NEOTROPICAL *MACROBRACHIUM* (CARIDEA: PALAEMONIDAE): ON THE BIOLOGY, ORIGIN, AND RADIATION OF FRESHWATER-INVADING SHRIMP

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ABSTRACT

Comprising >240 extant species, *Macrobrachium* Bate, 1868 is the most speciose caridean genus in Palaemonidae. It is generally considered as a monophyletic clade that lives exclusively in limnic and brackish habitats. Thus, it may provide a suitable model for the reconstruction of evolutionary transitions of euryhaline shrimp from ancestral state of living in the sea towards invasions of freshwater environments. Reviewing patterns of the biology (adaptative physiological and reproductive traits) and modern biogeographic distribution of this clade, I propose here a scenario for its tentative origin and evolutionary invasion of limnic inland waters, especially in the Americas. *Macrobrachium* shows: 1) a world-wide tropical to subtropical distribution, with only few species occurring in temperate regions and none in cold waters at high latitudes; 2) a clear preference for low salinity conditions (based on strong osmoregulatory capacities); 3) larval export strategies in coastal species (with diadromous migrations and invariably an extended larval development in estuaries); and 4) almost exclusively an abbreviated and lecithotrophic mode of larval development in hololimnetic inland species. The extant patterns of geographic distribution of this genus are strikingly disjunct, with completely separate groups of species occurring in the Indo-Pacific region (where maximum diversity occurs), in West Africa, and in the Americas. In a clade with common ancestry, this pattern can only be explained with a Tethyan origin and dispersal. Hence, I suggest an origin of ancestral *Macrobrachium* in the Mesozoic. As a consequence of the breakup of Gondwana and fragmentation of the Tethys Sea, mainly during the Late Cretaceous and Palaeogene, Neotropical and West African clades became isolated from the remaining congeners and thus can be considered as Tethyan relics. In the Neotropics, the closure of the Central American landbridge in the Late Pliocene was a significant vicariant event that caused diversification of coastal *Macrobrachium* in the Caribbean region, so that two separate groups of extant species live now in the Atlantic and Pacific drainage systems. The distribution of hololimnetic inland species can be explained by continental floodings occurring during the Miocene sea level highstand. Due to concomitant sub-Andean subsidence and impounded by the uplift of the Andes, the huge Pebas wetland system was formed at that time, covering the vast proto-Amazonas-Orinoco catchment area with sub-Andean lowlands reaching from Columbia to southern Bolivia. This allowed for incursions of marine-derived lineages of euryhaline shrimp and other coastal animals throughout northern and central South America, followed by adaptive radiations in freshwater. After the breaching of the continental divide (mainly the Purus Arch) in central Amazonia, probably in the Late Miocene, the modern eastward flow of the Amazon developed, draining to the Atlantic Ocean. Fluctuation but trending to a general decrease in global sea levels during the Pliocene and Pleistocene caused fragmentation of previously interconnected inland waters, promoting vicariant diversification of hololimnetic lineages. However, some hydrological connections between different catchment areas remained transitorily open, providing limited dispersal routes that also may have influenced speciation, e.g., through hybridisation. Thus, the modern distribution patterns of Neotropical *Macrobrachium* reflect interacting effects of tectonic events including Andean orogeny and the closure of the Panamaian landbridge, Miocene marine incursions, and possible cross-drainage dispersal through historical connections between river basins.

KEY WORDS: adaptation, biogeography, diadromy, evolutionary invasions, fresh water

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INTRODUCTION

Macrobrachium and Decapod Crustacean Diversity

De Grave et al. (2009), in a recent account of the currently known decapod crustacean diversity, estimated total numbers of almost 15 000 extant and 3000 fossil species. Outnumbered only by the brachyuran crabs (approximately 6800 species; Ng et al., 2008), the caridean shrimp have around 3300 species, the second highest diversity within the order Decapoda, followed by the infraorder Anomura (ca. 3100 species; Fransen and De Grave, 2009; De Grave and Fransen, 2011). Palaemonidae Rafinesque, 1815 constitutes the largest shrimp family, comprising almost 900 species,

i.e., more than 25% of the total number known for the infraorder Caridea.

It is a generally accepted view that Palaemonidae originated from an ancestral tropical marine clade, which has shown a conspicuous evolutionary tendency to adapt to non-marine conditions, successfully invading estuarine and limnic environments (Jalihal et al., 1993; Freire et al., 2003; Bauer, 2004; Augusto et al., 2009). As a consequence of adaptive radiations (Schluter, 2000; Glor, 2010), almost 300 extant palaemonid species (>30%) live in brackish or freshwater habitats (De Grave et al., 2008). Only Atyidae have radiated more successfully in fresh water, comprising 40 genera with about 400 species, >90% of these being limnic.

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Among the currently recognised 116 genera of Palae-monidae, *Macrobrachium* Bate, 1868, has most success-fully colonised estuarine and freshwater habitats, showing a world-wide distribution in tropical and subtropical re-gions. Comprising more than 240 species, it is also the most speciose genus among all Caridea (De Grave et al., 2009). Most of its species live in southern, southeastern, and eastern Asia, as well as in Australia (Jayachandran, 2001; Murphy and Austin, 2005; De Grave et al., 2008; Chen et al., 2009). Other clusters of *Macrobrachium* occur along the West African coast (Holthuis, 1951) and in the Ameri-cas (Holthuis, 1952; Pereira, 1997; Magalhães and Pereira, 2007). Remarkably, none of the New World species, which is the main focus of this review, is shared with other biogeo-graphic regions. Also, very few *Macrobrachium* spp. have been found on oceanic islands in the Pacific or Atlantic Ocean. In conclusion, the extant Neotropical species of *Mac-robrachium* are geographically isolated from all Palaeotrop-ical congeners, which raises the question how this disjunct pattern of distribution can be explained.

Macrobrachium in Aquaculture and Fisheries

Besides serving basic scientific disciplines including bio-geography and evolutionary biology, the genus *Macro-brachium* is relevant also for applied aquatic biology. Simi-lar to the penaeid shrimp, large species of *Macrobrachium*, commonly referred to as "giant freshwater prawns," have gained an enormous economic importance as a resource for commercial fisheries and aquaculture (Bauer, 2004; New, 2005; FAO, 2007; New et al., 2010). Their utilization for hu-man consumption is clearly dominated by a complex of two or more species from Southeast Asia, including *M. dacqueti* and *M. rosenbergii* (for recent discussion of their taxonomy, see De Bruyn et al., 2004a; Wowor and Ng, 2007; Iketani et al., 2011; following Wowor and Ng, 2008, the Interna-tional Commission on Zoological Nomenclature, 2010, and Ng and Wowor, 2011, the cultured species is here referred to as *M. rosenbergii*, although strictly this is a junior synonym of *M. dacqueti*). In addition, various congeners from other regions are also commercially exploited or have recently been considered as promising candidates for fisheries and artificial mass cultivation (Enin, 1998; Nwosu et al., 2007; Maciel and Valenti, 2009; New et al., 2010). The taxonomic references for all species names mentioned in this review are provided in Tables 1-4.

Macrobrachium as an Introduced Taxon

As a result of importing live *Macrobrachium* for aquaculture purposes, some species have escaped from rearing facilities and became "invasive" outside their native range of distri-bution. *Macrobrachium rosenbergii* has repeatedly been in-troduced in more than 40 countries world-wide (Iketani et al., 2011), for instance on Madagascar (Hanamura et al., 2008), in the USA (Woodley et al., 2002), and in Central and South America, where viable populations have estab-lished in recent decades (Magalhães et al., 2005; Loebmann et al., 2010; Silva-Oliveira et al., 2011). Further examples of artificial introductions are *M. lar* on Hawaii (Brock, 1960), *M. equidens* on the northern Brazilian coast (Maciel et al., 2011), and *M. nipponense* in the Caspian Sea (De Grave and Ghane, 2006; Gorgin and Sudagar, 2008). So far, there is no

Table 1. List of crustacean species mentioned in the text; neotropical species of *Macrobrachium* are listed in Tables 2-4.

Macrobrachium spp.:	Taxonomic reference
M. australe	(Guérin-Méneville, 1838)
M. chevalieri	(Roux, 1935)
M. dacqueti	(Sunier, 1925)
M. dux	(Lenz, 1910)
M. equidens	(Dana, 1852)
M. felicinum	Holthuis, 1949
M. feunteuni	Keith and Vigneux, 2002
M. foai	(Coutière, 1902)
M. grandimanus	(Randall, 1840)
M. intermedium	(Stimpson, 1860)
M. lanceifrons	(Dana, 1852)
M. lanchesteri	(De Man, 1911)
M. lar	(Fabricius, 1798)
M. lujae	(De Man, 1902)
M. macrobrachion	(Herklots, 1851)
M. niloticum	(Roux, 1831)
M. nipponense	(De Haan, 1852)
M. rosenbergii	(De Man, 1879)
M. sollaudii	(De Man, 1912)
M. thysi	Powell, 1980
M. vollenhovenii	(Herklots, 1857)
M. walvanensis	Almelkar, Jalihal and Sankoli, 1999
M. zariquieyi	Holthuis, 1949
Other taxa:	
Hippolyte sapphica	d'Udekem d'Acoz, 1993
Palaeopalaemon newberry	Whitfield, 1880
Paratya australienses	Kemp, 1917

evidence for serious consequences such as competitive re-placement of native species, as observed in various crayfish world-wide (see Gherardi et al., 2011). Nevertheless, a con-tinued spread of alien species to new environments enhances the likelihood of future detrimental effects including the in-troduction of viral and bacterial desease (New et al., 2010), and it therefore remains a permanent environmental concern (Williams et al., 2001; Iketani et al., 2011; Silva-Oliveira et al., 2011).

Since applied aspects including aquaculture, fisheries and invasions of *Macrobrachium* spp. have recently been re-viewed at length (New et al., 2010; Silva-Oliveira et al., 2011), these issues will not be further treated in this paper. Likewise, I am not attempting to review the biology of this genus on a global scale, as this would exceed the scope of a single article. In this review, I am rather concentrating on the biology, biogeography and ecology of Neotropical *Mac-robrachium* spp., focussing on their tentative evolutionary origin and historical patterns of radiation.

BIOLOGY OF *MACROBRACHIUM*: GENERAL PATTERNS

Physiological Adaptations to Estuarine and Freshwater Environments

Adult shrimp belonging to the genus *Macrobrachium*, in general, prefer limnic conditions (Freire et al., 2003; Bauer, 2004; Murphy and Austin, 2005; De Grave et al., 2008; Augusto et al., 2009; Charmantier and Anger, 2011). Al-though the estuarine species *M. intermedium* occurs also in seawater (Williamson, 1972; Gray, 1991), there is no

Table 2. Coastal Pacific species of Neotropical *Macrobrachium* with extended larval developments, diadromous reproductive migrations, and larval development in estuarine waters. Boldface: Species occurring also in rivers draining to the Atlantic (cf. Table 3). Geographic subregions are in boldface. PS = Pacific coast of South America; PC = Pacific coast of Central America (Panama to southern Mexico); PI = Pacific islands (Cocos Island or Galapagos); PN = Pacific coast of North America (northwestern Mexico). References: 1, Holthuis (1952); 2, Abele and Kim (1984); 3, Abele and Kim (1989); 4, Villalobos-Hiriart and Nates-Rodríguez (1990); 5, Rodríguez-Almaraz and Campos (1996); 6, Hernández et al. (2007); 7, Valencia and Campos (2007); 8, Rólier-Lara and Wehrtmann (2011); 9, Villalobos-Hiriart et al. (2010); 10, Vargas and Wehrtmann (2009).

Species	PS	PC	PN	PI	References
M. americanum Bate, 1868	×	×	×	×	1, 2, 3, 6, 7, 9, 10
M. cocoense Abele and Kim, 1984				×	2
M. crebrum Abele and Kim, 1989		×			3
M. digitum Abele and Kim, 1989		×			3
M. digueti (Bouvier, 1895)	×	×	×		1, 3, 6, 7, 8
M. gallus Holthuis, 1952	×				1
M. hancocki Holthuis, 1950	×	×		×	1, 2, 7, 10
M. hobbsi Villalobos-Hiriart and Nates-Rodríguez, 1990		×	×		4, 5, 6, 7, 9
M. inca Holthuis, 1950	×				1
M. michoacanum Villalobos-Hiriart and Nates-Rodríguez (1990)		×	×		4, 6, 9
M. occidentale Holthuis, 1950		×	×		1, 8, 9
***M. olfersi* (Wiegmann, 1836)**		×	×		1, 5, 6, 7
M. panamense Rathbun, 1912	×	×			1, 3, 7, 10
M. rathbunae Holthuis, 1950	×	×			1, 3, 7
M. tenellum (Smith, 1871)	×	×	×		1, 3, 6, 7, 8, 10
M. transandicum Holthuis, 1950	×				1, 7

Table 3. Coastal Atlantic species of Neotropical *Macrobrachium* with extended larval developments, diadromous reproductive migrations, and larval development in estuarine waters. Highlighted with bold letters: species occurring also in rivers draining to the Pacific (cf. Table 2). Geographic subregions: CS = Caribbean coast of South America; CC = Caribbean and Gulf of Mexico coasts of Central America; CI = Caribbean islands; GN = Gulf of Mexico coast of North America; AN = Atlantic coast of North America; AS = Atlantic coast of South America. References: 1, Holthuis (1952); 2, Ostrovski et al. (1996); 3, Rodríguez-Almaraz and Campos (1996); 4, Juarrero de Varona (1997); 5, Holthuis (1974); 6, Debrot (2003); 7, Bowles et al. (2000); 8, Valencia and Campos (2007); 9, García-Pérez and Villamizar (2009); 10, Magalhães and Pereira (2007); 11, Vargas and Wehrtmann (2009); 12, Rocha and Bueno (2004); 13, Abele and Kim (1989).

Species	CS	CC	CI	GN	AN	AS	References
M. acanthurus (Wiegmann, 1836)	×	×	×	×	×	×	1, 3, 8, 10, 11, 12, 13
M. amazonicum (Heller, 1862)	×					×	1, 8, 10
M. carcinus (Linnaeus, 1758)	×	×	×	×	×	×	1, 6, 8, 10, 11, 12, 13
M. crenulatum Holthuis, 1950	×	×	×				1, 6, 8, 12, 13
M. denticulatum Ostrovski et al., 1996						×	2
M. faustinum (de Saussure, 1857)	×		×	×	×		1, 4, 6, 7, 8
M. heterochirus (Wiegmann, 1836)	×	×	×	×	×	×	1, 6, 7, 8, 9, 12, 13
***M. hobbsi* Villalobos-Hiriart and Nates-Rodríguez, 1990**		×					3
M. lucifugum Holthuis, 1974			×				4, 5, 6, 7
M. ohione (Smith, 1874)				×	×		1, 7
***M. olfersi* (Wiegmann, 1836)**	×	×		×	×	×	1, 3, 7, 8, 10, 12, 13
M. praecox (Roux 1928)	×						8, 9
M. surinamicum Holthuis, 1948	×						1, 8, 10

truely marine representative among the currently recognized >240 extant species of *Macrobrachium* world-wide. Their capability to tolerate freshwater and oligohaline conditions is based on the capability of hyper-osmoregulation (Charmantier and Anger, 2011). This adaptive physiological function occurs in specialised cells, tissues and organs, which actively transport ions against concentration gradients from a hypo-osmotic external medium across cell membranes into the hypertonic haemolymph (for review of physiological mechanisms, see Péqueux, 1995; Lucu and Towle, 2003; Freire et al., 2008). Infering from the general occurrence of hyper-osmoregulation in euryhaline and freshwater-inhabiting shrimp (Augusto et al., 2009; Belli et al., 2009; Charmantier and Anger, 2011; Faria et al., 2011), I suggest

that the preference for low salinities is an ancient phylogenetic trait of *Macrobrachium*. Similarly, an early evolutionary transition to fresh water was proposed also for Atyidae (Ortmann, 1894; Fryer, 1977).

