

*Michael Türkay Memorial Issue***PALAEOGENE AND NEOGENE BRACHYURANS OF THE AMAZON BASIN: A REVISED FIRST APPEARANCE DATE FOR PRIMARY FRESHWATER CRABS (BRACHYURA, TRICHODACTYLIDAE)**

BY

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ABSTRACT

We describe claw fragments of fossil primary freshwater crabs from three areas in the Amazon basin, Tarapoto (Early Oligocene) and Contamana (Middle Eocene to early Late Miocene) in Peru, and Eirunepé (Late Miocene) in Brazil. All these fragments most likely belong to the family Trichodactylidae. We show a continuous presence of primary freshwater crabs in proto-Amazonian lowlands from the Middle Eocene to the Late Miocene and can thus shift the earliest appearance date of freshwater-adapted brachyurans into the Eocene, at least in the Neotropics.

Key words. — Freshwater crabs, Trichodactylidae, Cenozoic, Proto-Amazonia, Neotropics

ZUSAMMENFASSUNG

Wir beschreiben fossile Scherenfragmente von primären Süßwasserkrabben, die von drei Lokalisationen innerhalb des Amazonasbeckens stammen: Aus Tarapoto (Frühes Oligozän) und Contamana (Mittleres Eozän – frühes Spätes Miozän) in Peru, und aus Eirunepé (Spätes Miozän) in Brasilien. Alle Fragmente gehören vermutlich zur Familie der Trichodactylidae. Damit können wir vom Mittleren Eozän bis zum Späten Miozän eine kontinuierliche Präsenz von primären Süßwasserkrabben im proto-Amazonischen Tiefland nachweisen; und, zumindest für die Neotropen, das erste Auftreten von Süßwasser-angepassten Brachyuren bis in das Eozän verschieben.

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INTRODUCTION

A long-standing opinion regarding freshwater crabs is that their fossil record is notoriously poor. Contrasting the extant diversity patterns, we currently have the best knowledge on fossil freshwater crabs from Europe and the Near East, with 35 documented sites ranging from the early Middle Miocene to the Pleistocene (Klaus & Gross, 2010; Klaus & Prieto, 2014). Much scarcer is our knowledge of the fossil record of Asian freshwater crabs that date from the Miocene/Pliocene (Klaus & Gross, 2010; Klaus et al., 2011, in press) and Pleistocene/Holocene (Naruse et al., 2003; Rabett et al., 2009; Ng & Cranbrook, 2014; Conrad et al., 2016), and from Africa (Morris, 1976; Carriol & Secrétan, 1992; Martin & Trautwein, 2003). The latter landmass yields the earliest representative of Old World freshwater crabs, the Oligocene *Tanzanonautes tuerkayi* Feldmann, O'Connor, Stevens, Gottfried, Roberts, Ngasala, Rasmusson & Kapilima, 2007 from the East African Rift Valley. The fossil freshwater crabs of the Neotropics, however, so far represent a terra incognita for both systematists and palaeontologists. Currently there is only one undisputed record of fossil claw fragments, originating from the Middle Miocene Honda group in the upper Río Magdalena River, at La Venta, Colombia (Rodríguez, 1997). These have been assigned to the extant species *Sylviocarcinus piriformis* (Pretzmann, 1968), of the family Trichodactylidae. Trace fossils from fluvial deposits of the Early Oligocene to Miocene Vinchina Formation, La Rioja, Argentina have been suggested to represent trichodactylid crab burrows (Melchor et al., 2010), but this evidence is indirect. Additionally, subfossil remains of *Eudaniela garmani* (Rathbun, 1898) (= *Rodriguezus garmani*) of the Pseudothelphusidae were found in an anthropogenic shell midden disposed between 2925 and 3485 years ago near the Guacharo cave, Monagas state, Venezuela (Rodríguez & Díaz, 1977).

In the Neotropics two families of freshwater crabs occur today, the Pseudothelphusidae (278 species) and the Trichodactylidae (51 species) (Yeo et al., 2008), that most likely represent independent colonization events of the limnic habitat as indicated by morphology (Sternberg & Cumberlidge, 2003) and molecular phylogenetics (Tsang et al., 2014). The centre of taxonomic diversity of the Pseudothelphusidae is northwestern South America and Central America (Rodríguez, 1982, 1986), while the range of the Trichodactylidae extends much more south, with a disjunctive occurrence of few species in Central America (Magalhães & Türkay, 2012).

