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Fossil glochidia (Bivalvia: Unionida: Hyriidae) from the middle Miocene of western Amazonia (Peru)

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Unionid bivalves are a common and widely distributed group of freshwater mussels, presumably known since the Triassic. One peculiar trait is their life cycle, with brooding of eggs in portions of the gills and release of usually fish-parasitizing larvae. The morphology of these larvae (glochidia or lasidia) is an important character for unionid classification and hence for phylogenetic reconstructions. Dispersal capacity and success of unionids through geological times is assumed to be largely affected by the evolution of temporary parasitism. Nevertheless, pre-Quaternary fossil proof of unionid larvae has been lacking until now, which renders some palaeobiological, phylogenetic and palaeobiogeographical scenarios arguable. Here we document late middle Miocene glochidia from the Pebas Formation (Porvenir, north-eastern Peru). Based on morphological comparisons with Recent glochidia and the accompanying fossil record, these larvae are related to the Hyriidae genus *Diplodon* Spix, 1827. Due to the lack of ‘hooks’ (inward-directed projections on the ventral edge of the glochidium) the larvae probably did not parasitize (fish) hosts, which restricted their dispersal ability. In this case, ‘unhooked’ is presumably a derived feature related to direct larval development. The strata containing these glochidia have been interpreted as marginal marine deposits with high-frequency salinity fluctuations. The associated mollusc and ostracod fauna is strongly dominated by euryhaline, endemic species. Only subordinately ‘freshwater’ and ‘marginal marine’ taxa co-occur, as well as euryhaline foraminifers. Stable isotope analyses ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) performed on ostracods and foraminifers furnished very light ratios, indicative of freshwater conditions. It remains unresolved if some marine-derived ostracods and also foraminifers were able to adapt to freshwater settings or if marine incursions affected western Amazonia in late middle Miocene times. Possibly the combination of, for example, fluctuating oxygenation and/or salinity and the complex reproductive strategy diminished the competitiveness of unionids within the Pebas wetlands.

Keywords: freshwater mussels; Hyriidae; mussel larvae; glochidium; Pebas Formation; palaeoenvironment

Introduction

Unionid bivalves have a worldwide distribution and have formed an important component of freshwater ecosystems at least since the Triassic (e.g. Watters 2001; Graf & Cummings 2007; Bogan & Roe 2008; Skawina & Dzik 2011; Miyahira *et al.* 2017). Characteristically, these mussels brood fertilized eggs in modified gill portions (marsupia) and release specialized larvae, which commonly parasitize fish until metamorphosis is complete and the juvenile mussels leave their hosts (e.g. Wächtler *et al.* 2001; Haag 2012). The type of immature larva is assumed to be an important trait for internal systematic grouping and thus for reconstructing the phylogeny of unionids (e.g. Parodiz & Bonetto 1963; Pfeiffer & Graf 2015).

There are two basic unionid larval types: the glochidium (i.e. larva with bivalved, calcitic shells), and the lasidium (i.e. larva with univalved, non-calcareous

shell). Unionidae, Hyriidae and Margaritiferidae have glochidia; Etheriidae, Mycetopodidae and Iridinidae produce lasidia (e.g. Wächtler *et al.* 2001; Graf & Cummings 2007; Graf *et al.* 2015; Pfeiffer & Graf 2015). Due to the lack of mineralized parts the preservation potential of lasidia is low. Similarly, the small (~50–350 μm) and poorly calcified glochidia are prone to be lost during fossilization. In fact, fossil glochidia have been reliably documented so far only from Quaternary strata (late Pleistocene and Holocene; Brodniewicz 1968; Aldridge & Horne 1998). Early Eocene occurrences from the Green River Basin, USA (Hanley 1979; Hartman *et al.* 2002), need further affirmation. Indirect hints suggesting glochidia development already in the Jurassic remain highly speculative (Richard *et al.* 1991; Watters 2001).

Hence, important questions about how and when unionids developed their peculiar life cycle, and the

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palaeobiological and geological considerations derived therefrom (e.g. potential hosts, mussel-host interactions, host population structure, palaeoenvironmental parameters, dispersal pathways, palaeobiogeography: e.g. Aldridge & Horne 1998; Watters 2001; Good 2004; Wesselingh 2007; Rinehart & Lucas 2013) are pending fossil evidence.

The present work describes the first findings of pre-Quaternary glochidia from the late middle Miocene of western Amazonia (Peru) and discusses their potential systematic assessment, as well as their palaeoecological and phylogenetic implications.

Geological background

The investigated material originates from the locality Porvenir, about 55 km south of Iquitos, Loreto Department, north-east Peru (Fig. 1). The exposed sediments are attributed to the Pebas Formation and considered to be of late middle to early late Miocene age (*Grimsdalea* pollen zone, MZ9 mollusc zone: Räsänen *et al.* 1998; Wesselingh *et al.* 2002, 2006a; Vonhof *et al.* 2003; Hovikoski *et al.* 2007). Based on recent

correlations for the nearby locality Nuevo Horizonte (Boonstra *et al.* 2015; also MZ9 according to Wesselingh *et al.* 2006a; fig. 1B), a late middle Miocene age (~14.2–12.7 Ma; palynological zone T-15 of Jaramillo *et al.* 2011) is most likely for Porvenir.