Environmental factors such as low salt concentrations exert selective pressure not only on the adults but on all life-history stages, including the embryos and larvae (Charmantier, 1998; Charmantier and Charmantier-Daures, 2001). In most freshwater-tolerant shrimp, however, adaptive osmoregulatory functions are still absent or weakly expressed during the larval stages, so that these are unable to survive and develop in limnic habitats where the conspecific adults can permanently live (Huong et al., 2004; Augusto et al., 2007; Rome et al., 2009; Charmantier and Anger, 2011). In

Table 4. Hololimnetic inland species of Neotropical *Macrobrachium* with (known or presumably) abbreviated larval developments in freshwater; only exception (in boldface): *M. amazonicum*, with extended larval development (see Table 3). Geographic subregions: CS = Caribbean region of northern South America (including drainage of the northeastern Andes to the Caribbean, Orinoco plain, northern Guayana drainage to the Atlantic); AM = Amazon plain; PP = Paraná-Paraguay plain; LP = La Plata region; SE = southeastern Brazil (Atlantic slope of the Serra do Mar); CC = Caribbean slope of Central America. References: 1, Holthuis (1952); 2, Holthuis (1977); 3, Magalhães and Pereira (2007); 4, Collins et al. (2011); 5, Hobbs and Hobbs (1995); 6, Mejía-Ortíz and López-Mejía (2011); 7, Valencia and Campos (2007); 8, Pereira, 1986; 9, García-Pérez and Villamizar (2009); 10, Magalhães (2002); 11, Mejía-Ortiz et al. (2008); 12, Mejía et al. (2003); 13, Villalobos and Álvarez (1999); 14, Román et al. (2000); 15, Hobbs (1994); 16, Rodríguez (1982); 17, Rocha and Bueno (2004).

Species	CS	AM	PP	LP	SE	CC	References
M. acherontium Holthuis, 1977						×	2
M. amazonicum (Heller, 1862)	×	×	×				1, 3, 4, 7, 16
M. aracamuni Rodríguez, 1982	×	×					3
M. atabapense Pereira, 1986	×						3
M. borellii (Nobili, 1896)			×	×			1, 4
M. brasiliense (Heller, 1862)	×	×	×				1, 3, 4, 7, 9, 10, 16
M. catonium Hobbs and Hobbs, 1995						×	5
M. cortezi Rodríguez, 1982	×						3, 7, 9
M. cosolapaense Mejía-Ortíz and López-Mejía, 2011						×	6
M. depressimanum Pereira, 1993			×				10
M. dierythrum Pereira, 1986	×						8
M. ferreirai Kensley and Walker, 1982	×	×	×				3, 4, 7
M. iheringi (Ortmann, 1898)			×		×		1, 4
M. inpa Kensley and Walker, 1982		×					3
M. jacatepecense Mejía-Ortíz and López-Mejía, 2011						×	6
M. jelskii (Miers, 1877)	×	×	×				1, 3, 4, 10, 16
M. mazatecum Mejía-Ortíz and López-Mejía, 2011						×	6
M. nattereri (Heller, 1862)	×	×	×				1, 3, 4, 7, 16
M. oaxacae Mejía-Ortíz and López-Mejía, 2011						×	6
M. pectinatum Pereira, 1986	×						3
M. potiuna (Müller, 1880)					×		1, 17
M. pumilum Pereira, 1986	×						8
M. quelchi (De Man, 1900)	×						1, 3
M. reyesi Pereira, 1986	×						7, 8, 9
M. rodriguezi Pereira, 1986	×						3, 8, 9
M. santanderensis Garcia-Pérez and Villamizar, 2009	×						9
M. sbordonii Mejia-Ortiz et al., 2008						×	11
M. totonacum Mejía et al., 2003						×	12
M. tuxtlaense Villalobos and Álvarez, 1999						×	13
M. vicconi Román et al., 2000						×	14
M. villalobosi Hobbs, 1973						×	15

such species, the evolutionary transition to freshwater habitats must therefore be considered as incomplete.

Figure 1 compares the ontogeny of osmoregulatory functions in two very closely related species belonging to the *M. amazonicum* complex (for discussion of its taxonomy, see specific section below; Tables 3 and 4). In hololimnetic shrimp from the Pantanal (central South America), it is not surprising that all life-history stages are capable of strong hyper-osmoregulation in fresh water. Estuarine relatives from the mouth of the Amazon River, by contrast, show this capability only in the first larval stage and, again, as late juveniles and adults.

The peculiar pattern of an early expression, subsequent loss, and later reappearance of hyper-osmoregulation (Fig. 1A) makes sense in species that show a larval "export strategy" (Strathmann, 1982; Strathmann et al., 2002). This life-history pattern is considered as a common plesiomorphic trait of freshwater-invading coastal and estuarine clades (see Miller and Labandeira, 2002). It is typically associated with larval hatching in fresh water and a subse-

quent rapid passive downstream transport of the earliest larval stages towards the sea (thus, requiring an expression of hyper-osmoregulation at hatching; Anger et al., 2008; Charmantier and Anger, 2011). In some species, the ovigerous females show active diadromous migrations (frequently also referred to as "amphidromous" [for terminology and definitions of migratory patterns, see Myers, 1949; McDowall, 2007]). In both cases, larval development occurs in estuarine waters, avoiding hypo-osmotic stress.

The capability of hypo-osmoregulation in seawater (Fig. 1A) allows in estuarine species for larval transport also in coastal marine waters and subsequent colonization of estuaries and rivers other than those of origin. The salt-dependent early phase of the life cycle is followed by active upstream migrations of the freshwater-tolerant postlarval stages, and eventually, recruitment to the limnic adult populations.

In species of *Macrobrachium* that follow an export strategy, the larval dependence on brackish conditions indicates an incomplete evolutionary adaptation to fresh water, reflect-
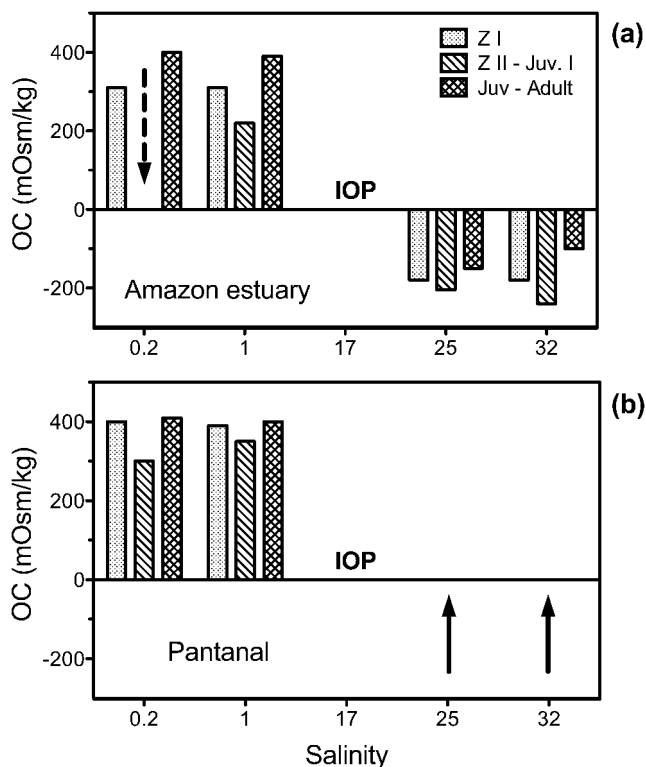
Fig. 1. Ontogeny of the osmoregulatory capacity (OC = difference between osmolalities of the extenal medium and haemolymph; IOP = isosmotic point) in successive life-history stages of two shrimp populations belonging to the *M. amazonicum*-species complex (after Charmantier and Anger, 2011). A, diadromous population from the Amazon estuary; B, hololimnetic inland population from the Pantanal, central South America; experimental short-term exposure (ca 15 hours) to fresh water and various salinities (data partially pooled for different stages and treatments. For more detailed information including statistical analysis, see Charmantier and Anger, 2011); developmental phases: Z I, newly hatched larvae, zoea I; Z II-Juv. I, later larval stages (zoea II-IX) and first-stage juveniles; Juv.-Adult, later juveniles and adults; note: expression of hyper-osmoregulation in newly hatched larvae and, again, in late juveniles and adults during exposure to freshwater, but lack of this physiological function in intermediate zoeal stages (II+) and early juveniles in the Amazon population (dashed arrow line, graph A); lack of hypo-osmoregulation during exposure to seawater in all life-history stages of the Pantanal population (solid arrow lines, graph B).

ing the evolutionary origin of this clade from coastal marine ancestors. In hololimnetic (non-exporting) species, by contrast, the larvae have evolved the capability to grow and develop in fresh water (see e.g. Odinetz Collart and Magalhães, 1994). As a trade-off, however, such species may lose the physiological function of hypo-osmoregulation (Fig. 1B), and thus, the capability to survive and develop in seawater. Similar shifts in the patterns of salinity tolerance have been observed also in freshwater-invading fish and molluscs, indicating an advanced level of adaptation to limnic conditions (Lee and Bell, 1999). The loss of hypo-osmoregulation fits in a rule of adaptive evolution, which suggests that losses and modifications of pre-existing molecular functions represent the most common adaptive changes (Behe, 2010).

Reproductive Adaptations to Limnic Environments

When reproductive and developmental traits such as the size and number of eggs, amounts of yolk stored per egg,

larval size at hatching, and early larval feeding behaviour are compared within a group of closely related aquatic decapods, some conspicuous modifications have commonly been observed in species that have successfully adapted to fresh water. As noted already, one century ago by Sollaud (1914, 1923), many freshwater-inhabiting *Macrobrachium* and other palaemonid shrimp produce, compared to marine relatives, much larger eggs with higher quantities of yolk. Females of similar body size show therefore a clearly lower fecundity, and newly hatched larvae are larger and contain more yolk. Also, the larvae show commonly benthic behaviour, are non-feeding (lecithotrophic), and the entire larval phase is strongly reduced both in terms of the duration of development and the number of stages passed from hatching to metamorphosis (Rabalais and Gore, 1985; Anger, 2001). This abbreviation of the larval phase is associated with heterochrony, viz., a marked predisplacement of the development of the antennae and of locomotory appendages, including an early expression of pereiopods as functional walking legs and of pleopods as swimming appendages (Fig. 2; cf. larval stages I-III of *M. iheringi*, with an abbreviated mode, and a species belonging to the *M. amazonicum* complex, with an extended developmental pattern; for taxonomic citations, see Table 4).

Such patterns of abbreviated larval development have frequently been found not only in *Macrobrachium* from various biogeographic regions (Alekhnovich and Kulesh, 2001; Murphy and Austin, 2005; Wowor et al., 2009), but also in other carideans as well as in anomuran and brachyuran crabs (Dobkin, 1969; Rabalais and Gore, 1985; Anger et al., 2007). This suggests a widespread convergent evolution of abbreviated modes of development among Decapoda, but also in other aquatic invertebrates (Lee and Bell, 1999). Supposedly, these traits have an adaptive value in limnic (especially lotic), terrestrial, and subpolar environments, where unpredictable or generally poor plankton productivity selects for a reduction of early larval dependence on suspended particulate food sources (Rabalais and Gore, 1985; Anger, 1995, 2001; Thatje et al., 2005). This is consistent with the fact that all fully limnic decapods including the true freshwater crabs (Pseudothelphusoidea, Potamoidea, Gecarcinucoidea), crayfish (Astacidea), and aeglids (Anomura) show a direct mode of development within the egg membrane (Bond-Buckup et al., 2008; Crandall and Buhay, 2008; Yeo et al., 2008; Cumberlidge and Ng, 2009). All these taxa have completely eliminated the free-living larval phase, which is generally considered as a plesiomorphic trait (Nielsen, 1998, 2009; McEdward, 2000; Strathmann, 2000). An opposite evolutionary course, i.e., an abbreviated larval development representing the ancestral state and extended patterns being derived, was proposed by Pereira and García (1995). However, this hypothesis requires a multiple convergent evolution of extendend larval development including the formation of morphologically and functionally similar, complex feeding and swimming appendages. By comparison, a secondary loss or a heterochronic shift (predisplacement) of larval characters into the embryonic phase seems to be a more parsimonious explanation.

The production of large eggs and an abbreviation of the planktonic larval phase, which are frequently associated
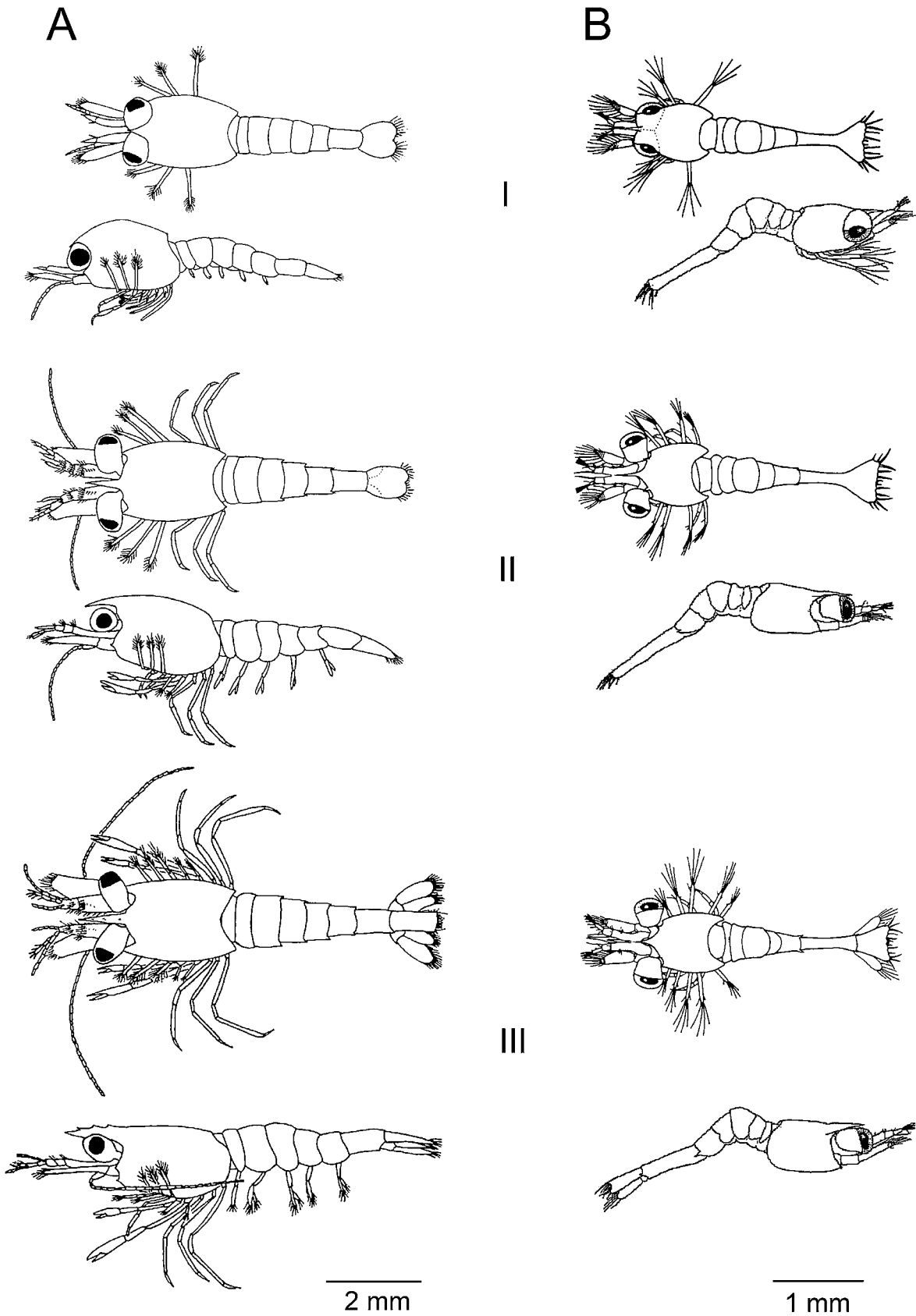
Fig. 2.   A, abbreviated, non-feeding larval development through three larval stages in a hololimnetic inland species, *M. iheringi* (after Bueno and Rodrigues, 1995); B, first three larval stages (I-III) of the extended, planktotrophic larval development of *M. amazonicum* (after Magalhães, 1985); note morphologically advanced development of equivalent stages in A.

with limnic invasions, were suggested to result from a gradual evolutionary change termed "freshwaterization" (Jalihal et al., 1993). This hypothesis was supported by studies of local variations in egg size and larval characteristics of a Japanese species of *Macrobrachium*, *M. nippoense*, where significantly larger eggs are produced by limnic as compared to estuarine populations (Mashiko, 1999; and earlier papers cited therein). A similar trend was observed also in the intraspecific variation of egg size in a Neotropical species complex, *M. amazonicum* (Odinetz Collart and Rabelo, 1996), and in an atyid shrimp from Australia, *Paratya australienses* (Walsh, 1993). However, these two species also represent striking exceptions from the patterns of "freshwaterization" because both show extended modes of larval development in fresh water (Guest, 1979; Magalhães, 1985; Walsh, 1993). Among the Palaeotropical *Macrobrachium* spp., extended modes of larval development in fully limnic inland waters have been observed in *M. lanceifrons* from the Philippines (Rasalan et al., 1969), in *M. niloticum* from Lake Chad in the northwestern centre of Africa (Williamson, 1972), in *M. walvanensis* from northwestern India (Almelkar et al., 2000), and probably (infering from the morphology of the first zoeal stage) in *M. lanchesteri* from Singapore (Chong and Khoo, 1988).

