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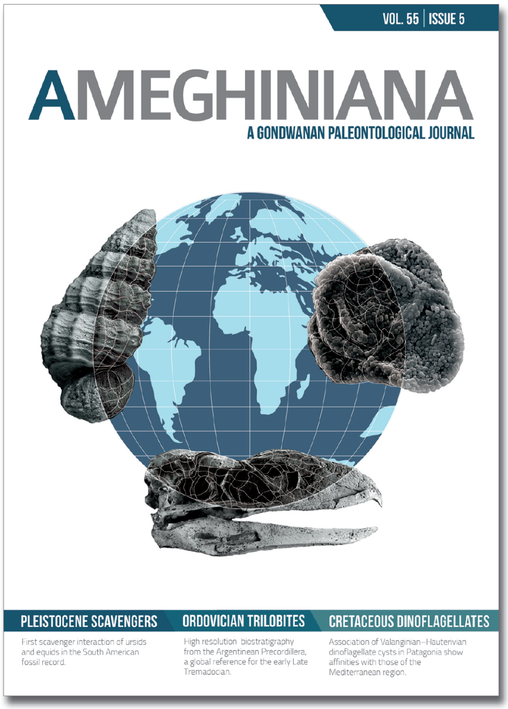

A REVIEW OF THE FOSSIL RECORD OF ECUADOR, WITH INSIGHTS ABOUT ITS CHALLENGES AND FUTURE DEVELOPMENT

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A REVIEW OF THE FOSSIL RECORD OF ECUADOR, WITH INSIGHTS ABOUT ITS CHALLENGES AND FUTURE DEVELOPMENT

EDWIN ALBERTO CADENA[1], AND JOSE LUIS ROMÁN-CARRIÓN[2]

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Abstract. Here we present a review of paleontology in Ecuador for the last three centuries, including the most significant studies, localities and their fossil record. This review is focused on four major fields of paleontology, which are: vertebrate paleontology, invertebrate paleontology, paleobotany and micropaleontology-palynology. The main fossil discoveries for each of these fields are ordered chronologically by date of publication and summarized in tables, maps and figures. Finally, we briefly discuss the current and near future challenges of paleontological research in the country.

Key words. Ecuador. Paleontology. South America. Paleobiodiversity. Fossils.

Resumen. UNA REVISIÓN DEL REGISTRO FÓSIL DE ECUADOR, CON IDEAS SOBRE SUS DESAFIOS Y FUTURO DESARROLLO. Aquí presentamos una revisión de la paleontología del Ecuador para los últimos tres siglos, incluyendo los estudios más significativos, localidades y su registro fósil. Esta revisión se centra en cuatro grandes campos de la paleontología, los cuales son: paleontología de vertebrados, paleontología de invertebrados, paleobotánica y micropaleontología-palinología. Los principales descubrimientos de fósiles para cada uno de estos campos son cronológicamente ordenados por la fecha de publicación, y resumidos en tablas, mapas y figuras. Finalmente, discutimos brevemente los desafíos actuales y del futuro cercano de la investigación paleontológica en el país.

Palabras clave. Ecuador. Paleontología. América del Sur. Paleobiodiversidad. Fósiles.

Ecuador is a country located around latitude 0° and known worldwide because of its rich biodiversity, which is spread along four major geographical regions: the Galápagos Islands, the Pacific coast, the Andes Cordillera, and the tropical Amazonia. A major question concerning not only the biodiversity of Ecuador but also the entire tropical region of South America is related to when and under which conditions all this biodiversity originated and evolved. The answers are recorded in part in the genome of each species, but also in their fossil record. The latter is of particular relevance for time-calibrated phylogenies and lineage branching (Futuyma and Agrawal, 2009; Ksepka *et al.*, 2011). Despite its importance, the fossil record of Ecuador is still poorly explored and studied, as is shown and summarized in this review paper.