Vonhof *et al.* (2003) measured the isotopic composition ($^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of some mollusc shells (inclusively ‘marginal marine’ taxa) from Porvenir and concluded a freshwater (<1 PSU) palaeoenvironment for these deposits. Wesselingh *et al.* (2006a) presented a comprehensive register of the mollusc fauna of Porvenir (see also Aartsen & Wesselingh 2000, 2005; Wesselingh *et al.* 2002; Wesselingh 2006). Among an overwhelming majority of endemic, ‘Pebasian’ molluscs are a few ‘freshwater’ (i.e. *Diplodon* spp.) and ‘marginal marine’ species (Wesselingh & Ramos 2010). Hovikoski *et al.* (2007: location 9, fig. DR3 in GSA data repository item 2007210) provided a detailed lithological section of this locality, which corresponds well (apart from some differences in bed thickness) with our observations (see below). Based on sedimentological and ichnological data, these authors interpreted the sedimentary succession as tidally influenced bay-margin deposits.

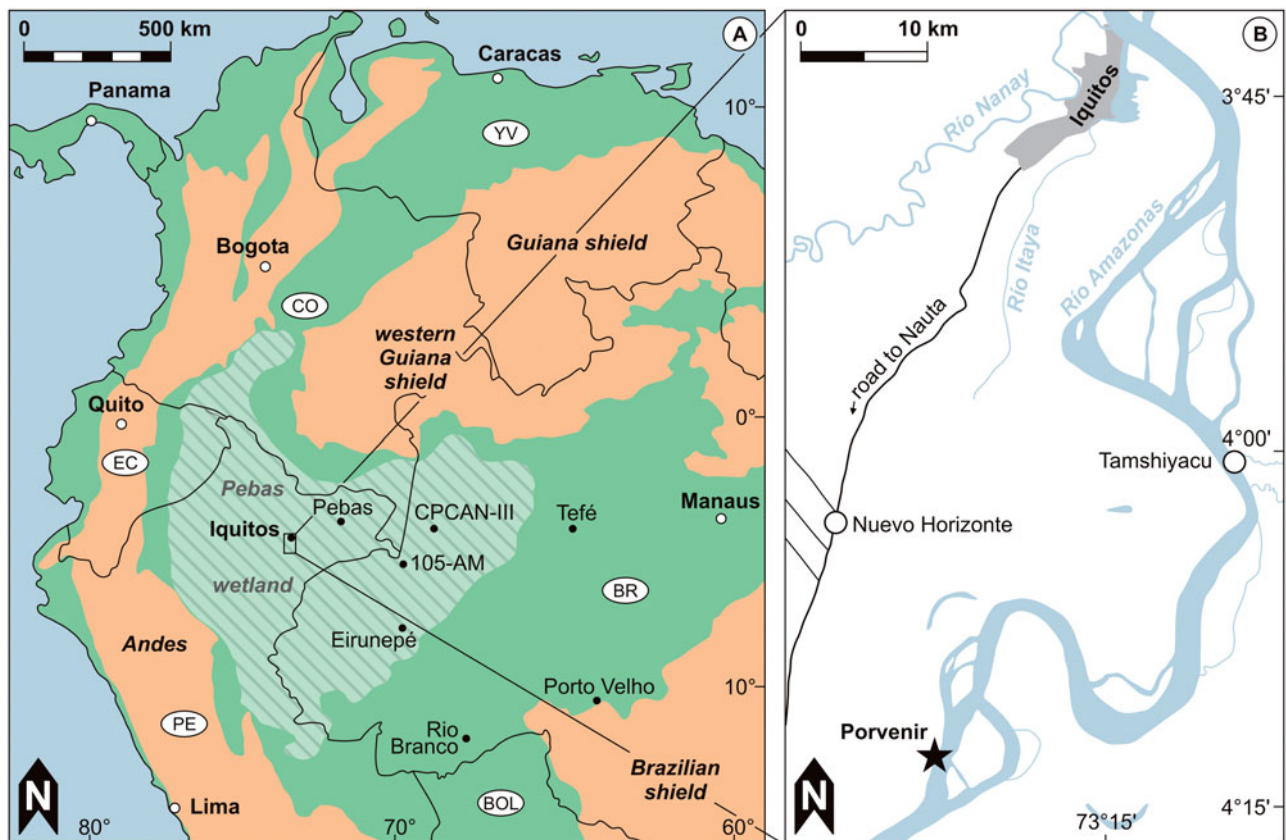


Figure 1. Location of the studied outcrop, Porvenir, south of Iquitos. **A**, sketch of the maximal extent of the ‘Pebas wetland’ during the middle Miocene (=hatched area; after Wesselingh 2008). **B**, location of the village of Porvenir (=star) on the left cutbank of the Amazon River.

These previous investigations at Porvenir mirror well the controversy concerning the presence or absence of marine incursions into the Pebas ‘mega-wetland’, which shaped western Amazonia and its biota for several million years (e.g. Wesselingh *et al.* 2002; Hoorn *et al.* 2010a, b; Hoorn & Wesselingh 2010; Latrubesse *et al.* 2010; Jaramillo *et al.* 2017).