Here, we describe freshwater crab remains from several localities of Palaeogene and Neogene age in the Amazon basin that push the first appearance of primary freshwater crabs back to the Eocene and point to their probable continuous presence in the area throughout the last 40 million years in Neotropical lowlands. For nomenclature used to describe the claw morphology, see fig. 1.

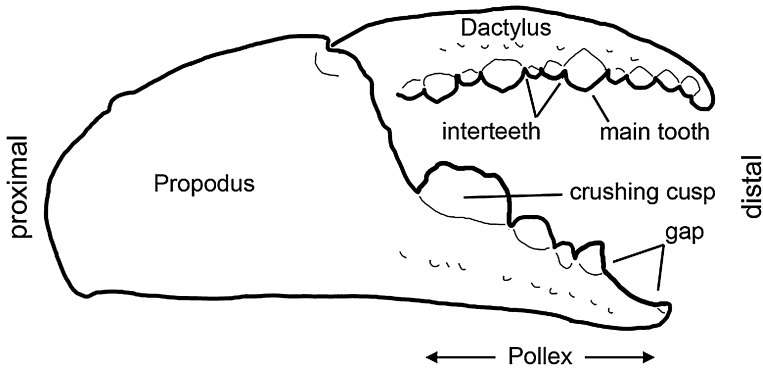


Fig. 1. Habitus of the brachyuran claw (right chela).

GEOLOGICAL SETTING

The claw fragments originate from three locations: Eirunepé area, Amazonas state, Brazil; Tarapoto area, San Martín province, Peru; and from several sites ranging from the Middle Eocene to the early Late Miocene in the Contamana area, Loreto province, Peru (fig. 2).

Sedimentological and palaeontological evidence (e.g., palynomorphs, charophytes, molluscs, fish, anurans, turtles and crocodiles) are primarily pointing to freshwater environments at Contamana for the crab-yielding levels, be them referred to the Pozo Formation (low-energy small streams of fluvial origin: CTA-47, CTA-27, CT-66, and CTA-29, Antoine et al., 2012, 2016) or to the overlying Chambira Formation (oxbow lake: CTA-32; Antoine et al., 2016a, b; Boivin et al.,

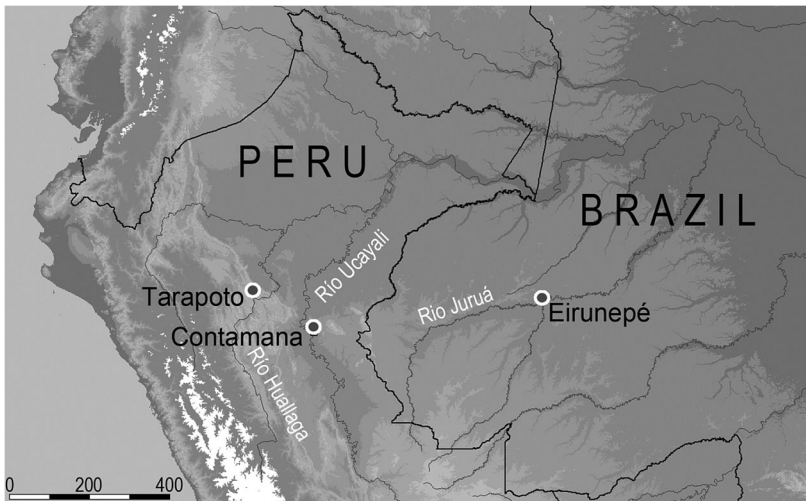


Fig. 2. Location of the sampling sites within the Amazon drainage in Peru and Brazil.

2017). A marine influence is supported by the presence of dinoflagellate cysts in CTA-47, but all other aquatic components of the concerned assemblage indicate a fluvial setting instead (Antoine et al., 2016). In the same section, the CTA-44 top (Middle-Late Miocene transition) and CTA-43 localities (early Late Miocene) have also yielded crab claws, referred to Trichodactylidae. These levels have gathered a mixture of fluvial, lacustrine, and estuarine faunal elements associated with tropical rainforest dwellers (dominated by mammals: Antoine et al., 2016; Marivaux et al., 2016).

