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Taxonomic study of the genus *Cyprideis* JONES, 1857 from the Pebas formation (Miocene), Iquitos (Peru), with description of three new species

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ABSTRACT

The taxonomic analysis of the ostracods from the Pebas Formation, Iquitos, Peru, allowed the identification of eight genera and twenty-two species of which *Cyprideis* Jones, 1857 is the most abundant and diverse with three new species described: *Cyprideis indianaensis* sp. nov., *Cyprideis soledadensis* sp. nov., and *Cyprideis santaelenae* sp. nov. The species *C. anterospinosa* Purper and Ornellas1991, *Cyprideis marginuspinosa* Purper and Ornellas1991, *Cyprideis retrobispinosa* Purper and Pinto1983, and *Cyprideis krsticae* Purper and Pinto1985 are registered for the first time in the Pebas Formation. Based on the taxonomic composition of the ostracods an oligohaline lake or a slightly confined brackish water lagoon predominated during the middle to late Miocene in the studied area.

1. Introduction

The study of ostracods from the Neogene of Western Amazonia have contributed to the knowledge of biodiversity, biostratigraphy, and evolution of northwestern South American landscape (Purper and Pinto, 1983; Purper and Ornellas, 1991; Muñoz-Torres et al., 2006; Gross et al., 2013, 2014, 2015; Linhares et al., 2011, 2017, 2019; Medeiros et al., 2019; Gross and Piller, 2020).

The Neogene deposits of Western Amazonia are characterized by a Mega-Wetland System called "Pebas lake", which extended over a huge area in the central part of northwestern South America comprising parts of Ecuador, Colombia, Peru and Brazil (Wesselingh et al., 2002, 2006a). In eastern Ecuador, this system is recognized in the Oriente basin, Curaray Formation and in Colombia in the Putumayo Basin, La Tagua layers (Wesselingh *et al.*, 2022; Rebata et al., 2006). While in the Peru it is recorded in the Neogene portion of the Marañon Basin and in Brazil in the Solimões Basin, represented by the Pebas and Solimões formations, respectively. The Mega-Wetland System is assumed as a network of lakes and temporary pools, which occupied most of western Amazonia between c. 23 and 8 Ma (Wesselingh et al., 2006a); marine influence has been continuously discussed (Hoorn, 1994b; Linhares et al., 2017; Antoine et al., 2016; Gross and Piller, 2020; Leandro et al., 2022). A particular paleoenvironmental evolution during the Neogene in the Western Amazonia promoted a remarkable radiation that directly influenced the diversity of an endemic fauna, where mollusks and ostracods are a good example (Wesselingh et al., 2002, 2006a; Wesselingh and Ramos, 2010).

Taxonomic and isotope data from the mollusks shells indicated freshwater settings during the deposition of the Pebas Formation, with the exception of a few incursion levels that were deposited under oligohaline-mesohaline conditions (Wesselingh et al., 2002). Recently, studies on isotope analysis using different proxies infer a freshwater system predominating in the early Miocene and oligohaline conditions during the Middle and early Late Miocene influenced by shallow marine incursions in the Pebas Megawetland System (Alvim et al., 2021).

Taxonomic studies of ostracods from the Pebas Formation in Peru and Colombia began with Sheppard and Bate (1980), and Swain (1998) who recognized a diverse ostracods fauna characteristic from lagoons, lakes, estuaries, and bays, typical of transitional systems. Later Muñoz-Torres et al. (1998) and Whatley et al. (1998) studied outcrops and wells from Brazil, Peru, and Colombia and identified a similar fauna when compared to the ostracods studied by Purper (1977, 1979), Purper and Pinto (1983), and Purper and Ornellas (1991) from Solimões Formation. These last authors identified an endemic fauna and proposed a high number of new genera and species; however, this fauna was reviewed by Muñoz-Torres et al. (1998) and Whatley et al. (1998), who placed many of these new genera in synonymy of the genus *Cyprideis* Jones, 1857, making it the most abundant and diverse genus. According

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[1] SOUSA AND RAMOS: OSTRACODS OF PEBAS FORMATION, PERU.

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to Whatley et al. (1998) this "*Cyprideis* flocks" developed in a brackish, lacustrine system; a phylogenetic model and a regional biozonation covering the early Miocene to early late Miocene in the area were also proposed (Muñoz-Torres et al., 2006).

The present study is a new contribution to the records of ostracods from the Pebas Formation, in Iquitos (Peru), contributing with the biodiversity and database increment of Neogene ostracods from Western Amazonia helping in the paleoenvironmental reconstitution as well as in the correlation between different sites already studied.

Morphological abbreviations: **C** = carapace; **LV** = left valve; **RV** = right valve; **H** = height; **L** = length; **W** = width.

2. Material and methods

The studied material originated from nine sites outcropping along the Amazonas and Napo rivers banks, Peru (Fig. 1). Samples were kindly donated by Frank Wesselingh (Museum Naturalis, The Netherlands). Additional information about the localities can be found in Wesselingh et al. (2002).

For micropaleontological analyses the samples were processed by conventional methods and washed through standard sieves (0.5 mm, 0.250 mm, 0.180 mm, and 0.125 mm). Wet sieve residuals were dried at 60 °C; from that 60 g of dried sediment per sample were picked out completely for microfossil analysis using a stereomicroscope, for subsequent identification. Scanning electron microscope images were taken with a Mirae3 Tescan (Museu Paraense Emilio Goeldi). The suprageneric classification follows Liebau (2005) and species determination is based on Purper (1979), Purper and Pinto (1983, 1985), Purper and Ornellas (1991), Muñoz-Torres et al. (1998), Whatley et al. (1998), and Gross et al. (2013, 2014). Additional type-material from Gross et al. (2013, 2014) housed in the micropaleontological collection, Coordenação de Ciências da Terra e Ecologia (COCTE), Museu Paraense Emilio Goeldi (MPEG), was also consulted for comparative studies. The type-material of this work as well as figured specimens are housed in the micropaleontological collection of the COCTE, MPEG, Pará, Brazil, under catalogue numbers MPEG-857-M to MPEG-928-M, and MPEG-986-M to MPEG-991-M.

3. Geological setting

The studied samples stem from the Pebas Formation, outcropping in the banks of the Amazonas and Napo rivers, in the north of Iquitos, capital of Loreto department (Peru) in the area of the Iquitos Arch, close to the eastern border of the Marañon Basin (Fig. 1).

The Marañon Basin is a foreland sub-Andean basin, covering an area of about 320,000 km^2 (Mathalone and Montoya, 1995); it is geographically situated in the north of Peru and geologically limited to the west by the Campanquiz-Cahuapanas and Cushabatay structural high; to the east by the Iquitos forebulge (Rebata et al., 2006; Roddaz et al., 2005; Parra et al., 2020) dividing it from Solimões Basin (Caputo, 1991; Roddaz et al., 2005; Parra et al., 2020). To the south, the basin is bordered by the Ucayali and Acre basins, by Contaya Arch (Roddaz et al., 2005). The Cretaceous-Eocene interval is marked by a depocenter located between the Andes mountains and cratonic domains (Eude et al., 2015). The minimum thickness of the Marañon Basin is to the east, in direction to the Iquitos Arch (Sanchez et al., 1999). The stratigraphy of the basin is known through oil drilling developed by PARSEP and published by PeruPetro in 2000 (PARSEP, 2001); a summary can be found in Roddaz et al. (2010) and Calves et al. (2018).

The Pebas Formation, with a thickness of approximately 1000 m (Wesselingh et al., 2006a), transitionally overlies the Chambira Formation (Oligocene) and underlying the Marañon Formation, in a concordant contact. The transition is characterized by blue clay, fine-grained lithic sandstone, and lignite layers rich in diverse and well-preserved invertebrate and vertebrate fossils; the base of this formation was dated around 23.9–22.5 Ma (Oligocene–Miocene boundary) (Wesselingh et al., 2006a). Palynology significantly contributed to the biostratigraphy and paleoenvironmental reconstructions (Hoorn, 1993) of the studied area. The biostratigraphy presented by Hoorn (1993), and later with mollusks by Wesselingh et al. (2006b), and ostracods by Muñoz-Torres et al. (2006), allowed to infer an early to middle Miocene age for the Neogene deposits of western Amazonia (Pebas and Solimões formations). According to Antoine et al. (2016), based on palynological studies, the Pebas Formation span from late early to early late Miocene and, more recently Parra et al. (2020) infer early Miocene to the latest Miocene.

Some outcrops studied herein have been dated previously based on palynology and mollusks (Hoorn, 1993; Wesselingh et al., 2006a), of which Indiana outcrop is equivalent to the *Psiladiporites-Crototricolpites* palynozone (Burdigalian to Langhian), early to middle Miocene, while the Pebas outcrop to the *Crassoretitriletes* palynozone (Langhian to Serravalian), middle Miocene. In addition, Wesselingh et al. (2006a) infer that Indiana covers the *Toxosoma carinatum* and *Diplodon indianensis* biozones (MZ4 and MZ5), corresponding to Langhian; Pebas is equivalent to *Dyris pebasensis* (MZ7), and Santa Elena to *Dyris lanceolatus* biozones (MZ8), both corresponding to Serravallian; and Buen Pasa is equivalent to *Diplodon indianensis* biozone (MZ5), Langhian, all restricted to the middle Miocene.

Based on the fossil and sedimentological records the paleoenvironment of Pebas system was characterized as lacustrine with marine influence (Hoorn, 1994b; Sheppard and Bate, 1980; Whatley et al., 1998; Wesselingh et al., 2002; Gingras et al., 2002). Additionally, Alvim et al. (2021) infer that freshwater conditions occur in the early Miocene, in the Pebas system, while in the middle and early late Miocene, oligohaline conditions predominated. Palynological studies and investigations on marine influence in the sites Nuevo Horizonte and Porvenir/Amazon, suggest a brackish environment, such as a lagoon, or a slightly confined infralittoral environment affected by freshwater in the late middle Miocene (Boonstra et al., 2015). On the other hand, Gross and Piller (2020), infer to nearby sites of the studied area (Porvenir/Amazon) that the salinity variations are related to groundwater influx.

4. Results

4.1. Qualitative and quantitative analysis of the ostracods in the studied sections

The ostracod recovery from the studied samples comprises a general assemblage of eight genera and twenty-two species. Among the genera identified (*Cyprideis*, *Perissocytheridea*, *?Macrocypris*, *Skopaeocythere*, *Cypria*, *Heterocypris*, *Pelocypris* and *?Penthesilenula*), *Cyprideis* is the most abundant and diverse with wide geographic distribution in the studied area occurring in the most samples; it corresponds to 92.5% of the total number of specimens. It is represented by fifteen species (Figs. 3–7) including three new ones: *Cyprideis soledadensis* sp. nov., *Cyprideis santaelenae* sp. nov., and *Cyprideis indianaensis* sp. nov. described and illustrated herein (Figs. 3 and 4). Twelve species were previously recorded in the Miocene of the Pebas and Solimões Formations (Table 1). Detailed information about the species distribution in the studied samples is show in Table 2. *Cyprideis caraionae* Purper and Pinto (1985) is the most abundant species while *Cyprideis sulcosigmoidalis* Purper (1979) is the most frequent in the studied outcrops. The genus *Perissocytheridea* is also frequent and abundant although occurs in less number than *Cyprideis* and is represent by the species *Perissocytheridea ornellasae* Purper (1979). Additional genera and species as ?*Macrocypris*, *Skopaeocythere tetrakanthos* Whatley et al., 2000, *Cypria aqualica* Sheppard and Bate (1980), *Heterocypris*, *Pelocypris zilchi* Triebel (1953) and *? Penthesilenula olivencae* (Purper, 1979) are rare and occur only at the Indiana outcrop (Fig. 2); the exception to *Skopaeocythere tetrakanthos* and other very small and rare specimens, which need future taxonomic investigation, that were registered in Santa Elena outcrop.