Material and methods

The section of Porvenir was vertically logged by inspection of bed thickness, colour, sedimentary structures, grain size and macrofossil content (Fig. 2). For micropalaeontological investigations, bulk samples (~1–2 kg) were collected from various beds (Fig. 2); in this study, only the sample from bed number 8 (PO-N-8) is further considered. A total of 500 g of dried sediment (40 °C, 24 h) was washed through standard sieves (63/125/250/500 µm) using diluted hydrogen peroxide for disintegration (H₂O₂: H₂O = 1:5). Sieve residues were washed with ethanol (70%) before drying (40 °C, 24 h). Microfossils from residues ≥250 µm were picked completely; half of the residual ≥125 µm was screened for its foraminifer, ostracod and glochidia content.

Glochidia shells were photographed in transmitted light (Leitz Orthoplan microscope, camera: Leica DFC290) and measured (Leica Application Suite V3.6.0). For focus-stacked images up to 50 transmitted light photographs per specimen (covered with distilled water) were combined (software CombineZP 2010). Scanning electron microscope images were taken with a JEOL JSM-6610LV at the Universalmuseum Joanneum.

Adult ostracod valves (*Cyprideis*: three species; *Perissocytheridea*: one species) and foraminiferan tests (*Ammonia* sp., *Elphidium* sp.) were additionally washed with distilled water and rinsed in ethanol prior to stable isotope analyses (δ¹⁸O, δ¹³C; 24 measurements). Between two (ostracods) and 10 (foraminifers) specimens were necessary (>50 µg) per analysis (equipment: Thermo-Finnigan Kiel II automated reaction system and Thermo-Finnigan Delta Plus isotope-ratio mass spectrometer; University of Graz; standard deviation = 0.1 ‰ relative to NBS-19; results in per mille relative to Vienna Pee Dee Belemite (VPDB) standard).

Length, height, dorsal hinge line length and angle of obliquity of glochidia were measured according to Mansur & Silva (1999). The orientation of glochidial valves follows Hoggarth (1987, 1999), the terminology used adapted from Hoggarth (1999) and Pimpão *et al.* (2012). For basic statistics (mean and standard error) the software PAST 3.20 was used (Hammer *et al.* 2001).

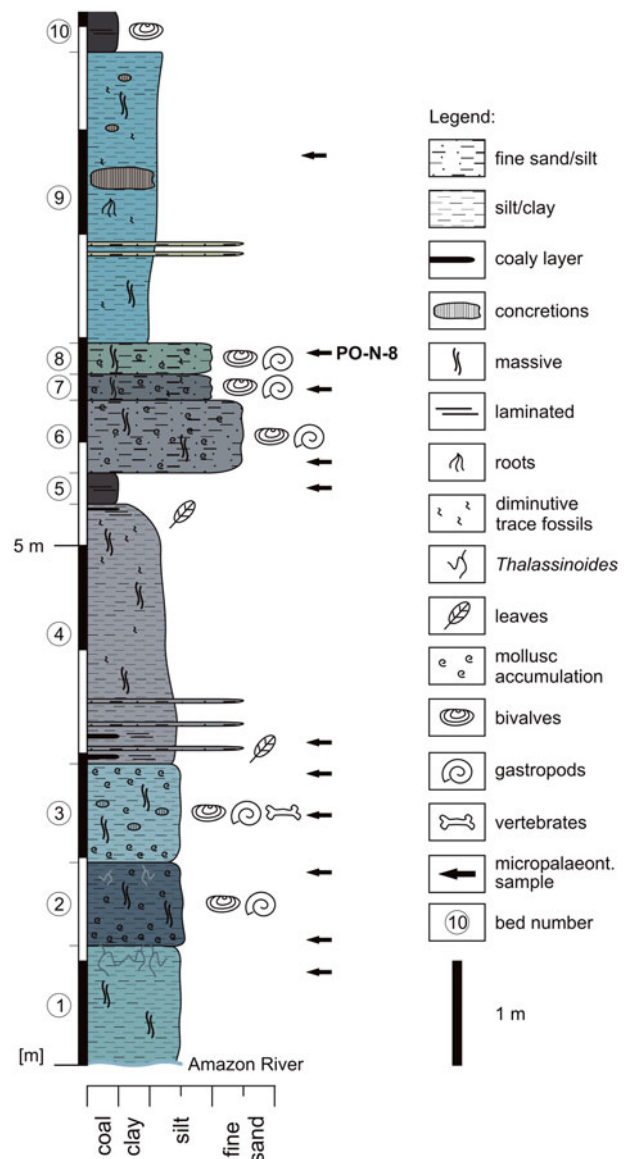


Figure 2. Lithological section of Porvenir. The glochidia described here originate from bed number 8 (sample PO-N-8).

All specimens are stored in the collection of the Universalmuseum Joanneum, Department for Geology & Palaeontology, Graz, under inventory number UMJG&P 213.854.

Results

Location. Porvenir. The studied section is located ~55 km S Iquitos (S 04°13'34.9" W 073°22'11.8"), on the left cutbank of the Amazon River, ~500 m NNE of the port of Porvenir (Fig. 1B).