This review explores the fossil record of Ecuador as unveiled during the last three centuries (19th to present) and focuses on four major fields of paleontology, *i.e.*, vertebrate paleontology, invertebrate paleontology, paleobotany, and micropaleontology-palynology. For each of these four disciplines, we summarize the main literature, focused mainly on works published in indexed journals, and in particular those in which fossil taxa were originally reported, described or extensively explored. Informal publications, as well as undergraduate or graduate theses or dissertations are only mentioned if they are considered key for the understanding of the paleontological history of Ecuador; however, many of them are summarized in Appendix 1. Together with the literature review, we present summary tables and figures of the most relevant fossil taxa for each of the four paleontological disciplines discussed herein (vertebrates, invertebrates, plants, and microfossils-palynomorphs). Finally, we briefly discuss the current and near future status and challenges of paleontological research in the country.

GENERAL GEOLOGICAL FRAMEWORK OF ECUADOR

The geology of Ecuador is the result of intense tectonic activity expressed in volcanism (intrusive, extrusive, islands), orogeny (uplifting and erosion) and dynamic deformation (earthquakes, folding, and faulting) among other processes. This makes Ecuador a highly diverse country geologically speaking despite its relatively small geographical area, with abundant outcrops of igneous and metamorphic rocks, principally in the Cordillera Real and Cordillera Occidental, as well as in the Galápagos Islands, and sedimentary rocks spread all over the country, with major exposures located near the foothills of both cordilleras, intra-basins, in the Pacific coastal area, and occasionally in the Amazon basin (Bristow and Hoffstetter, 1977; Duque, 2000; Vera, 2013). Figure 1 shows a map of the distribution of the Paleozoic, Mesozoic and Cenozoic sedimentary and volcaniclastic rocks of Ecuador from where most of the fossils mentioned in this review came. It also includes the most important fossil localities and Ecuadorian provinces.

ECUADORIAN PALEONTOLOGY IN THE LAST THREE CENTURIES

Paleontology in Ecuador during the 19th century

Paleontological discoveries in Ecuador started with the arrival of Europeans and the explorations they made by the end of the 18th century, including for example Alexander von Humboldt, who collected a mastodon molar near Imbabura volcano, which was studied by Cuvier (1806) (Housed at the Muséum National d'Histoire Naturelle, Paris, **MNHN AC** 1738; see Montellano-Ballesteros and Román-Carrión, 2011 for discussion about this particular fossil). During a great part of the 19th century, several expeditions and studies revealed more fossils and localities in Ecuador, including the discovery of fossil mammals in the Chimborazo region by Wagner (1860). Later in that century, more geological and paleontological data on fossil localities in Ecuador were presented, including the work of Wolf (1892) and the reports of some fossil mammals assigned to *Neohippus*, currently included in *Equus (Amerhippus)* and *Protauchenia (Palaeolama)* genera near Riobamba by Branco (1883).

In the field of paleobotany, fossil leaves from Loja Province were published by Wolf and von Rath (1876). Years later Engerlhardt (1895) also described and reported more fossil leaves from Loja, showing the abundant occurrence of these fossils in that region of the country.

Microfossils from Ecuador were firstly reported in the iconic work "Geografía y Geología del Ecuador" by Wolf (1892), particularly the occurrence of foraminifera and ostracods from Esmeraldas Province.