Such cases of extended development in fully limnic species have generally been interpreted as indications of recent evolutionary transitions from coastal marine to freshwater habitats. This hypothesis implies that slightly older transitions should then be associated with partially abbreviated modes, and only very old limnic clades should show strongly abbreviated development. Inconsistent with these expectations of the "freshwaterization" hypothesis, palaemonid and atyids very rarely show transitional patterns in the number of larval stages. In both families, most species pass either through an abbreviated mode with ⩽3 stages (Benzie and De Silva, 1983; Magalhães and Medeiros, 1998; Magalhães, 2000a; Shy et al., 2001), or through an extended pattern with mostly ⩾8 stages (Hunte, 1980; Benzie, 1982; Willführ-Nast et al., 1993).

This dichotomy suggests that radical changes in the mode of development might be caused by a few effective mutations (for review and examples of fast evolutionary changes in ontogeny, see Damuth, 2001; Abouheif and Wray, 2002) rather than through numerous small genetic changes occurring over extended evolutionary time scales. This patterns resembles a case of extreme intraspecific variability in the relative length and morphology of the rostrum of a hippolytid shrimp, *Hippolyte sapphica*, which occurs in adult individuals with two clearly distinct forms but no intermediates. This dichotomous trait is expressed during juvenile growth, apparently being controlled by a single gene in a Mendelian way (Ntakis et al., 2010).

Dramatic evolutionary changes in developmental patterns do not necessarily concur with conspicuous changes in adult morphology. This may be exemplified with a comparison of sympatric Neotropical species assigned to *M. amazonicum* and *M. jelski*, respectively (Table 4). While the former pass through an extended development with ⩾8 larval stages (Magalhães, 1985), the latter shows consistently an abbreviated mode with only 3 stages (Magalhães, 2000a). Interme-

diate patterns or signs of successful interspecific mating have never been observed. According to the Biological Species Concept (Mayr, 2000), there is thus no doubt that these are two reproductively separate, hence valid species. Nevertheless, the adults are morphologically so similar to each other that their identification is difficult, and numerous erroneous and doubtful records of distribution occur in the scientific literature (for examples and references, see Holthuis, 1952).

In conclusion, there may be no simple or close relationship between limnic invasions and an evolution of abbreviated modes of larval development, and the transition from an extended to an abbreviated mode might evolve abruptly and not as gradually as suggested by the "freshwaterization" hypothesis. Future comparative studies of differential gene expression coding for abbreviated or extended delopments, respectively, may be a promising tool for deepening our understanding of life-history evolution in the context of limnic invasions by *Macrobrachium* spp. and other decapod crustaceans.

Implications of Physiological and Reproductive Traits for Connectivity Among Populations

The presumably ancient evolutionary tendency of palaemonids to invade estuarine and freshwater environments has implications for their dispersal potential, the genetic structure of populations, and geographic range (Cook et al., 2009; Liu et al., 2011). A long-distance oceanic transport between continents may take from several months to about one year. This has been observed in some marine molluscs and spiny lobsters (Scheltema, 1979, 1989; Polovina et al., 1999; Feng et al., 2011) but never in euryhaline palaemonids. Even in estuarine species with an export strategy, the planktonic phase takes a few to several weeks at most, so that larval offshore or alongshore transport is restricted to estuarine and adjacent coastal waters (Provenzano et al., 1978; Bauer and Delahoussaye, 2008). In freshwater-adapted clades with physiological adaptations to low osmotic pressures (including the possible loss of the capability of hypo-osmoregulation in seawater), extended periods of larval dispersal with coastal currents are very unlikely or impossible, especially when these physiological adaptations occur together with an abbreviated mode of larval development. In conclusion, life-history traits that are typical of successful limnic invaders must have enhanced the decisive role of sea floor spreading as a vicariant event, favouring reliction and allopatric speciation in Palaeo- and Neotropical *Macrobrachium*.

ORIGIN AND RADIATION OF *MACROBRACHIUM*

The world-wide range of extant *Macrobrachium* shows three distinct centres of occurrence, with different groups of species in the Indo-West-Pacific, West Africa, and the Americas (Fig. 3). As all >240 species of *Macrobrachium* are restricted to freshwater and estuarine habitats, this clearly disjunct pattern of geographic distribution has raised the question whether *Macrobrachium* really can be a monophyletic clade (Holthuis and Ng, 2010). However, various morphological and molecular phylogenetic studies (Pereira, 1997; Liu et al., 2007; Fransen and De Grave, 2009; Pileggi and Mantelatto, 2010) have consistently concluded that *Macrobrachium* is indeed monophyletic, or perhaps paraphyletic
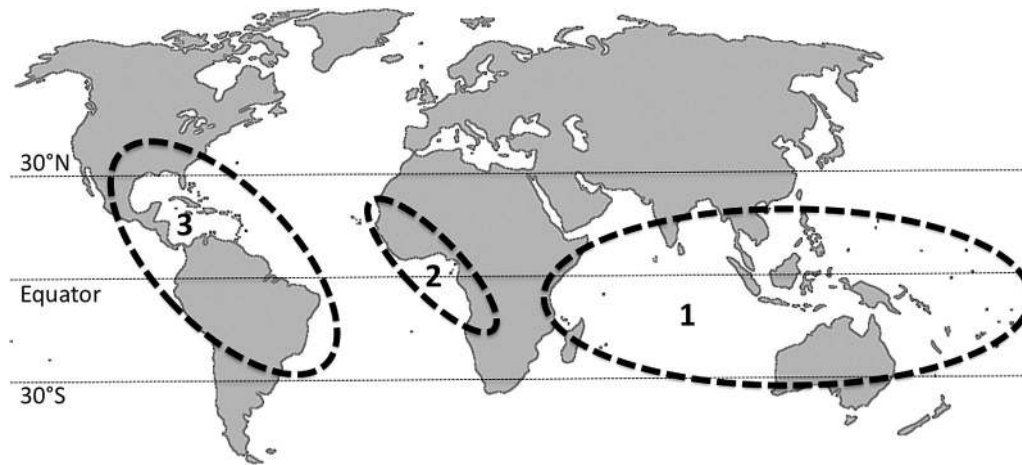
Fig. 3.   Biogeographic distribution of *Macrobrachium* spp. (oval areas as a rough sketch) in tropical regions. 1, the Indo-West-Pacific; 2, along the West African coast; and 3, in the Americas. The three disjunct centres of distribution show no overlap of species; world map from Wikimedia Commons.

(some species currently assigned to other genera may additionally be accomodated within *Macrobrachium*). Regardless whether monophyly or paraphyly is assumed, all Palaeo- and Neotropical *Macrobrachium* originate from the same ancestor. Consequently, radiation must have begun in a single region of origin, and the age of this clade must be older than the modern biogeographic barriers separating different groups of species. For instance, *Macrobrachium* must thus be older than the Atlantic Ocean. This raises questions as to the hypothetical ancestor, when and where the spectacular world-wide radiation of this clade began, and how the disjunct patterns of distribution of extant *Macrobrachium* spp. can be explained.

Criteria for a Biogeographic Reconstruction

Choosing an empirical biogeographic approach (Rull, 2011), but attempting to avoid a merely intuitive or "narrative" biogeography (for critical review of methods, see Posadas et al., 2006; Crisp et al., 2011), I attempt to develop here testable hypotheses on the origin, radiation, and life-history evolution of *Macrobrachium*. These hypotheses can be scrutinized with new evidence from phylogenetic analyses of both morphological and molecular data (consult Lohman et al., 2011; Matzen Da Silva et al., 2011; Page and Hughes, 2011; Robe et al., 2012), the use of more reliable molecular clocks (for basic assumptions and limitations of this method, see Lessios, 2008; Li and Makova, 2008), and an improved fossil record (Glaessner, 1969; Fransen and De Grave, 2009; Schram, 2009).

Examples for all these approaches can be found in the literature. In Palaeotropical *Macrobrachium*, molecular genetic studies have recently contributed to the understanding of regional phylogeographic relationships (Murphy and Austin, 2003; De Bruyn et al., 2004a, b; De Bruyn and Mather, 2007; Liu et al., 2007; Parhi et al., 2008) and of the evolution of life-history patterns (Murphy and Austin, 2005; Wowor et al., 2009). For Neotropical congeners, some comparative morphological (Holthuis, 1993; Pereira, 1997) and molecular phylogenetic studies have been published as well (Pereira et al., 2002; Pileggi and Mantelatto, 2010; Vergamini et al., 2011). Overall, however, the cur-

rently available data are still limited (especially phylogenetic analyses including both Neo- and Palaeotropical *Macrobrachium*), do not yet provide reliable estimates of diversification rates, and have produced inconsistent results. Progress in the development of molecular genetic techniques, the use of additional gene markers, and a rapidly growing molecular data base may soon improve our understanding of the phylogeny and diversification of *Macrobrachium*, and this may subsequently allow for further testing of the hypotheses proposed in this paper.

Palaeontological evidence provides another powerful tool for the evaluation of biogeographic scenarios (Crisp et al., 2011). However, the fossil record for Caridea is meager compared to that available for other Decapoda. This is due at least in part to the relatively thin shrimp cuticle and therefore mostly poor preservation of caridean fossils (Glaessner, 1969; Fransen and De Grave, 2009; Schram, 2009). As a consequence, the hypotheses on the origin and radiation of *Macrobrachium* proposed in this review are principally based on the analysis of modern patterns of distribution in relation to paleogeographic, palaeoecological, physiological, and life-history patterns.

Another problem in studies of biodiversity and phylogeny is associated with an inconsistent and often unclear use of the species concept (Mayden, 1997; Wheeler and Meier, 2000; Ghiselin, 2010). Most authors claim to follow the Biological Species Concept (BSC), which considers species as interbreeding or potentially interbreeding units (Mayr, 2000). However, most species descriptions are actually based on a merely phenetic and morphology-based concept. The BSC is hardly practicable in studies of speciose groups of aquatic invertebrates such as the carideans, and it cannot be applied to the fossil record or to organisms with asexual reproduction including numerous microorganisms and plants. Also, there is the problem of hybridisation occurring between closely related but otherwise "good" species of shrimp (Parhi et al., 2008). Hybridisation is common also in many other groups of animals and plants, especially when populations invade new environments. In this ecological situation, which must have occurred very often in the evolution of *Macrobrachium*, it may be an impor-

tant mechanism enhancing the responsiveness to divergent selection, and thus, accelerate adaptive diversification (Seehausen, 2004). Among the numerous other species concepts competing with the BSC, the varieties of the phylogenetic concept (Mishler and Theriot, 2000; Wheeler and Platnick, 2000) are based on a statistical approach that may be suitable for the analysis of extensive molecular and morphological data sets, but maybe not for that of complex biological information from reproduction, development, physiology, life style, behaviour, etc., which cannot easily be expressed and analysed in numerical terms. I am not discussing this problem further in the present review, but we should remain aware of it when we consider different views of species diversity and phylogeny occurring in the literature.

Timing of the Appearance of *Macrobrachium*

The earliest known decapod currently recognized is *Palaeopalaemon newberry*, a fossil lobster from the upper Devonian (Schram et al., 1978; Schram and Dixon, 2004; Karasawa et al., 2013). This corresponds with estimates of molecular divergence rates suggesting a Palaeozoic origin of Decapoda (Porter et al., 2005). The plesiomorphic Dendrobranchiata date back at least to the Triassic, and the Caridea have probably appeared in the Jurassic, although the fossil record does not provide conclusive evidence (for references and recent discussion, see Fransen and De Grave, 2009; Schram, 2009).

The currently available fossil record for *Macrobrachium* does not provide much information on the time and geographic region of its origin, or on later pathways of spread and radiation. Based mainly on a fossil fragment from Panama that was considered as being close to *Macrobrachium* (Rathbun, 1918), a Late Oligocene or Early Miocene, i.e., about 20-25 Ma, origin of this genus was proposed (Short, 2000; unpublished thesis cited in Murphy and Austin, 2005). However, if we assume that adaptations to brackish and freshwater conditions were already evolved in the ancestral stock, then the disjunct distribution of extant *Macrobrachium* spp. on both sides of the Atlantic Ocean renders this estimate unrealistic. The Atlantic began to open already during the Mesozoic, and the last land connection between West Africa and northeastern South America was dissected in the Cretaceous, about 112 Ma (Torsvik et al., 2009; for terminology and units of geological time scales, see Aubry et al., 2009). The new Atlantic sea floor widened throughout the Late Cretaceous and the Palaeogene, reaching in the Late Oligocene or Early Miocene nearly its present dimensions. This implies that connectivity between West African and South American populations of *Macrobrachium* through planktonic larval transport must have weakened already during the Late Mesozoic. Gene flow should have been completely interrupted before the Cretaceous-Cenozoic boundary (65 Ma), when the Atlantic Ocean became an effective vicariant barrier between freshwater-adapted clades of Palaeo- and Neotropical *Macrobrachium*.

Indications for a Tethyan Origin

Our estimate of a Mesozoic origin of *Macrobrachium* is consistent with the fact that the earliest reliably dated caridean shrimp fossils were found in Cretaceous strata.

Interestingly, these fossils were assigned to the families Palaemonidae and Atyidae, i.e., to those two shrimp families that are known as the most successful invaders of brackish and freshwater environments world-wide (for the Neotropic, see e.g. Beurlen, 1950; for recent review, see Schram, 2009). This supports the assumption that physiological and life-history adaptations to habitats with low salinities appeared early in the evolutionary history of the Caridea and, among them, especially in ancestral *Macrobrachium*.

