



New Mesozoic and Cenozoic fossils from Ecuador: Invertebrates, vertebrates, plants, and microfossils

Edwin A. Cadena*, Alejandra Mejia-Molina, Carla M. Brito, Sofia Peñafiel, Kleber J. Sanmartin, Luis B. Sarmiento

School of Geological Sciences and Engineering, Yachay Tech, San Miguel de Urcuquí, Ecuador



ARTICLE INFO

Article history:

Received 19 December 2017
Received in revised form
7 February 2018
Accepted 8 February 2018
Available online 10 February 2018

Keywords:

Paleobiodiversity
Neotropics
Northern south america
Paleontology

ABSTRACT

Ecuador is well known for its extensive extant biodiversity, however, its paleobiodiversity is still poorly explored. Here we report seven new Mesozoic and Cenozoic fossil localities from the Pacific coast, inter-Andean depression and Napo basin of Ecuador, including vertebrates, invertebrates, plants, and microfossils. The first of these localities is called El Refugio, located near the small town of Chota, Imbabura Province, from where we report several morphotypes of fossil leaves and a mycetopodid freshwater mussel of the Upper Miocene Chota Formation. A second site is also located near the town of Chota, corresponding to potentially Pleistocene to Holocene lake deposits from which we report the occurrence of leaves and fossil diatoms. A third locality is at the Pacific coast of the country, near Rocafuerte, a town in Esmeraldas Province, from which we report a late Miocene palm leaf. We also report the first partially articulated skull with teeth from a Miocene scombridid (*Mackerels*) fish from El Cruce locality, and completely preserved seeds from La Pila locality, both sites from Manabí Province. Two late Cretaceous fossil sites from the Napo Province, one near Puerto Napo showing a good record of fossil shrimps and a second near the town of Loreto shows the occurrence of granular amber and small gymnosperms seeds and cuticles. All these new sites and fossils show the high potential of the sedimentary sequences and basins of Ecuador for paleontological studies and for a better understanding of the fossil record of the country and northern South America.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

The fossil record of Ecuador is still poorly explored and documented as has been recently discussed in a review study on the paleontology of the country (Cadena and Román-Carrión, *in press*). This is due to several factors including for instance the lack of specific and permanent paleontological fieldwork. In the following paragraphs we briefly describe some of the most famous localities of Ecuador where fossil vertebrates, invertebrates, plants, and microfossils have been reported and studied.

In terms of fossil vertebrates, Ecuador has shown to be rich, particularly for Neogene faunas, including several Pleistocene and Holocene localities from Santa Elena Province (southwestern region of the country) (Ruiz-Sánchez et al., 2014; Lindsey and Lopez, 2015; Lindsey and Seymour, 2015; Tanaka et al., 2017; Cadena et al.,

2017, references therein), an important number of localities from the inter-Andean basin, including one from the historic center of Quito (capital of the country) (Román-Carrión, 2012a, 2012b, 2012c, 2012d; Carlini et al., 2013), and the localities near the small town of Bolívar, Carchi Province (northern of the country) (Ficcarelli et al., 1992, 1995; Fejfar et al., 1993, 1996; Ferretti, 2010; Tomiati and Abbazzi, 2002; Ficcarelli et al., 2003).

Fossil invertebrates of Ecuador include freshwater, marine, and terrestrial forms. For instance, Mesozoic mollusks reported and described from several localities of the eastern region of the country (Amazon basin) (Aspden and Ivimey-Cook, 1992; Dommergues et al., 2004; Bulot et al., 2005; Dhondt and Jaillard, 2005). Cenozoic invertebrates, particularly mollusks, arthropods and ichnofossils have been reported and described from the inter-Andean depression, the Pacific coast and the Galápagos Islands (Walker, 2001; Di Celma et al., 2002; Landini et al., 2002; Ragagni et al., 2002; Ragagni and Di Celma, 2009; Herrera and Román-Carrión, 2012; Sánchez et al., 2013; Zunino, 2013, references therein).

The fossil record of plants in Ecuador is restricted principally to

* Corresponding author.

E-mail address: ecadena@yachaytech.edu.ec (E.A. Cadena).

the southern provinces in Mesozoic and Cenozoic sequences that include the famous petrified forest of Puyango (Shoemaker, 1982), and reports of leaves and seeds from different localities in Loja, El Oro, and Azuay provinces (Berry, 1933; Burnham, 1995; Kowalski, 2001).

The micropaleontology of Ecuador, as in many other countries has resulted highly beneficiated by the oil-exploration. However, as usual, much of this knowledge has not been published and makes part of internal reports or classified documents of the oil companies. In spite of this, some studies describing microfossils and fossil palynomorphs of Ecuador include: Landini et al., 2002; Vallejo et al., 2002; Ordóñez et al., 2006; Niemann and Behling, 2007; Collins et al., 2013; Bush et al., 2014, and references therein.

Here we report and briefly describe seven new Mesozoic and Cenozoic localities and their fossil content from different regions of Ecuador, including vertebrates, invertebrates, plants, and microfossils. We also discuss the relevance of these fossil findings for understanding the biodiversity history of Ecuador and tropical South America, as well as their potential importance for future paleobiological, paleoclimatic, and paleobiogeographical studies.

2. New fossil localities and their geological setting

2.1. El Refugio locality

Situated along the highway 35, which goes from Quito to Tulcán, approximately 800 m past the Ambuqui toll station, on the right side of the road ($0^{\circ}28'3.50''N$, $78^{\circ}2'1.17''W$) (Fig. 1.1), town of Chota, Ibarra Canton, Imbabura Province. The stratigraphic section (Fig. 2) makes part of the upper sequence (sequence S2) of the Chota Formation following Barragán et al., 1996, including fine-grained lithic sandstones interbedded with siltstones, and layers of dark grey organic rich mudstones and laminated gypsum. Radiometric ages for the entire Chota Formation varies from 28 ± 2.0 to 1.1 ± 0.6 Ma, with four of the five samples giving a range between 4.8 ± 0.4 to 1.1 ± 0.6 Ma (Pliocene-Pleistocene), based on Winkler et al. (2005). In particular, radiometric ages obtained from volcanic rocks overlying the Chota Formation along the Chota river by Barberi et al. (1988) indicate an age between 6.31 ± 0.1 Ma and 6.30 ± 0.06 Ma, suggesting that the fluvio-lacustrine deposits of the Chota Formation are the oldest of the stratigraphy sequence in this region and should be at least Miocene in age (Barragán et al., 1996).

2.2. Chota locality

Located 200 m after the small town of Chota, crossing the Chota River bridge, on the left margin of the road ($0^{\circ}28'30.13''N$, $78^{\circ}3'57.37''W$) (Fig. 1.2), Mira Canton, Carchi Province. This outcrop is characterized by a thick bed of approximately 6 m of laminated white to pink diatomite, pinched laterally and in contact with poorly consolidated fluvial deposits dominated by conglomerates and conglomeratic sandstones. According to this stratigraphic configuration and the diatoms content (see microfossils section of this study) the age for this deposit is hypothesized as Pleistocene to Holocene.