The species *Cyprideis anterospinosa*, *Cyprideis marginuspinosa*,

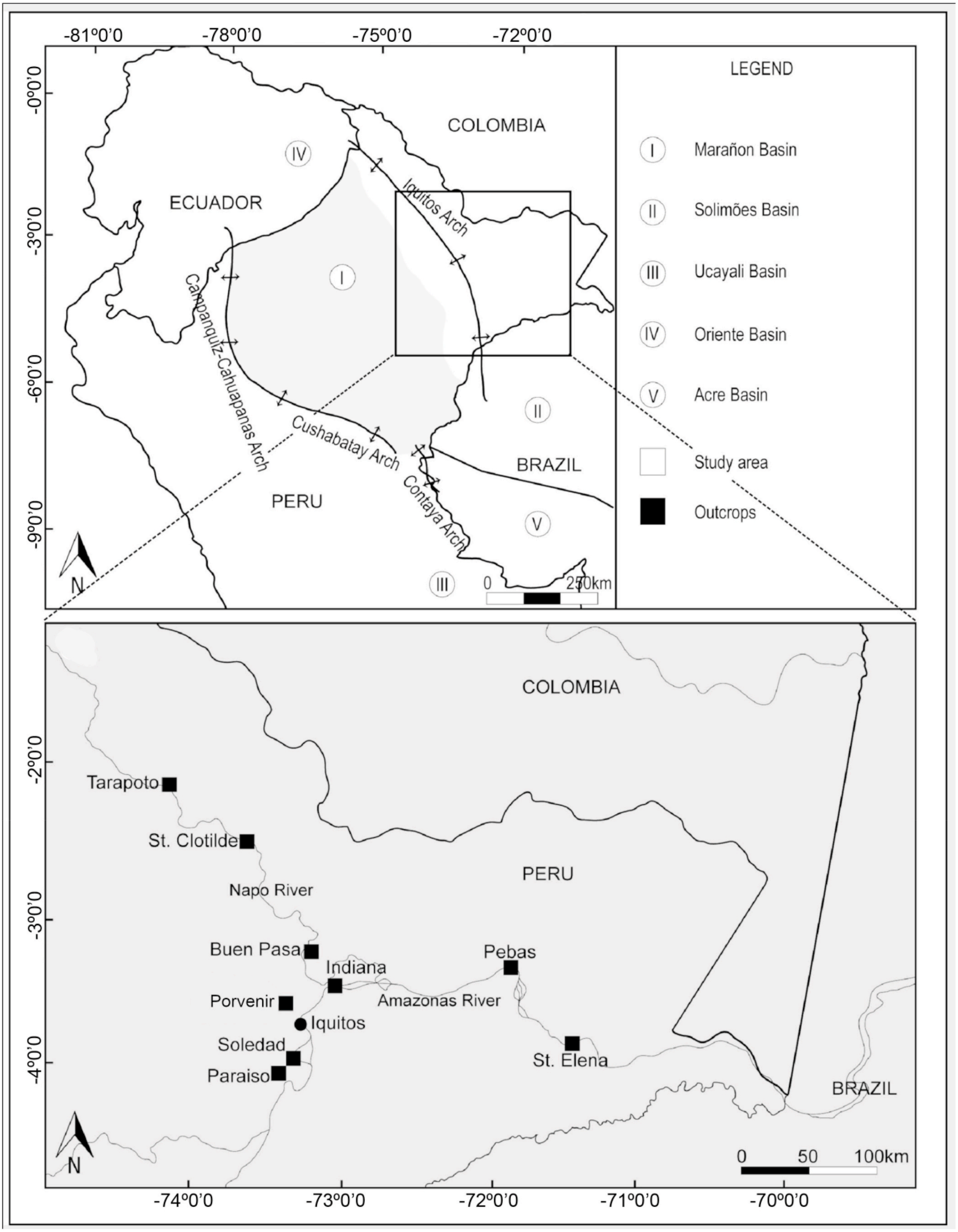

Fig. 1. Overview map of the Marañon Basin with structural highs and neighboring basins. The highlighted dashed area corresponds to the study area and studied localities.

Fig. 2. Distribution map of the species identified in the study area.

Cyprideis retrobispinosa, and *Cyprideis krsticae* are recorded herein for the first time in the Pebas Formation and are rare in the Solimões Formation (Table 1).

4.2. Systematic paleontology

Class Ostracoda Latreille, 1802.
Order Podocopida Sars, 1866.
Superfamily Cytheroidea Baird, 1850.
Family Cytherideidae Sars, 1925.
Subfamily Cytherideinae Sars, 1925.
Genus Cyprideis Jones, 1857.

Type-species. Candona *torosa* Jones (1850). Pleistocene Beds of Newbury Copford, England.

Cyprideis indianaensis sp. nov.

Diagnosis: Subrectangular species, dorsal margin slightly arched in

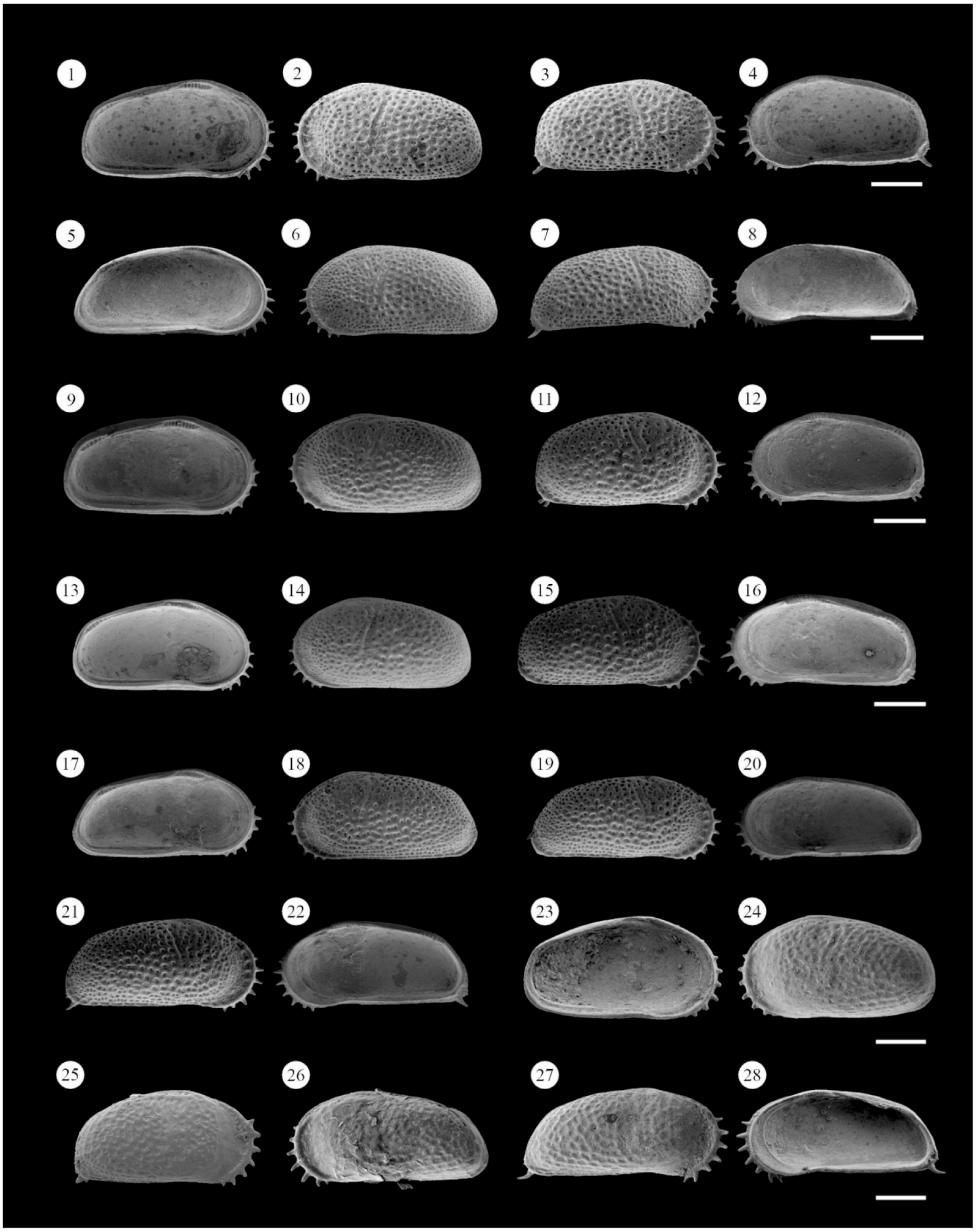

Fig. 3. 1–2. MPEG-902-M (paratype), female, left valve, inside view and external view; 3–4. MPEG-903-M (holotype), female, right valve, external view and inside view; 5–6. MPEG-904-M (paratype), male, left valve, inside view and external view; 7–8, MPEG-905-M (paratype), male, right valve, external view and inside view; 9–22. *Cyprideis soledadensis* sp. nov., 9–10. MPEG-906-M (holotype), female, left valve, inside view and external view; 11–12. MPEG-907-M (paratype), female, right valve, external view and inside view; 13–14. MPEG-908-M (paratype), Female, left valve, inside view and external view; 15–16. MPEG-909-M (paratype), female, right valve, external view and inside view; 17–18, MPEG-910-M (paratype), male, left valve, inside view and external view; 19–20. MPEG-911-M (paratype), male, right valve, external view and inside view; 21–22. MPEG-912-M (paratype), male, right valve, external view and inside view; Scale 200 μm. 23–28. *Cyprideis santaelenae* sp. nov., 23–24. MPEG-913-M (holotype), female, left valve, inside view and external view; 25. MPEG-986-M (holotype), female, right valve, external view; 26. MPEG-914-M (paratype), male, left valve, inside view and external view; 27–28. MPEG-915-M (paratype), male, right valve, external view and inside view; Scale 200 μm.

the anterodorsal region, anterior margin broad, thick marginal rib and with seven, exceptionally eight, very expressive spines in its margin. Three to four spines in the posteroventral region of RV, with the lowermost spine more developed than the others, absent in the LV. Vertical sulcus extending from the median dorsal margin to over 2/3 of the central region of the valve surface. Surface strongly reticulated in the most of the surface to punctuated in the extremities. Inner lamella moderately thick. Sexual dimorphism evident, males shorter and more elongated than females.

Etymology: In reference to the type-locality, Indiana.

Holotype: Female, RV (MPEG-903-M).

Paratypes: Female, LV (MPEG-902-M). Males, LV (MPEG-904-M), and RV (MPEG-905-M).

Type-locality: Indiana outcrop.