In order to identify a tentative region of origin where the radiation of this clade begun, we should consider also the patterns of climatic distribution in a geohistorical context. Extant species of *Macrobrachium* show a world-wide distribution in the tropical belt, with a strongly decreasing diversity in subtropical regions, only few species in temperate zones, and none in cold waters at high latitudes (see e.g. Holthuis, 1993; Pereira, 1997; Bauer, 2004; Murphy and Austin, 2005; Wowor et al., 2009). This suggests that we are dealing with an originally tropical clade that has only secondarily spread into adjacent regions with slightly cooler climates.

The "Centre of Origin Hypothesis" assumes that there is a correlation between extant diversity and the time available for diversification (for general discussion and examples, see Briggs, 2000; Wiens and Donoghue, 2004; Wiens, 2011; Wiens et al., 2011). Based on this biogeographic rule (which probably has exceptions in some groups, see Anker and Baeza, 2012), we may localise a tentative geographic center of origin within the tropical belt: A clear maximum of extant species diversity occurs in the Indo-West Pacific. This suggests that *Macrobrachium* originated from the eastern Palaeotropical region, which roughly covers the area once occupied by an ancient tropical ocean, the Tethys Sea (Fig. 4).

The formation of the Tethys began in the Triassic when the supercontinent Pangea began to split into Laurasia and Gondwana. While drifting apart, these new continents gradually opened a growing space in between, where the Tethys could expand throughout the Mesozoic (for details, see Bortolotti and Principi, 2005). The breakup of Pangea was largely completed in the Early Cretaceous. The Tethys formed at that time a marine waterway that comprised the Indo-West-Pacific, the Mediterranean, the North Atlantic, and the Caribbean and the eastern Pacific coasts of the Americas. The Central American landbridge was absent, while North America remained partially connected to Europe. From the Jurassic until the Late Oligocene, i.e., throughout the Cretaceous and Palaeogene, the Tethys Sea remained an important dispersal pathway for tropical decapod crustaceans (Feldmann and Schweitzer, 2006). The hydrological connections around the southern tips of Africa and South America, by contrast, were most probably too cold for the dispersal of tropical forms, at least since the formation of the Circumpolar Current subsequent the opening of the Tasman Sea and the Drake Passage in the Oligocene (Ortiz-Jaureguizar and Cladera, 2006).

Shallow coastal and estuarine waters fringing the Tethys Sea must have provided optimal living conditions for palaemonid shrimp and other marine shelf fauna, allowing also for spread and radiation of various other crustacean groups
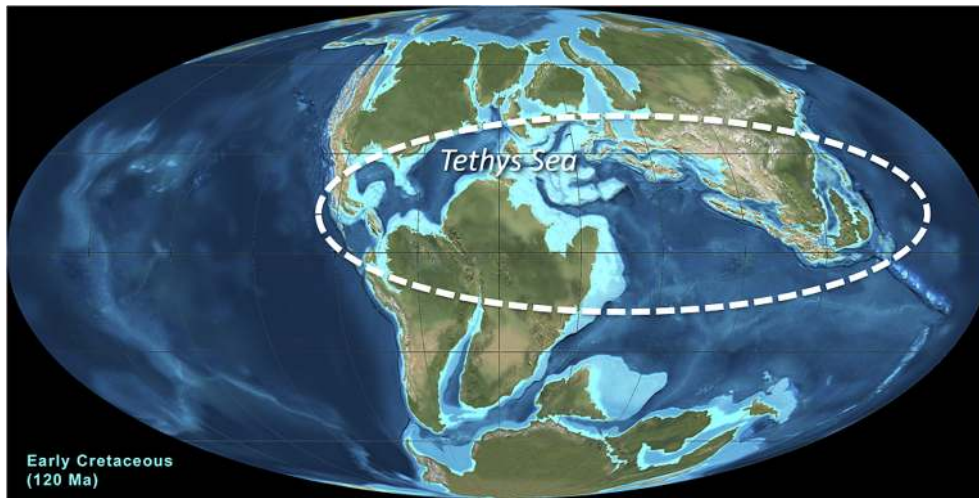
Fig. 4.   Palaeogeographic map showing the Gondwana breakup and the extension of the Tethys Sea in the Early Cretaceous (Mollweide projection; © Ron Blakey and Colorado Plateau Geosystems Inc., USA). Hypothetical range of ancestral *Macrobrachium* in the Tethys Sea, with in principle panmictic populations ranging from the Indo-West-Pacific through the Mediterranean, North Atlantica and Caribbean, to the Pacific coasts of the Americas. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

such as cirripedes (for references, see Newman, 1991), spiny lobsters (George, 2006), and freshwater crabs (Yeo et al., 2008). After the appearance of angiosperms in the Cretaceous, transitional zones between aquatic and terrestrial, as well as those between marine, brackish and freshwater habitats, were increasingly inhabited by newly evolving mangroves (Saenger, 1998; Ellison et al., 1999). These coastal plants probably played a significant role in the evolution of amphibious and estuarine biota world-wide (Schweitzer et al., 2003; Greb et al., 2006). In extant coastal communities of tropical regions, brackish mangrove swamps represent significant nursery habitats for shallow-water fish and aquatic crustaceans including palaemonids (Duke et al., 2007; Meynecke et al., 2007; Vargas and Wehrtmann, 2009). Their fossil record in inland regions such as upper Amazonia has been used as a palaeoecological indicator of estuarine conditions caused by marine transgressions (Hoorn, 2006). In summary, I conclude that the Tethys Sea was, especially during the Cretaceous period, crucial for the evolutionary appearance and initial dispersal of *Macrobrachium* in tropical zones world-wide.

Tethyan Fragmentation and Vicariance

Since the Middle Cretaceous, the gradual separation of North America from Europe and the beginning breakup of Gondwana caused an increasing fragmentation of the Tethys Sea (Torsvik et al., 2009). This geological process favoured parapatric speciation in populations that became increasingly isolated by growing distances, reduced genetic connectivity, and adaptations to different regional environments (for review of speciation mechanisms in the presence of potential gene flow, see Ritchie, 2001; Pinho and Hey, 2010). Eventually, diversification occurred even in fully marine clades with extended periods of planktonic development and long-distance transport of pelagic larvae by ocean currents, for instance in spiny lobsters (Newman, 1991; George, 2005, 2006). In estuarine and freshwater-adapted forms such as *Macrobrachium*, isolation must have occurred earlier than in

marine groups. The opening of the South Atlantic Ocean became thus a significant vicariant event that caused reproductive isolation between Palaeotropical (African and Asian) and Neotropical (American) clades. This was followed by independent regional radiations, producing high endemic diversity in the Central American region (Feldmann and Schweitzer, 2006). In conclusion, I suggest that all Neotropical representatives of *Macrobrachium* became Tethyan relicts during the Late Cretaceous (Fig. 5).

Reliction occurred eventually also in the West African species of *Macrobrachium*. Due to the formation of the South Atlantic during the Late Cretaceous and throughout the Palaeogene (Torsvik et al., 2009), they first became isolated from the western Tethyan congeners in the Americas. Later, they were also separated from their eastern Tethyan, i.e., Asian and East African, relatives (Fig. 6). This vicariant event was associated with the northward drift of the African continent and its subsequent collision with the Eurasian plate in the Turkish-Arabian region (building of the Zagros mountain range in Iraq). In the Oligocene, the Tethys in that region became narrow and shallow, until the separation of the eastern Mediterranean Sea from the Indian Ocean became complete in the Early to Mid-Miocene (19-12 Ma). This closure of the Tethys seaway subsequently also caused a blockage of the global equatorial current that had previously connected distant eastern and western regions in the tropics (Von Der Heydt and Dijkstra, 2008; García-Castellanos et al., 2009; Potter and Szatmari, 2009). It is possible that *Macrobrachium* living in the Mediterranean and along the West African coast remained connected throughout the Miocene.

Due to a later orogenetic process, this time in the region of the Strait of Gibraltar, the Mediterranean Sea became in the Messinian (Late Miocene, ca. 6 Ma) also completely separated from the Atlantic Ocean. As a consequence of this isolation, it became hypersaline and eventually dried out, so that the aquatic fauna and flora of the Mediterranean must have become largely extinct, including previously
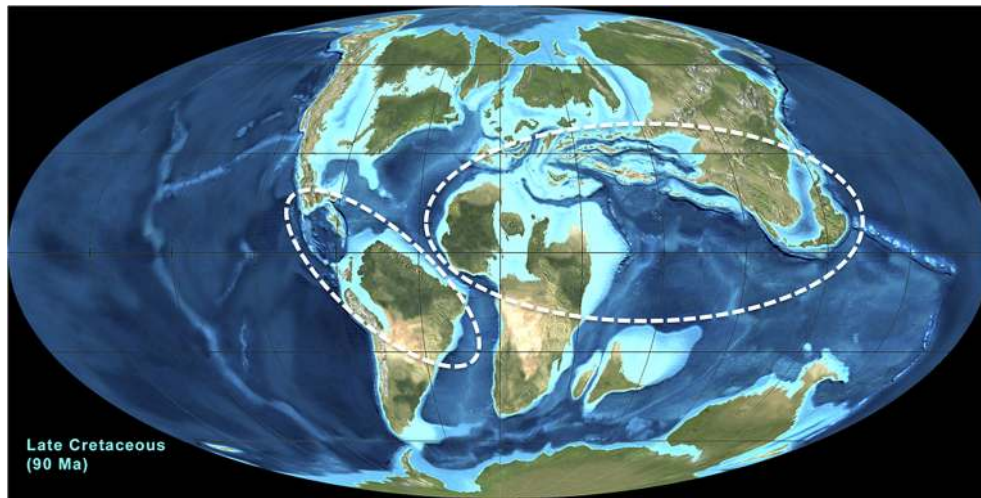
Fig. 5. Palaeogeographic map showing the advanced opening of the South Atlantic and the fragmentation of the Tethys Sea in the Late Cretaceous (Mollweide projection; © Ron Blakey and Colorado Plateau Geosystems Inc., USA). Freshwater-adapted Palaeo- and Neotropical *Macrobrachium* genetically separated, the latter becoming thus a Tethyan relict group. Note extensive world-wide continental floodings at high sea level. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

existing populations of estuarine *Macrobrachium*. When the Gibraltar land barrier breached about 700 ka later, a catastrophic flood event re-filled the Mediterranean with oceanic water from the Atlantic (García-Castellanos et al., 2009).

After the Messinian Salinity Crisis, a recolonisation of the Mediterreanean would theoretically have been possible through an immigration of coastal species of *Macrobrachium* from West Africa, but this process was probably prevented by arid climatic conditions in northwestern and northern Africa, which implies a lack of large river systems allowing for the formation of estuarine and brackish coastal lagoon habitats. High salinities in the Mediterranean may have been another unfavourable precondition for a recolonization by *Macrobrachium* spp.

In conclusion, the West African species of *Macrobrachium* became in the Miocene isolated from the remaining congeners, remaining the last Tethyan relicts of this genus in the westernmost part of the Palaeotropical region. This group, which comprises only 11 currently known species (*M. chevalieri*, *M. dux*, *M. felicinum*, *M. foai*, *M. lujae*, *M. macrobrachion*, *M. raridens*, *M. sollaudii*, *M. thysi*, *M. vollenhovenii*, and *M. zariquieyi*; taxonomic citations in Table 1), lives within a limited geographic range between Senegal and Angola, mostly in the estuarine reaches of the major West African rivers Senegal, Volta, Niger, and Congo. Additionally, there is most probably a complex of hololimnetic inland species that is currently assigned to a single species (*M. niloticum*). It has been reported from the upper Nile River, from the endorheic Lake Chad in

Fig. 6. Palaeogeographic map showing the complete opening of the South Atlantic and the closure of the eastern Mediterranean due to mountain building in the Early Miocene (Mollweide projection; © Ron Blakey and Colorado Plateau Geosystems Inc., USA). West African (and possibly remaining Mediterranean) *Macrobrachium* genetically separated from populations in the Indo-West-Pacific, becoming another Tethyan relict group; Mediterranean populations extinct during the Messinian Salinity Crisis (Late Miocene). This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

northwestern Central Africa, and from the alkaline Lake Turkana in the Rift Valley of East Africa (Williamson, 1972). Their origin and phylogenetic relationships with East or West African congeners remain unexplored.

Obviously, the West African *Macrobrachium* have not radiated as successfully as the eastern Palaeotropical (Indo-Pacific) and the Neotropical congeners (Holthuis, 1951, 1980; Kensley, 1981; Jayachandran, 2001; Kutty and Valenti, 2010). Their limited range is probably due to the unfavourable arid conditions prevailing along the northern, northwestern and southwestern coasts of the African continent, which are dominated by the Sahara and Namib deserts, respectively. The Neotropical congeners, by contrast, continued to thrive and spread in a moist monsoon climate that remained comparable to the ancestral conditions in the Mesozoic Tethys Ocean (Ohba and Ueda, 2010).

Among the West African *Macrobrachium*, only *M. thysi* is known to produce large eggs, passing most probably through an abbreviated mode of larval development (Powell, 1980). The same pattern may be presumed to occur also in *M. foai*, which lives far inland in the upper Congo basin. All remaining species produce small eggs and follow, as far as this is known, a larval export strategy, which implies a greater dispersal potential and favours a wider geographic range. However, except for *M. chevalieri* and *M. vollenhovenii*, whose presence has been recorded on the Cape Verde Islands (about 570 kilometres off the coast of Western Africa; for references, see Holthuis, 1951, 1980), there is no indication that members of this genus have ever colonised oceanic Atlantic islands such as the Macaronesian Archipelago (Azores, Madeira, Savage, Canary, and Cape Verde Islands). An alleged previous record of *M. vollenhovenii* on St. Helena Island by Bate is highly doubtful and most probably due to an erroneous citation in the early literature (for discussion, see Holthuis, 1951).

Remarkably, there is a complete lack of distributional overlap in the species of *Macrobrachium* between West Africa (Atlantic) and East Africa (Indian Ocean). This is surprising insofar, as the coastal faunas of the Indian Ocean and the Atlantic are hydrologically connected already since the opening of the South Atlantic in the Mesozoic. Hence, gene flow must have been blocked by some vicariant biogeographic barrier other than a landbridge. Most probably, the dispersal of tropical species around the southern tip of Africa has been prevented by low water temperatures prevailing south of the Angola-Benguela Front, especially in the Cape region and along the coast of Namibia. Upwelling conditions associated with the cold northward flowing Benguela Current have been recognised as one of the major biogeographic boundaries also for other tropical taxa (Lessios et al., 2003).

In conclusion, the connections between eastern and western Tethyan *Macrobrachium* were gradually reduced and eventually terminated when larval exchange and gene flow over the expanding Atlantic Ocean became impossible, probably since the Late Cretaceous. Likewise, the West African *Macrobrachium* became, probably since the Middle Miocene, completely separated also from their congeners in the Indian Ocean, when the hydrological connection from the Atlantic through the Mediterranean was interrupted.