2.3. El Cruce locality

Located 300 m before the round-point on road 15 that goes from Manta to Rocafuerte, approximately 3 km before this town, Rocafuerte Cantón, Manabí Province ($00^{\circ}54'47.32''S$, $80^{\circ}29'16.526''W$) (Fig. 1.3). The outcrop is dominated by calcareous mudstones, mapped as belonging to the Dos Bocas Formation (Egüez et al., 2017), which is considered late Oligocene to middle Miocene by Bristow and Hoffstetter (1977). A sample for calcareous

nannofossils (YT-Nan-0001) was studied from this locality and the results and implications for the age of the section are presented in the discussion section of this study.

2.4. La Pila locality

Located 80 m after La Pila town on the road that goes from Montecristi to Jipijapa, Montecristi Cantón, Manabí Province ($01^{\circ}61'41.84''S$, $80^{\circ}34'53.10''W$) (Fig. 1.4). This outcrop is represented by siliceous siltstones, mapped as belonging to the Dos Bocas Formation (Egüez et al., 2017), which is considered late Oligocene to middle Miocene by Bristow and Hoffstetter (1977).

2.5. Rocafuerte locality

Located 1.2 km west of Rio Fuerte town, along the beach, Pacific coast, Rio Verde Canton, Esmeraldas Province ($1^{\circ}04'28.62''N$, $79^{\circ}23'17.95''W$) (Fig. 1.5). The outcrop is dominated by calcareous fine-grained sandstones with abundant hematite laminae and nodules, mapped as belonging to the Viche Formation (Egüez et al., 2017), which is considered as lower to lower middle Miocene in age (Cantalamessa et al., 2007).

2.6. Puerto Napo locality

Located 200 m before the town of Puerto Napo on the right margin of road 45 that goes from Tena to Puyo, Napo Province ($1^{\circ}02'31.76''S$, $77^{\circ}47'38.54''W$) (Fig. 1.6). This section is represented by an interbedded sequence of biomicrites and grey to black shales, belonging to the upper segment of Napo Formation, Coniacian age (Bristow and Hoffstetter, 1977).

2.7. Pungarayacu quarry

Located 7 km after the small town of Jondachi, along 20 road that goes from Tena to Loreto, Loreto Canton, Napo Province ($0^{\circ}42'24.14''S$, $77^{\circ}44'28.78''W$) (Fig. 1.7). An old quarry in the middle of a dense tropical forest exposes a sequence of limestones, interbedded with grey to black-oily siltstones and claystones potentially belonging to the middle segment of Napo Formation, Turonian in age (Bristow and Hoffstetter, 1977).

3. Materials and methods

All macro fossil specimens and nannofossil samples reported and figured herein were prepared, studied, and deposited at the Paleontology Lab collections of Yachay Tech, San Miguel de Urcuquí, Imbabura Province, Ecuador. Specimens and micropaleontological slides receive a collection identification number starting with the university initials (YT) followed by an abbreviation of the group to which they belong e.g.: Ver (vertebrates), and finally a consecutive serial number of four digits e.g.: 0001.

Most of the specimens were studied and photographed using an Olympus SZX16 stereomicroscope. Additionally some specimens of diatoms and small seeds were observed and studied using a Phenom ProX Scanning Electron Microscope under 5 and 10 kV conditions (YT Paleontology Lab facility). Preliminary taxonomic identifications of the fossils described herein were consulted with experts in each of these groups, and are referred to as personal communications in each of the sections that we described the fossils.

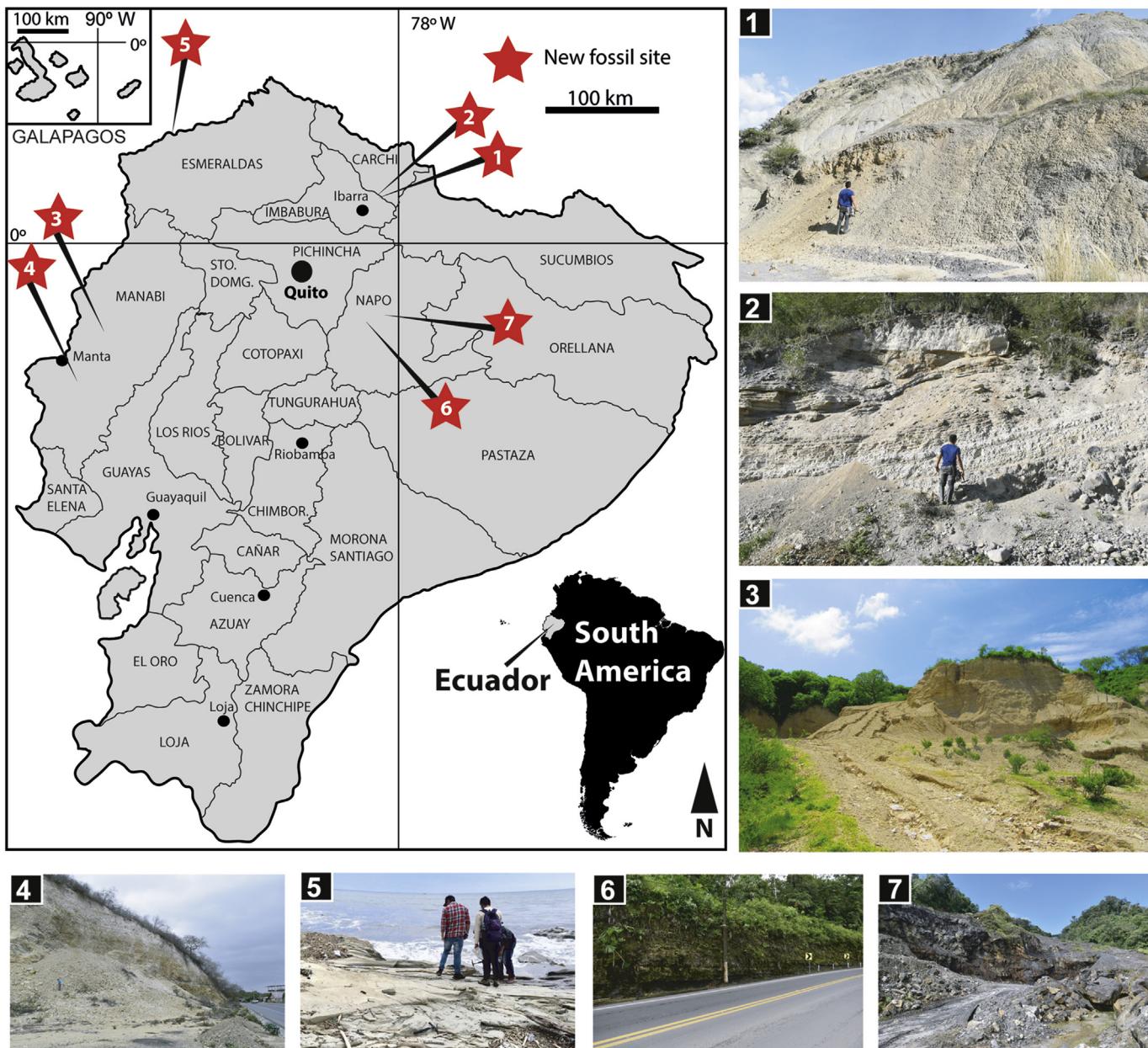


Fig. 1. Map of Ecuador showing the new six fossil localities described herein: (1) El Refugio locality, Chota Formation, Imbabura Province; (2) Chota locality, paleolake deposits, Carchi Province; (3) El Cruce locality, Dos Bocas Formation, Manabí Province; (4) La Pila locality, Dos Bocas Formation, Manabí Province; (5) Rocafuerte locality, Viche Formation, Esmeraldas Province; (6) Puerto Napo locality, Napo Formation, Napo Province; (7) Pungarayacu quarry, Napo Formation, Napo Province.