Paleontology in Ecuador during the 20th century

Vertebrate paleontology. During the 20th century, the number of paleontological discoveries in Ecuador increased, particularly in terms of fossil vertebrates. One of these early studies described a new Pleistocene rodent species, *Drytomomys aequatorialis* (Anthony, 1922), from Azuay Province. Years later, the first fossil fish from Ecuador was described as *Carrionellus diumortuus* from the late Miocene of Loja Province (White, 1927). Quaternary fossil mammals including several new species of *Equus* (*Amerhippus*) were described by Spillmann (1938) from Chimborazo, Santa Elena and Nabón provinces, as well as from the Chiche and Ambato River outcrops. A species of capybara, *Prohydrochoerus* (*Neochoerus*) *sirasakae* was described by Spillmann in 1941 from the Pleistocene of the Santa Elena Province. A nearly complete skull and some other bone elements of two new species of Pleistocene birds: *Protoconurus* (*Aratinga*) *roosevelti* and *Archeoquerquedula lambrechti*, were described also by Spillmann (1942) based on material from the same two provinces. Isolated marine fish scales were mentioned by Liddle and Palmer (1941) from the Lower Cretaceous of the Cuenca Basin, Azogues valley, near Biblián. A couple of years later, Spillmann (1948) described a new species of mammal: *Eremotherium carolinense*, a new Megatheriinae from the Pleistocene of Guayas Province.

By mid-century the arrival of the taxonomist and paleontologist Robert Hoffstetter to Ecuador resulted in increased paleontological activity in the country reflected in new publications such as notes about Pleistocene xenarthrans, felids, equids, megatherids and gomphotherids (Hoffstetter, 1948a, 1949a, 1949b, 1949c, 1950a, b), and an extensive memoir about all the Pleistocene mammals from Ecuador (Hoffstetter, 1952). Hoffstetter was not only interested in describing new fossil mammals, as shown by his description of the first marine snake from the Eocene of the Ancon region, Santa Elena Province (Hoffstetter, 1958), as well as his reports of fragments of a giant tortoise (*Testudo* (*Che-*