Similar to the Atlantic, the vast marine area of the Early Mesozoic Panthalassa, which later developed to the Pacific Ocean, has always been an effective biogeographic barrier for coastal, shallow-water, estuarine, and freshwater-adapted groups. In contrast to the Atlantic, however, the presence of numerous scattered archipelagos in the western and central Pacific allowed some Indo-West Pacific species with an extended, salt-dependent larval development to spread eastward and colonise remote oceanic islands, where also a few endemic species may have evolved, e.g., *M. feunteuni* on the Marquesas (Keith and Vigneux, 2002). Examples for particularly widely distributed species are *M. grandimanus*, *M. australe* and *M. lar* (see Brock, 1960; Shokita, 1985; Chace and Bruce, 1993; Fouilland and Fossati, 1998; Concepcion and Nelson, 1999; Carey et al., 2011). Altogether, these few exceptions only confirm the rule that the Pacific Ocean has remained a huge and impermeable biogeographic barrier for *Macrobrachium*. With distances of 4000-6000 km between the easternmost islands of Polynesia and the continental Americas, a vast oceanic area that is almost void of islands constitutes a large and ancient oceanic barrier, which has completely impeded a colonization of the Neotropics by *Macrobrachium* from Asia or Australia, or *vice versa* (Newman, 1991).

Although Palaeo- and Neotropical regions do not share any species of *Macrobrachium*, there are indications of close phylogenetic relationships between species from both sides of the Atlantic. Cladistic analyses of morphological characters showed, for instance, a proximity of the Neotropical shrimp *M. carcinus* and *M. heterochirus* to the West African species *M. vollenhoveni* (Pereira, 1997). *M. heterochirus* also appears to be closely related to *M. chevalieri* from West Africa (Holthuis, 1952). All these species live in coastal regions and follow, as far as we know, an export strategy with salt-dependent and extended patterns of larval development (Choudhury, 1971; Vega Pérez, 1984; Willführ-Nast et al., 1993). Their close molecular genetic relationships reflect a relatively late evolutionary divergence (Pereira, 1997; Pileggi and Mantelatto, 2010), suggesting that coastal species with extended development maintained their contact through longer periods (possibly throughout the Late Cretaceous), wheras the gene flow between hololimnetic clades must have terminated at an earlier stage of the Gondwana breakup.

Macrobrachium in the Americas
General Remarks: Species Number and Range

From the taxonomical, biogeographical, and ecological literature, 57 New World species of *Macrobrachium* were identified (see distributional checklists, Tables 2-4), none of them occurring in geographic regions other than the Americas. The real species number, however, remains to some degree uncertain. It might actually be slightly lower, as some of the species listed here may be considered as doubtful, for instance because they have never been found again since their description (in some cases published in the 19th century), the type material deposited in museums has been lost or is in a poor condition of preservation, or recent molecular genetic or morphological studies suggest synonymizations. Species that are generally considered as junior synonyms are excluded from the present review (for instance *M. petronioi*

Melo, Lobão and Fernandes, 1986 = *M. potiuna* (Müller, 1880); both *M. birai* Lobão, Melo and Fernandes, 1986 and *M. holthuisi* Genofre and Lobão, 1978 = *M. olfersi* (Wiegmann, 1836); for recent discussion and references, see Pileggi and Mantelatto, 2010). The same applies to *M. fluviale* Streets, 1871, which was described from a coastal river draining to the Gulf of Mexico. This species is considered as highly doubtful, probably representing juveniles of another species (Holthuis, 1952), and it has never been found again in spite of extensive taxonomical and ecological studies carried out in Mexico (Román et al., 2000; Villalobos-Hiriart et al., 2010; Mejía-Ortíz and López-Mejía, 2011, and regional literature cited therein). Numerous further examples of synonyms, doubtful species, and misidentifications can be found in taxonomical revisions and comprehensive faunistic reviews (Holthuis, 1952; Chace and Hobbs, 1969; Bowles et al., 2000; Magalhães and Pereira, 2007). Recently introduced species such as *M. rosenbergii* and *M. equidens* are not considered either in the present review.

While a few of the species listed here might later turn out to be invalid, it is more likely that numerous others have not yet been discovered, so that the real number of Neotropical species of *Macrobrachium* may actually be much higher. New discoveries are particularly likely in large remote rainforest areas in the interior of South America, where almost inaccessible systems of creeks, streams and ponds have remained practically unexplored (García-Pérez and Villamizar, 2009). Also, some currently recognised species with an uncommonly large distibutional range may actually be species complexes that remain to be resolved through further phylogenetic studies and taxonomic revision (for examples, see below). According to recent molecular genetic data (Pileggi and Mantelatto, 2010), also members of the genus *Cryphiops* should be included within *Macrobrachium*. This would imply paraphyly, and thus, a further enhancement of the number of species in this genus. Awaiting additional taxonomic confirmation, *Cryphiops* spp. are not considered in the present review.

Overall, the latitudinal range of American *Macrobrachium* extends over 8000 km from the Rio de la Plata, Argentina/Uruguay (35°S), to the Ohio River in the USA (38°N). Only few species, however, occur in temperate zones; among these, the northernmost ranging species is *M. ohione* in the continental USA (Bowles et al., 2000; Bauer, 2004), while the southernmost is *M. borellii* in the Province of Buenos Aires, Argentina (Boschi, 1981; Collins et al., 2011). In east-west direction, the generic range extends over almost 5000 km across the tropical zone of South America, where the great majority of New World *Macrobrachium* lives. The westernmost occurrence of *Macrobrachium* has been reported from Baja California, northwestern Mexico (115°W; Hernández et al., 2007), the easternmost from northeastern Brazil (35°W; Coelho et al., 1990; Ramos-Porto and Coelho, 1998).

The overall distribution pattern of Neotropical *Macrobrachium* along the Pacific and Atlantic coasts, respectively, is quite asymmetrical, showing a much larger range in the Atlantic (Fig. 7). Similar to the patterns observed along the southern African coasts (see above), the main limiting factor is obviously water temperature: the occurrence of *Mac-robrachium* spp. coincides clearly with the prevalence of warm ocean currents such as the Gulf Stream as well as the Brazil and North Brazil Currents in the Atlantic, or the North Equatorial Countercurrent in the Pacific. On the other hand, their absence is correlated with cold currents including the Labrador and Malvinas Currents in the Atlantic, or the Humboldt and California Currents in the Pacific. On the Pacific coasts, however, lack of freshwater supply through large rivers in the arid region of Baja California and along the Peruvian and Chilean Atacama desert is probably an additional limiting factor, comparable to the Sahara and Namib regions in West Africa.

In the following account of the biology, diversity and distribution of American *Macrobrachium* spp., I will first further characterise and exemplify the two principal life-history patterns: 1) "coastal (or estuarine) species": adults living in rivers or estuaries; invariably with an extended mode of larval development in estuarine or coastal marine waters; diadromous migrations; and 2) "hololimnetic species": entire life cycle in fresh water, typically with an abbreviated developmental mode (only one exception in the Neotropic, see below). For biogeographic considerations, I distinguish within each of these two life-history categories two distributional designations with occurrence in waters draining either to the Pacific or the Atlantic slopes of the Andes or the Central American landbridge.

Diversity and Geographic Distribution of Coastal Species

The distributional checklists provided in Tables 2 and 3 comprise in total 27 American species of *Macrobrachium* that live in estuaries or rivers draining to the Pacific or the Atlantic slope, respectively. Within each of these two biogeographic categories, various regions are distinguished. As references, I cite here preferably recent distributional and ecological studies, unless the occurrence of a species was reported only in older papers or in its original description. Simões Ferreira et al. (2010) provided detailed distributional maps for coastal and estuarine species of *Macrobrachium* (and other palaemonids) in the Americas.

As adults, all these species can live in fresh water, whereas their larvae are known (or in some cases infered from small egg size or habitat location near the coast) to develop in brackish estuarine or coastal marine waters. Most probably, all of these species show diadromous migrations and pass through an extended larval development with numerous (typically ≥8) planktonic stages.

About one half (14 species) of all coastal *Macrobrachium* live exclusively in rivers draining to the Pacific side of the Americas, while 11 others are restricted to the Atlantic slope. Only two species (*M. hobbsi* and *M. olfersi*) have been reported from both sides of the Central American landbridge (Tables 2 and 3). This pattern, with two almost completely separated groups of coastal species, reflects the enormous biogeographic significance of this barrier, which will be discussed below.

Among the 16 coastal Pacific species of *Macrobrachium* (including the two amphi-istmian species), 9 live in South American rivers of Peru, Equador or Colombia, 12 have been found in Central America (Panama to southern Mexico), and 7 in northwestern Mexico. Most of these species are shared between two or more subregions (Table 2), while

Fig. 7.   Biogeographic distribution of coastal *Macrobrachium* in the Americas. Highly asymmetrical patterns with presence (marked regions) or absence along the Atlantic and Pacific coasts are related to the occurrence of warm and cold ocean currents, respectively; lack of *Macrobrachium* along the Pacific coasts of Peru and Chile also congruent with arid zones (lack of freshwater supply through large rivers). Map: Mollweide projection; © Ron Blakey and Colorado Plateau Geosystems Inc., USA. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

three are endemic to the western slope of the Andes (*M. transandicum*, *M. inca*, *M. gallus*). In *M. gallus*, however, the reproductive mode has remained uncertain, as no ovigerous females have become available (Holthuis, 1952).

Only three Neotropical species of *Macrobrachium* occur on oceanic Pacific islands. On Cocos Island, 500 km off the coast of Costa Rica, an apparently endemic species (*M. cocoense*) has been found, together with the widespread congeners *M. americanum* and *M. hancocki* (Abele and Kim, 1984). The two latter occur also on the Galapagos Islands, more than 900 km off the shore of Ecuador (Holthuis, 1952; Abele and Kim, 1984).

Among the coastal Pacific species, *M. americanum* shows the widest geographic distribution, ranging from Peru to northwestern Mexico. A similarly wide distribution along the shoreline, but not on offshore oceanic islands, has been observed in *M. digueti* and *M. tenellum*. Together with *M.*

americanum, these two species reach in the Gulf of California the northernmost boundary of the genus on the Pacific slope (up to 26°N; Hernández et al., 2007). The highest diversity of palaemonid shrimp, in general, was found in Costa Rica, Central America, where *Macrobrachium* spp. also show particularly high population densities, contributing up to over 90% of all Caridea in benthos samples (Vargas and Wehrtmann, 2009; Rólier-Lara and Wehrtmann, 2011).

On the Atlantic side of the Central American landbridge, the highest regional diversity of *Macrobrachium* has been documented for the Caribbean and Atlantic coasts of northern South America (region CS in Table 3; for topology and hydrology, see Rodríguez-Olarte et al., 2011). This includes the Magdalena, Maracaibo and Orinoco basins, the northern slope of the Guayana shield, e.g., the Essequibo drainage system, and northern Brazil (Holthuis, 1952; Magalhães and Pereira, 2007). Nine out of 13 coastal Atlantic species have

been recorded in this region. As only exceptions, the amphi-isthmian congener *M. hobbsi* (Hernández et al., 2007), the strictly North American *M. ohione* (Bauer, 2004), and *M. denticulatum*, which seems to be restricted to the São Francisco River in northeastern Brazil (Ostrovski et al., 1996), have not been found at this hotspot of coastal diversity for *Macrobrachium*.

Among the coastal Atlantic species of *Macrobrachium*, the largest areas of geographic distribution have been observed in *M. acanthurus*, *M. carcinus*, and *M. heterochirus*. They all range from subtropical regions of southern Brazil (Rio Grande do Sul State, ca. 32°S) to the continental USA (Simões Ferreira et al., 2010; Table 3). Their northernmost limits of distribution were found in northeastern Florida (*M. carcinus*; ca. 31°N) and North Carolina (*M. acanthurus*, *M. heterochirus*; ca. 37°N), respectively (Bowles et al., 2000; Holthuis and Provenzano, 1970). Only the "Mississippi shrimp," *M. ohione*, has been found further north, reaching ca. 38°N in the Missouri and Ohio Rivers (Illinois, Indiana, Ohio; see Bowles et al., 2000; Bauer and Delahoussaye, 2008).

Within the enormous geographic range of coastal Atlantic *Macrobrachium*, surprisingly few species occur on the Caribbean coasts of Central America, in the Gulf of Mexico, and on the Caribbean Islands (Table 3). Most species reported from these subregions are widespread (*M. acanthurus*, *M. carcinus*, *M. heterochirus*) and thus not characteristic. It is noteworthy, however, that one of the otherwise most widely ranging Atlantic species, *M. olfersi*, does not occur on Caribbean islands. *Macrobrachium lucifugum* and, to a lesser degree *M. faustinum* and *M. crenulatum*, might be considered as the most typical *Macrobrachium* spp. on the Caribbean islands.

M. lucifugum was originally described as a subspecies of *M. faustinum* (Holthuis, 1974), but later elevated to species rank (Juarrero De Varona, 1997). This view has been widely accepted, as *M. lucifugum* shows a troglobitic life style, living in anchialine caves, i.e., in subterranean waters that are connected to the sea, usually with brackish conditions (see Smith and Wier, 1999; Debrot, 2003). *M. faustinum*, by contrast, is an epigean species (Hunte, 1978; Barnish, 1984). While troglobitic shrimp living in land-locked, freshwater-filled inland caves show typically an abbreviated larval development and a small area of distribution (Komai and Fujita, 2005; Mejía-Ortiz et al., 2008), a wide distributional range of *M. lucifugum* on the Antilles islands (see Hobbs, 1994; Juarrero De Varona, 1997) suggests that this anchialine species passes through an extended larval development in marine waters, as shown for the closely related *M. faustinum* (Hunte, 1980).

Biology and Inland Distribution of Coastal Species

Coastal species of *Macrobrachium* live as opportunistic omnivores in major rivers and their tributaries (Bauer, 2004). Being strong hyper-osmoregulators, the benthic juveniles and adults tolerate fresh water, while the planktonic larval stages of these species require brackish or marine salinity conditions and must therefore be "exported" to estuarine or coastal waters (Freire et al., 2003; Augusto et al., 2007; Charmantier and Anger, 2011). This implies that either the larvae hatch upstream and are then passively transported

towards the sea, or the ovigerous females must perform active downstream migrations to release their offspring close to or within estuaries. However, there are surprisingly few studies that have tested the relative importance of these two differential export strategies. For the continental North American species *M. ohione*, field and laboratory studies (Bauer and Delahoussaye, 2008; Rome et al., 2009; Oliver and Bauer, 2011) have recently provided evidence that the females do migrate downstream over apparently large distances, but not necessarily all the way to the sea. On the other hand, first-stage larvae occur in river water 150 km upstream (although at much lower densities than in estuaries), and in laboratory experiments they tolerate for several days an exposure to fresh water. These findings indicate that there is, in this species, a combination of both catadromous female migrations and at least a limited larval drift with river currents.

Besides physical stress exerted by hypo-osmotic conditions in fresh water (Miller and Labandeira, 2002; Freire et al., 2003), planktonic food limitation is considered as another key variable that selects for special adaptations in the larval stages, or alternatively, for an export strategy with larval development outside the parental habitat. In diadromous species where an initial period of larval drift in river currents occurs, e.g., in *M. ohione* and estuarine shrimp belonging to the *M. amazonicum*-complex (Odinetz Collart, 1991; Bauer and Delahoussaye, 2008), the newly hatched zoeae must show a strong hyper-osmoregulatory capacity providing euryhalinity (Anger et al., 2008; Charmantier and Anger, 2011), as well as an enhanced endotrophic potential providing a reduced nutritional vulnerability (Diesel and Schuh, 1998; Anger, 2001; Anger and Hayd, 2009).

Fully or facultatively lecithotrophic first-stage larvae have been observed also in hololimnetic (non-exporting) palaemonid species with extended modes of larval development, e.g. in inland populations tentatively assigned to *M. amazonicum* (Anger and Hayd, 2010) as well as in *Palaemonetes argentinus* (Ituarte et al., 2005). This suggests that reduced early larval dependence on planktonic food sources may be an ancient phylogenetic trait in this clade, consistent with the hypotheses that the tendency to invade limnic systems has appeared early in the evolution of the palaemonids (see above), and that larval export strategies represent ancestral traits of evolutionary invaders in freshwater environments, in general (Miller and Labandeira, 2002).