4. Fossil invertebrates

4.1. Bivalvia

Large pearly freshwater mussels were found in a siltstone layer at the El Refugio locality (middle segment of the section, Fig. 2) (Fig. 3.1). At least six specimens (YT-Inv-0001-0006) were collected, being the largest one being 10.5 cm long. These bivalves belong to the Mycetopodidae family (F.P. Wesselingh, personal communication, 2017).

4.2. Decapoda

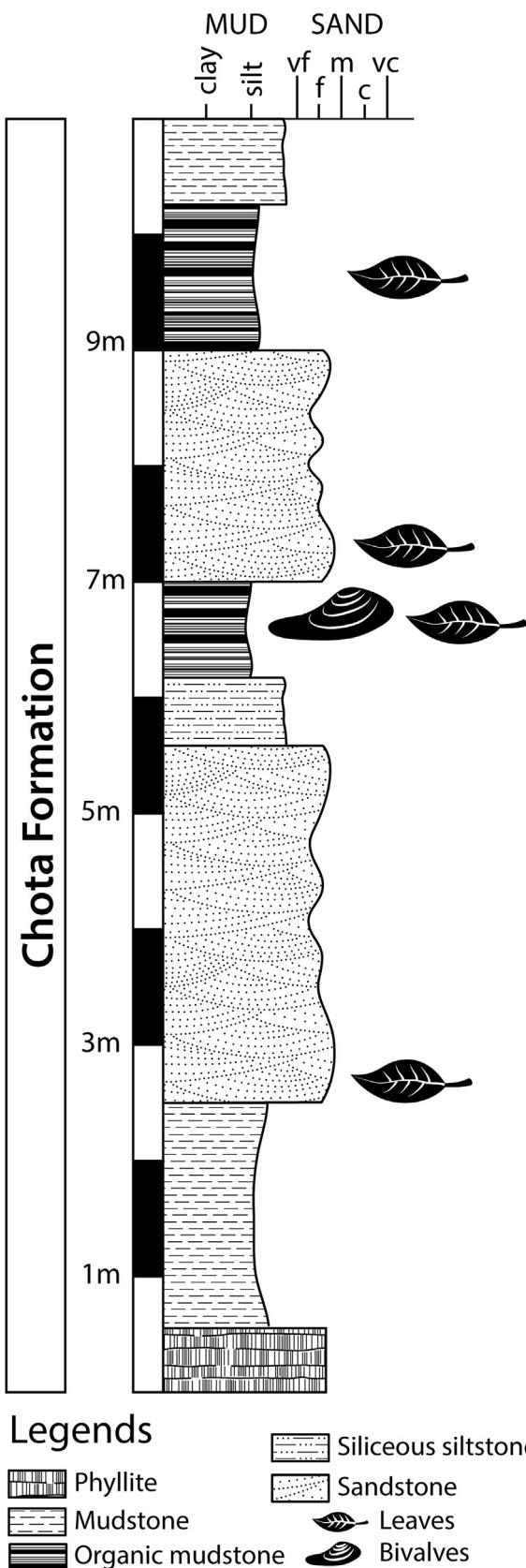
Shrimps preserving tails, arms, and claws with delicate cuticles were found in the Puerto Napo locality, Napo Formation

(Fig. 3.2–3.5) (YT-Inv-0007-0011). A total of seven specimens were found, and these seem to belong to the infraorder Thalassinidea (J. Luque, personal communication, 2017).

5. Fossil vertebrates

5.1. Actinopterygii

A partially complete skull, considerably crushed, but preserving in place most of its teeth in the premaxilla and dentary (Fig. 4.1–4.3) (YT-Ver-0001). The specimen was found at El Cruce locality, Manabí Province. This fish is potentially a representative of the Scombridae family, resembling the *Scomberomorus* genus, which include also the extant mackerels (J. Carrillo, personal communication, 2018).



6. Fossil plants

6.1. Angiosperms

Several indeterminate families of fossil leaves and seeds were found in four different horizons at the El Refugio locality, Chota Formation (Fig. 2). At least thirteen different morphotypes have been identified, including large leaves with entire margin, some with dentate margin, two different type of grasses, and two potential small seeds (Fig. 5.1–5.8) (YT-Bot-0001-0022, 0028) (Supplementary data 1). Insect damage has also been recognized in some of these fossil leaves, as well as different levels of veins structures (Fig. 5.3).

Other locality from which we have found fossil leaves is the Rocafuerte locality, Viche Formation. Here we found only one small leaf that potentially represents a palm, with abundant oily micro-bubbles attached to the cuticle surface (Fig. 5.9) (YT-Bot-0025).

Fossil leaves have also been found in the paleolake deposits of the Chota basin particularly at the Chota locality. The fossils are found well-preserved in the diatomite layers; however we only have identified one morphotype characterized by long leaves with entire margin and low degree of venation (Fig. 5.10) (YT-Bot-0023-0024).

A large drift seed was found associated with abundant plant remains in La Pila locality, Dos Bocas Formation (YT-Bot-0029) (Supplementary data 1). This fossil seed resembles in shape and size the seeds of the extant *Hura* genus (S. Manchester, personal communication, 2017).

6.2. Gymnosperms

Small seeds and cuticle remains well-preserved were recovered from grey siltstones rich in organic matter and other plant remains (Fig. 6.1–6.5) (YT-Bot-0026), found at the Pungarayacu quarry, Napo Province. These seeds potentially belong to the Gnetales order (F. Herrera, personal communication, 2017).

6.3. Amber

Granular amber that varies from coarse grains to pebbles, are very abundant in the same siltstones that the Gnetales seeds and cuticles were found (YT-Bot-0027, Supplementary data 1). At present, none of these amber granules have shown to preserve fossils, only abundant “dusty” like inclusions and potentially microbubbles.

7. Microfossils

7.1. Diatoms

At least twelve different taxa have been found in the diatomites from the paleolake deposits of the Chota basin, Chota locality. Some of the taxa identify include: *Cocconeis placentula* (Fig. 6.6) and *Navicula cryptocephala* (Fig. 6.7) (YT-Dia-0001-0002). (S. Fritz, personal communication, 2017), (Supplementary data 2).