Cenozoic deposits from the Tarapoto area (fig. 2) are much less constrained from a chronostratigraphical point of view (Hermoza et al., 2005; Eude et al., 2015). Continuing fieldwork by an international team of palaeontologists coordinated by POA and RSG led to the recent discovery of a rich vertebrate locality termed TAR-01, currently under study (Antoine et al., data not shown). The concerned level was considered to be part of the Oligocene-Miocene Chambira Formation (Hermoza et al., 2005), but it might instead be referred to the upper part of the underlying Pozo Formation (Late Eocene to Early Oligocene; Roddaz et al., 2010). Be it as it may, the preliminary faunal list of TAR-01 points to an early Oligocene age, based on the co-occurrence of undisputable prepidolopid/polydolopid and argyrolagoid polydolopimorphian metatherians. Such a co-occurrence was only attested in early Oligocene assemblages from Chile and Argentina thus far (Tinguirirican South American Land Mammal Age; Flynn & Wyss, 1999; Goin et al., 2010). TAR-01 was deposited by a low-energy fluvial stream, as consistently attested by sedimentological evidence (sandy channel with millimetre-sized carbonate nodules and blue clayish matrix) and its palaeontological content (charophytes, freshwater malacofauna and ichthyofauna, and putative gharial caimans). Nevertheless, the presence of myliobatids (eagle rays) and pristids (sawfishes) lower in the same stratigraphical section suggests a deltaic/marine influence for the corresponding member (unpubl. data).

Close to the city of Eirunepé three sections (Pau d'Alho, Morada Nova, Remanso) yielded fossil crab remains. The exposed strata belong to the upper part of the Solimões Formation and are biostratigraphically dated to the Late Miocene (Gross et al., 2011, 2013). Sedimentological observations indicate a fluvial, possibly anastomosing river system as depositional setting. The chelae originate from layers which were interpreted as partly crevasse splay influenced floodplain lake sediments. Palaeontological and geochemical ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) data derived from molluscs and ostracods refer to exclusively freshwater conditions (Gross et al., 2011, 2013).

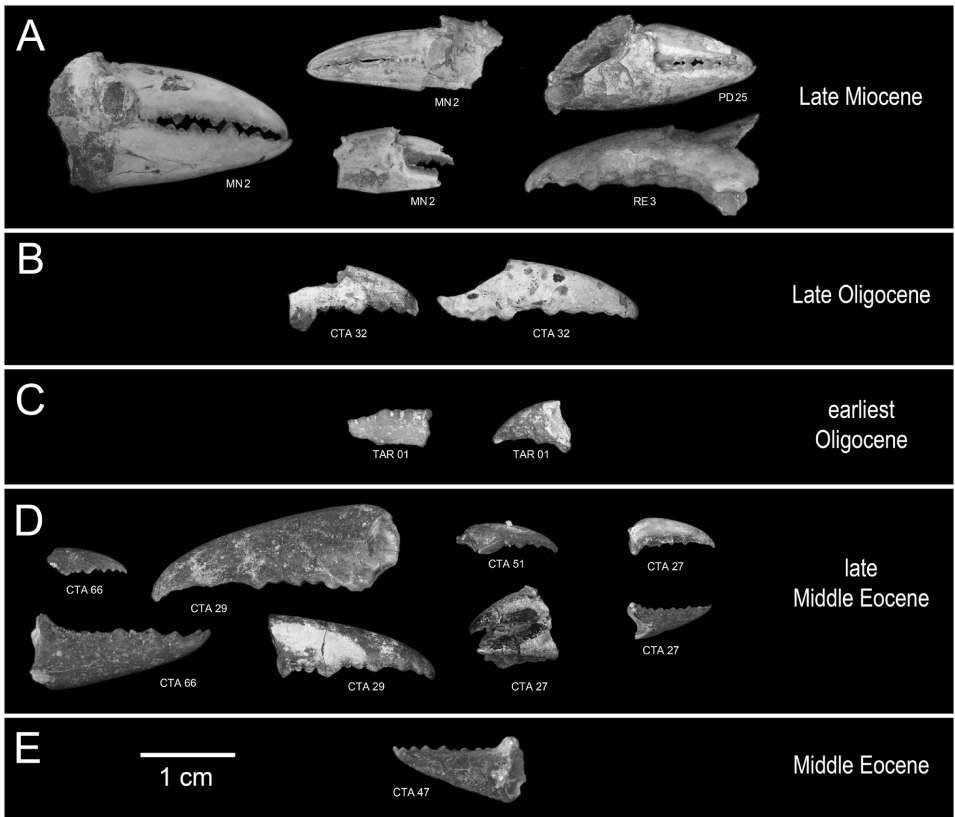


Fig. 3. Freshwater crab claw fragments from Peru and Brazil grouped according to their stratigraphical position: A, Eirunepé, Brazil; B, D, E, sites at Contamana, Peru; C, Tarapoto, Peru. Likely identity as pollex or dactylus is indicated by orientation of the claws' cutting edge (upwards vs. downwards). All claws are of the same scale.