Description. The sedimentary succession (Fig. 2) starts with more than 1.15 m of thick green-grey, massive

clayey silt (bed 1) with centimetre-thick *Thalassinoides* burrows filled with dark grey pelite and mollusc shells in the upper 0.30 m. Bed 2 consists of 0.80 m of dark grey, massive pelite, which is rich in molluscs and burrowed by *Thalassinoides* in the uppermost part. Up-section (bed 3), 0.95 m of green-grey, partly brown mottled, massive fine sandy pelites follows, enclosing abundant mollusc remains at the top and base. Centimetre-scale calcitic concretions and rare turtle remains have been found. This bed is overlain by 2.50 m of dark brown to grey, massive clay (bed 4). In the lower 0.80 m coaly (with leaf remains) and silty fine sand layers are intercalated. The upper part is bioturbated and contains coaly layers (with leaf fragments in the uppermost 0.10 m). The transition to bed 5, consisting of brown, laminated lignite, is gradual. Above, 0.70 m of grey to grey-brown, massive silty fine sand, rich in molluscs forms, bed 6, followed by 0.25 m of brown-grey, massive (bioturbated), mollusc-rich, fine sandy silt (bed 7). Bed 8 is composed of 0.30 m of green-grey, massive fine sandy silt, rich in molluscs. The next 2.80 m of the section (bed 9) comprises blue-grey, massive (bioturbated) clay with some discontinuous fine sand layers, centimetre-scale concretions and root traces. At section-metre 8.50 m a layer of metre-scale (decimetre-thick) calcitic concretions is developed. The top of the outcrop is formed by 0.40 m of thick, brown, laminated lignite with bivalves (bed 10). The glochidia described here originate from bed 8/sample PO-N-8 (~section metre 7.5 in Hovikoski *et al.* 2007).

Calcareous microfossils. The following microfossils were recorded from bed 8 (sample PO-N-8). Ostracods: *Alicenula olivencae* (Purper, 1984), *Cyprideis* aff. *graciosa* (Purper, 1979), *Cyprideis curucae* Gross *et al.*, 2014, *Cyprideis cyrtoma* Muñoz-Torres *et al.*, 1998, *Cyprideis inversa* (Purper & Pinto, 1983), *Cyprideis ituiaie* Gross *et al.*, 2014, *Cyprideis machadoi* (Purper, 1979), *Cyprideis multiradiata* (Purper, 1979), *Cyprideis munoztorresi* Gross *et al.*, 2014, *Cyprideis paralela* (Purper, 1979), *Cyprideis sulcosigmoidalis* (Purper, 1979), *Pellucistoma curupira* Gross *et al.*, 2016, *Perissocytheridea acuminata* (Purper, 1979), *Perissocytheridea akistron* Muñoz-Torres *et al.*, 1998, *Perissocytheridea ornellasae* (Purper, 1979), *Perissocytheridea* spp. 1 and 2, *Rhadinocytherura amazonsis* Sheppard & Bate, 1980, *Rhadinocytherura* spp. 1 and 2, *Skopaeocythere tetrakanthos* Whatley *et al.*, 2000; foraminifers: *Ammonia* sp., *Elphidium* sp.; and unionid glochidia.

Stable isotope ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) data from bed 8 (sample PO-N-8). Ostracods: *C. machadoi* ($\delta^{18}\text{O}$: -4.1 to -7.1‰ , $\delta^{13}\text{C}$: -7.7 to -11.2‰ ; five measurements), *C. multiradiata* ($\delta^{18}\text{O}$: -6.0 to -7.1‰ , $\delta^{13}\text{C}$: -8.6 to

-10.1‰ ; six measurements), *C. sulcosigmoidalis* ($\delta^{18}\text{O}$: -3.2 to -6.7‰ , $\delta^{13}\text{C}$: -8.4 to -11.1‰ ; six measurements) and *P. acuminata* ($\delta^{18}\text{O}$: -6.6‰ , $\delta^{13}\text{C}$: -11.7‰ ; one measurement); foraminifers: *Ammonia* sp. ($\delta^{18}\text{O}$: -4.5 to -7.4‰ , $\delta^{13}\text{C}$: -9.2 to -11.5‰ ; three measurements) and *Elphidium* sp. ($\delta^{18}\text{O}$: -5.4 to -7.2‰ , $\delta^{13}\text{C}$: -11.1 to -12.1‰ ; three measurements).

Systematic palaeontology

For suprageneric classification of unionids, see Bogan & Roe (2008), Graf *et al.* (2015), Santos-Neto *et al.* (2016) and Miyahira *et al.* (2017).

Class **Bivalvia** Linnaeus, 1758
 Order **Unionida** Stoliczka, 1871
 Family **Hyriidae** Swainson, 1840
 Genus **Diplodon** Spix, 1827
Diplodon sp. (**glochidia**)
 (Fig. 3A–P)

Material. Over 100 isolated valves. Middle Miocene, Pebas Formation, bed 8; Porvenir, north-eastern Peru.

Dimensions. Number of measured specimens = 33; length = 266–291 μm (mean = 278.8 ± 1.1 μm); height = 230–260 μm (mean = 241.0 ± 1.3 μm); dorsal hinge line length = 167–195 μm (mean = 181.8 ± 1.3 μm); angle of obliquity = $2\text{--}8^\circ$ (mean = $5.2 \pm 0.3^\circ$).