8. Discussion

8.1. Relevance of the new fossils

The fossil fish reported here from El Cruce locality, Manabí Province represents the first skeletal remain with in-place dentition reported for this region of Ecuador, and potentially the first fossil record of scombridid from the Pacific margin of South America, from the late Miocene, based on the identification of the

Fig. 2. Stratigraphic column of the Chota Formation, El Refugio locality, showing the fossil leaves and freshwater bivalves horizons.

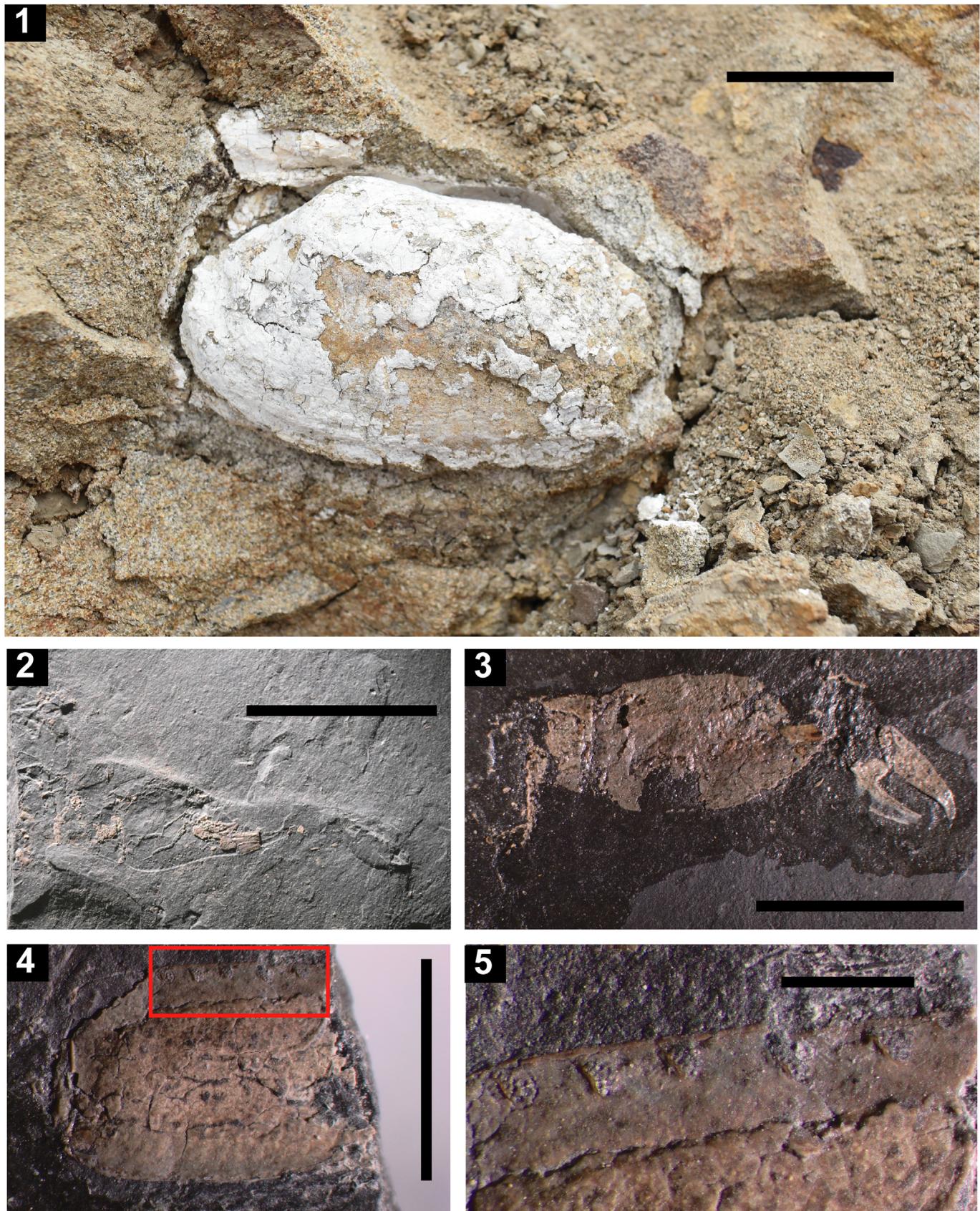


Fig. 3. Fossil invertebrates from Ecuador reported herein: (1) Freshwater mussel (YT-Inv-0005) belonging to the Mycetopodidae family (F.P. Wesselingh, personal communication, 2017) from El Refugio locality; (2) Posterior portion of a fossil shrimp with the tail (YT-Inv-0009), Puerto Napo locality; (3) Partial arm with claw of a fossil shrimp (YT-Inv-0007), Puerto Napo locality; (4) Proximal segment of an arm of a fossil shrimp (YT-Inv-0010), Puerto Napo locality; (5) Close-up of margin of YT-Inv-0010 (red rectangle in (4)). Scale bars are (1) 2 cm; (2) 3 cm; (3, 4) 10 mm; (5) 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