While early larvae are transported downstream, they are not only exposed to osmotic and nutritional stress, but also to the risk of predation. Field observations in Puerto Rico (March et al., 1998) revealed that larval drift showed a peak occurrence at night in streams where visually oriented predatory fish were abundant, while no such diel pattern was discernible in stream reaches with low predation pressure. This may be explained with two alternative or combined mechanisms: 1) As adult shrimp are known to respond to the scent of predators (Hein and Crowl, 2010), and ovigerous females can control the release of their offspring (March et al., 1998), maximum larval hatching at night may reflect a maternal response; and 2) After hatching, also the larvae are able to perceive chemical cues from the environment (Anger, 2001, 2006). In the

presence of predators, they may show vertical migrations in the water column, with predominantly benthic behaviour during daytime (predator avoidance) and upward swimming during darkness (nocturnal feeding of surface plankton). Among freshwater-dwelling palaemonids, such diel vertical migrations have been observed in *M. amazonicum* in the lower Amazon (Moreira and Odinetz Collart, 1993). Future studies of larval behaviour and sensory physiology should further elucidate the complex life histories of diadromous shrimp, including the relative importance of female and larval adaptations to predation pressure.

After completion of the planktonic larval development in estuarine waters, the benthic juveniles must migrate upstream to recruit to the parental populations living in limnic habitats. In *M. ohione*, field studies have shown that post-larval body size tends to increase from downstream to upstream, which indicates that the juveniles are growing during their anadromous migration (Bauer and Delahoussaye, 2008). During this phase of the life cycle, the recruitment success of diadromous species is particularly prone to anthropogenic disturbance such as road and dam constructions (Kikkert et al., 2009; Hein et al., 2011).

Interestingly, diadromous species of *Macrobrachium* with a large geographic range tend to show also particularly large altitudinal and horizontal distributions within river systems. The coastal Pacific *M. americanum*, *M. digueti*, and *M. occidentale*, for instance, have been found upstream at altitudes > 500 m above sea level, with a maximum of 750 m observed in *M. digueti* (Rólier-Lara and Wehrtmann, 2011). Also, populations of the Atlantic species *M. olfersi* and *M. acanthurus* occur as far as 200 and 360 km, respectively, away from the coastline (Rodríguez-Almaraz and Campos, 1996; Mejía-Ortiz and Álvarez, 2010), and *M. ohione* inhabits riverine habitats up to more than 1000 km inland (Bauer and Delahoussaye, 2008).

Special Case of *Macrobrachium amazonicum*: One Highly Flexible Species or a Species Complex?

The most spectacular case of limnic invasions by supposedly coastal species of *Macrobrachium* seems to be *M. amazonicum*. Individuals assigned to this species live in not only coastal rivers draining to the northern and northeastern coasts of South America (for recent review, see Magalhães and Pereira, 2007; Maciel and Valenti, 2009), but also inland waters of both the Amazon and Orinoco plains, up to about 3400 km away from the Atlantic coast (Odinetz Collart and Rabelo, 1996; García-Dávila and Magalhães, 2004). Further populations live in the upper Paraguay and Paraná rivers and adjacent inland waters of the Pantanal plains, which belong to the La Plata drainage system (Bialetzki et al., 1997; Magalhães, 2000b; Magalhães et al., 2005; Pantaleão et al., 2012; Hayd and Anger, in press). This catchment area has been hydrologically separated from the Amazon and Orinoco plains maybe since the Miocene (about 10 Ma; Hubert and Renno, 2006) or at least since the Pliocene (ca. 4 Ma; Espurt et al., 2007). Its exceptionally large range of distribution makes *M. amazonicum* a special case among the Neotropical *Macrobrachium*. Moreover, shrimp assigned to this species are exceptional also insofar as they consistently show an extended mode of larval development not only in estuarine habitats but also in land-locked inland waters.

In inland populations, e.g., in those living in the Pantanal in the geographic centre of South America, female downstream migrations or a passive larval export to estuarine waters over thousands of kilometres have never been observed and must be considered as biologically impossible. This implies that such populations complete their entire life cycle in fresh water, which raises the question if coastal, estuarine, and hololimnetic inland populations assigned to *M. amazonicum* can really belong to the same species.

Although the currently available molecular data have not revealed statistically significant genetic diversification on the species level (Vergamini et al., 2011; Robe et al., 2012), recent comparative studies of reproductive, developmental, and physiological traits have revealed consistent and biologically significant differences between populations living in the Pantanal and in the Amazon estuary, respectively (Anger and Hayd, 2010; Charmantier and Anger, 2011; Urzúa and Anger, 2011; Hayd and Anger, in press). In hololimnetic populations from the Pantanal, there is no conspicuous sexual dimorphism (which suggests a reduced male-male competition compared to the estuarine population; see Baeza and Asorey, 2012). Moreover, males of the Pantanal population do not express different morphotypes, reach a smaller maximum body size than females, and show pure-search instead of mate-guarding behaviour (for details, see Hayd and Anger, in press). All these differences in reproductive systems indicate that long vicariant separation has indeed allowed for diversification in different catchment areas, implying that *M. amazonicum* is actually a complex of closely related but separate species. While estuarine populations are biologically similar to other coastal *Macrobrachium* spp. such as *M. acanthurus*, *M. olfersi*, *M. carcinus*, or *M. heterochirus* (cf. Anger and Moreira, 1998; Anger et al., 2002), hololimnetic inland populations, at least those in the Pantanal, are thus considered here as separate species (dos Santos et al., in prep.), which will be treated in the sections below.

Diversity and Geographic Distribution of Hololimnetic Inland Species

Table 4 compiles 31 currently known Neotropical species of *Macrobrachium* that are considered as hololimnetic, i.e., passing their entire life cycle in freshwater habitats. The assignment to this reproductive category is in some cases based on circumstantial evidence, infered from large egg size or land-locked habitats such as subterranean caves. All of these species occur in inland waters of South or Central America, living exclusively in waters on the Atlantic slope of the Andes or the Central American landbridge; there is not a single known hololimnetic species of *Macrobrachium* occurring in waters draining to the Pacific. Except for shrimp belonging to the *M. amazonicum*-complex, all of these species develop through an abbreviated and food-independent larval phase.

The highest diversity of species with an abbreviated mode of larval development has been recorded in continental inland waters around the Caribbean and the Gulf of Mexico. Within this tropical region between the Americas, 13 species live in northern South America (including the northeastern slope of the Andes, the Orinoco plain, and the northern drainage of the Guyana shield to the Atlantic), another 11

in Central America (eastern Mexico and Belize). Five of the northern South American species (*M. aracamuni, M. brasiliense, M. ferreirai, M. jelskii, M. nattereri*) occur also in the adjacent Amazon drainage system, together with two apparently endemic Amazonian species (*M. inpa* and *M. depressimanum*).

In the Paraguay-Paraná system, which drains southeast to the La Plata River, six inland species with abbreviated larval development have been recorded. Four of these (*M. brasiliense, M. ferreirai, M. jelskii,* and *M. nattereri*) are shared with both the Amazon plain and the northernmost region of South America, while only two species (*M. borelli* and *M. iheringi*) are restricted to the subtropical or temperate southern regions of the Paraguay and Uruguay river plains (Collins et al., 2011). Remarkably, the latter species occurs on both the western and the eastern slopes of the Serra do Mar mountain range (Uruguayan and Atlantic drainage systems, respectively), which suggests recent cross-drainage connections through headwater capture (Hubert and Renno, 2006; Ribeiro et al., 2006). An additional species with abbreviated larval development, *M. potiuna*, lives exclusively in rivers of the Atlantic slope of southeastern Brazil (Mueller and Carpes, 1991; Moulton et al., 2010).

The most widespread Neotropical species belonging to this category may be *M. brasiliense, M. ferreirai, M. jelskii,* and *M. nattereri*, which all occur in the Orinoco, the Amazon, as well as the Paraná-Paraguay plains (Table 4; Kensley and Walker, 1982; Rodríguez, 1982; Magalhães and Pereira, 2003, 2007; Collins et al., 2011).

Biology of Hololimnetic Inland Species

In the Amazon and Orinoco plains of northern South America, where the diversity of hololimnetic palaemonids is maximum, species of *Macrobrachium* and other shrimp with abbreviated modes of larval development, e.g., *Palaemonetes, Pseudopalaemon, Eurhynchus* spp., have most typically been found in nutrient-poor streams, rivers, and "*Igapó*" habitats (seasonal floodplains with blackwater characteristics, e.g., those connected to the Rio Negro; for ecological characterization, see Parolin et al., 2004; for records of *Macrobrachium*, see Holthuis, 1966; Kensley and Walker, 1982; Walker and Ferreira, 1985; Henderson and Walker, 1986; Walker, 1992). Blackwater habitats, which are named after their high content of dark-coloured tannins originating from plant degradation, show generally low nutrient concentrations and, as a consequence, low primary production (Fittkau et al., 1975; Saint-Paul et al., 2000; Junk et al., 2010). The prime source of organic matter and energy in such systems is leaf litter and other organic debris that is washed into streams, subsequently shredded by shrimp and other benthic invertebrates, and eventually degraded by microorganisms (Walker et al., 1991; Walker, 1994; Wright and Covich, 2005). Since other invertebrates are scarce in such habitats, shrimp occupy an important intermediate trophic position, sustaining fish populations in blackwater habitats (Kensley and Walker, 1982). Similarly, clearwater rivers and creeks in cratonic inland regions of the Brazilian and Guayana Shields show in general nutrient poverty (McClain and Naiman, 2008), which selects for abbreviated and lecithotrophic modes of larval development.

Freshwater-filled subterranean caves and groundwater streams (aquifers) represent another kind of typically nutrient-limited inland habitats, where detritus washed in from the surface may be the main food source for aquatic particle feeders. Cave systems with a characteristic toglobitic fauna (often with reduced or modified eyes; see Mejía-Ortiz and Hartnoll, 2005, 2006) are very common throughout the Neotropical region including the Caribbean Islands, Central America and the continental USA. Among the obligatorily cave-dwelling crustaceans, there are numerous species of cambarid crayfish as well as atyid and palaemonid shrimp including various *Macrobrachium* spp. (Hobbs et al., 1977; Reddell, 1981; Culver et al., 2000). As far as the mode of reproduction (size of eggs or larvae) is known, troglybitic shrimp such as *M. villalobosi* (Hobbs, 1973), *M. acherontium* (Holthuis, 1977), *M. catonium* (Hobbs and Hobbs, 1995), and *M. sbordonii* (Mejía-Ortiz et al., 2008) belong to the category with an abbreviated, lecithotrophic larval development. This is consistent with the practical impossibility of a larval export to estuaries as well as an almost complete lack of plankton production.

While low nutrient concentrations and weak plankton productivity may have played a crucial role in the evolution of hololimnetic *Macrobrachium* and other palaemonids with abbreviated and food-independent larval development, this category of species may be found also in the lower reaches of rivers as well as in lentic waters with higher productivity. In nutrient-rich "*Varzea*" habitats (areas that are periodically inundated by overflowing whitewater rivers such as the Upper Amazon or Solimões; for chemical and biological characterization, see Henderson and Crampton, 1997; Finck et al., 2011), shrimp belonging to the *M. amazonicum*-complex may be most typical. Consistent with their extended planktotrophic mode of larval development, these are rare or absent in nutrient-poor blackwater and clearwater environments, where congeners with abbreviated development are common (Magalhães and Walker, 1988; Odinetz Collart, 1991; Walker, 1992; Odinetz Collart and Magalhães, 1994).

The available literature indicates that an extended type of larval development depends obligatorily on a reliable production of freshwater plankton, which is most abundant in seasonally occurring Varzea lakes. As molecular data have shown that the *M. amazonicum* complex is a monophyletic clade (Vergamini et al., 2011), a single ancestral (estuarine) lineage with an extended mode of larval development must have invaded a large area with highly productive inland freshwater habitats, followed by vicariant diversification at least between the Amazon and upper Paraguay drainage systems. With its plesiomorphic developmental characteristics, the *M. amazonicum* complex may represent a suitable model for the reconstruction of the early steps of evolutionary transitions to limnic environments.

Species of *Macrobrachium* with abbreviated modes of larval development also originate from coastal ancestors that have successfully invaded inland waters, where they subsequently radiated, adapting to diverse regional and ecological habitat conditions. The presumable evolutionary course and palaeoenvironmental drivers of diversification in New World *Macrobrachium* will be discussed below,

relating modern distribution patterns (Tables 2-4) with the geological and climatic history of the Neotropics and adjacent temperate regions.

DRIVERS OF AQUATIC NEOTROPICAL DIVERSIFICATION

Central American Landbridge: Vicariant Diversification of Coastal Lineages

Diadromous *Macrobrachium* found in rivers draining to the Eastern Pacific or the Western Atlantic (including the Caribbean and Gulf of Mexico), respectively (Tables 2 and 3), show similar diversity but almost completely different species composition on each side of the Central American landbridge. This extant biogeographic pattern indicates a crucial role of the Panamanian landbridge for the diversification of coastal lineages of shrimp.

The timing of the geological separation of the Neotropical Atlantic from the Pacific is rather precisely known and generally considered as a highly influencial vicariant event that has driven regional diversifications in numerous groups of aquatic and terrestrial organisms (Lessios, 2008). As a consequence of a collision and subsequent subduction of the Cocos Plate beneath the less dense Caribbean Plate since the Late Miocene, the formation of the Central American landbridge occurred gradually, terminating only during the Pliocene, at ca. 3.7-2.8 Ma (Ibaraki, 1997; Kirby et al., 2008; Lessios, 2008). The final closure of the Central American waterway caused extensive changes in regional ocean circulation and climate (Haug and Tiedemann, 1998), and it might even have triggered the beginning of the Pleistocene Ice Ages (for discussion of controversial hypotheses, see Molnar, 2008). Undoubtly, this event caused vicariant speciation and differential extinction on both sides of the isthmus. These evolutionary effects are well documented in the fossil record, especially for molluscs (Vermeij, 1978, 1993; Beu, 2001), but also through molecular genetic analyses of extant trans-isthmian sister species of echinoids, crustaceans, fishes, bivalves, and gastropods (see Knowlton and Weigt, 1998; Anker et al., 2007; Lessios, 2008). Biological comparisons of geminate species pairs from the Pacific and Atlantic, e.g., in fishes (Wellington and Robertson, 2001) and decapod crustaceans (Wehrtmann and Albornoz, 2002), have revealed significant reproductive and developmental differences associated with divergence in nutritional conditions and other environmental facters exerting differential selection pressures. A recent molecular genetic study of grapsid crabs (Schubart, 2011) showed more pronounced divergence between species or population pairs living on different sides of the isthmus than between those on different sides of the Alantic. These data suggest that the Isthmus of Panama has been a more effective barrier for gene flow during the past ca. 3 Myr than the Atlantic Ocean. In Grapsidae, this is plausible; this crab family is characterised by extremely long periods of larval development in marine waters (Cuesta et al., 2011).