SYSTEMATIC PALAEOONTOLOGY

Infraorder BRACHYURA Latreille, 1802

Family TRICHODACTYLIDAE H. Milne Edwards, 1853

Trichodactylidae indet.

Material.— Four articulated claws (propodus and dactylus), 2 pollices (fig. 3A), housed in the Universalmuseum Joanneum, Graz under references UMJG&P 211469, 211470, 211471.

Locality.— Eirunepé municipality; left bank of Juruá River, downstream from Eirunepé, Amazonas State, Brazil (Gross et al., 2011, 2013); sites Pau d'Alho: layer PD 25 (UMJG&P 211470); Morada Nova: layer MN 2 (UMJG&P 211469); Remanso: layer: RE 3 (UMJG&P 211471).

Stratigraphy and age.— Solimões Formation; Late Miocene (Gross et al., 2011; Gross et al., 2013).

Palaeoenvironment.— Floodplain lake within a possibly anastomosing river system.

Description.— Well preserved fragments. On the cutting edge of the larger claw's pollex (fig. 3A, left) triangular main teeth and interteeth are alternating; on the dactylus the number of smaller interteeth between the main teeth varies between one and three. One more slender claw (fig. 3A, upper row middle) most likely presents a smaller claw of a left-handed crab with hardly visible teeth on the dactylus, and on the pollex several larger teeth in the distal third and equally sized smaller teeth in the proximal part with a gap in-between.

Trichodactylidae indet.

Material.— Sixty-five claw fragments, housed in the Museo de Historia Natural de la Universidad Nacional Mayor San Marcos de Lima, Peru (MUSM) (fig. 3B).

Locality.— Contamana area, Loreto, Peru (site CTA-32; Antoine et al., 2016).

Stratigraphy and age.— Base of Chambira Formation; Late Oligocene (Antoine et al., 2016a).

Palaeoenvironment.— Oxbow lake (see Boivin et al., 2017).

Description.— Most claws are highly fragmented. The better preserved specimens (dactyli) show distally up to six larger, triangular teeth followed by two interteeth and one large main tooth.

Trichodactylidae indet.

Material.— More than 340 smaller claw fragments, housed in the MUSM (fig. 3C).

Locality.— Tarapoto area, San Martín, Peru (site TAR-01).

Stratigraphy and age.— Pozo Formation, upper member; most probably earliest Oligocene (Tinguirirican, approximately 33-30 Ma) based on mammalian biochronology (unpubl. data).

Palaeoenvironment.— Low-energy fluvial setting, with deltaic/estuarine influence (presence of myliobatid rays in the assemblage; unpubl. data).

Description.— The claws from site TAR-01 are highly fragmented and appear to be strongly eroded. Nevertheless, main and interteeth can be identified.

Trichodactylidae indet.

Material.— Fifty-one claw fragments (site CTA-27: 35; site CTA-29: 5; site CTA-51: 9; site CTA-66: 2), housed in the MUSM (fig. 3D).

Locality.— Contamana area, Loreto, Peru (sites CTA-27; CTA-29; CTA-51; CTA-66; Antoine et al., 2016a).

Stratigraphy and age.— Pozo Formation, lower member; Late Middle Eocene (early Barrancan, >41.6-40.94 Ma) based on mammalian biochronology; site CTA-29: 43.44 ± 2.5 Ma ($^{40}\text{Ar}/^{39}\text{Ar}$ age; Antoine et al., 2016a).

Palaeoenvironment.— Fluvial setting.

Description.— The claw fragments are of different size and include one fragment of an articulated claw. The dactylus' distal teeth are very small (abraded? gap?). The claw fragments from CTA-66 are of different size bearing triangular teeth, the smaller fragment showing more prominent teeth in the distal part. The larger pollex bears at its tip a small cup formed by two teeth that held the tip of the dactylus.

Trichodactylidae indet.

Material.— One claw fragment, housed in the DIPP-MUSM (fig. 3E).

Locality.— Contamana area, Loreto, Peru (site CTA-47; Antoine et al., 2016a).

Stratigraphy and age.— Pozo Formation, lower member; Middle Eocene (Barancan) (Antoine et al., 2016a).

Palaeoenvironment.— Fluvial setting, with marine influence (presence of dinoflagellates in the palynomorph assemblage; Antoine et al., 2016a).