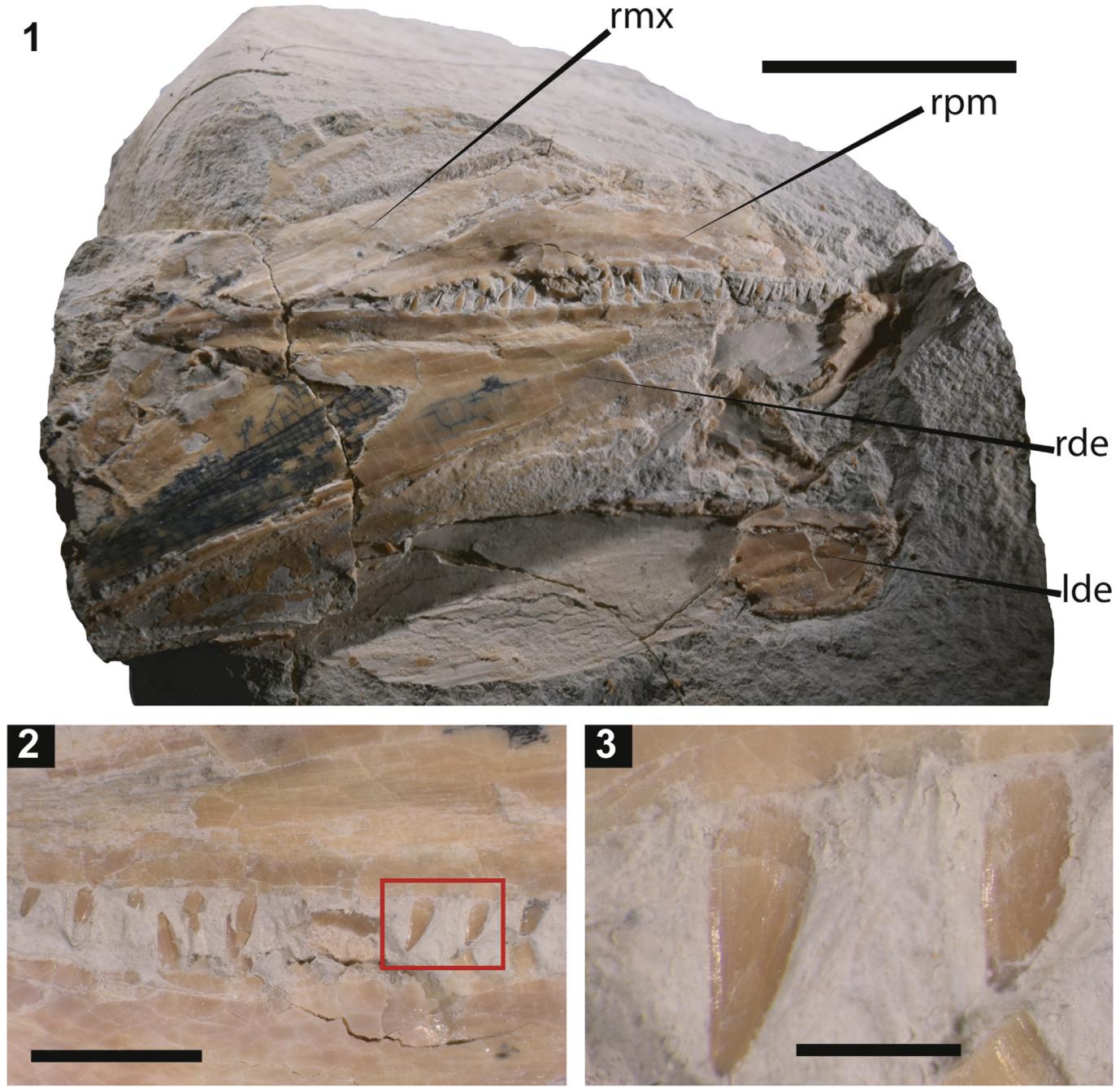


Fig. 4. Scombridid (J. Carrillo, personal communication, 2017) partial fossil fish skull, from El Cruce locality (YT-Ver-0001): (1) Dorsolateral view showing the articulated (crushed) right maxilla, premaxilla and dentary; the print and a fragment of the right dentary also can be observed (2) Close-up of the premaxilla and dentary showing teeth in-place; (3) Close-up of the teeth (red rectangle in (2)). Scale bars are (1) 3 cm; (2) 5 mm; (3) 1 mm. Abbreviations: lde, left dentary; rde, right dentary; rmx, right maxilla; rpm, right premaxilla. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

calcareous nannofossils NN8 zone, represented by *Catinaster coalitus* (this study). Isolated marine fish remains principally teeth and otoliths assemblages have been reported from the Pliocene Onzole Formation, Esmeraldas Province (Bianucci et al., 1993; Carnevale et al., 2011), and nearly complete freshwater fish skeletons have been reported from the Loja Province (White, 1927; Costa, 2011).

The marine fossil shrimps from Puerto Napo locality represent the first record of these decapods in the Mesozoic of Ecuador. Fossils of freshwater shrimps have been reported from the Miocene of southern Ecuador (Herrera and Román-Carrión, 2012).

The freshwater mussels from the Chota Formation represent the

first report of these bivalves in the Chota basin and at the same time represent the westernmost fossil record of the Mycetopodidae family in South America. Thus, considering that the age of this sequence is potentially late Miocene (Barragán et al., 1996), make these fossil bivalves have relevance to establish a possible west extension of the late Miocene Pebas wet-land system that existed previous to the origin of the current Amazon drainage system, a study that is currently being developed by the senior author. Fossil invertebrates particularly gastropods were only previously mentioned in the general description of the Chota Formation (Barragán et al., 1996), however, we did not find evidence of these