Considering the generally dramatic effects of the closure of the Central American seaway, the extant amphi-isthmian distribution of *M. hobbsi* and *M. olfersi* (Tables 2 and 3) is puzzling. It may raise doubts whether tentatively conspecific populations living on both the Pacific and Atlantic slopes, respectively, really belong to the same species. The contact between previously panmictic Pacific

and Atlantic populations must have terminated at the latest about 2 Ma. This is a minimum estimate, assuming that the Central American landbridge remained initially for some time permeable, due to intermittent marine connections at Late Pliocene and Early Pleistocene interglacial periods of high sea level alternating with complete closures during glacial periods of low sea level (Beu, 2001). Identical species on both sides of the isthmus, i.e., lack of allopatric speciation in spite of diverging environmental conditions through an extended period in vicariance, would indicate very slow genetic drift. This would be in contrast to fast divergence suggested for East Asian *Macrobrachium*, where a monophyletic clade is believed to have split during the Late Pleistocene within a short geologic period of 0.5-1 Myr into separate species with completely different modes of larval development (Mashiko and Shy, 2008). On the other hand, regional populations of the Southeast Asian *M. rosenbergii* seem to have diverged relatively little since Miocene times, suggesting in this case low divergence rates (De Bruyn et al., 2004a). Such discrepancies between estimates of fast diversification in subtropical East Asian *Macrobrachium* vs. much slower rates in tropical regions of South East Asia and Central America are surprising also insofar as diversification is generally assumed to be faster in tropical compared to cooler climates (Mittelbach et al., 2007). Also in other palaemonids, large and highly disjunct patterns of distribution suggest slow diversification in some lineages (Simões Ferreira et al., 2010), while very high endemic diversity in northern South America suggest rapid diversification in others (Holthuis, 1952; Pereira, 1997).

Discrepant estimates may indicate great variability in molecular divergence rates even within closely related lineages, which should caution against a possibly premature use of global molecular clocks (Li and Makova, 2008; Voloch et al., 2009; Lanfear et al., 2010). As an alternative explanation, variability may be high in the times rather than rates of divergence. For instance, over fourfold variability observed in the genetic divergence of transisthmian sister pairs of alpheids was interpreted as an indication of variable divergence times ranging from 3-15 Myr (Knowlton and Weigt, 1998).

If future morphological and molecular studies confirm the identity of disjunct populations of *M. hobbsi* and *M. olfersi* on both sides of the Central American land bridge, then a recent human-aided introduction through the Panama Canal could be an alternative explanation for these two rare cases of amphi-isthmian distribution. This mechanism is plausible for the widely distributed Atlantic species *M. olfersi*, which has also been found inside the canal (Abele and Kim, 1989). Immigrating from the Caribbean, it might have reached the Pacific already several decades ago, where it could spread northward to the Gulf of California (Hernández et al., 2007). In the predominantly Pacific species *M. hobbsi*, the situation is less clear. It was described only after Abele's and Kim's comprehensive study (1986) of the decapod fauna of the Panama Canal (see Villalobos-Hiriart and Nates-Rodríguez, 1990), so that it might have been previously overlooked or confused with other species of *Macrobrachium*. However, its amphi-isthmian distribution along the northeastern and northwestern coasts of Mexico render it more likely that

these two populations may actually represent two separate species, possibly a geminate pair of sister species.

Another taxonomical problem seems to occur in the type species of the genus *Macrobrachium*, *M. americanum*. From consideration of morphological and molecular genetic data, this species has been interpreted as a subspecies of *M. carcinus* (Holthuis, 1952; Pileggi and Mantelatto, 2010). The problem with this view, however, is that *M. americanum* is widely distributed along the Pacific coast and even on offshore Pacific islands, while *M. carcinus* ranges exclusively along the Atlantic coasts and throughout the Caribbean region. Synomization of these two allopatric, currently valid, species would thus raise the same questions as those related to trans-isthmian divergence in *M. hobbsi* and *M. olfersi*. The description of *M. americanum* by Bate already in the 19th century, i.e., before the construction of the Panama Canal, rules out that it represents a Pacific population of *M. carcinus* that was recently introduced from the Atlantic. Also, its extremely wide distributional range in the Pacific, comprising the South and Central American coasts, the Galapagos Islands and Baja California (Table 2), renders a recent invasion unlikely. The interpretation of *M. americanum* and *M. carcinus* as a geminate pair of trans-isthmian species (as proposed by Hernández et al., 2007) seems thus to be the most parsimonious explanation for their great morphological and molecular similarity.

In summary, except for a few unclear cases (*M. hobbsi*, *M. olfersi*, *M. americanum*), coastal *Macrobrachium* on the two sides of the Central American landbridge constitute two clearly distinct groups of species, reflecting vicariant speciation since the uplift and closure of this biogeographic barrier near the end of the Pliocene. As in numerous other groups of aquatic organisms (Lessios, 2008), these patterns show that the formation of the Isthmus of Panama has been one of the most significant drivers of diversification in coastal Neotropical *Macrobrachium*.

Andean Orogeny and Marine Incursions: Origin of Hololimnetic Inland Lineages

It is striking that hololimnetic inland species of *Macrobrachium* are highly diverse on the eastern slopes (Atlantic drainage systems) of the Andes and the Central American landbridge, while they seem to be completely absent from the western slopes (Pacific drainage; Table 4). This seems to suggest that the rise of the Isthmus of Panama might have influenced the diversification not only in coastal but also in inland lineages of *Macrobrachium*. However, if the uplift of the Andes and the Panamanian landbridge were mere vicariant events that separated previously panmictic populations, then we should expect to find similar species numbers, including geminate species pairs, on both sides of these barriers, as we can see in coastal *Macrobrachium* (cf. Tables 2, 3). Hence, the diversification of inland clades in Central and northern South America may actually have been driven by Palaeogeographic and ecological changes other than those associated with the formation of the Central American landbridge.

The physiographic history of the Neotropics, especially of the Amazon and Orinoco basins (where *Macrobrachium* diversity is maximum) is still to some extent subject to controversial discussions (see e.g. recent debates in Irion et al.,

2005; Rossetti et al., 2005; Figueiredo et al., 2009; Campbell, 2010; Figueiredo et al., 2010). Analysing an enormous set of data from multidisciplinary studies, however, several comprehensive reviews (Hovikoski et al., 2007b; Hoorn and Wesselingh, 2010; Hoorn et al., 2010; Wesselingh and Hoorn, 2011) have recently provided a largely consistent and plausible scenario of the origin and diversification of aquatic Neotropical biota. Although there is still some controversy as to details and the precise timing of some geologic events, these uncertainties do not severely affect the overall patterns outlined below.

Soon after the beginning of the Gondwana breakup in the Mesozoic era, a subduction of the oceanic Nazca plate underneath the westward drifting continental South American plate began to cause an uplift of the earth crust along the western margins of the newly forming continent (for details and references, see Capitanio et al., 2011). Although the Western Cordillera tectonics began already in the Early Cretaceous (ca. 140 Ma), Andean orogeny continued throughout an extended geologic period thereafter. The modern elevations of the central Andes were reached only after a strongly increasing tectonic activity in the Mid-Miocene, and the uplift of the northern Andes (Columbia, Venezuela), which was caused by a subduction of the Caribbean plate beneath the South American Plate, occurred even later, in the Pliocene (Potter and Szatmari, 2009; Ramos, 2010; Schaefer, 2011). Throughout this extended period, the palaeogeography of northern South America has changed continuously and sometimes dramatically.

In the Late Cretaceous, a river system originating from a cratonic area near the modern Amazon estuary ran westward through an ancient rift zone between the Guyana and the Brazilian Shields, draining initially to the Pacific Ocean (Lundberg, 1998; Hoorn et al., 2010; Wesselingh and Hoorn, 2011). The uplift of a continental divide in Central Amazonia at ca. 62°W, mainly the Purus Arch, separated since the Palaeocene the western drainage system of the "pan-Amazonian region" (Hoorn et al., 2010), or "proto-Amazonas-Orinoco river basin" (Rodríguez-Olarte et al., 2011), from an intercratonic eastern basin that drained to the Atlantic. Due to a sinking global sea level, marine settings disappeared at that time in northern South America, and terrestrial and limnic conditions prevailed.

Throughout the Palaeogene, the pan-Amazonian region extended over northwestern South America including the eastern slopes of the uplifting Andean chains in the west, the western drainages of the Guyana and Brazilian Shields in the east, and the upper Paraguay-Paraná basin in the south (Lundberg, 1998; Lundberg et al., 1998). Due to marine transgressions in the Late Eocene (Santos et al., 2008), major parts of this vast lowland became an epicontinental embayment, referred to as Pozo system (Hoorn et al., 2010; Wesselingh and Hoorn, 2011). Brackish and shallow marine waters occupied at that time the entire western part of modern Amazonia including the Ecuadorian Oriente, the Peruvian Marañón and Ucayali basins, as well as the Colombian and Venezuelan Llanos. The major connections to the sea included not only a large opening to the Caribbean (Roblecito embayment) but also a smaller one to the Pacific (Santos et al., 2008).

The continental divide in Central Amazonia that separated east- and westward flowing rivers migrated westward during the course of the Palaeogene (Wanderley-Filho et al., 2010), so that the Atlantic catchment area increased in size. This drainage system became later the precursor of the modern lower Amazon River (see below). Concomitantly, the Pacific drainage was increasingly constrained by continuing Andean orogeny, so that the main palaeodrainage was deflected northward. As a consequence, the whole Subandean foreland basin drained throughout the Oligocene and most of the Miocene exclusively to the Caribbean Sea (Lundberg, 1998; Hoorn et al., 2010; Rodríguez-Olarte et al., 2011; Wesselingh and Hoorn, 2011).

Besides tectonic processes such as Andean mountain building and associated vertical movements of the earth crust, eustatic sea level variations belong to the major drivers of palaeogeographic and –ecological changes. Sea level fluctuations are mainly driven by sea floor spreading (the opening of the Atlantic since the Cretaceous), continental collisions (that between India and Eurasia in the Eocene), and variations in global climate (alternating periods of glaciation and deglaciation during the Pleistocene; for review, see Miller et al., 2005). Although it seems that their amplitudes had previously been overestimated (cf. Haq et al., 1987; Miller et al., 2005; Müller et al., 2008), sea level fluctuations are definitely among the principal causes of continental floodings.

During periods of high sea level in the Late Cretaceous, in the Late Eocene, and again in the Miocene, low-gradient coastal regions and continental lowlands were repeatedly flooded by seawater (Lundberg et al., 1998; Sousa et al., 2009; Bloom and Lovejoy, 2011; Wesselingh and Hoorn, 2011). Each of these major palaeoenvironmental events must have allowed for marine invasions and subsequent diversification of marine-derived lineages in limnic inland waters of northern South America. However, the results of earlier invasions and radiations in fresh water might have been erased due to extinction of freshwater-adapted clades by later marine transgressions. This might explain why there is to date no indication of a Cretaceous or Eocene origin of marine-derived Amazonian freshwater clades (Lovejoy et al., 1998, 2006; Bloom and Lovejoy, 2011). The latest flooding events, occurring during the Miocene (23-10 Ma), may thus be the most influential marine transgressions in relation to the extant biogeographic distribution patterns. It will therefore be discussed here in more detail.

Miocene incursions of Caribbean waters onto the northern South American lowlands (Fig. 8) were caused by combined effects of increasing sea levels (Miller et al., 2005; Müller et al., 2008) and tectonic subsidence of the Subandean region (Lundberg, 1998; Albert et al., 2006; Wesselingh and

Fig. 8. Marine incursions, extension of the partially brackish Pebas wetland system in northwestern South America during the Early and Middle Miocene (23-11 Ma; after Wesselingh and Hoorn, 2011, modified). This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

Hoorn, 2011). Due to extended continental flooding, the western Amazonas-Orinoco and Subandean river basins became a large system of coastal embayments, interconnected lakes, anastomosing rivers, brackish swamps, and seasonally flooded tropical wetlands, collectively referred to as "Pebas system" (Hovikoski et al., 2007a, b; Hoorn et al., 2010; Wesselingh and Hoorn, 2011). Besides by marine transgressions from the Caribbean, the formation of this megawetland was favoured also by climatic changes associated with mountain building. The modern wet monsoon climate was probably established in the Early Miocene, when the Andes reached a critical elevation of about 2000 m (for references, see Wesselingh and Hoorn, 2011). The ascent of humid easterly air currents caused increasing condensation and rainfall along the eastern flank of the Andes, which enhanced the freshwater supply to the Subandean foreland (see supporting online material in Hoorn et al., 2010).

Radiations of endemic limnic mollusc and ostracod groups indicate the occurrence of major lacustrine environments in some areas of the Pebas system (for references, see Wesselingh and Hoorn, 2011). On the other hand, palynological evidence such as pollen analyses (Hoorn, 2006) showed that the epicontinental waters were partially fringed by mangrove forests, which indicates estuarine conditions in other parts of the upper Amazonian region. As evidenced by both sedimentological and palaeontological data (mangrove pollen, teeth of euryhaline sharks, foraminifera, cirripedes, marine gastropods, brachiopods), tidally influenced brackish environments reached in the Miocene southward as far as to the Subandean region of southern Bolivia, which was hydrologically connected also with the precursor of the upper Rio Paraguay-Paraná basin (Lundberg, 1998; Lundberg et al., 1998; Hovikoski et al., 2007b).

The extent of the Miocene marine incursions might have been even larger than this. Infering mainly from sedimentological data, some authors (Räsänen et al., 1995; Webb, 1995) proposed the temporary existence of a huge marine waterway, referred to as "Paranean Sea" or "Paranaense Sea." This hypothetical intracontinental sea stretched across the Llanos (Colombia-Venezuela) through western Amazonia and the La Plata basin, conncecting the Caribbean directly with the South Atlantic. However, details of its geographic extent, regional hydrological connections, salinity conditions, and the chronological development, especially in the southern part of the Subandean foreland, are subject to controversial debates (see Latrubesse et al., 2007, 2010; Ruskin et al., 2011). While a continuously marine character of the "Paranean seaway" may thus be doubtful, there is no controversy related to the existence of the huge, partially marine or brackish Miocene Pebas system, with extensive hydrological connections between the Caribbean Sea, the proto-Amazonas-Orinoco basin, the Subandean forelands, and the modern upper La Plata basin (Hoorn et al., 2010; Albert et al., 2011; Wesselingh and Hoorn, 2011).

As a consequence of transgressions, marine organisms invaded previously terrestrial and limnic inland regions. During later regressions, those immigrants became isolated from their ancestral environment, the sea, and were eventually "trapped" in their new, gradually changing and fragmenting aquatic inland habitats. While most marine invaders may have become extinct, some lineages adapted successfully to limnic conditions. The Miocene Pebas system may thus be considered as a "lineage pump" that "injected" marine taxa into limnic inland environments (Lovejoy et al., 2006). In continental South America, marine transgressions are responsible, for instance, for the widespread occurrence of marine-derived freshwater lineages of mammals (dolphins, manatees), fish (stingrays, drums, anchovies, needlefish), invertebrates (crabs, shrimp, molluscs), and various parasite groups specifically associated with these invaders (for references, see Lovejoy et al., 1998, 2006; Hubert and Renno, 2006). Numerous further examples for limnic radiations in the Pebas megawetland are listed in the reviews by Horn et al. (2010) and Wesselingh and Hoorn (2011).

Considering the conditions prevailing in the Pebas system, with shallow, partially brackish, and warm epicontinental waters (Fig. 8), it is plausible that estuarine species from the Caribbean coast, including palaemonids, found here ideal living conditions. Due to the enormous extension of this tropical wetland system, with large distances and probably great regional variations in hydrological connectedness, salinities, vegetation, productivity, and other palaeoecological variables, *Macrobrachium* must have thrived, dispersed, and successfully radiated throughout the approximately 13 Myr of existence of this vast tropical Miocene environment (ca. 23-10 Ma; Hoorn et al., 2010). In conclusion, the high extant diversity of hololimnetic *Macrobrachium* observed in inland waters of northern and central South America must be based on marine incursions, especially in the Miocene, which were followed by diversification of marine-derived lineages in the proto-Amazon-Orinoco basin as well as in the adjacent, transitorily connected river plains such as the modern upper Paraguay and Paraná basins.