Description. Depressed pyriform, slightly scalene outline with length greater than height; dorsal hinge line straight, anterior margin slightly more arched and longer than posterior margin; base edge (ventral projection) pointed, prominent and slightly displaced from the centre (Fig. 3A–J, M–P). External surface with faint relief formed by micropores ($\sim 1\text{--}2$ μm in diameter) and ridges with commarginal orientation; valve border smooth, without pores (Fig. 3B, D, E, G, L); internal surface regularly pitted due to micropore perforation (Fig. 3A, C, F, H); a row of delicate, blunt micropoints is visible along the free valve margin (Fig. 3K); hookless, without microstylets or protuberances (Fig. 3I, J).

Discussion

Previous fossil glochidia records

Unequivocal pre-Quaternary fossil glochidia are previously unknown. Brodniewicz (1968) documented fossil Unionidae glochidia from upper Pleistocene (~ 120 kyr; Eemian interglacial) and Holocene deposits of Poland. The *Anodonta* glochidia (Unionidae) of Aldridge &

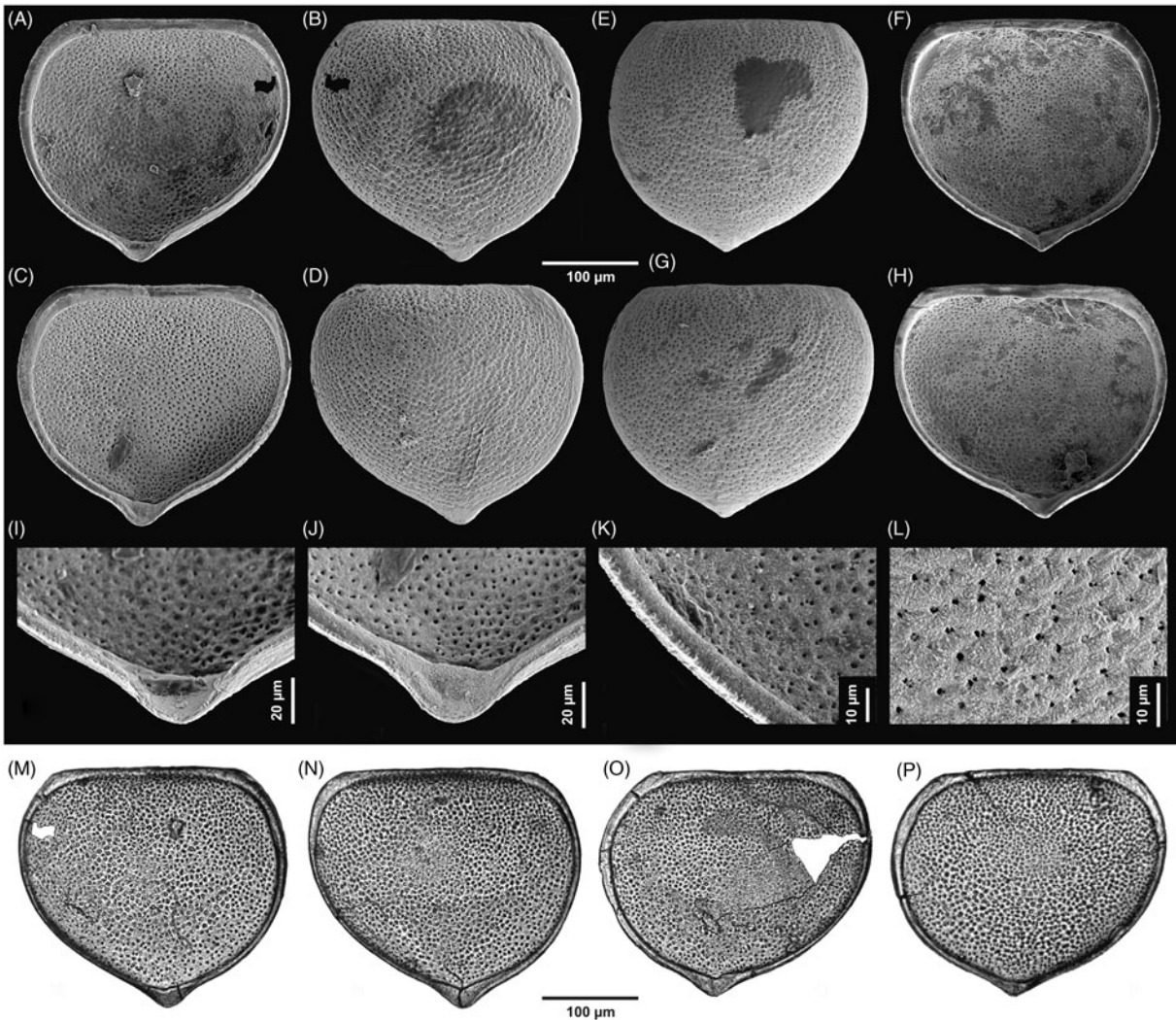


Figure 3. *Diplodon* sp. glochidia; scanning electron microscope (SEM) photographs (A–L) and transmitted light photographs, focus stacked (M–P). A, B, left valve in internal and external view; C, D, left valve in internal and external view; E, F, right valve in external and internal view; G, H, right valve in external and internal view; I, detail (base edge) of A; J, detail (base edge) of C; K, detail (valve border) of F; L, detail of external surface with micropores; M, left valve in external view; N, left valve in external view; O, right valve in external view; P, right valve in external view.