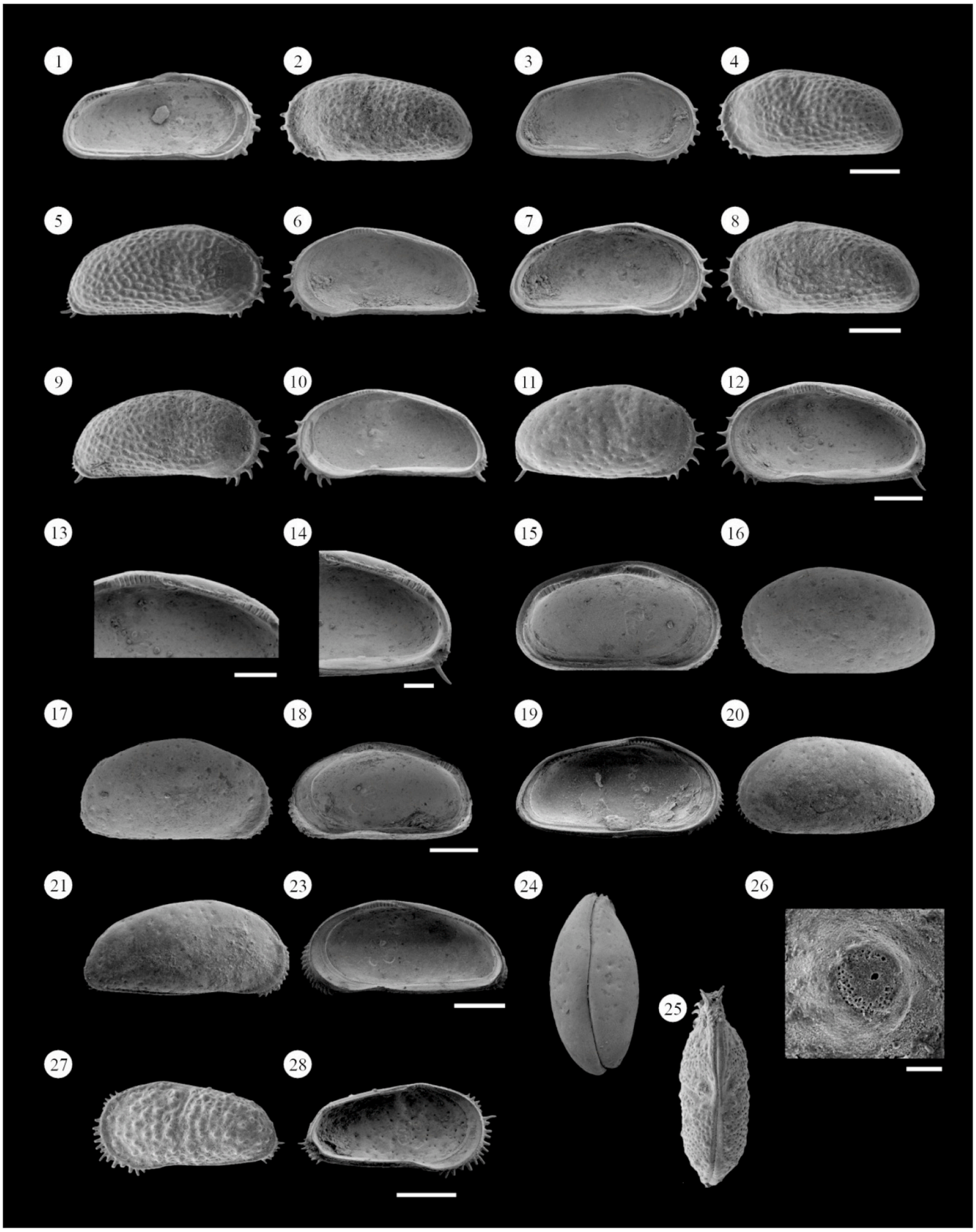

Fig. 4. 1–10. Cyprideis santaelenae sp. nov., 1–2. MPEG-916-M (paratype), male, left valve, inside view and external view; 3–4. MPEG-917-M (paratype), male, left valve, inside view and external view; 5–6. MPEG-918-M (paratype), male, right valve, external view and inside view; 7–8. MPEG-919-M (paratype), male, left valve, inside view and external view; 9–10. MPEG-920-M (paratype), male, right valve, external view and inside view. Scale 200 µm; 11–14. Cyprideis anterospinosa, 11–12. MPEG-857-M, female, right valve, external and inside view. Scale 200 µm; 13. MPEG-857-M, female, dorsal margin and hinge elements; 14. MPEG-857-M, female, right valve, inside view, posterior spines. Scale 100 µm; 15–23. Cyprideis caraionae, 15–16. MPEG-858-M, female, left valve, inside view and external view; 17–18. MPEG-859-M, female, right valve, external view and inside view; 19–20. MPEG-860-M, male, left valve, inside view and external view; 21–22. MPEG-861-M, male, right valve, external view and inside view; 23. MPEG-862-M, female, dorsal view; 24–27. Cyprideis inversa, 24. MPEG-863-M, male, dorsal view. Scale 100 µm; 25–26. MPEG-864-M, male, left valve, external view and inside view. Scale 200 µm; 27. detail of the pore canals of MPEG-864-M. Scale 5 µm.

Description: Subrectangular valves in lateral view; dorsal margin slightly arched in the anterodorsal region. Ventral margin with slight concavity in the anteroventral region of both valves. Anterior margin of both valves is broad, with a thick marginal rib with seven, exceptionally eight, expressive spines. Posterior margin truncated with a small projection in the posteroventral region in the RV of the females; elongated in the males. Three to four spines in the posteroventral region of RV, with the lowermost spine more developed than the others, absent in the LV. Vertical sulcus evident in both valves, extending from the median dorsal margin to over 2/3 of the central region of the valve surface. Females with large reticulation in both valves through the surface except in the extremities that are more punctuated; males reticulated only in the central region, and punctuate in the extremities of both valves. Internal view: Inner lamella moderately thick; hinge with positive elements in the RV, elongated anterior element with ten teeth, crenulated and short anteromedian elements, posteromedian element consists of a

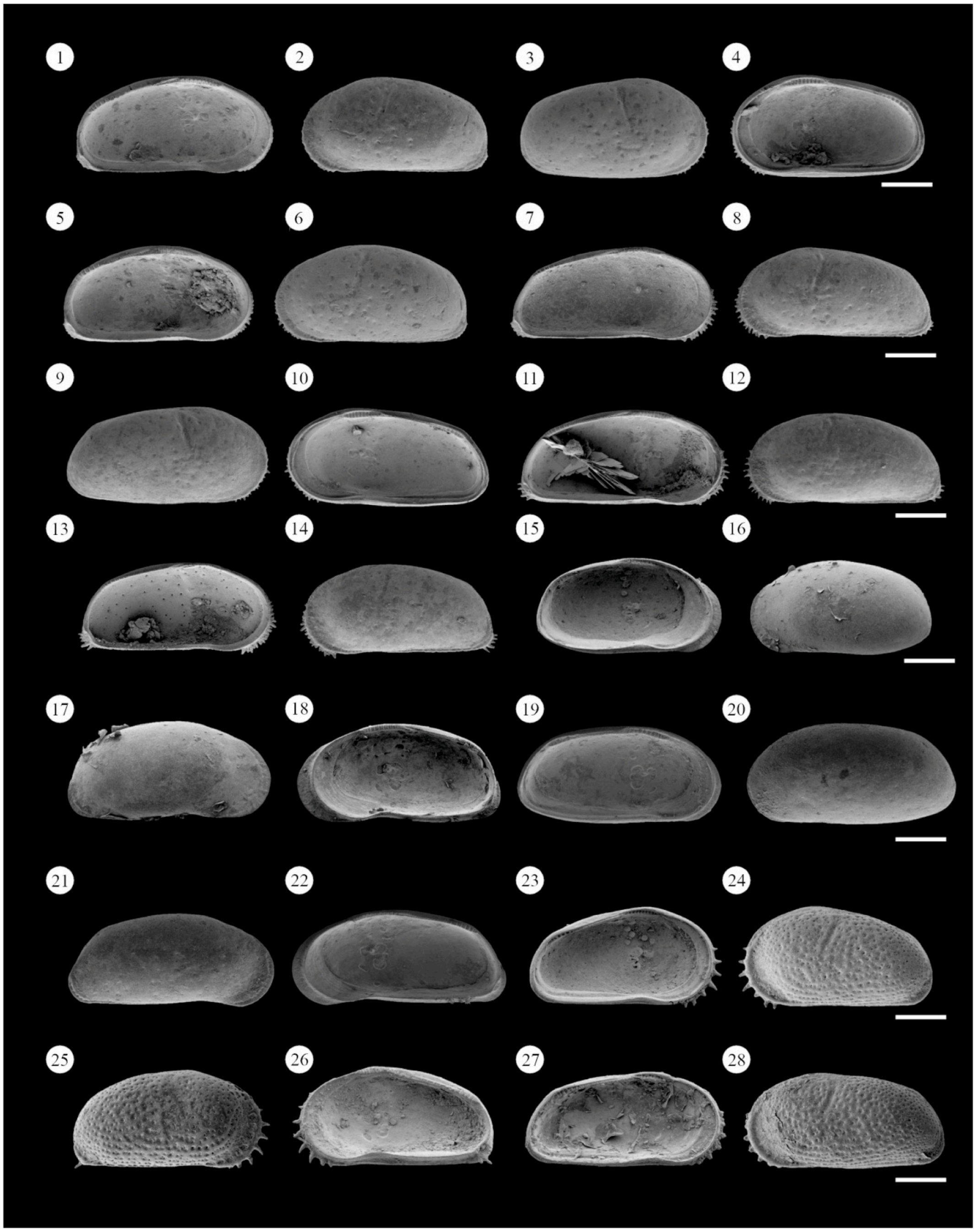

Fig. 5. 1–14. Cyprideis krsticae, 1–2. MPEG-865-M, female, left valve, inside view and external view; 3–4. MPEG-866-M, female, right valve, external view and inside view; 5–6. MPEG-867-M, female, left valve, inside view and external view; 7–8. MPEG-868-M, male, left valve, inside view and external view; 9–10. MPEG-869-M, male, right valve, external view and inside view; 11–12. MPEG-870-M, male, left valve, inside view and external view; 13–14. Cyprideis krsticae, MPEG-871-M, male, left valve, inside view and external view; 15–22. Cyprideis machadoi, 15–16. MPEG-872-M, female, left valve, inside view and external view; 17–18. MPEG-873-M, female, right valve, external view and inside view; 19–20. MPEG-874-M, male, left valve, inside view and external view; 21–22. MPEG-875-M, male, right valve, external view and inside view; 23–28. Cyprideis marginuspinosa, 23–24. MPEG-876-M, female, left valve, inside view and external view; 25–26. MPEG-877-M, female, right valve, external view and inside view; 27–28. MPEG-878-M, male, left valve, inside view and external view; All scales: 200 μm.

long crenulated bar, posterior element with six teeth; normal sieve type pores; hinge of the LV with complementary elements. Central muscle scars composed of four adductor and a V-shaped frontal scar; fulcral point almost imperceptible as well as the two mandibular impressions. Strong sexual dimorphism, with females more inflated than males that are more elongated with a pointed posterior margin.

Occurrence: Outcrops Indiana (T350) and, Pebas (T421) both the bank of Amazonas River, and Tarapoto (T859), in the bank of Napo River, Iquitos, Peru.

Material: One hundred thirty-six valves and ten carapaces.

Dimensions (mm): MPEG-903-M (holotype), female, RV: L: 0.73, H: 0.39; MPEG-902-M (paratype), female, LV: L: 0.76, H: 0.41; MPEG-904-M (paratype), male, LV: L: 0.80, H: 0.39; MPEG-905-M (paratype), male, RV: L: 0.76, H: 0.35.

Remarks: Cyprideis *indianaensis* sp. nov is similar to *Cyprideis graciosa* (Purper, 1979) differing in the contour, which is more subrectangular in the species herein described and in the ornamentation that is more reticulated than punctuated comparing to *C. graciosa.*

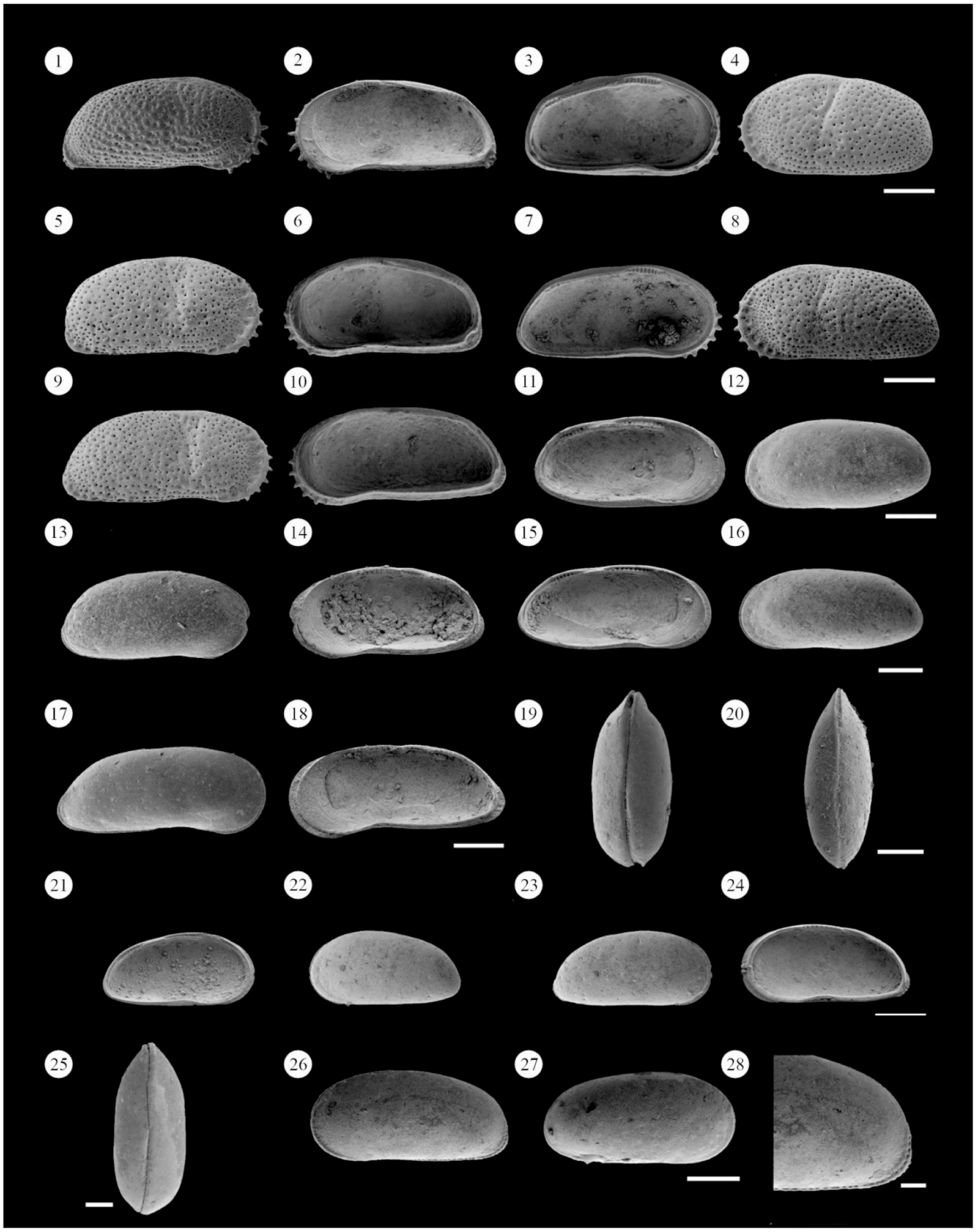

Fig. 6. 1–2. Cyprideis marginuspinosa, 1–2. MPEG-879-M, male, right valve, external view and inside view; 3–10. Cyprideis minipunctata, 3–4. MPEG-880-M, female, left valve, inside view and external view; 5–6. MPEG-881-M, female, right valve, external view and inside view; 7–8. MPEG-882-M, male, left valve, inside view and external view; 9–10. MPEG-883-M, male, right valve, external view and inside view; 11–24. Cyprideis multiradiata, 11–12. MPEG-884-M, female, left valve, inside view and external view. Scales: 200 μm. 13–14. MPEG-885-M, female, right valve, external view and inside view; 15–16. MPEG-886-M, male, left valve, inside view and external view; 17–18. MPEG-887-M, male, right valve, external view and inside view; 19. MPEG-888-M, female, dorsal view; 20. MPEG-889-M, male, dorsal view. Scale 200 μm; 21–22. MPEG-890-M, left valve, inside view and external view, juvenile; 23–24. MPEG-891-M, right valve, external view and inside view, juvenile; 25–28. Cyprideis paralela, MPEG-892-M, 25. female, dorsal view. Scale 100 μm; 26. female, left valve and external view; 27. female, right valve and external view; 28. detail of the posterior margin. Scale 50 μm.