Description.— The fragment represents most likely a pollex with nine preserved triangular teeth, the distal five being larger than the following teeth.

DISCUSSION

Claw morphology is hardly used in brachyuran systematics as a diagnostic character, especially as its variability within populations and — ontogenetically — within an individual is not explored yet. As claw morphology appears to be highly susceptible to selection related to ecology (Marijnissen, 2007), its phylogenetic bearing is difficult to assess, especially in a palaeontological context when neither carapace and gonopodial morphology nor genetic information is available. For freshwater crabs there are few endeavours to assign isolated fossil claw fragments to extant species. Ng & Cranbrook (2014) used comparative morphology to assign claw fragments from historical cave deposits to extant species. Pretzmann (1972) and Bachmayer & Pretzmann (1971) investigated patterns of main and interteeth in extant and fossil *Potamon*, but failed to find consistent data within the fossil assemblages and in the extant species. More successful was a morphometric approach that could assign (sub)fossil Pleistocene claws to an extant species, and also point out evolutionary changes (Ashkenazi et al., 2005). For these approaches, however, large series of completely preserved claws of the same size are necessary, what is not given with the present material. Therefore, we have to rely on a mere qualitative approach that makes species identification impossible and also hampers family and genus assignment.

With a reasonable degree of certainty, the present findings belong to the freshwater crab family Trichodactylidae. Claws of Pseudothelphusidae usually

have a well-marked row of rather similar sized teeth and longitudinal rows of granules along dactylus and pollex. The latter might be eroded in fossil remains, but especially the fragments from Eirunepé (fig. 3A) are quite well-preserved and lack any granules. Ecological differences, i.e., differential altitudinal distribution of both Neotropical freshwater crab families, would also corroborate the assignment of the present remains to the Trichodactylidae. The species of this family are widely distributed in the lowland areas of the main South American river basins, with the highest diversity in lentic and lotic environments of the Amazon drainage (Rodríguez, 1981; Magalhães, 2003). The pseudothelphusid crabs, on the other hand, are a mountainous group that supposedly evolved along the Andean mountains (Rodríguez, 1981, 1982) and are not distributed in the periodically flooded areas of the Amazon drainage (Magalhães, 2003). Considering that the fossil claw fragments originate from floodplain deposits of the palaeo-Amazon-Orinoco lowland system characterized by rivers, small streams and lakes, with recurrent marine incursions and with no palynological trace of high elevation habitats by the considered interval (Lundberg et al., 1998; Hoorn et al., 2010; Antoine et al., 2016a), it is very likely that the crabs inhabiting this region were indeed Trichodactylidae (given that the occurrence at higher altitudes represents the ancestral state for South American pseudothelphusids). All the specimens described here originate from oxbow lakes and low-energy streams, whereas higher-energy fluvial deposits from the Cenozoic of Western Amazonia (CTA-61, Late Oligocene, Contamana: Marivaux et al., 2016; Fitzcarrald local fauna, Middle Miocene: Tejada-Lara et al., 2015) and/or the Subandean Zone (MD-61, Early Miocene: Marivaux et al., 2012; MD-67, early Middle Miocene: Antoine et al., 2013) have yielded no crab remains thus far.

A putative Middle Miocene decapod claw fragment from a drilling core at the Ituí river, Amazonas state, Brazil (Linhares & Ramos, 2011) is most likely not of brachyuran origin, as its very small size (0.2 mm length) is far below the range even of juveniles' claws. Two claws from the Pebas section, Peru (Middle Miocene, 14-13 Ma; Mollusc Zone 7 of Wesselingh et al., 2006) are illustrated by Wesselingh & Ramos (2010: 309, fig. 18.6c, d). Based on the palaeoenvironment these fragments might be of freshwater crab origin, as they were found in the "type" locality of the Pebas Megawetland System, known to predate the major Miocene marine incursion. This record is slightly prior to the Colombian occurrence of trichodactylids at La Venta (Rodríguez, 1997), which would have biogeographical implications concerning potential dispersal pathways, as La Venta and Pebas belong to two distinct (palaeo)biogeographical areas within the Pebas System at that time (Salas-Gismondi et al., 2015; Salas-Gismondi et al., 2016). Morphologically, however, the claw fragments are unlikely to be of trichodactylid origin. One of the fragments (Wesselingh & Ramos, 2010:

309, fig. 18.6d) cannot be assigned unequivocally to the Trichodactylidae due to the extremely elongated distal tooth, while the other (Wesselingh & Ramos, 2010: 309, fig. 18.6c) is a strongly curved dactylus, a situation that very rarely (and less prominent) occurs in very large trichodactylid specimens only, e.g., in *Trichodactylus fluviatilis* Latreille, 1828 from southeast Brazil.

