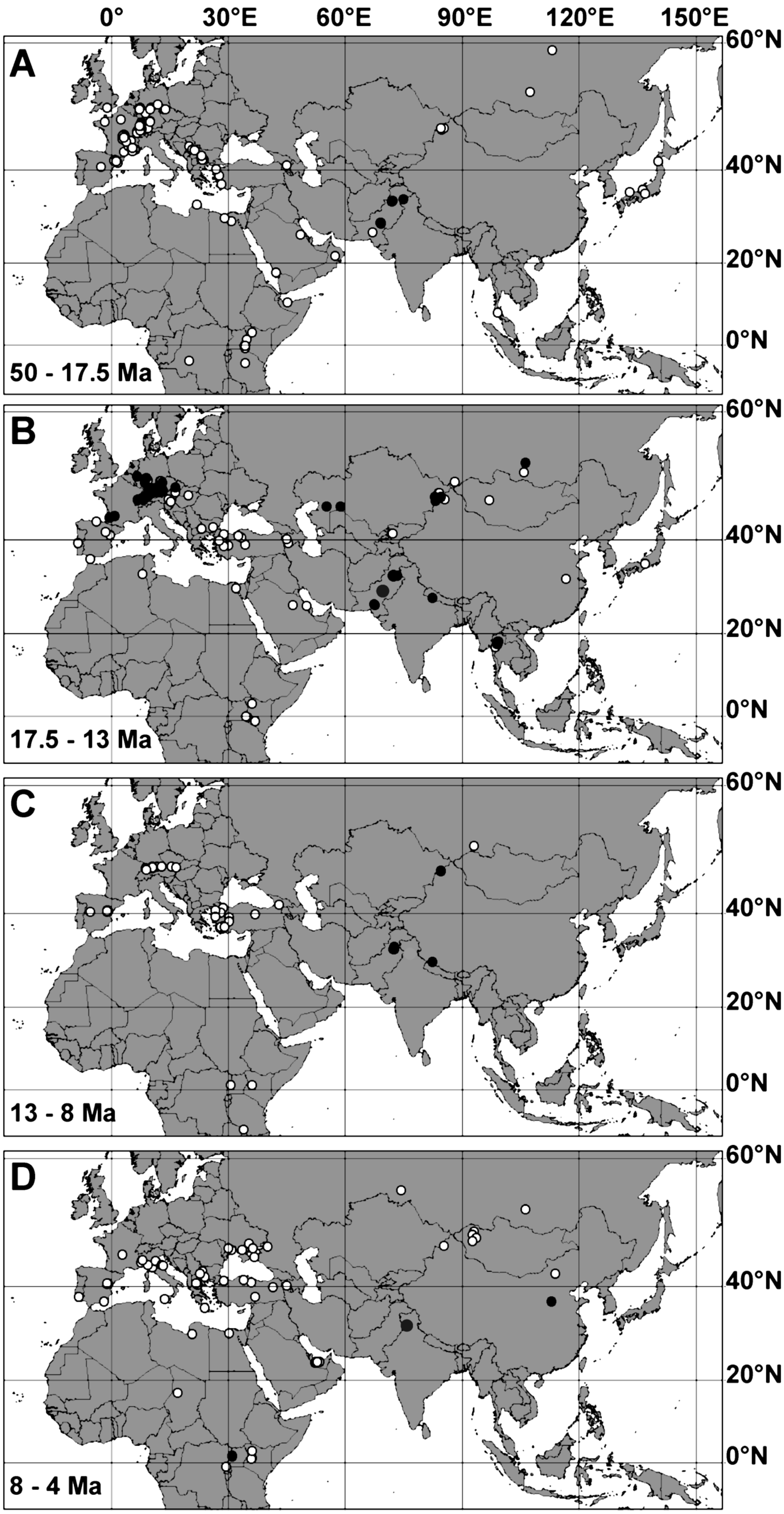

Figure 2. Distribution maps of fossil snakeheads (Channidae). Black dots—occurrences of snakehead fishes; white dots—freshwater fish localities without snakeheads. A: 50 to 17.5 Ma (latest early Eocene to late early Miocene; n = 61). B: 17.5 to 13 Ma (latest early to late middle Miocene; n = 347). C: 13 to 8 Ma (late middle to late Miocene; n = 43). D: 8 to 4 Ma (late Miocene to early Pliocene; n = 64; n = number of localities investigated).

The zonality in summer precipitation in western Europe could have been caused by both orography and atmospheric circulation. The summer perhumidization north of the European orogen and the drying to its south may be explained by northerly or northeasterly winds, which produced precipitation upwind and dryness downwind of the orogen. Significant northerly winds in central Europe are indicated by studies of fall direction of trees and eccentricity of tree growth rings in the lower middle Miocene (ca. 16 Ma) brown coal deposits of the Lower Rhine embayment (Utescher and Bruch, 2000). This wind system had a stronger east to northeast component ca. 14 Ma, also manifested in north Alpine volcanic ash layers (dated 15–14 Ma) whose source was in the Pannonian Basin (Unger et al., 1990).