Besides the differences in the ornamentation, the well-developed posteroventral spine of both valves in *C. graciosa*, is absent in the LV of the study material; it is present only in the right valve.

Cyprideis indianaensis sp. nov. is also similar to *Cyprideis ituiae* Gross et al. (2014) in the outline, however the species described herein has the dorsal margin more arched, marked in dorsomedian portion by the sulcus, with more evident ventral incurvature in both valves and with the posterior cardinal angles less developed; anterior region without the typical distally broadened and idented antero-marginal denticles and the uppermost and smallest one cone-shaped spines present in *C. ituiae*; the anteromarginal spines in *C. indianaensis* sp. nov. are finer than in the *C. ituiae* and has one well developed posteroventral spines in the RV, absent in *C. ituiae*. Anteromarginally and posteroventrally with a discreet rib and flange not robust as in *C. ituiae*. Similarities between *Cyprideis indianaensis* and *C. soledadensis* is discussed in the *C. soledadensis* remarks.

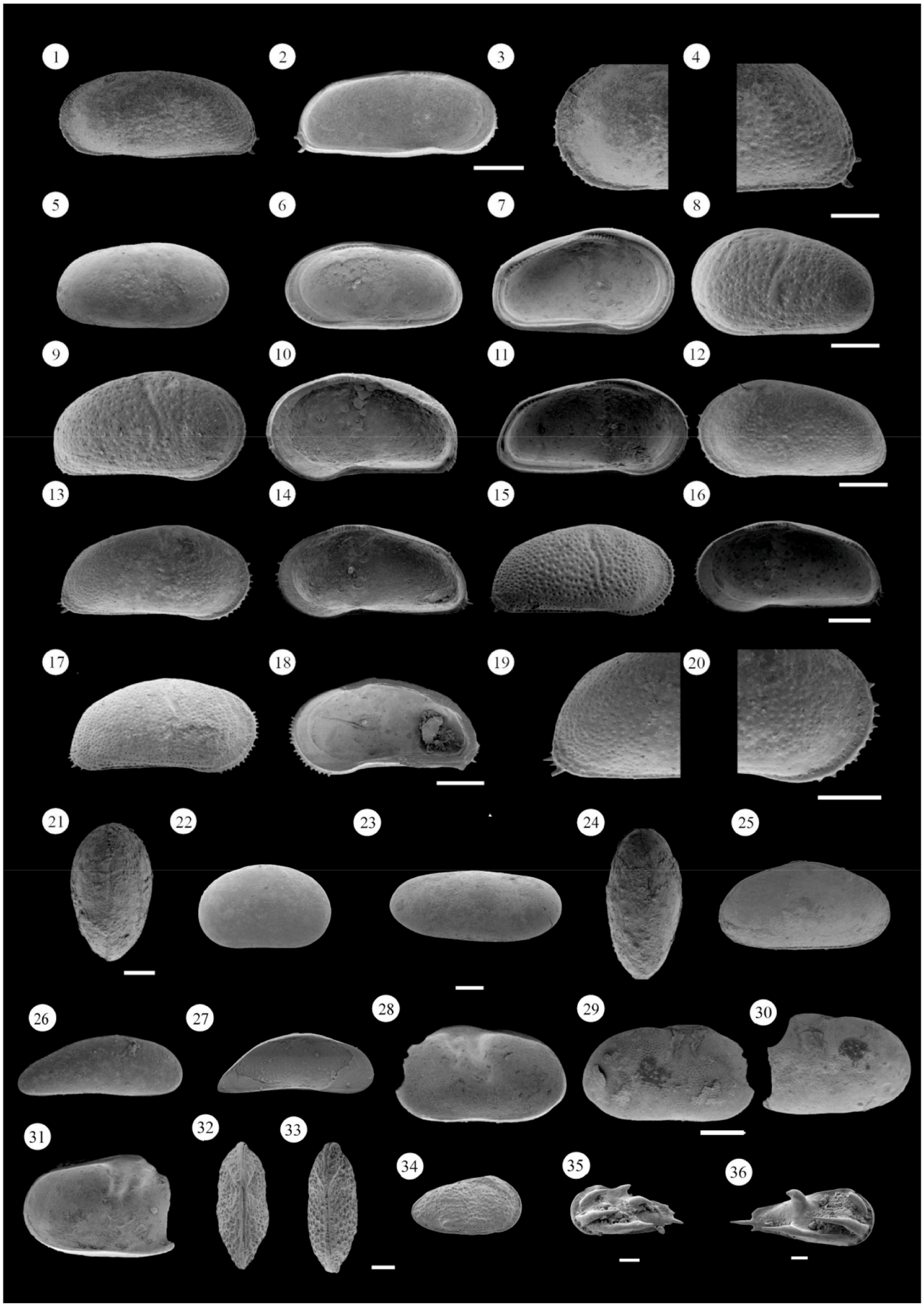

Fig. 7. 1–4. *Cyprideis retrobispinosa*, MPEG-894-M, 1–2. male, left valve, external view and inside view. Scale 200 μm; 3. detail of the anterior margin. Scale 100 μm; 4. detail of the posterior margin; 5–6. *Cyprideis simplex*, MPEG-895-M, male, right valve, external view and inside view; 7–20. *Cyprideis sulcosigmoidalis*, 7–8. MPEG-896-M, female, left valve, inside view and external view; 9–10. MPEG-897-M, female, right valve, external view and inside view; 11–12. MPEG-898-M, male, left valve, inside view and external view. Scale 200 μm. 13–14. MPEG-899-M, male, right valve, external view and inside view; 15–16. MPEG-900-M, male, right valve, external view and inside view, 17–18. MPEG-901-M, male, right valve, external view and inside view. Scale 200 μm; 19. detail of the posterior margin of MPEG-899-M; 20. detail of the anterior margin of MPEG-899-M. Scale 100 μm. 21–22. *Cypria aqualica*, 21. MPEG-921-M, dorsal view; 22. MPEG-987-M, right valve, external view; 23. ?*Penthesilenula olivencae*, MPEG-988-M, left valve, external view. Scale 100 μm; 24–25. *Heterocypris* sp., MPEG-923-M, dorsal view and right valve, external view. Scale 200 μm; 26–27. ?*Macrocypris* sp., MPEG-924-M, right valve, external view; 27- MPEG-989-M, left valve, internal view. Scale 100 μm; 28–31. *Pelocypris zilchi*, 28–29. MPEG-925-M, right valve, inside view and external view; 30–31. MPEG-926-M, left valve, external view and inside view. Scale 500 μm; 32–34. *Perissocytheridea ornellasae*, 32. MPEG-923-M, female, dorsal view; 33. MPEG-893-M, male, dorsal view; 34. MPEG-990-M, female, right valve external view. Scale 100 μm; 35–36. *Skopaecythere tetrakantos*, 35. MPEG-928-M, left valve, external view, 36. MPEG-991-M, right valve, external view. Scale 100 μm.

Table 1
Cyprideis species identified in the study area with previous recorded in the Pebas Formation (Peru) and in the Solimões Formation (Brazil).

	C. anterospinosa	C. caraionae	C. inversa	C. krsticae	C. machadoi	C. marginuspinosa	C. minipunctata	C. multiradiata	C. paralela	C. retrobispinosa	C. simplex	C. sulcosigmoidalis
Pebas Formation	*	X	X	*	X	*	X	X	X	*	X	X
Solimões Formation	X	X	X	X	X	X	X	X	X	X	X	X

Species with (*) have the first occurrence in the Pebas Formation from the studied material.

Table 2
Number of specimens per species recovered in the studied samples (number of samples are the same mentioned by Wesselingh et al., 2002).

Species	Outcrops and samples														Total
	Pebas	St. Elena	Indiana					Soledad	Paraiso	B.Pasa		Tarapoto	St.Clotilde	Porvenir/Momon	
	(T421)	(T488)	(T346)	(T347)	(T348)	(T349)	(T350)	(T821)	(T808)	(T898)	(T899)	(T859)	(T881)	(T832)	
C. anterospinosa		1													1
C. caraionae				35	126		179				65	71	343		819
C. inversa	5	13		11									19		48
C. krsticae			10		16	15				18	20	53			132
C. machadoi	115	12						30							157
C. marginuspinosa		61													61
C. minipunctata	167														167
C. multiradiata	10	174													184
C. paralela	16	4						8							28
C. retrobispinosa								1							1
C. simplex								5							5
C. sulcosigmoidalis	80	67		8			6		8		48		65		282
C. indianaensis sp. nov.	15						53					79			147
C. soledadensis sp. nov.								154							154
C. santaelenae sp. nov.		38													38
Cypria aqualica					9										9
?Penthesilenula. olivencae							1								1
Heterocypris sp.1					2										2
?Macrocypris				2											2
Pelecocypris. zilchi			2												2
Perissocytheridea ornellasae	5	30		50			53		5				20		163
S. tetrakanthos		3													3

Diagnosis: *Cyprideis* species of subrectangular shape, with punctuated surface, reticulated in the central portion. Dorsal margin slightly sinuous and slightly concave marked by the sulcus. Ventral margin straight in the LV, with an oral incurvature evident in the RV. Anterior margin with an evident rib rounded in the border and seven to eight spines spaced along its margin. Short, and sinuous sulcus extending to 1/3 of the valve.

Etymology: In reference to the type-locality Soledad.

Holotype: Female, RV (MPEG-906-M).

Paratypes: Females, LV (MPEG-907-M), LV (MPEG-908-M), and RV (MPEG-909-M). Males, LV (MPEG-910-M), RV (MPEG-911-M), and RV (MPEG-912-M).

Type-locality: Soledad outcrop.

Description: Subrectangular species in side view; the dorsal margin slightly sinuous and slightly concave marked by the sulcus. Ventral margin of both valves almost straight, with a slight concavity in the anteroventral region of the RV. The anterior margin of both valves is rounded with an evident rib rounded in the border. The presence of spines on the anterior margin of both valves is variable, ranging from seven to eight spines. In some specimens these are evident and expressive, while in others they are not so expressive. Posterior margin of the RV with a more developed inferior spine in the posteroventral region. In some valves, there is the development of a second spine in the posteroventral region or, they are absence (Figs. 3 and 11; 3,15). Surface moderately reticulate in the central portion to punctuated at margins. In both valves there is a slight sulcus in the middle-dorsal region extending to 1/3 of the valve. Internal view: hinge with positive elements in the RV, elongated anterior element with nine teeth, short antero-median element, posteromedian element consists of a long crenulated bar, posterior element with six teeth; hinge elements are complementary in the LV. Inner lamella moderately thick. Central muscle scars with four adductor muscle impressions, a V-shaped frontal impression; fulcral point almost imperceptible as well as the two mandibular impressions. Strong sexual dimorphism, with females more inflated than the males that are more elongated with a pointed posterior margin.

Occurrence: Outcrops Soledad (T821), and St. Clotilde (T881), banks of the Amazon River, Iquitos, Peru.

Material: One hundred and fifty valves and four carapaces.

Dimensions (mm): MPEG-906-M (holotype), female, RV: L: 0.86, H: 0.46; MPEG-907-M (paratype), female, LV: L:0.89, H: 0.48; MPEG-908-M (paratype), female, LV: L: 0.81, H: 0.44; MPEG-909-M (paratype), female, RV: L: 0.89, H: 0.46; MPEG-910-M (paratype), male, LV: L: 1.02, H: 0.51; MPEG-911-M (paratype), male, RV: L: 0.97, H: 0.46; MPEG-912-M (paratype), male, RV: L: 0.98, H: 0.48.