Most of the remains described here show affinities to the claws of the trichodactylid tribe Valdiviini (the genera *Sylviocarcinus*, *Valdivia* and *Zilchiopsis*), based on the presence of generally triangular teeth with alternating main and inter-teeth. This applies for fig. 3A left, 3D, 3E middle and 3F. However, several claws could as well belong to genera of the Dilocarcinini (*Dilocarcinus*, *Fredilocarcinus* and *Moreirocarcinus*), e.g., fig. 3A left, 3A upper row middle, 3E lower row middle, 3F. One claw from Eirunepé is extremely slender and resembles the smaller chela of species of the genus *Valdivia* (fig. 3A upper row middle). Table I gives an overview of the extant species occurring in the drainages of the three fossil sites. However, based on the preservation of most claws and the minor phylogenetic signal in freshwater crab claws in general, the present fragments might or might not be of conspecific origin.

The significance of these findings — despite the unsatisfying inability for a more precise taxonomic identification — is the Middle Eocene age of the earliest sites (CTA-47, 51, 27, 66 and 29), as this pushes the first appearance date of primary freshwater crabs more than ten million years deeper into the Palaeogene (compared to Early Oligocene *Tanzanonautes tuerkayi* from East

TABLE I

Occurrence of extant trichodactylid species within the drainages of the fossil sites of Tarapoto (Río Huallaga), Contamana (Río Ucayali) and Eirunepé (Río Juruá). Based on Magalhães (2003) and Magalhães & Türkay (1996a, b, 2008a, b)

Species	Río Huallaga	Río Ucayali	Río Juruá
<i>Dilocarcinus pagei</i> Stimpson, 1861	✓	✓	✓
<i>Dilocarcinus septemdentatus</i> (Herbst, 1783)			✓
<i>Fredilocarcinus musmuschiae</i> (Pretzmann & Mayta, 1980)		✓	
<i>Fredilocarcinus raddai</i> (Pretzmann, 1978)	✓		
<i>Fredilocarcinus apyratii</i> Magalhães & Türkay, 1996			✓
<i>Goyazana rotundicauda</i> Magalhães & Türkay, 1996		✓	
<i>Rotundavaldivia latidens</i> (A. Milne-Edwards, 1869)		✓	
<i>Sylviocarcinus devillei</i> H. Milne Edwards, 1853	✓	✓	✓
<i>Sylviocarcinus maldonadoensis</i> (Pretzmann, 1978)		✓	
<i>Sylviocarcinus pictus</i> (H. Milne Edwards, 1853)		✓	
<i>Trichodactylus faxoni</i> Rathbun, 1906	✓		
<i>Valdivia serrata</i> White, 1847		✓	
<i>Zilchiopsis cryptodus</i> (Ortmann, 1893)		✓	

Africa). This reduces the vast gap between the freshwater crab's first appearance date in the fossil record and the age of primary freshwater crabs as estimated by molecular clock techniques. The divergence of the monophyletic clade of Old World freshwater crabs (Potamidae, Gecarcinucidae and Potamonautidae) and Pseudothelphusidae from their marine relatives was estimated at 151-127 Ma; and that of the Trichodactylidae at about 102-73 Ma (Tsang et al., 2014). The temporal discrepancy between the hypothesised split and the available fossil record is thus still enormous, and is usually explained by the incompleteness of the latter for freshwater crabs (Klaus et al., 2011; Tsang et al., 2014). It has to be stressed, however, that also molecular clock calibration is subject to error that might not be reflected by credibility intervals of divergence time alone, and includes uncertainty of taxonomical assignment of fossils used to calibrate the clock, as well as the dating of these fossils (Klaus & Prieto, 2014).

The present study is only the second undisputed report of fossil primary freshwater crabs at the South American scale (since Rodríguez, 1997). Given that, it is likely that more intense future work — and a better awareness of crustacean remains by palaeontologists — will lead to a more detailed picture of the ?Cretaceous-Palaeogene freshwater crab fauna of South America. This might not only shed light on the biogeographical connection between the crab faunas of South and Middle America and the Caribbean, but can also contribute to our understanding of tropical palaeoecosystems, given the importance of freshwater crabs in extant tropical limnic food webs as main shredders (Dobson et al., 2002).

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