Horne (1998) are of Holocene age (~5 kyr BP) and in a strict sense ‘subfossil’. Late Cretaceous ‘glochidia?’ shown in Gasiński *et al.* (2013) represent juvenile bivalve shells. Hanley (1979) and Hartman *et al.* (2002) mentioned Unionidae glochidia from the early Eocene of the Green River Basin (USA). However, this material has been never described and seems to be lost (Joseph Hartman pers. comm.).

Interestingly, Purper (1979) documented doubtless glochidia from the Pebas Formation (drilling CPCAN-III-São Paulo de Olivença; ~S 03°27’/W 068°48’, ~510 km WSW of Porvenir; Fig. 1A) but regarded these fossils as juvenile cyclopyridine ostracods (for a similar misinterpretation of recent *Anodonta* glochidia as

ostracods compare *Goniocypris mitra* Brady & Robertson, 1870; Scott 1883). Solely based on the description, the specimens from Purper (1979) are more scalene and significantly smaller (length ~240 µm, height ~180 µm) than the current material. Probably, they belong to another unionid genus or species. However, a careful re-evaluation is required.

Classification of the fossil glochidia

In general, Unionidae and Margaritiferidae can have similar glochidia to Hyriidae but the latter lack – like our specimens – microstylets (e.g. Ortmann 1921; Mansur *et al.* 2012; Pimpão *et al.* 2012; Pereira *et al.* 2014; compare also Hoggarth 1999). Moreover, hyriid

mussels are the only glochidium-bearing unionids recognized in native South American freshwater faunas today and through the entire Cenozoic as well (Parodiz & Bonetto 1963; Parodiz 1969; Nuttall 1990; Wesselingh 2006; Bogan & Roe 2008; Miyahira *et al.* 2017). This renders an attribution of the current material to the Hyriidae plausible.

Currently, eight hyriid genera (in part quoted as subgenera) occur in South America (tribe Hyriini: *Paxyodon* Schumacher, 1817, *Prisodon* Schumacher, 1817, *Triplodon* Spix, 1827; tribe Castaliini: *Callonaia* Simpson, 1900, *Castalia* Lamarck, 1819, *Castaliella* Simpson, 1900; tribe Rhipidodontini: *Diplodon* Spix, 1827, *Rhipidodonta* Mörch, 1853; Graf & Cummings 2007; Graf *et al.* 2015; Santos-Neto *et al.* 2016; Miyahira *et al.* 2017). Compared with our specimens, Recent Hyriini glochidia diverge in outline (*Paxyodon*, *Prisodon*: isosceliform, nearly equilateral; *Triplodon*: more scalene with base edge more displaced from centre), external surface ornament (*Paxyodon*, *Prisodon*: small spines or spikes), and development of hooks (Parodiz & Bonetto 1963; Mansur *et al.* 2012; Pimpão *et al.* 2012; note that *Triplodon* is sometimes considered a synonym of *Prisodon*; Simone 2006; Mansur & Pimpão 2008). Glochidia of the Castaliini (*Castalia*, *Callonaia*, *Castaliella*) differ in their more equilateral outlines, lower angle of obliquity and triangular teeth (Ortmann 1921; Parodiz & Bonetto 1963; Bonetto & Ezcurra 1965; Vale *et al.* 2005; Mansur *et al.* 2012; Pimpão *et al.* 2012).

Rhipidodontini glochidia bear either a hook (and protuberance) or are hookless (without protuberance). In addition to shell characters, these are used to differentiate two genera/subgenera: *Diplodon* and *Rhipidodonta* (Pimpão *et al.* 2012; Miyahira *et al.* 2017). The hooked forms (*Diplodon*) are regarded as parasitic glochidia, and unhooked glochidia (*Rhipidodonta*) are regarded as non-parasitic larvae, which develop directly in the marsupium of the female to a juvenile mussel (Parodiz & Bonetto 1963; Mansur & Silva 1999; Mansur *et al.* 2012).

A plethora of *Diplodon* sensu lato species has been described from South America, including both hooked and unhooked glochidia (for a review see Miyahira *et al.* 2017). Although the presence/absence of glochidial hooks is an important taxonomical and biological feature, several uncertainties remain concerning this trait: (1) there is still need for (re-)descriptions of Rhipidodontini glochidia (e.g. *Diplodon suavidicus* (Lea, 1856) went from being 'non-parasitic/hookless' in Bonetto 1961 to 'parasitic/hooked' in Pimpão *et al.* 2012); (2) glochidia can be released by the female immature and unhooked under stressed conditions (i.e.

hypoxia: e.g. Aldridge & McIvor 2002); (3) there is some unexplained variability in the development of hooks (e.g. Khalloufi *et al.* 2011); (4) hooks could be lost during the fossilization process (Brodniewicz 1968; Aldridge & Horne 1998); and (5) since fossil glochidia are unknown, it is unclear whether this specific adaptation was already established in, for example, Miocene times.