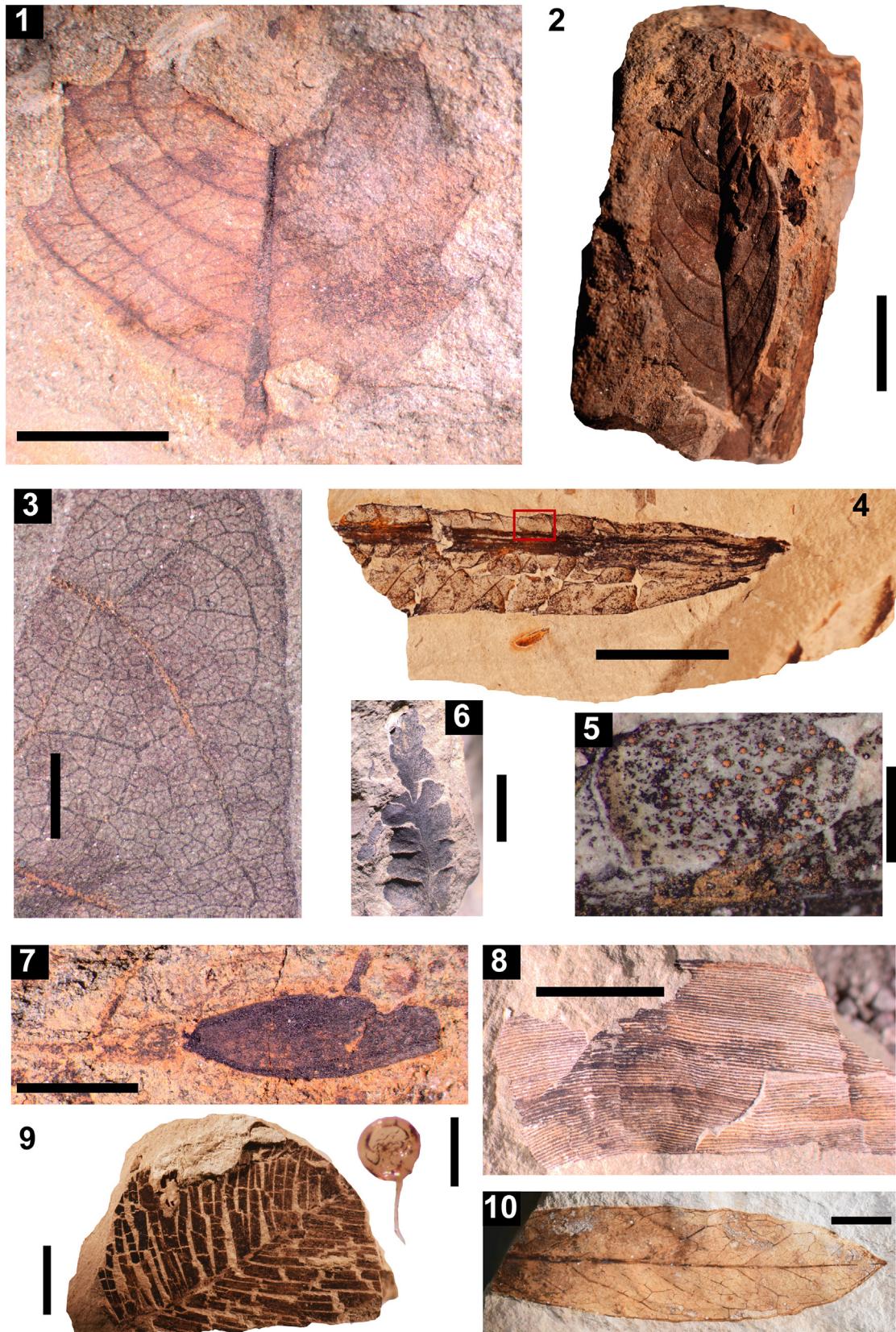


Fig. 5. Fossil leaves and seeds from El Refugio (1–7), Rocafuerte (8), and Chota (9) localities: (1) Leaf with dentate margin (YT-Bot-0001); (2) Leaf with entire margin (YT-Bot-0014); (3) Detail of the venation pattern of YT-Bot-0012; (4) Leaf elongated with entire margin (YT-Bot-0019); (5) Close-up of red rectangle area in (4), showing microvortex texture; (6) Fern leaf (YT-Bot-0028); (7) Potential fossil seed (YT-Bot-0005); (8) Grass leaf (YT-Bot-0022); (9) Palm leaf fragment (YT-Bot-0025), and one of its oily microbubbles shown at the upper right corner (scale bar 5 µm); (10) Leaf with entire margin (YT-Bot-0024), from the paleolake deposits of Chota locality. Scale bars are (1, 6, 8, 10) 5 mm; (2, 4, 9) 10 mm; (3, 7) 2 mm; (5) 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

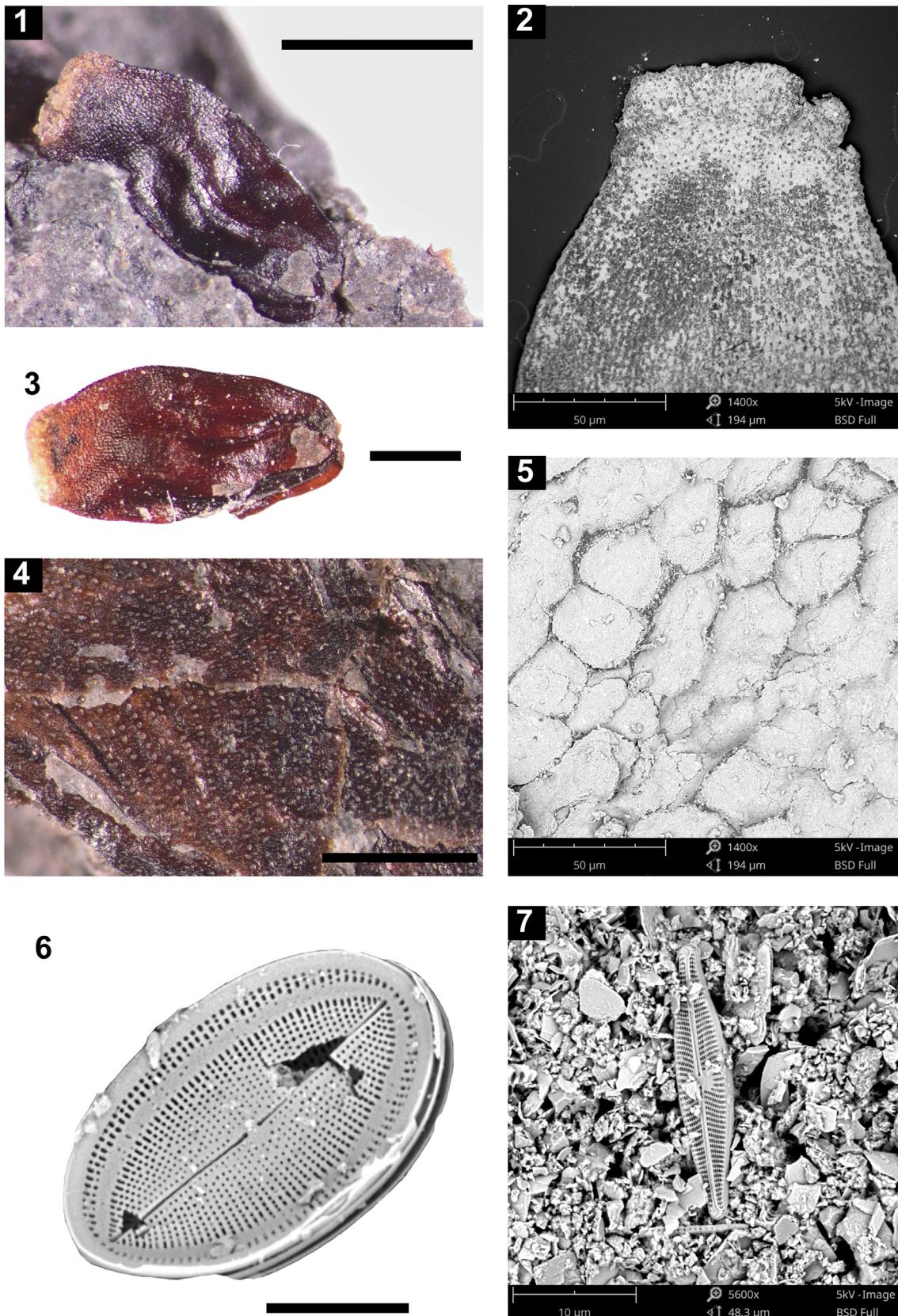


Fig. 6. Small seeds and diatoms from the Pungarayacu and Chota localities respectively: (1) Small seed from Gnetales (F. Herrea, personal communication, 2017) (YT-Bot-0026); (2) SEM-photograph of the proximal region of YT-Bot-0026; (3) YT-Bot-0026 after being released from the rock; (4) Fragment of a cuticle (YT-Bot-0026); (5) SEM-photograph of the cuticle shown in (4); (6) *Cocconeis placentula* diatom from Chota locality (YT-Dia-0001); (7) SEM-photograph of *Navicula cryptocephala* diatom (YT-Dia-0001), from Chota locality. Scale bars are (1, 4) 1 mm; (3) 0.5 mm; (6) 10 µm. SEM-photographs have the scale at the bottom black stripe, as well as the magnification and voltage information.

at the Chota Formation localities explored.

Fossil leaves from the El Refugio locality (Chota Formation) represent the first occurrence of this type of fossils in northern Ecuador and could contribute to the understanding of paleo-vegetation changes of this region during the onset of the uplifting of this part of South American Andes. As well as, represent a good site for comparisons with the floristic composition and paleobiogeography distribution between this and the Miocene south localities of the country, particularly with the Nabón basin fossils (Kowalski, 2001).