Remarks: Cyprideis *soledadensis* sp. nov. is similar to *Cyprideis indianaensis* sp. nov in the presence and position of the anterior spines of both valves; although *Cyprideis soledadensis* sp. nov. has a more robust carapace, with almost parallel sides and the ventral margin is straighter, mainly in the LV, than in *C. indianaensis* sp. nov.; these species differ also in the posteroventral spines where *C. soledadensis* do not have the longer and fine posteroventral spine, with two shorter instead, when present; the dorsal sulcus is shorter in *C. soledadensis* than in *C. indianaensis*. Some specimens of this species was classified in *Cyprideis graciosa* (Purper (1979) by Muñoz-Torres et al. (1998), Whatley et al. (1998) and Linhares et al. (2011), and in *Cyprideis* aff. *graciosa* by Gross et al. (2014), and Medeiros et al. (2019) – see synonym list. However, *C. soledadensis* sp. nov. differs significantly from *C. graciosa* in many aspects, as in the outline that is more subretangular than *C. graciosa*, in the ornamentation that is more reticulated and in the marginal posteroventral spines that is absent in the LV of the *C. soledadensis* sp. nov.

Geographic and stratigraphic occurrence: Borehole 1AS-4a-AM (Whatley et al., 1998; Muñoz-Torres et al., 1998), 1AS-31-AM, close to the Ituí River, southwest of the Amazonas state (Linhares et al., 2011); 1AS-33-AM, Curuçá river, Amazonas state (Medeiros et al., 2019), 1AS-10-AM, close to the Ituí River. Brazil. Solimões Formation, Miocene; many localities from Peru and Colombia (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Cyprideis santaelenae sp. nov.

Diagnosis: Subrectangular species in lateral view. Dorsal margin slightly concave in the middle, turned downwards in to the posterior region. Anterior margin rounded with an evident rib and seven evident marginal spines. Posterior margin with a lower spine, sometimes well-developed, and curved in the posteroventral region of the RV. Four to five grouped spines in the posteroventral region can occur. Moderately reticulated in the posterior region and smoother in the anterior region; sulcus shallow and discreet in the middle-dorsal region.

Etymology: In reference to the type-locality Santa Elena outcrop.

Holotype: Female, RV (MPEG-913-M), LV (MPEG-986-M).

Paratypes: Males, LV (MPEG-914-M), RV (MPEG-915-M), LV (MPEG-916-M), RV (MPEG-918-M), LV (MPEG-919-M) and, RV (MPEG-920-M).

Type-locality: Santa Elena outcrop.

Description: Subrectangular species in lateral view. Dorsal margin slightly concave, turned downwards in to the posterior region. Ventral margin with subtle anteroventral concavity in the RV. Anterior margin of both valves rounded with an evident rib, with seven evident and expressive spines along its margin. Posterior margin of the RV with four to five spines grouped in the posteroventral region, in some valves (Figs. 4–6 and 9–10), where the upper ones are shorter and discreet and the lower one is curved and longer than the others, mainly in the males. Surface moderately reticulated in the posterior region to smooth in the anterior region. Sulcus shallow and discreet in the middle-dorsal region. Internal view: hinge with positive elements in the RV, elongated anterior element with nine teeth, short anteromedian element, posteromedian element consists of a long crenulated bar, posterior element with six teeth; hinge elements are complementary in the LV. Inner lamella moderately thick. Central muscle scars with four adductor muscle impressions, a V-shaped frontal impression; fulcral point almost imperceptible as well as the two mandibular impressions. Strong sexual dimorphism, with females more inflated than males which are more elongated with a pointed posterior margin.

Occurrence: Outcrop Santa Elena (T488), bank of the Amazon River, Iquitos, Peru.

Material: Thirty-eight valves.

Dimensions (mm): MPEG-913-M (holotype), female, LV: L: 0.77, H: 0.43; MPEG-986-M (holotype), female, RV: L: 0.79, H: 0.41; MPEG-914-M (paratype), male, LV: L: 0.92, H: 0.45; MPEG-915-M (paratype), male, RV: L: 0.90, H: 0.42; MPEG-916-M (paratype), male, LV: L: 0.91, H: 0.45; MPEG-917-M (paratype), male, LV: L: 0.90, H: 0.45; MPEG-918-M (paratype), male, RV: L: 0.85, H: 0.41; MPEG-919-M (paratype), male, LV: L: 0.90, H: 0.45; MPEG-920-M (paratype), male, RV: L: 0.87, H: 0.43.

Remarks: This species is similar to *C. soledadensis* sp. nov. in the arrangement of spines on the anterior and posterior margins; however, *C. santaelenae* sp. nov. differs from this species by the ornamentation that is smoother mainly in the anterior region, in addition to the more prominent and thicker marginal spines, mainly in the RV of the males. Gross et al. (2014) illustrated similar specimens (Pl. 7, Figs. 6–11) that were grouped in *Cyprideis* aff. *graciosa* but these specimens are much more reticulated in the surface, mainly in the posterior region, cardinal angles are more prominent (mainly in the males), and with a longer, stronger and more evident antero and posteroventral spines than those from *Cyprideis santaelenae* sp. nov.

Cyprideis santaelenae sp. nov. is also similar to *Cyprideis marginuspinosa*, however this new species is smaller, with a smoother ornamentation, mainly in the anterior region to slightly reticulated in the posterior region. *Cyprideis marginuspinosa* has a strongly punctuated ornamentation for all surface, and the median sulcus that is deeper and more evident than in *Cyprideis santaelenae* sp. nov.

Cyprideis anterospinosa Purper and Ornellas, 1991.

Occurrence: Outcrop St. Elena (T488), bank of Amazonas River, Iquitos, Peru, Pebas Formation (Miocene), Marañon Basin.

Material: one valve.

Dimensions (mm): MPEG-857-M, female, LV: L: 0.84, H: 0.46.

Remarks: *Cyprideis anterospinosa* Purper and Ornellas, 1991 has a rare record in the Neogene strata from western Amazonia. The studied material is similar to the type-material illustrated by Purper and Ornellas (1991) but it is more inflated and with a more punctuated surface; postero ventral spine is finer and longer. Although just one valve was recovered, we expand the geographic distribution of the species, as it was so far restricted to strata of the Solimões Formation, in Brazil.

Geographic and stratigraphic occurrence: Borehole: 1AS-32-AM (122 m), Solimões Basin, Brazil (Purper and Ornellas, 1991), Solimões Formation, Miocene.

Cyprideis caraionae Purper and Pinto, 1985.

Occurrence: Outcrops Indiana (T347 and T348), St. Clotilde (T881), Tarapoto (T859) and Buen Pasa (T898 and T899), Iquitos, Peru.

Material: seven hundred and fifty-five valves and sixty-four carapaces.

Dimensions: MPEG-858-M, female, LV: L: 0.83, H: 0.49; MPEG-859-M, female, RV: L: 0.79, H: 0.44; MPEG-860-M, female, C: L: 0.82, H: 0.48, W: 0.39; MPEG-861-M, male, LV: L: 0.84, H: 0.44; MPEG-862-M, male, RV: L: 0.84, H: 0.41.

Remarks: Besides the specimens studied herein are not well-preserved they share the same characteristics of the type-material of *C. caraionae* Purper and Pinto, 1985 as to the most illustration cited in the synonym list.

Geographic and stratigraphic occurrence: Boreholes: 1AS-33-AM, southwest of the locality of Benjamin Constant (Purper and Pinto, 1985); 1AS-31-AM, next to the Ituí River, southwest of the Amazonas state (Linhares et al., 2011); 1AS-33-AM, Curuçá River, District of Canamã, Municipality of Atalaia do Norte (Medeiros et al., 2019); 1AS-7D-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Brazil. Solimões Formation, Miocene; Outcrops: Iquitos and Pebas, Peru (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Cyprideis inversa (Purper and Pinto, 1983).

Occurrence: Outcrops of Indiana (T347), bank of Amazonas River, Iquitos, Peru.

Referred material: forty-five valves and three carapaces.

Dimensions (mm): MPEG-863-M, male, C: L: 0.65, H: 0.30, W: 0.15; MPEG-864-M, female, LV: L: 0.62, H: 0.32.

Remarks: The specimens of *C. inversa* identified in the present study have variations in the ornamentation, from a more punctuated surface, across the entire valve, as illustrated by Muñoz-Torres et al. (1998), Whatley et al. (1998), and Gross et al. (2014) to a less punctuated surface with small and evident tubercles, as illustrated by Purper and Pinto (1983), Linhares et al. (2011, 2017), Gross et al. (2014), and Medeiros et al. (2019). Despite these variations in ornament, the specimens match with the diagnosis by Purper and Pinto (1983).

Geographic and stratigraphic occurrence: Boreholes 1AS-32-AM, northwest of the Amazonas state (Purper and Pinto, 1983), 1AS-31-AM, next to the Ituí River, southwest of the Amazonas state (Linhares et al., 2011), 1AS-10-AM, Sucuriju, next to the Ituí River, southwest of Benjamin Constant (Gross et al., 2014), 1AS-33-AM (Medeiros et al., 2019), and 1AS-7D-AM, next to the Quixitó River, northwest of the Amazonas state (Linhares et al., 2017); 1AS-7D-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Brazil. Solimões Formation, Miocene; outcrops in the Pebas (Whatley et al., 1998; Muñoz-Torres et al., 1998) and Porvenir localities, in the area of the Iquitos Arch (Gross and Piller, 2020), in Peru; Villareal and Los Chorros, Colombia (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Cyprideis krsticae Purper and Pinto, 1985.

Occurrence: Outcrops of Indiana (T346, T347, T348, and T349), bank of the Amazonas River; Buen Pasa (T898 and T899) and Tarapoto (T859), the bank of the Napo River, all located in Iquitos, Peru.

Material: one hundred eighteen valves and fourteen carapaces.

Dimensions (mm): MPEG-865-M, female, LV: L:0.82, H: 0.44; MPEG-866-M, female, RV: L: 0.87, H: 0.48; MPEG-867-M, female, LV: L: 0.82, H: 0.44; MPEG-868-M, male, LV: L: 0.94, H: 0.45; MPEG-869-M, male, RV: L: 0.94, H: 0.48; MPEG-870-M, male, LV: L: 0.90, H: 0.43; MPEG-871-M, male, LV: L: 0.94, H: 0.47.

Remarks: The specimens identified herein are similar to the type-material of *C. krsticae* Purper and Pinto, 1985, however with the development of more expressive spines on the anterior and posterior margins of both valves. Purper and Pinto (1985) mentioned the occurrence of small spines at the ends of the valves, however they do not mention the degree of their development or possible morphological variation in the species, as was observed in the present material; in the analyzed material we observed specimens with one or two expressive spines in the posteroventral region of the LV; however, it is observed only among specimens of the Tarapoto outcrop. This species has a rare record in the Solimões Formation (Purper and Pinto, 1985), therefore, the species is no longer restricted to the Solimões Formation, having now the first record in the Pebas Formation.

Geographic and stratigraphic occurrence: Borehole 1AS-4-AM, northwest of the Amazonas state (Purper and Pinto, 1985). Solimões Formation, Miocene.

Occurrence: Outcrops of Pebas (T421), Soledad (T821), and St. Elena (T488), all located on the banks of the Amazonas River, Iquitos, Peru.

Material: one hundred fifty-three valves and four carapaces.

Dimensions (mm): MPEG-872-M, female, LV: L: 0.82, H: 0.48; MPEG-873-M, female, RV: L: 1.14, H: 0.58; MPEG-874-M, male, LV: L: 1.09, H: 0.54; MPEG-875-M, male, RV: L: 1.08, H: 0.51.

Remarks: This species was originally described as *Chlamydocytheridea machadoi* by Purper (1979), and transferred later to the genus *Cyprideis* by Muñoz-Torres et al. (1998). The specimens recovered herein have the typical characteristics of the type-species. Muñoz-Torres et al. (1998), corroborated by Whatley et al. (1998), highlighted variations in the curvature of the anterior margin in the RV, in the degree of development of the flange, that may or may not be present and in the shape and contour of the anterior margin of the LV. Such variations were not observed in the present material, except for the intermediate extension of the flange, as mentioned by Gross et al. (2014).