Our specimens consistently lack a hook, and no traces of hooks or damage could be observed under high magnifications (Fig. 3I, J). We compared the current material with the glochidia of the following South American *Diplodon* sensu lato species described in Ortmann (1921), Bonetto (1961), Bonetto & Ezcurra (1965), Bonetto *et al.* (1986), Parada *et al.* (1989), Mansur (1999), Mansur & Silva (1999), Mansur *et al.* (2012) and Pimpão *et al.* (2012): (1) hookless forms: *D. asuncionis* Marshall, 1926, *D. bulloides* (Lea, 1859), *D. burroughianus* (Lea, 1834), *D. charruanus* (d'Orbigny, 1835), *D. garbei* Ihering, 1910, *D. hasemani* Ortmann, 1921, *D. hildae* Ortmann, 1921, *D. hylaeus* (d'Orbigny, 1835), *D. iheringi* Simpson, 1900, *D. koseritzi* (Clessin, 1888), *D. paranensis* (Lea, 1834), *D. peraeiformis* (Lea, 1860), *D. subquadratus* Marshall, 1922, *D. suppositus* Simpson, 1914 and *D. variabilis* (Maton, 1811); and (2) hooked forms: *D. atratus* (Sowerby, 1839), *D. berthae* Ortmann, 1921, *D. chilensis* (Gray, 1828), *D. decipiens* Ortmann, 1921, *D. delodontus* (Lamarck, 1819), *D. ellipticus* var. *santanus* Ihering, 1910, *D. expansus* (Küster, 1856), *D. fontainianus* (d'Orbigny, 1835), *D. frenzelii* (Ihering, 1893), *D. hartwrighti* Ihering, 1910, *D. huapensis* Bartsch, 1906, *D. imitator* Ortmann, 1921, *D. martensi* (Ihering, 1893), *D. mogymirim* Ortmann, 1921, *D. multistriatus* (Lea, 1831), *D. obsolescens* Baker, 1914, *D. parallelopipedon* (Lea, 1834), *D. paulista* (Ihering, 1893), *D. piceus* (Lea, 1860), *D. simillimus* Ortmann, 1921, *D. solidulus* (Philippi, 1869), *D. suavidicus* (Lea, 1856), *D. trivialis* (Simpson, 1914), *D. vicarius* Ortmann, 1921, *D. wagnerianus* Simpson, 1900 and *D. yaguaronis* Marshall, 1930.

All hookless and almost all hooked glochidia are more scalene, with a higher angle of obliquity and a basal edge that is more displaced from the centre. Most similar are the hooked glochidia of *D. solidulus* shown in Bonetto *et al.* (1986) from Puerto Montt, Chile (compare also Parada & Peredo 2002), and *D. piceus* in Bonetto (1961) from Itaquí, Brazil, but the former are more equilateral and the latter slightly more scalene.

The only known hyriid genera from the Miocene of the western Amazon Basin are *Diplodon*, *Callonaia* and *Castalia*. The latter two have not been recorded from the Pebas Formation (Nuttall 1990; Wesselingh 2006, Wesselingh *et al.* 2006a, Wesselingh & Ramos 2010).

In this formation *Diplodon* is represented by three species: *D. longulus* (Conrad, 1874), *D. amygdalaeformis* Wesselingh, 2006 and *D. indianensis* Wesselingh, 2006. At Porvenir only *D. longulus* (Wesselingh *et al.* 2002: sample 707) and *D. amygdalaeformis* (Wesselingh 2006: sample 702) have been reported.

In considering the morphological differences with Recent Hyriini and Castaliini glochidia mentioned above, and the fact that only *Diplodon* shells have been found at Porvenir and in the Pebas Formation, it is most likely that the current material belongs to the Rhipidodontini. The hookless appearance of the fossil glochidia could argue for an assignment to *Rhipidodonta*. Nevertheless, two hooked forms (*D. solidulus* and *D. piceus*) were found to be most similar. Therefore, and in view of the uncertainties concerning the character ‘hook/hookless’, we refrain from an attribution to either *Diplodon* or *Rhipidodonta* and refer these glochidia to *Diplodon* sensu lato.

Palaeoecological remarks

Hovikoski *et al.* (2007) interpreted the deposits of Porvenir as a marginal marine succession. For Bed 8, a deltaic/protected shoreface palaeoenvironment was inferred. Discrepancies resulting from geochemical data obtained from mollusc shells (Vanhof *et al.* 2003; see also Kaandorp *et al.* 2005, 2006; Wesselingh *et al.* 2006b) are explained by potential sampling biases, biologically induced offsets or uncertain calculation assumptions. The high endemicity of the aquatic Pebas fauna was linked to very low salinity and/or high-frequency brackish-freshwater water fluctuations due to short-lived marine incursions into an otherwise fluvio-lacustrine environment (Hovikoski *et al.* 2010; compare also Wesselingh *et al.* 2006b; Boonstra *et al.* 2015).