The small seeds and cuticles potentially from gymnosperms (Gnetales), as well as the granular amber from Pungarayacu locality offer a new opportunity for understanding aspects of the vegetation and possibly climatic conditions of this part of South America during the late Cretaceous.

Finally, the fossil diatoms from the lake deposits of the Chota basin, particularly from the Chota locality constitute the first fossil record of this type of microfossils in northern Ecuador and could shed light on paleoenvironmental conditions of this region of the country during the Neogene and the Quaternary, as well as for correlation with other paleolake deposits along the South American Andes.

9. Conclusions

The fossil sites and fossils reported and briefly described herein are evidence of the high potential that the sedimentary rocks of Ecuador have to improve our knowledge on the paleobiodiversity not only of the country but also of northern South America. At the same time, with this work we show the poorly explored state in which many of the basins and sequences of Ecuador are in terms of their fossil content. We hope this study will trigger other near future contributions describing and studying in detail the taxonomic, systematic paleontology, as well as to establish the paleoenvironmental, paleobiogeographical and paleoclimatic implications of the fossils described herein. Also with this type of contributions we hope to promote and support the paleontological activity and research in Ecuador.

Funding

Funding for this study was provided by the School of Geological Sciences and Engineering of Yachay Tech, and the internal grants program of this university, grants 27 and 09.

Acknowledgments

We thank to E. Mariño, D. Rojas, R. Madden, J. Román, K. Choez for assisting during the fieldwork. We also thank to F. Mejia from the Instituto Nacional de Patrimonio Cultural (INPC) of Ecuador for helping us to obtain permits to work at the Chota basin. Special thanks to J. Carrillo, G. Ballen, J. Luque, S. Fritz, F. Herrera, S. Manchester, and F. Wesselingh for their personal comments on the taxonomy of the fossils reported here. Thanks to the reviewers J. Carrillo and J. Abella for their comments and suggestions to improve this manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jsames.2018.02.004>.

References

- Aspden, J.A., Ivimey-Cook, H.C., 1992. Nuevos datos paleontológicos del Centro y Sureste del Ecuador. Bol. Geol. Ecuat. 3, 85–88 (in Spanish).
- Barberi, F., Coltellini, M., Ferrara, G., Innocent, F., Navarro, J.M., Santacroce, R., 1988. Plio-Quaternary volcanism in Ecuador. Geol. Mag. 125, 1–14.
- Barragán, R., Baudino, R., Marocco, R., 1996. Geodynamic evolution of the Neogene intermontane Chota basin, northern Andes of Ecuador. J. S. Am. Earth Sci. 9, 309–319.
- Berry, E.W., 1933. A new *Lygodium* from the late Tertiary of Ecuador. Johns Hopkins Univ. Stud. Geol. 23, 208–210.
- Bianucci, G., Cantalamessa, G., Landini, W., Ragagni, L., Valleri, G., 1993. Fossil assemblages from the Pliocene Onzole Formation (Esmeraldas, NW Ecuador) and their implications in the Panamic bioprovince evolution. Doc. Lab. Geol. Lyon 125, 43–58.
- Bristow, C.R., Hoffstetter, R., 1977. Lexique Stratigraphique International, Volume V Amérique Latine, Fascicule 5 a 2 Ecuador. Centre National de la Recherche Scientifique Paris, p. 410.
- Bulot, L.G., Kennedy, W.J., Jaillard, E., Robert, E., 2005. Late middle-early late albian ammonites from Ecuador. Cretac. Res. 26, 450–459.
- Burnham, R.J., 1995. A new species of winged fruit from the Miocene of Ecuador: *Tipuana ecuatoriana* (Leguminosae). Am. J. Bot. 82, 1599–1607.
- Bush, M.B., Restrepo, A., Collins, A.F., 2014. Galápagos history, restoration, and a shifted baseline. Restor. Ecol. 22, 296–298.
- Cadena, E.A., and Román-Carrión, J.L., in press. A review of the fossil record of Ecuador, with insights about its challenges and future development: Ameghiniana.
- Cadena, E.A., Abella, J., Gregori, M.D., 2017. New findings of Pleistocene fossil turtles (Geoemydidae, kinosternidae and chelydridae) from Santa Elena province, Ecuador. Peer J. <https://doi.org/10.7717/peerj.3215>.
- Cantalamessa, G., Di Celma, C., Ragagni, L., Valleri, G., Landini, W., 2007. Sedimentology and high-resolution sequence stratigraphy of the late middle to late Miocene Angostura Formation (western Brobón Basin, northwestern Ecuador). J. Geol. Soc. Lond. 164, 653–665.
- Carlini, A.A., Castro, M.C., Madden, R.H., Scillato-Yané, G., 2013. A new species of dasypodidae (Xenarthra: cingulata) from the late Miocene of northwestern south America: implications in the dasypodina phylogeny and diversity, historical Biology. Int. J. Paleobiol. <https://doi.org/10.1080/08912963.2013.840832>.
- Carnevale, G., Landini, W., Ragagni, L., Di Celma, C., Cantalamessa, G., 2011. Taphonomic and paleoecological analyses (mollusks and fishes) of the Súa Member condensed shellbed, upper Onzole Formation (Early Pliocene, Ecuador). Palaios 26, 160–172.
- Collins, A.F., Bush, M.B., Sachs, J.P., 2013. Microrefugia and species persistence in the Galápagos highlands: a 26,000-year paleoecological perspective. Front. Genet. 4, 1–16.
- Costa, W.J.E.M., 2011. Redescription and phylogenetic position of the fossil killifish *Carriomelus diumontii* white from the lower Miocene of Ecuador (teleostei: cyprinodontiformes). Cybium 35, 181–187.
- Dhondt, A.V., Jaillard, E., 2005. Cretaceous bivalves from Ecuador and northern Peru. J. S. Am. Earth Sci. 19, 325–342.
- Di Celma, C., Ragagni, L., Cantalamessa, G., Curzio, P., 2002. Shell concentrations as tools in characterizing sedimentary dynamics at sequence-bounding unconformities: examples from the lower unit of the Canoa Formation (Late Pliocene, Ecuador). Geobios - Mem. Spec. 24, 72–85.
- Dommergues, J.L., Meister, C., Jaillard, E., 2004. Ammonites de la formation Santiago de la zone urbaine subandine de S-E de l'Équateur (Jurassique inférieur, Sinémurien). Rev. Paléobiol. 23, 355–371 (in French).
- Egüez, A., Gaona, M., Albán, A., 2017. Mapa geológico de la República del Ecuador, Escala 1:1.000.000. Ministerio de Minería y Instituto Nacional de Investigación Geológico Minero Metalúrgico, Quito (in Spanish).
- Fejfar, O., Blasetti, A., Calderoni, G., Coltorti, M., Ficcarelli, G., Masini, F., Rook, L., Torre, D., 1993. New finds of cricetids (mammalia, rodentia) from the late Pleistocene-holocene of northern Ecuador. Documents du Laboratoire de Géologie de Lyon 125, 151–167.
- Fejfar, O., Ficcarelli, G., Mezzabotta, C., Moreno-Espinosa, M., Rook, L., Torre, D., 1996. First record a copemymeine-peromyscine cricetid (Rodentia, Mammalia) in South America: hypotheses regarding its ancestry in the Palaearctic. Acta Zool. Cracov. (Engl. Transl.) 39, 137–145.
- Ferretti, M.P., 2010. Anatomy of *Haplomastodon chimborazi* (mammalia, Proboscidea) from the late Pleistocene of Ecuador and its bearing on the phylogeny and systematics of south american gomphotheres. Geodiversitas 32, 663–721.
- Ficcarelli, G., Borselli, V., Moreno-Espinosa, N., Torre, D., 1992. New *haplomastodon* finds from the late Pleistocene of northern Ecuador. Geobios 26, 231–240.
- Ficcarelli, G., Borselli, V., Herrera, G., Moreno, M., Torres, D., 1995. Taxonomic remarks on the south american mastodons referred to *haplomastodon* and *cuvieroni*. Geobios 28, 745–756.
- Ficcarelli, G., Coltorti, M., Moreno-Espinosa, M., Pieruccini, P.L., Rook, L., Torre, D., 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. J. S. Am. Earth Sci. 15, 835–845.
- Herrera, M.M., Román-Carrión, J.L., 2012. Registro de camarones de río en el Mioceno Superior del Sur de Ecuador. Revista Politécnica 30, 211–213 (in Spanish).
- Kowalski, E.A., 2001. Middle to Late Miocene Environment of Southern Ecuador: Temperature, Elevation, and Fossil Plants of the Nabón Basin. Ph.D. thesis. The University of Michigan, Ann Arbor, p. 451.
- Landini, W., Bianucci, G., Carnevale, G., Ragagni, L., Sorbini, C., Valleri, G., Bisconti, M., Cantalamessa, G., Di Celma, C., 2002. Late Pliocene fossils of Ecuador and their role in the development of the Panamic bioprovince after the rising of Central American Isthmus. Can. J. Earth Sci. 39, 27–41.