Geographic and stratigraphic occurrence: In Brazil, it occurs in the boreholes: CPCAN–III–São Paulo de Olivença, CPCAN–II–Porerê and 1AS-32-AM, all northwest of the Amazonas state (Purper, 1979; Purper and Pinto, 1983); 1AS-31-AM and 1AS-10-AM, both near the Ituí River, Amazonas state (Linhares et al., 2011; Gross et al., 2014); 1AS-7D-AM, near the Quixitó River, northwest of the Amazonas state and 1AS-33-AM, southwest of the locality of Benjamin Constant, Curuçá River, District of Canamã, Atalaia do Norte, Amazonas state (Linhares et al., 2017; Medeiros et al., 2019); 1AS-7D-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022) and outcrops the southeast of Eirunepé, Morada Nova, and Pau D'Alho, Amazonas state (Wesselingh and Ramos, 2010; Gross et al., 2013). Brazil. Solimões Formation, Miocene; Outcrops: Pichua, in Marañon River; Pebas, Santa Júlia, Iquitos (Whatley et al., 1998; Muñoz-Torres et al., 1998), and Porvenir in area of Iquitos Arch (Gross and Piller, 2020), Peru; in Colombia, outcrops of Los Chorros, Villareal, and Salado (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Occurrence: Outcrop St. Elena (T488), bank of the Amazonas River, Iquitos, Peru **Material:** fifty-six valves and five carapaces.

Dimensions (mm): MPEG-876-M, female, LV: L: 0.89, H: 0.50; MPEG-877-M, female, RV: L: 0.93, H: 0.50; MPEG-878-M, male, LV: L: 1.06, H: 0.52; MPEG-879-M, male, RV: L: 1.06, H: 0.52.

Remarks: *C. marginuspinosa* is similar to the type-material described by Purper and Ornellas (1991), although the studied specimens have anterior cardinal angle more evident, mainly in the LV, with the dorsal margin turning downwards in the posterior region. This species has a rare record in the Solimões Formation, so it is no longer restricted to this formation, having now the first record for the Pebas Formation, in Peru.

Geographic and stratigraphic occurrence. Borehole: 1AS-32-AM, Solimões Basin, Brazil (Purper and Ornellas, 1991); Solimões Formation, Miocene.

Occurrence: Outcrop of Pebas (T421), bank of the Amazonas River, Iquitos, Peru.

Material: one hundred fifty-five valves and twelve carapaces.

Dimensions (mm): MPEG-880-M, female, LV: L: 0.79, H: 0.43; MPEG-881-M, female, RV: L: 0.75, H: 0.39; MPEG-882-M, male, LV, L: 0.90, H: 0.44; MPEG-883-M, male, RV: L: 0.88, H: 0.41.

Remarks: The specimens recovered in the Iquitos region share the same characteristics as the type-material described by Purper and Ornellas (1991); this species is one of the *Cyprideis* from the Neogene of Amazonia that does not present significant morphological variations, with a very typical ornamentation pattern being also similar to the specimens recovered from previous studies by Muñoz-Torres et al. (1998), Gross et al. (2014- Fig. 6/e; Pl. 7; Figs. 32–33; Pl. 8, Figs. 1–9), Linhares et al. (2017), and Linhares and Ramos (2022).

Geographic and stratigraphic occurrence: In Brazil, the species occurs in the boreholes 1AS-32-AM and 1AS-7D-AM (near the Quixitó River), both northwest of the Amazonas state (Purper and Ornellas, 1991; Linhares et al., 2017); 1AS-10-AM, Sucuriju, near the Ituí River, southwest of the Amazonas state (Gross et al., 2014); 1AS-7D-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Solimões Formation, Miocene; Outcrops: Pebas and Pichua, Peru (Sheppard and Bate, 1980; Whatley et al., 1998; Muñoz-Torres et al., 1998); and Villareal, Colombia (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Occurrence: Outcrops of Pebas (T421) and St. Elena (T488), both at the bank of the Amazonas River, Iquitos, Peru.

Material: one hundred and eighty-four valves.

Dimensions (mm): MPEG-884-M, female, LV: L: 0.81, H: 0.41; MPEG-885-M, female, RV: L: 0.78, H: 0.38; MPEG-886-M, male, LV: L: 0.85, H: 0.39; MPEG-887-M, male, RV: L: 0.82, H: 0.36; MPEG-888-M, female, C: L: 0.83, W: 0.36; MPEG-889-M, male, C: L: 0.81, W: 0.29; MPEG-890-M, juvenile, LV: L: 0.64, H: 0.32; MPEG-891-M, juvenile, RV: L: 0.62, H: 0.30.

Remarks: The specimens analyzed herein share the same morphological characteristics as the type-material, originally identified as *Amazonacytherideа multiradiata* by Purper (1979). Purper and Pinto (1985) suggest an evolutionary trend for the species based on the variations in internal morphological characteristics and in the contour of the valves. These variations were not observed in the specimens identified in the present study. Muñoz-Torres et al. (1998) and Whatley et al. (1998), placed this species into the synonymy of *Cyprideis olivencai* (Purper, 1979), as well as *C. paralela* (Purper, 1979) and *C. simplex* (Sheppard and Bate, 1980). However, according to Gross et al. (2014) these species form a distinct lineage and *C. multiradiata* is a valid taxon. We agree with the taxonomic position proposed by Gross et al. (2014) as the specimens related to *Cyprideis multiradiata*, *C. paralela* and *C. simplex* recovered from the studied material show clear differences between then.

Geographic and stratigraphic occurrence: In Brazil, it occurs in the boreholes CPCAN–III–São Paulo de Olivença, CPCAN-I-Tamanduá, 1AS-32-AM, 1AS-7D-AM, near the Quixitó River, all northwest of the Amazonas state (Purper, 1979; Purper and Pinto, 1985; Linhares et al., 2017); 1AS-33-AM, southwest of Benjamin Constant, Curuçá River, Distrito de Canamã, Atalaia do Norte, Amazonas state (Medeiros et al., 2019); 1AS-10-AM, Sucuríju, near of Ituí River, southwest of the Amazonas state (Gross et al., 2014); 1AS-7D-AM, 1AS-31-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Solimões Formation, Miocene; Outcrops: Pebas, Santa Julia (Whatley et al., 1998; Muñoz-Torres et al., 1998) and Porvenir in area of Iquitos Arch (Gross and Piller, 2020) Peru; Mocagua, Los Chorros and Buenos Aires, Colombia (Whatley et al., 1998; Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Occurrence: Outcrops of Pebas (T421), Soledad (T821), and St. Elena (T488), all located on the banks of the Amazonas River, Iquitos, Peru.

Material: twenty-eight valves.

Dimensions (mm): MPEG-892-M, C: L: 0.65, H: 0.32, W: 0.26.

Remarks: The specimens from the studied samples are similar to the material illustrated and described by Purper (1979). They share the same characteristic from the material illustrated by Gross et al. (2014, Figs. 36–45), however the eye spot was not observed as mentioned by Purper (1985) and Gross et al. (2014) and it has a distinct posteroventral marginal punctuation (Fig. 6–28).

Geographic and stratigraphic occurrence: In Brazil, the species occurs in the boreholes CPCAN–III–São Paulo de Olivença, CPCAN-I-Tamanduá, 1AS-32-AM, 1AS-7D-AM, near the Quixitó River, northwest of the Amazonas state (Purper, 1979; Purper and Pinto, 1983, 1985; Linhares et al., 2017); 1AS-10-AM, Sucuríju, near Ituí River, southwest of the Amazonas state (Gross et al., 2014); 1AS-7D-AM Quixitó River, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Solimões Formation, Miocene; Outcrop: Porvenir, in area of Iquitos Arch, Peru (Gross and Piller, 2020). Pebas Formation, Miocene.

Occurrence: Outcrop Soledad (T821), bank of Amazonas River, Peru.

Material: one valve.

Dimensions (mm): MPEG-894-M, LV: L: 1.00, H: 0.48.

Remarks: the specimens of *C. retrobispinosa* Purper and Pinto, 1983 do not differs from the type-material. This species has a rare occurrence in the Solimões Formation and it is the first record for the Pebas Formation.

Geographic and stratigraphic occurrence: Borehole: 1AS-32-AM, northwestern of the Amazonas state, Brazil (Purper and Pinto, 1983) and 1AS-31-AM Ituí River, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Solimões Formation, Miocene.

Occurrence: Outcrop Soledad (T821), bank of Amazonas River, Iquitos, Peru.

Material: four valves and one carapace.

Dimensions (mm): MPEG-895-M, RV: L: 0.85, H: 0.44.

Remarks: The recovered material comprises only five specimens of males, which differ slightly from that illustrated by Sheppard and Bate (1980), being less elongated and inflated, and with the dorsal margin of the RV slightly turn downwards in direction to the posterior region. Differ also from those illustrated by Purper and Pinto (1983), where the dorsal and ventral margins are more parallel.

Geographic and stratigraphic occurrence: Boreholes: 1AS-32-AM, northwestern of the Amazonas state (Purper and Pinto, 1983, 1985); 1AS-10-AM, Sucuríju, near Ituí River, southwest of the Amazonas state (Gross et al., 2014); 1AS-33-AM, southwest of Benjamin Constant, Curuçá River, District of Canamã, Atalaia do Norte (Medeiros et al., 2019); 1AS-7D-AM Quixitó River, Municipality of Atalaia do Norte (Linhares and Ramos, 2022), Brazil. Solimões Formation, Miocene; Outcrop: Pichua, the bank of Marañon River, Peru (Sheppard and Bate, 1980). Pebas Formation, Miocene.

Occurrence: Outcrops of Indiana (T347 and T350), Pebas (T421), St. Elena (T488), and Paraiso (T808) bank of Amazonas River; Tarapoto (T859), Buen Pasa (T899), and St. Clotilde (T881), bank of Napo River, Iquitos, Peru.

Material: two hundred and seventy-nine valves and three carapaces.

Dimensions (mm): MPEG-896-M, female, LV: L: 1.01, H: 0.63; MPEG-897-M, female, RV: L: 1.03, H: 0.63; MPEG-898-M, male, LV: L: 0.92, H: 0.50; MPEG-899-M, male, RV: L: 0.96, H: 0.48; MPEG-900-M, male, RV: L: 1.09, H: 0.56; MPEG-901-M, female, RV: L: 1.15, H: 0.62.

Remarks: This is a widely distributed species in the Neogene beds of the western Amazonia. *Cyprideis sulcosigmoidalis* (Purper, 1979) and *Cyprideis aulakos* Muñoz-Torres et al., 1998 are considered synonym by Gross et al. (2014), since the morphological differences are not clear between these two species. The authors mentioned that the presence of marginal denticles and parallel punctuation in the peripheral regions in *C. sulcosigmoidalis*, in contrast with the smoother ornamentation in

C. aulakos, are the main differences between these species; however, they do not consider these differences enough for the separation in two species. The specimens identified in the present work are similar to the type-material in Purper (1979) with the addition of the morphological variations as mentioned by Whatley et al. (1998), Muñoz-Torres et al. (1998), and discussed by Gross et al. (2014), such as the presence of denticles on the posterior and anterior margins of the RV, which is not described by Purper (1979). Among the morphological variations observed in the recovered material there are variations in the ornamentation pattern from smooth to punctuated, and mainly of denticulation in the anterior margin of the RV, where in some specimens the denticles are more evident; well-developed spines occur in the posteroventral region of the RV.

Geographic and stratigraphic occurrence: In Brazil, boreholes: CPCAN–III–São Paulo de Olivença and CPCAN-I-Tamanduá, northwestern of the Amazonas state (Purper, 1979); 1AS-31-AM, near Ituí River, southwestern of the state of Amazonas (Linhares et al., 2011); 1AS-10-AM, Sucuríju, near Ituí River, southwestern of the Amazonas state (Gross et al., 2014); 1AS-8-AM, near Quixitó River, northwestern of the state of Amazonas (Linhares et al., 2017); 1AS-33-AM, southwestern of Benjamin Constant, Curuçá River, District of Canamã, Atalaia do Norte, Amazonas state (Medeiros et al., 2019); 1AS-7D-AM, 1AS-31-AM and 1AS-8-AM, Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022). Brazil. Solimões Formation, Miocene; Outcrops of Pichua, the bank of Marañon River (Sheppard and Bate, 1980); Santa Julia, Santa Sofia (Whatley et al., 1998; Muñoz-Torres et al., 1998) and Porvenir, in area of Iquitos Arch (Gross and Piller, 2020), Peru; and Mocagua, Colombia (Muñoz-Torres et al., 1998). Pebas Formation, Miocene.

Superfamily Cypridacea Baird, 1845.

Family Cyclocyprididae Kaufmann, 1900.

Genus Cypria Zenker, 1954.

Type-species. *Cypria exsculpta* (Fischer, 1855). Recent, United Kingdon.

Cypria aqualica Sheppard and Bate, 1980.

Occurrence: Outcrop of Indiana (T348), the bank of Amazonas River, Iquitos, Peru.

Material: four valves and five carapaces.