I hypothesize here that these north to northeasterly winds are part of the trade wind circulation resulting from an early middle Miocene northward shift of the Intertropical Convergence Zone (ITCZ), which during this time was situated over North Africa (John et al., 2003). A subtropical high-pressure zone supposedly was over northeast and east Europe and produced dry climate in the central and eastern Paratethys region. The northernmost fossil distribution of channids implies that the boundary between the westerlies and trade winds in the Northern Hemisphere may have been north of 47°N paleolatitude, which is in agreement with suggestions of Rea (1994).

The expansion of the distribution area of snakeheads into western Eurasia between ca. 17.5 and ca. 13 Ma may therefore have been related to the warming of the Northern Hemisphere, producing an asymmetrical thermal gradient between both hemispheres (Flohn, 1981). The weaker thermal gradient of the Northern Hemisphere displaced the ITCZ northward and brought the southern part of western Eurasia under the influence of the northern trade winds. Over the North Sea Basin and the Paratethys, the trade winds accumulated water vapor and represented a moist onshore flow. The generally east-west–oriented mountain ranges (Pyrenees, Alps) produced upwind precipitation by the rising trade winds and downwind aridity by the descending winds. The subtropical high-pressure zone created dry summers over eastern Europe, as documented by extensive evaporite deposits in the central Paratethys (Rögl, 1998).

In the late middle Miocene, ca. 13 Ma, the snakeheads disappeared from western Eurasia. This regional extinction event postdates the middle Miocene global cooling between 14 and 13.5 Ma when, on the basis of ectothermic vertebrate data, the minimal summer temperature in central Europe dropped to between 14 and 15 °C (Böhme, 2003). The disappearance occurred during a time of increasing aridity in the western Paratethys, between 13 and 11.5

Ma (Sarmatian; Jung and Mayr, 1980). These data suggest that the extinction of channids in western Eurasia ca. 13 Ma was caused by decreasing humidity rather than decreasing temperature. The climatic requirements of channids lead me to suggest a decrease of the mean monthly precipitation during summer to below 50–100 mm and a mean summer temperature of ~20 °C for the Sarmatian of the western Paratethys. Stepwise global cooling between 15 and 10 Ma (Zachos et al., 2001) may be responsible for a southward shift of the boundary between the westerlies and trade winds in the Northern Hemisphere.

During the late Miocene and early Pliocene (8–4 Ma), snakeheads reached their present-day distribution (Fig. 2D), documented by their oldest African and East Asian occurrences. For both migrations—beginning ca. 17.5 and ca. 8 Ma—a causal relationship to the intensification of the Asian monsoon system can be suggested. The migration into Africa implies summer precipitation maxima in eastern North Africa and Arabia during the Messinian. This inference is supported by data of Griffin (2002), who showed that during the Zeit wet phase (7.5–4.6 Ma) the initiating Southwest Asian monsoon had two phases. One of them, the Southeast monsoon, transferred moisture from the Indian Ocean to Africa at the precessional cycle. The lack of snakeheads in East Asia during the early and middle Miocene and their first appearance there in the early Pliocene are consistent with other continental-scale evidence (An et al., 2001) that the Asian summer monsoon was not established before the late Miocene.

CONCLUSIONS

The extant distribution of snakehead fishes is limited by temperature and precipitation and is best characterized by high precipitation during a warm season. Snakeheads occur if the wettest month has a precipitation of >50–100 mm and a mean temperature of >20 °C, indicating a summer precipitation maximum in subtropical and temperate regions. I have shown that the paleobiogeography of snakeheads can be related to changes in the atmospheric circulation pattern, and that their past migrations and extinctions are associated with climate shifts.

The most remarkable changes in their distribution occurred in the late early to early middle Miocene (17.5–13 Ma) with the migration into western Eurasia, and in the latest Miocene to early Pliocene (8–4 Ma) with the migration into Africa and eastern Asia. Both events could be related to increasing summer precipitation in these areas. The older event is associated with the Miocene climatic optimum. It is hypothesized that owing to a northward shift of the ITCZ, western Eurasia came under the influence of the northern trade winds, bringing moisture from the central Paratethys and the North Sea Basin. The east-west–oriented orogens (Pyrenees, Alps) produced a strong zonality in summer precipitation (summer perhumid upwind, arid downwind). The younger event is associated with the intensification of the Asian monsoon circulation. The Southeast Asian monsoon of the Messinian Zeit wet phase brought moisture into previously arid Arabia and northeast Africa and enabled the migration of snakeheads from South Asia to Africa. The same can be shown for east Eurasia, where the East Asian monsoon triggered the snakehead migration from South Asia into China.

The present-day distribution of snakeheads can therefore be understood as the result of the late Neogene establishment of the Asian monsoon system.

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