- Lindsey, E.L., Lopez, R., 2015. Tanque Loma, a new late-Pleistocene megafaunal tar seep locality from southwest Ecuador. *J. S. Am. Earth Sci.* 57, 61–82.
- Lindsey, E.L., Seymour, K.L., 2015. “Tar pits” of the western neotropics: Paleoecology, taphonomy, and mammalian biogeography. In: Harris, J.M. (Ed.), *La Brea and beyond: the Paleontology of Asphalt-preserved Biotas*. Natural History Museum of Los Angeles County Science Series n° 42, pp. 111–124.
- Niemann, H., Behling, H., 2007. Late Quaternary vegetation, climate and fire dynamics inferred from the El Tiro record in the southeastern Ecuadorian Andes. *J. Quat. Sci.* 23, 203–212.
- Ordóñez, M., Jiménez, N., Suárez, J., 2006. Micropaleontología ecuatoriana. Centro de Investigaciones Geológicas. Guayaquil 634 (in Spanish).
- Ragaini, L., Bianucci, G., Cantalamessa, G., Valleri, G., Landini, W., 2002. Paleoecology and paleobiogeography of fossil mollusks from isla isabela (Galápagos Ecuador). *J. S. Am. Earth Sci.* 13, 381–389.
- Ragaini, L., Di Celma, C., 2009. Shell structure, taphonomy and mode of life of a Pleistocene ostreid from Ecuador. *Bollettino della Soc. Paleontol. Ital.* 48, 79–87.
- Román-Carrión, J.L., 2012a. Hallazgo de megafauna pleistocénica en el centro histórico de Quito. *Revista Politécnica* 30, 136–146 (in Spanish).
- Román-Carrión, J.L., 2012b. Registro de fauna pleistocénica en Caraburo, Nor-Oriente de Quito. *Revista Politécnica* 30, 205–210 (in Spanish).
- Román-Carrión, J.L., 2012c. Nuevo registro de un mylodonte (*Glossotherium wegneri* Spillmann, 1931) en Conocoto. Quito. *Revista Politécnica* 30, 218–221 (in Spanish).
- Román-Carrión, J.L., 2012d. Nuevo registro de un mastodonte (*Stegomastodon waringi*) en San Vicente, Provincia de Manabí - Ecuador. *Revista Politécnica* 30, 147–155 (in Spanish).
- Ruiz-Sánchez, F.J., Abella, J., Román-Carrión, J.L., Lindsey, E., Santana, J., López, E., Marquina, R., Crespo, V.D., Mansino, S., Díez, N., Ramírez, M., Vera, D., Escalante, K.M., Flores, F.F., Molina, J.O., Ramos, M.B., Ronquillo, I.L., Cornejo, M.H., 2014. Nuevos datos sobre las faunas fósiles de vertebrados de la zona de Quebrada Seca (Santa Elena, Ecuador). XXX Jornadas de Paleontología. Soc. Española de Paleontol. Teruel 215–218 (in Spanish).
- Sánchez, M.V., Genise, J.F., Bellosi, E.S., Román-Carrión, J.L., Cantil, L.F., 2013. Dung beetle brood balls from Pleistocene highland palaeosols of Andean Ecuador: a reassessment of Sauer's *Coprinisphaera* and their palaeoenvironments. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 386, 257–274.
- Shoemaker, R.E., 1982. Fossil leaves from the lower cretaceous ciano formation southwestern Ecuador. *Palaeontographica B* 180, 120–132.
- Tanaka, Y., Abella, J., Aguirre-Fernández, G., Gregori, M., Fordyce, R.E., 2017. A new tropical Oligocene dolphin from montanita/olón, Santa Elena, Ecuador. *PLoS One* 12, e0188380.
- Tomiati, C., Abbazzi, L., 2002. Deer fauna from Pleistocene and Holocene localities of Ecuador (south America). *Geobios* 35, 631–645.
- Vallejo, C., Hochuli, P.A., Winkler, W., von Salis, K., 2002. Palynological and sequence stratigraphic analysis of the Napo group in the Pungarayacu 30 well, sub-andean zone, Ecuador. *Cretac. Res.* 23, 845–859.
- Walker, S.E., 2001. Paleoecology of gastropods preserved in turbiditic slope deposits from the Upper Pliocene of Ecuador. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166, 141–163.
- White, E.I., 1927. On a fossil cyprinodont from Ecuador. *Ann. Mag. Nat. Hist.* 20, 519–522.
- Winkler, W., Villagómez, D., Spikings, R., Abegglen, P., Tobler, St., Egüez, A., 2005. The Chota basin and its significance for the inception and tectonic setting of the inter-Andean depression in Ecuador. *J. S. Am. Earth Sci.* 19, 5–19.
- Zunino, M., 2013. The first dung beetle retrieved from *Coprinisphaeridae* ichnofossils: *Phanaeus violetae* n. sp. (Coleoptera: scarabaeinae) from Ecuadorian Cangahua balls. *Acta Zool. Mexic.* 29, 219–226.