Dimensions (mm): MPEG-921-M, RV: L: 0.54, H: 0.39; MPEG-987-M, RV: L: 0.66, H: 0.36.

Remarks: The rare specimens identified herein are similar to *Cypria aqualica*, however some specimens are lower and with a ventral margin more convex. They are similar to *Physocypris* sp. illustrated by Gross et al. (2013) however there are higher and longer and with antero and posterior margin more symmetrically rounded. However, more material is necessary for further taxonomical analysis.

Geographic and stratigraphic occurrence: Borehole: CPCAN–III–São Paulo de Olivença, Benjamin Constant, northwest of the Amazonas state; 1AS-7D-AM and 1AS-31-AM Quixitó and Ituí rivers, respectively, Municipality of Atalaia do Norte (Linhares and Ramos, 2022); Outcrops: Torre da Lua, Eirunepé town (Ramos, 2006; Gross et al., 2013), Brazil. Solimões Formation, Miocene; Outcrops: La Tagua, Peru; Santa Sofia, Macedonia and Puerto Nariño, Colombia. Pebas Formation, Miocene.

Superfamily Darwinuloidea Brady and Norman, 1889.

Family Darwinulidae Brady and Norman, 1889.

Genus ***Penthesilenula*** Rossetti and Martens, 1998.

Type-species. *Penthesilenula brasiliensis* (Pinto and Kotzian, 1961), São Paulo state, Brazil, fresh water, Recent.

?Penthesilenula *olivencae* (Purper, 1979).

Occurrence: Outcrop of Indiana (T350), bank of Amazonas River, Iquitos, Peru.

Material: two valves.

Dimensions (mm): MPEG-922-M, RV: L: 0.49, H: 0.19; MPEG-988-M, RV: L: 0.52, H: 0.20.

Remarks: The specimen is tentatively classified as *Penthesilenula olivencae* as it was not possible to see the internal features and to the poor material available and the bad preservation.

Superfamily Cypridoidea Baird, 1845.

Family Cyprididae Baird, 1845.

Genus Heterocypris Clauss, 1893

Type-species. *Heterocypris incongruens* (Ramdohr, 1808), Rock-pool South Bass Island, Ohio, Recent.

Heterocypris sp.

Occurrence: Outcrop of Indiana (T348), bank of Amazonas River, Iquitos, Peru.

Material: two carapaces.

Dimensions (mm): MPEG-923-M, C: L: 0.77, H: 0.42, W: 0.35.

Remarks. The specimens identified as *Heterocypris* sp. has no distinction from the material illustrated by Muñoz-Torres et al. (1998), except for the size of the identified specimens, which are smaller than presented by Muñoz-Torres et al. (1998).

Geographic and stratigraphic occurrence: The species occurs sporadically in outcrops of Iquitos and Pebas, Peru. Pebas Formation, Miocene; Los Chorros, Mocagua, San Martín and Villareal, Miocene, Colombia (Muñoz-Torres et al., 1998).

Family Macrocypridinae Műller, 1912

Genus Macrocypris Brady, 1867.

Type-species. *Cythere minna* Baird, 1850, Shetland Isles, Cretaceous formation of England.

?Macrocypris sp.

Occurrence: Outcrop of Indiana (T347), bank of Amazonas River, Iquitos, Peru.

Material: five valves.

Dimensions (mm): MPEG-924-M, RV: L: 0.45, H: 0.17; MPEG-989-M, RV: L: 0.54, H: 0.18.

Remarks: Although the specimens are very fragile and break when handled, they macth well with some internal (adont hinge and very wide anterior and posterior duplicature) and external (subtriangular and elongated shape, rounded anterior margin and tapered posterior margin) generic characteristics of *Macrocypris*. However, they are tentatively classified as ?*Macrocypris* sp. as some diagnostic internal structures (mainly marginal pore canals and muscle scars), essential to the generic classification, were not seen. Some specimens are similar to the specimen illustrated by Muñoz-Torres et al. (1998), with broad and elongated outline, anterior margin rounded, posterior margin sub-acute (slightly rounded); convex dorsal margin and slightly concave ventral margin. However, some specimens have an acutely tapered posterior margin (Fig. 7. 27) similar to the specimens illustrated by Sheppard and Bate (1980) (Pl. 13; Fig. 10).

Family Ilyocyprididae Kaufmann, 1900.

Subfamily Pelocypridinae Triebel, 1962

Genus Pelocypris Klie, 1939.

Type-species: *Pelocypris lenzi* Klie, 1939, Brazil, Recent.

Pelocypris zilchi Triebel, 1953.

Occurrence: Outcrop of Indiana (T346), bank of Amazonas River, Iquitos, Peru.

Material: two fragmented valves.

Dimensions (mm): MPEG-925-M, RV: L: 1.40, H: ~0.85; MPEG-926-M, LV: L: 1.50, H: ~0.85.

Remarks: The material illustrated by Sheppard and Bate (1980), as *Pelocypris zilchi* has similarity with the specimens identified in the present work, as outline, ornamentation and presence of two sulci in the middle dorsal region. However, these authors mentioned the presence of little tubercles in anterior and posterior margin of the valves, as well as the presence of well-developed marginal denticles in RV of adult specimens. These features are absent in the recovered specimens. Gross et al. (2013) mentions the presence of tubercles in juvenile, as well as marginal denticles in the right valve, different than occur in the adults.

Geographic and stratigraphic occurrence: Outcrops: Aquidabã, southwest of the Amazonas state (Wesselingh and Ramos, 2010; Gross et al., 2013), Brazil. Solimões Formation, Miocene; La Tagua, in

Colombia (Sheppard and Bate, 1980) and Barranca El Sismico, El Salvador (Triebel, 1953).

Superfamily Cytherideoidea Liebau, 2005.

Family Cytherideidae Sars, 1925.

Genus Perissocytheridea Stephenson, 1938.

Type-species: *Perissocytheridea matsoni* (Stephenson, 1935), Mio-Pliocene Florida.

Perissocytheridea ornellasae (Purper, 1979).

Occurrence: Outcrops of Indiana (T347 and T350), Pebas (T421), Santa Elena (T488), and Paraiso (T808), bank of Amazonas River; Santa Clotilde (T881), the bank of Napo River, Iquitos, Peru.

Material: One hundred and six valves and fifty-seven carapaces.

Dimensions (mm): MPEG-927-M, female, C: L: 0.38, H: 0.20, W: 0.15; MPEG-893-M, male, C: L: 0.35, H: 0.15, W: 0.12; MPEG-990-M, female, C: L: 0.48, H: 0.20, W: 0.24.

Remarks: The specimens of *Perissocytheridea ornellasae* recovered herein have the same morphological characteristics of type-material and of most illustration listed in the synonym list.

Geographic and stratigraphic occurrence: Boreholes: CPCAN-I-Tamanduá and CPCAN–III–São Paulo de Olivença, Benjamin Constant, northwest of Amazonas state (Purper, 1979); 1AS-7D-AM, near the Quixitó River and 1AS-8-AM, near the Ituí River, Atalaia do Norte town, northwest of Amazonas state (Linhares et al., 2017; Linhares and Ramos, 2022); 1AS-33-AM southwest of Benjamin Constant, Curuçá River, District of Canamã, Atalaia do Norte (Medeiros et al., 2019), Brazil. Solimões Formation, Miocene; Outcrops: Pebas (Muñoz-Torres et al., 1998), Pichua (Sheppard and Bate, 1980) and Porvenir in area of Iquitos Arch, Peru (Gross and Piller, 2020). Pebas Formation, Miocene; Macedonia, Los Chorros, Buenos Aires and Villareal, Colombia (Muñoz-Torres et al., 1998).

Superfamily Cytheracea Baird, 1850.

Family Limnocytheridae Klie, 1938

Genus ***Skopaeocythere*** Whatley, Muñoz-Torres and Van Harten, 2000.

Type-species: *Skopaeocythere tetrakanthos* Whatley et al., 2000, Miocene, Los Chorros, northwest of the town of Leticia, Colombia.

Skopaeocythere tetrakanthos Whatley et al., 2000.

Occurrence: Outcrop Santa Elena (T488), bank of Amazonas River, Iquitos, Peru.

Material: Two valves and one carapace.

Dimension (mm): MPEG-928-M, RV: L: 0.40, H: 0.20; MPEG-991-M, L: 0.36, H: 0.24.

Remarks: The rare specimens of *S. tetrakanthos* do not have distinction from the type-material. Thus, this species has the first record for the Pebas Formation, Peru.

Geographic and stratigraphic occurrence: Boreholes: 1AS-7D-AM, near the Quixitó River, northwest of the Amazonas state (Linhares et al., 2017; Linhares and Ramos, 2022), Brazil. Solimões Formation, Miocene; Outcrops: Los Chorros, Colombia (Muñoz-Torres et al., 1998; Whatley et al., 2000) and Porvenir, in area of Iquitos Arch, Peru (Gross and Piller, 2020). Pebas Formation, Miocene.

5. Discussion

5.1. Cyprideis species distribution, age and correlation of the studied area

Some outcrops studied herein have age previously proposed based on palynology and on mollusks (Hoorn, 1993; Wesselingh et al., 2006a). The Indiana outcrop is equivalent to the *Psiladiporites-Crototricolpites* palynozone (Burdigalian to Langhian), early to middle Miocene), and the Pebas outcrop to the *Crassoretitriletes* palynozone (Langhian to Serravalian), middle Miocene.

In addition, Wesselingh et al. (2006a) infer that Indiana is equivalent to the *Toxosoma carinatum* zone (MZ4) and *Diplodon indianensis* zone (MZ5), both covering the Langhian; the Pebas outcrop is equivalent to the *Dyris pebasensis* zone (MZ7), and Santa Elena to *Dyris lanceolatus* zone (MZ8), both covering the Serravalian, and Buen Pasa is equivalent to *Diplodon indianensis* zone (MZ5), covering the Langhian, all them restricted to the middle Miocene.

Based on the ostracod faunas, the most studied sites (Indiana, Buen Pasa, Tarapoto, and Santa Clotilde) was positioned in the late middle to early late Miocene (Serravallian-Tortonian), extending them to the late Miocene, due to the occurrence of the index species *Cyprideis caraionae* (Tabel 2; Figs. 8 and 9). According to Linhares et al. (2019) *Cyprideis caraionae* zone reaches the interval between the middle Miocene (Serravallian) and early late Miocene (Tortonian), equivalent to part of the *Crassoretitriletes* and *Grimsdalea* zones (Hoorn, 1994a *sensu* Lorente, 1986).

The Pebas outcrop and Santa Elena were also extended to the Tortonian (Fig. 9). The Pebas was the only outcrops where *Cyprideis minipunctata* was recorded, an index species that gave name to the *Cyprideis minipunctata* zone. This zone extends from late Middle (Serravalian) to early late Miocene (Tortonian) having the base marked by the extinction of *Cyprideis caraionae* and the top marked by the extinction of *Cyprideis minipunctata sensu* Muñoz-Torres et al. (2006). According to Linhares et al. (2019) *Cyprideis minipunctata* zone corresponds to the *Grimsdalea* zone covering the Tortonian.

On the other hand, the Santa Elena and Soledad outcrops, the last dated herein for the first time, are here correlated to the *Cyprideis paralela* zone, a zone proposed by Linhares et al. (2019), correspondent to late Miocene (Tortonian) and equivalent to *Asteraceae* zone (Hoorn, 1993). The authors proposed that the base of this zone is marked by the extinction of *Cyprideis cyrtoma* and the top by the extinction of *Cyprideis paralela* (Fig. 9).

At the Paraiso outcrop only *Cyprideis sulcosigmoidalis* occurs. Due to the absence of other index species, it is impossible to infer the chronostratigraphic interval for this outcrop as this species has a wide stratigraphic range occurring from the early to late Miocene (Muñoz-Torres et al., 2006; Linhares et al., 2019).

5.2. Paleoenvironmental interpretation

The paleoenvironmental evolution of the “Pebas lake” or Pebas Mega-Wetland system has been deeply discussed (Vonhof et al., 2003; Leandro et al., 2022). This system is assumed as a network of freshwater lakes and temporary pools, which occupied most of western Amazonia between c. 23 and 8 Ma (Wesselingh et al., 2006a) and marine influence has been attested (Hoorn, 1994b; Linhares et al., 2017; Antoine et al., 2016; Leandro et al., 2022). Since the pioneer micropaleontological studies in the Neogene beds of Western Amazonia a mixture of fresh and brackish water, and rare marine taxa has been recorded (Purper, 1979; Sheppard and Bate, 1980; Hoorn, 1993; Linhares et al., 2011) which instigated an investigation on the marine influence on these deposits (Vonhof et al., 2003; Boonstra et al., 2015; Antoine et al., 2016; Alvim et al., 2021; Leandro et al., 2022). Isotopic analyses on mollusks shells were also applied to investigate the salinity variations from different localities from the Peru Neogene beds, which infer marine influence in a predominantly fresh water lacustrine environment (Wesselingh et al., 2002; Vonhof *et al.* 1998; 2003).