Wesselingh (2007) related the exceptional success of euryhaline corbulid (pachydotine) bivalves to their adaptability to dysoxic conditions, soft substrate and high predation pressure. While corbulids are broadcast spawners, unionids are brooders and mostly develop parasitic larvae. Accordingly, differences in reproductive modes might be additional constraints for competitiveness in the Pebas system (Wesselingh 2007; Anderson *et al.* 2010; for ostracods, see Gross *et al.* 2013). On the one hand, brood care and parasitism on (mainly) fish hosts provide shelter and some nutrient supply, and, most importantly, facilitate unionid larval dispersal in both lentic and lotic freshwater systems. On the other hand, brooding may reduce the respiration capacity of the female (especially critical under stressed, e.g. poorly oxygenated, conditions), and an appropriate (fish) host community, likewise sensitive to environmental changes, must be established (e.g. Bauer 2001; Wächtler *et al.*

2001; Aldridge & McIvor 2002; Barnhart *et al.* 2008; Fritts *et al.* 2013; Imscher & Vaughn 2015). Hence, oxygenation and/or salinity fluctuations, high predation pressure and a complex life cycle might have been responsible for the low success of unionids in the Pebas wetlands.

At Porvenir (bed 8) the ostracod fauna is strongly dominated by *Cyprideis* (10 species; > 90% of the specimens) accompanied by *Perissocytheridea*. Extant species of this genera are euryhaline, ‘brackish water’ taxa. The typically marine ostracod *Pellucistoma*, the freshwater darwinulid *Alicenula*, and the endemics *Rhadinocytherura* and *Skopaeocythere* (e.g. Sheppard & Bate 1980; Muñoz-Torres *et al.* 1998; Whatley *et al.* 2000; Gross *et al.* 2013, 2014, 2016) co-occur in low numbers. In addition, the glochidia of obligate freshwater unionids described here and the marginal marine foraminifers *Ammonia* and *Elphidium* have been found. Thus, the microfossil assemblage with a mixture of a few freshwater and marine forms among a wealth of endemic, euryhaline taxa coincides with the mollusc record (e.g. Wesselingh *et al.* 2006a).

Adaptation, or even a ‘supralimital evolution’ (Wesselingh 2007), to freshwater environments has been discussed for Pebasian ostracods (*Cyprideis*, *Perissocytheridea*, *Pellucistoma*: Gross *et al.* 2013, 2016) and ichnofossils (Wesselingh *et al.* 2006b), largely based on very light $\delta^{18}\text{O}$ - and $\delta^{13}\text{C}$ -ratios. O/C-stable isotope analyses performed on *Cyprideis* and *Perissocytheridea* valves, as well as on *Ammonia* and *Elphidium* tests from Porvenir (bed 8), gave depleted $\delta^{18}\text{O}$ - and $\delta^{13}\text{C}$ -values again, consistent with the data of Vanhof *et al.* (2003). In turn, these geochemical data would imply an extraordinary adaptation of foraminifers to freshwater settings too, which is – admittedly – a challenging interpretation and needs further investigation (compare Wesselingh *et al.* 2006b; Hovikoski *et al.* 2007, 2010). To date, the assumption of short-lived marine influences reaching the Pebas wetlands during the late middle Miocene (e.g. Boonstra *et al.* 2015: Nuevo Horizonte, fig. 1B; Jaramillo *et al.* 2017: drilling 105-AM, fig. 1A) seems to provide a more parsimonious explanation for the occurrence of foraminifers.

In contrast, due to their delicate shells, long-distance transport, either by water currents or by phoresy, is unlikely for the glochidia, and suitable freshwater habitats must have been at least very close.

Phylogenetical considerations

The characteristic reproductive strategy of unionids (brooding and parasitic larvae) is expected to have evolved very early (?Late Triassic, ~220 Ma) in their phylogeny as an adaptation to the colonization of lotic

freshwater environments (Watters 2001; Graf & Cummings 2006; Skawina & Dzik 2011).

In both traditional systematic and cladistic classifications, larval type (glochidium or lasidium) is an important but until now unproven trait in deep time (e.g. Parodiz & Bonetto 1963; Hoeh *et al.* 2001; Watters 2001; Graf & Cumming 2006, 2007; Graf *et al.* 2015). It remains ambiguous whether hookless glochida represent the ancestral condition in unionids in general (Graf & Cummings 2006). In the case of hookless *Diplodon* species, Hoeh *et al.* (2001) presumed the loss of hooks to be a derived feature, possibly related to direct larval development.

The ~13.5 Ma glochidia described here seem to be hookless, and conceivably they are derived forms. Nevertheless, 'hookless' in *Diplodon* could also be the plesiomorphic state, and 'hooked' parasitic larvae as well as phoresy via hosts might have appeared very late in hyriid evolution. If this is true, scenarios of unionid dispersal through time and phylogenetic reconstructions (e.g. Graf *et al.* 2015; Santo-Neto *et al.* 2016) will have to be reassessed. However, in respect to the enormous gap of more than 200 million years in the fossil record, this consideration remains speculative at present.

Conclusions

We recovered late middle Miocene unionid larvae from marginal marine or freshwater deposits of western Amazonia. Based on morphological comparisons and the ambient fossil record, these glochidia are attributed to the Hyriidae genus *Diplodon*. Our specimens prove the presence of such unionid-specific larvae in pre-Quaternary times. Probably, these hookless glochidia did not parasitize (fish) hosts. Aside from palaeoenvironmental parameters (i.e. fluctuating oxygenation and/or salinity), brooding of larvae within the gills of bivalves seems to have impaired the success of unionids within the Pebas system. Glochidia are most likely more frequent in the fossil record but have been either misinterpreted (e.g. as ostracods) or simply overlooked.

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