In the more saline northern parts of the Pebas system, *Macrobrachium* spp. may have remained incompletely adapted to fresh water, following an export strategy with reproductive migrations and larval development in brackish waters. In these lineages, life histories and other biological traits should have been similar to those of extant coastal *Macrobrachium* as described above. In cratonic rivers draining the Brazilian and Guyana shields, in the upper (high-gradient) reaches of newly forming Andean streams, and in blackwater habitats such as seasonal *Igapó* floodplains, by contrast, poor planktonic productivity may have selected, already at that time, for abbreviated and food-independent modes of larval development. In such environments, marine-derived lineages could either evolve physiological and reproductive adaptions to fully limnic conditions, or they became extinct.

The same kind of selection against a continued dependence of marine-derived lineages from brackish or marine conditions occurred most probably also in other Neotropical regions including Central America. Although the Panamanian landbridge closed only in the Late Pliocene, its emergence had begun already in the Mid-Miocene (Lessios, 2008). During the Miocene sea level highstand, coastal shrimp ecologically similar to *M. lucifugum* (see Debrot, 2003) and other Tethyan relics colonised anchialine limestone caves of Cretaceous origin, where some of them later adapted to a troglobitic or subterranean life style and limnic

conditions (see Jaume and Brehier, 2005; Jaume, 2008; Porter et al., 2008). This should explain the high diversity of endemic *Macrobrachium* and other troglobitic fauna observed in cave habitats and adjacent mountain streams in Central America, where this habitat type is wide-spread (Holthuis, 1977; Hobbs and Hobbs, 1995; Villalobos and Álvarez, 1999; Mejía-Ortiz et al., 2008; Baldari et al., 2010).

The conspicuous diversification of hololimnetic *Macrobrachium* spp. in the Atlantic drainage basins of northern South America, i.e., in the region once occupied by the Pebas system, is thus plausible, as a consequence of the ancient colonization of a large, shallow, and ecologically optimal palaeo-environment. By contrast, the absence of similar radiations in Pacific drainage systems might be a consequence of the lack of comparably large lowland habitats. The continuous Andean mountain building since the Cretaceous and the later uplift of the Panamaian landbridge in the Miocene and Pliocene generated along the western (Pacific) margins of South and Central America a continuous emergence of geologically young formations with steep slopes, while the coastal plains remained narrow. This did not allow for the formation of large river systems and extended lacustrine environments, which are common in the Amazonian and Caribbean (Atlantic) drainages. As a consequence, all rivers draining to the Pacific are short and show high-gradient characteristics as compared to those draining the Atlantic slopes of the Andes and Central America (for illustration, see drainage charts in Hulsey and López-Fernández, 2011). This type of landscape allows for a colonization of coastal rivers by diadromous estuarine species, but it may not select for an evolution of hololimnetic lineages.

Formation of Modern Amazonas: Fragmentation of Inland Waters and Allopatric Diversification of Hololimnetic Inland Lineages

While details concerning the precise timing of the formation of the modern, eastward flowing Amazon river are still under dispute (estimates ranging from Late Miocene to Late Pliocene; cf. Campbell et al., 2006; Figueiredo et al., 2009; Latrubesse et al., 2010), there is no doubt that this process caused great changes in the hydrological conditions of northern South America. It seems to have been associated with the incipient uplift of the northern Andes in Columbia and Venezuela, which increasingly restricted the Caribbean drainage of the huge proto-Amazonas-Orinoco basin, leading to a rising water level in the Pebas system. Possibly enhanced by erosion or tectonic subsidence, this impounding caused eventually a breaching of central Amazonian land barriers such as the Purus Arch and a subsequent drainage of the Pebas waters eastward to the Atlantic Ocean (Hoorn et al., 2010; Wesselingh and Hoorn, 2011). The earliest detection of sediments of Andean origin in layers deposited in the Amazon deep-sea fan ("Foz do Amazonas") suggest an onset of the Amazon reversal already in the Late Miocene (about 11 Ma; Figueiredo et al., 2009; for controversial discussion of these findings, cf. Campbell, 2010; Figueiredo et al., 2010). However, the formation of the eastward running modern Amazon river seems to have finished only at the end of the Miocene (ca. 7 Ma; Figueiredo et al., 2009).

Due to regional tectonic uplift and a falling global sea level (Miller et al., 2005; Müller et al., 2008), the Pebas
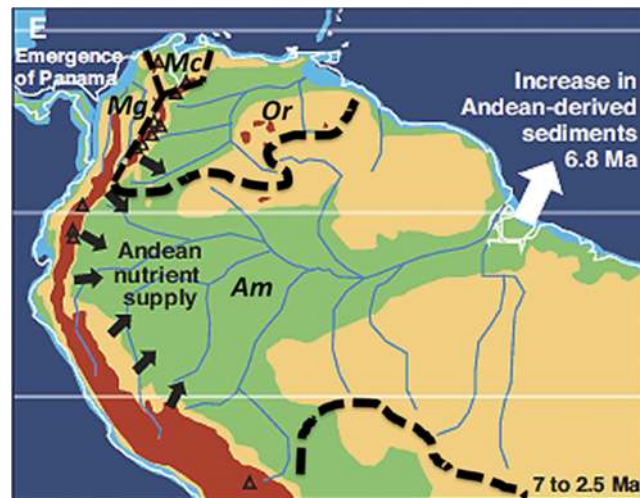

Fig. 9. Draining of the previously flooded Orinoco and Amazon basins (Pebas and Acre systems), fragmentation of epicontinental inland waters, and appearance of new watersheds during the Late Miocene and Pliocene, after the breaching of the main continental devide (Purus Arch) and subsequent reversal of the flow direction of the Amazon (becoming an eastward running drainage system; after Hoorn et al., 2010, modified); major catchment areas since the Pliocene: Am, Amazon; Or, Orinoco; Mg, Magdalena; Mc, Maracaibo. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1937240x.

system shrank during the Late Miocene in size and lost eventually the hydrological contact with the Caribbean drainage system to the north (Fig. 9). As a consequence, a new watershed between the modern Orinoco and Amazon drainages developed. In western and central Amazonia, a system of eastward draining rivers and lakes without marine influence, the "Acre System," developed at ca. 10-7 Ma (Hoorn et al., 2010; Hovikoski et al., 2010; Wesselingh and Hoorn, 2011). Some authors reported indications for marine settings persisting in lowland Amazonia until the Late Pliocene (implying a later reversal of the Amazon flow only in the Pliocene; see Campbell et al., 2006; Hubert and Renno, 2006), but this controversial interpretation has been questioned, as the data can also be interpreted with drainage valleys in seasonally flooded landscapes similar to those of the modern Pantanal (Figueiredo et al., 2010; Wesselingh and Hoorn, 2011). Western Amazonia developed in the Late Miocene an increasingly positive relief with entrenched river systems, high sedimentation, and a mosaic-type terrestrial landscape structure, which favoured limnic and terrestrial radiations as well as the development of modern rainforest communities (Albert et al., 2006; Hoorn et al., 2010).

Marine regressions and the depression of the overall level of South American inland waters led to the separation of the Paraguay catchment area, which later developed into the modern Pantanal (Carvalho and Albert, 2011), from the Amazon headwaters draining the sub-Andean foreland of southern Bolivia. The precise timing of this drainage compartimentalization in southwestern Amazonia remains uncertain, as headwater capture and local hydrological connections persisted through a long period (Carvalho and Albert, 2011). The final separation may have occurred already at about 10 Ma (Hubert and Renno, 2006) or the latest at 4 Ma (Espurt et al., 2007).

In the Early Pliocene, the rise of the Eastern Cordillera in northern South America (Columbia, Venezuela) separated the Magdalena basin from the proto-Orinoco drainage, and in the Late Pliocene also the Maracaibo basin became isolated due to the rise of the Andes of Merida (Fig. 9; for references, see Rodríguez-Olarte et al., 2011). All over the region of the former proto-Amazonas-Orinoco basin, emerging land masses and sinking water levels caused an increasing fragmentation of inland waters, although some temporary or local connections between different drainage systems may have persisted, offering limited dispersal routes between river plains. These connections include not only the well known Casiquiare between the Rio Negro (Amazon drainage) and the upper Orinoco (Winemiller and Willis, 2011), but also others between the Caribbean and Amazon drainages of the Guyana shield (Lujan and Armbruster, 2011), between the Amazon and Paraguay basins (Carvalho and Albert, 2011), and across the Serra do Mar watershed in southeastern Brazil (Ribeiro et al., 2006).

An increasing number of completely isolated or poorly connected freshwater refuges in northern South America must have promoted allopatric speciation of marine-derived aquatic lineages including *Macrobrachium*. Habitat fragmentation and regional reliction was probably further enhanced during the Pleistocene, when the climate was generally colder and dryer compared to both the preceding Late Neogene and the subsequent Holocene (Colinvaux and De Oliveira, 2000; Whitney et al., 2011). During glaciation cycles, dramatically decreasing sea levels caused headward erosion and, in consequence, strong downcutting processes in the lower Amazon and its tributaries (Irion and Kalliola, 2010). On the Caribbean islands, surface streams disappeared completely during such periods, so that only troglobitic or stygobitic shrimp (i.e. subsurface cave and groundwater dwellers) persisted (Covich and McDowell, 1996). This may explain also the high extant diversity of *Macrobrachium* spp. in subterranean caves and adjacent mountain streams in karst regions of Central America, especially Mexico and Belize (Table 4). On the other hand, marine transgressions occurring during Pleistocene interglacial periods caused the periodic drowning of extended river valleys, so that temporary connenctions between neigbouring drainage systems should have developed (Irion and Kalliola, 2010).

Based on the distribution patterns of South American freshwater fish (Hubert and Renno, 2006; Albert and Carvalho, 2011; Albert et al., 2011), the diversification of hololimnetic inland lineages of Neotropical *Macrobrachium* is the result mainly of interactions between marine transgressions, tectonic events associated with Andean orogeny, and transitory connections between catchment areas (Bilton et al., 2001; Hubert and Renno, 2006; Carvalho and Albert, 2011). Cross-drainage dispersal through historical connections between river basins may explain the wide distribution of some hololimnetic species with abbreviated and non-planktonic (benthic) modes of larval development, e.g., *M. brasiliense*, *M. ferreirai*, *M. jelskii*, and *M. nattereri*, which comprise allopatric populations in the Amazon, Orinoco and Paraná-Paraguay plains. Since they cannot disperse through planktonic larval stages, and hydrological connections across the major watersheds are absent

or limited, future phylogenetic analyses considering molecular, morphological, reproductive and developmental traits might also in these cases reveal diversification among populations living in different catchment areas. Also, such studies may show whether the diversification of Neotropical freshwater shrimp is due to one major colonisation event that took place in the Miocene, followed by radiations in inland waters, or reflecting several marine incursions that have occurred since the Late Cretaceous (see Bloom and Lovejoy, 2011). Infering from phylogenetic studies in Palaeotopical *Macrobrachium* (Murphy and Austin, 2004, 2005) and other Palaemoninae (Ashelby et al., 2012), we should expect that evidence for multiple invasions is more likely. Alternatively, evidence for the existence of a single monophyletic lineage may confirm the prime importance of the Miocene transgressions for the explanation of modern distribution patterns.

Concluding Remarks

Within their world-wide geographic range, the >240 extant species of *Macrobrachium* are largely restricted to equatorial regions, with only few exceptions occurring in temperate zones and none at high latitudes. All of these species live in limnic or brackish habitats, none in the sea. These general patterns render it highly unlikely that the preferences of this genus for warm-water and low-salinity conditions, or the expression of adaptive traits such as strong osmoregulatory functions, have independently evolved in various allopatric assemblages of species living in different continents. In conclusion, I suggest that preference for high temperatures and low salinities are ancestral characteristics of a monophyletic lineage. If these assumptions are correct, then a dispersal of *Macrobrachium* over vast oceanic distances of several thousand kilometres is impossible. This implies that phylogenetically closely related congeners living on both sides of the Atlantic must be older than the biogeographic barrier separating them. All this suggests that *Macrobrachium* represents an ancient lineage that must have appeared in Mesozoic times, before the opening of the Atlantic. The shallow tropical Tethys Sea connected at that time regions that later developed to the modern Indian Ocean, the Mediterranean Sea, the Atlantic Ocean, the Caribbean Sea, and the eastern Pacific Ocean. A Tethyan origin thus explains the modern pattern of distribution with three allopatric groups of congeners in the Indo-West-Pacific, West Africa, and the Americas.

Maximum diversity of hololimnetic *Macrobrachium* occurs in nutrient-poor blackwater and clearwater inland habitats in northern South America, as well as in Central American mountain streams and subterranean caves. These inland species originate from ancient marine transgressions, especially in the Miocene. The significance of older marine incursions for limnic radiations, e.g., in the Eocene, remains unknown. Subsequent to continental floodings, marine-derived lineages were "trapped" in fragmenting inland waters, where conditions of planktonic food limition select for abbreviated and food-independent modes of larval development. The exceptional case of the *M. amazonicum* complex indicates, however, that the ancestral pattern of an extended planktonic larval development can exceptionally persist also in fully limnic inland waters, if these pro-

vide sufficiently high plankton productivity, e.g., in Várzea lakes and other whitewater habitats. Besides nutritional factors, the ionic composition of such inland waters may be important. This is indicated by experimental observations in *M. amazonicum* from the Pantanal (Anger and Hayd, 2010) and in *M. niloticum* from the Central African Lake Chad (Williamson, 1972), whose larvae show higher survival in the presence of salts in low concentrations as compared to pure fresh water. However, it remains unknown whether such effects are due to general osmotic requirements of the larvae, or reflect the need for particular ions such as magnesium or calcium.

In summary, I suggest that the principal drivers of Neotropical diversification comprise: 1) ancient sea level fluctuations causing marine transgressions and continental flooding, "injecting" marine-derived lineages into inland environments; 2) tectonic events associated with Andean orogeny aiding to the formation of vast, partially brackish epicontinental inland waters, where marine-derived lineages could disperse and radiate; 3) "trapping" of invaders in habitats that lost during later marine regressions their contact with the sea, so that marine-derived lineages either adapted to fresh water or became extinct; and 4) fragmentation of inland waters during the Pliocene and Pleistocene promoted vicariant diversification in different catchment areas.

Among the "to do's" for future research, I suggest that further elaboration of molecular genetic techniques including the intercalibration of molecular clocks is required to enhance the reliability of phylogenetic analyses. Using improved techniques, such studies may also reveal the respective significance of different (Cretaceous, Eocene, Miocene) marine incursions for the origin and diversification of Neotropical *Macrobrachium*. The genus *Cryphiops*, which occur in South and Central America (including inland waters of the Amazon and Orinoco plains as well as the Pacific coast south to Chile), might have originated from such earlier incursions. Future phylogenetic studies will scrutinize their relationship to *Macrobrachium*. It also seems that the theoretical background and the practicability of different species concepts require further discussion, and the significance of interspecific hybridisation for diversification, especially in newly invaded invironments, may need more attention. Future palaeontologic, biogeographic, and phylogenetic studies of Palaeotropical *Macrobrachium* may show time frames and mechanisms of diversification comparable to those suggested here for the Neotropical congeners. Multidisciplinary studies may also reveal the origin and likely diversification of Central African inland species of *Macrobrachium* living in endorheic and alkaline lakes in Central Africa or in the East African Rift Valley, respectively. Altogether, multidisciplinary research may eventually allow for a more general understanding of evolutionary transitions of marine and estuarine animals to life in fresh water.

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