Taxonomic studies of ostracods from the Pebas Formation in Peru and Colombia began with Sheppard and Bate (1980), and Swain (1998) who recognized a diverse ostracods association from lagoons, lakes, estuaries, and bays, typical of transitional systems. Later, Whatley et al. (1998) identified a “*Cyprideis* flocks” developed in a brackish, lacustrine system during the early Miocene to early late Miocene (Muñoz-Torres et al., 2006). Palynological studies and investigations on marine influence in the sites Nuevo Horizonte and Porvenir/Amazon, in Peru, suggest a brackish environment, such as a lagoon, or a slightly confined infralittoral environment affected by freshwater in the late middle Miocene (Boonstra et al., 2015). On the other hand, Gross and Piller (2020), infer to Porvenir/Amazon site that the salinity variations are related to groundwater influx.

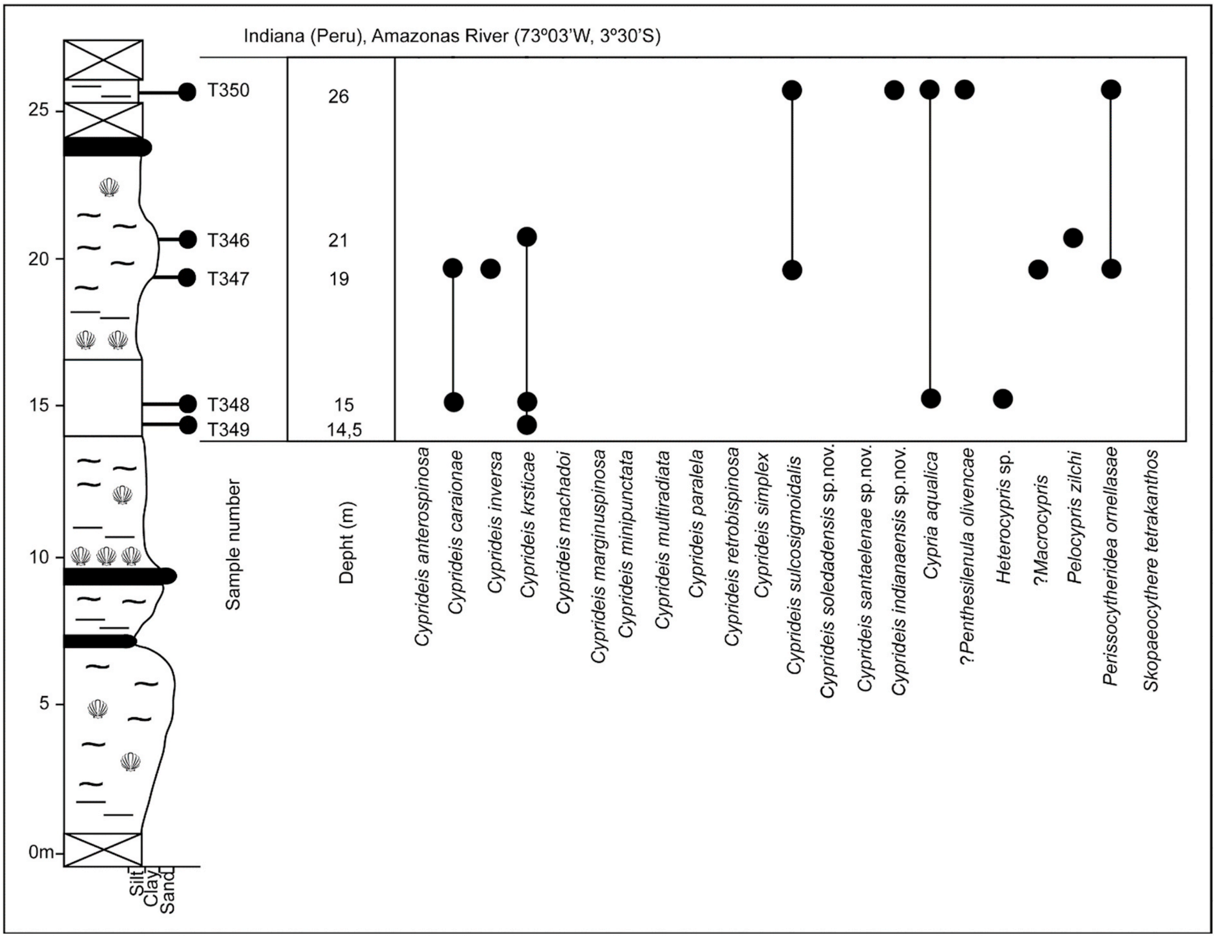

Fig. 8. Lithological profile of the outcrop Indiana with ostracods species distribution on the analyzed samples. Modified fromVonhof et al. (2003).

More recently, according to Alvim et al. (2021), freshwater predominated in the early Miocene in the Pebas System and oligohaline conditions were observed during the middle and early late Miocene, influenced by shallow marine incursions.

The particular paleoenvironmental evolution during the Neogene in the Western Amazonia promoted a remarkable radiation that directly influenced the diversity of an endemic fauna, mainly of the mollusks and ostracods (Muñoz-Torres et al., 1998; Wesselingh et al., 2006a; Wesselingh and Ramos, 2010).

The sites studied herein is marked by the predominance of the euryhaline genera *Cyprideis*, and *Perissocytheridea*; freshwater species are rare (*Cypria aqualica*, *Heterocypris* sp., *Penthesilenula olivencae* and *Pelocypris zilchi*); specimens probably of marine origen are also rare and very fragile (?*Macrocypris* sp. and *Skopaeocythere tetrakantos*) and marine influence cannot be attested.

The genus *Cyprideis* commonly occurs in estuaries, lakes and lagoons (Wouters, 2002). Furthermore, the genus *Cyprideis* is euryhaline, adapted to live in conditions of variable salinity related to daily and/or seasonal cycles (van Harten, 2000). Its adaptation to environmental stress caused by salinity changes involves physiological peculiarities, metabolic pathways and genetic configurations (van Harten, 1975).

Perissocytheridea is a euryhaline genus, common in mesohaline, marginal marine environments (e.g., lagoons), characteristic of a brackish environment (Whatley et al., 2000; Muñoz-Torres et al., 2006; Boonstra et al., 2015; Nogueira and Ramos, 2016; Gross and Piller, 2020); however, it can be also found in slightly saline inland lakes (e.g., Keyser, 1977; Gross et al., 2013; Gross and Piller, 2020).

In Santa Elena outcrop a very rare, fragile and dwarf fauna including brackish and probably marine water genera as *Perissocytheridea*, ?*Macrocypris*, ?*Pontocypris*, *Skopaeocythere*, ?*Rhadynocytherura* and *Pellucistoma* were found, that could indicate a proximity of coastal settings, but detailed taxonomic studied is necessary to attest this condition.

Based on the ostracods fauna we could infer to the studied area an oligohaline lake or a slightly confined brackish water lagoon with the possibility of relative proximity of coastal settings.

6. Conclusion

The taxonomic analysis allowed to recognize eight genera and twenty-two ostracods species with three new species described. Most species are common to Pebas and Solimões formations with the species *Cyprideis anterospinosa*, *Cyprideis krsticae*, *Cyprideis marginuspinosa* and *Cyprideis retrobispinosa* having their first records in the Pebas Formation and are rare in the Solimões Formation; *C. krsticae* is well represented in the studied area.

Among the outcrops of the study area, the Indiana outcrops is extended to the transition of middle Miocene to late Miocene, different from the age previously proposed based on palynological data and mollusks, which positioned this outcrop to the early Miocene to middle Miocene. The same occurs with the Pebas restricted before to middle Miocene, is extended to late Miocene (Tortonian); Buen Pasa restricted to the Langhian based on mollusks before, is restricted to Serravallian; and Santa Elena restricted to the late middle Miocene (Serravallian) before is attributed to the late Miocene (Tortonian). Tarapoto and St. Clotilde outcrops have age proposed from the Serravalian to the Tortonian and Soledad to the Tortonian, for the first time.

The fauna of ostracods is predominated by the genus *Cyprideis* followed by *Perissocytheridea* allowing to infer possibility of relative

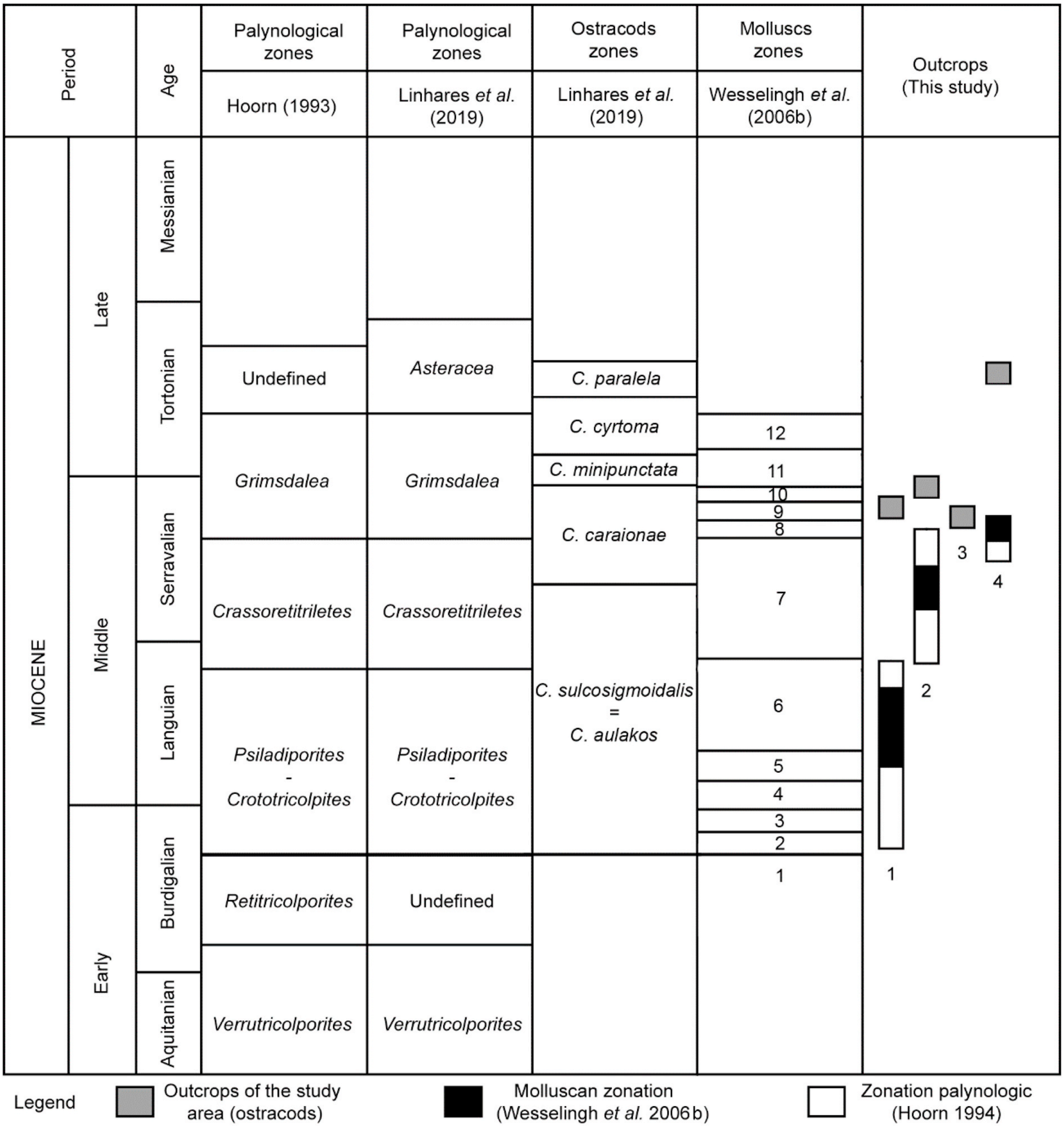

Fig. 9. Stratigraphic distribution of outcrops in the study area. (1) Indiana; (2) Pebas; (3) Buen Pasa, Tarapoto and St. Clotilde; (4) Santa Elena and Soledad. Modified from Linhares et al. (2019), Vonhof et al. (2003), and Kaandorp et al. (2006).

proximity of coastal settings. The rare presence of exclusively freshwater as well as marine taxa is probably attributed to a transitional environment.

CRediT authorship contribution statement

Fabricia Silva DE. Sousa: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Maria Inês Feijó Ramos:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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