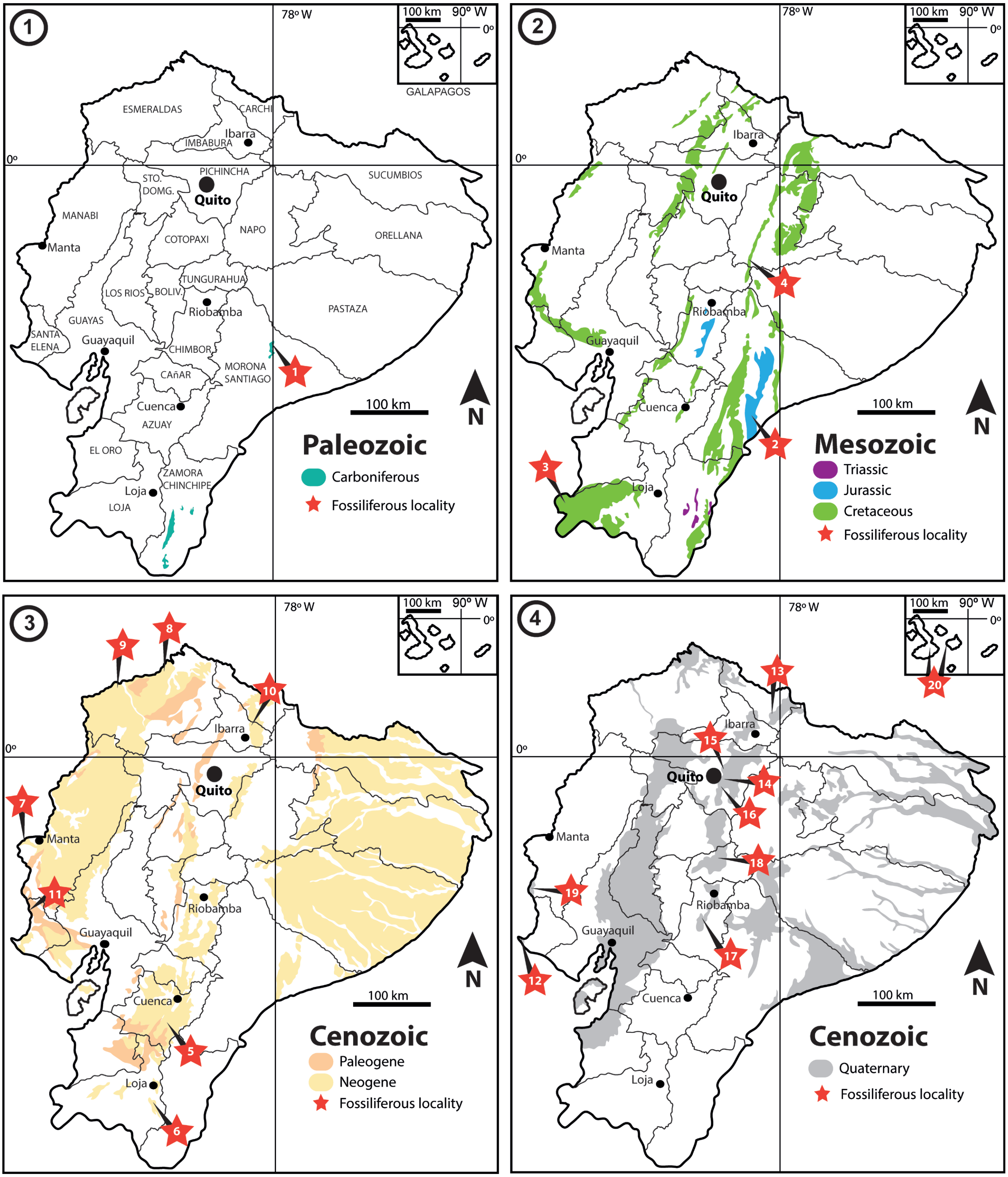

Figure 1. Map of Ecuador with all current provinces, distribution of sedimentary and volcanic-sedimentary rocks throughout geologic time based on Inigemm (2016) as well as the most important fossil localities-regions (red stars) for macrofossils; **1,** Paleozoic, locality: 1. Cordillera de Cutucu; **2,** Mesozoic, localities: 2. Santiago de Patuca region, 3. Puyango River basin, 4. Misahuali River basin; **3,** Cenozoic (Paleogene–Neogene), localities: 5. Nabón-Cuenca-Girón basins, 6. Loja region, 7. Cabo San Lorenzo region, 8. Las Peñas regíon, 9. Súa region, 10. Chota River basin, 11. Montañita/Olón region; **4,** Cenozoic (Quaternary), localities: 12. La Carolina - Tanque Loma region, 13. Bolivar region, 14. Chique River, 15. Calderón, 16. Alangasí, 17. Quebrada de Chalán, 18. Chimborazo region, 19. Machalila, 20. Galápagos islands.

lonoidis) sp.) at La Carolina site, Santa Elena Province (Hoffstetter, 1952). The late Pleistocene mammalian fauna from La Carolina was also described by Edmund (1965). A decade later, a highly diverse assemblage including at least four different families of fish was reported and described by Roberts (1975) based on fossil teeth from Miocene deposits in the Cuenca Basin. A year later, fossil birds were reported and described by Campbell (1976) from La Carolina site, Santa Elena Province. Before the end of the 1970 decade, the first Miocene sharks (currently considered as Pliocene in age, see Cione *et al.*, 2007) from Ecuador were described by Longbottom (1979) based on material collected at several localities in Manabí and Esmeraldas provinces, who acknowledged the occurrence of at least nine different genera.

The occurrence of Holocene fossils from the iconic Galápagos Islands, including mammals, birds, tortoises and lizards, from Floreana Island were reported by Steadman (1986). Almost a decade later, joint field expeditions of Ecuadorian and Italian paleontologists explored the fossil record of the northern region of the country, particularly in Carchi Province, finding and describing late Pleistocene gomphotherid remains identified as *Haplomastodon* (*Notiomastodon*) (Ficcarelli *et al.*, 1992, 1995), as well as new Pleistocene–Holocene material assigned to rodents (cf. *Peromyscus* sp., *Copemyodon ecuadorensis, Phyllotis* and *Akodon*) and the felid *Smilodon* (Fejfar *et al.*, 1993, 1996). More precise dating by Coltorti *et al.* (1998) of all the fossil localities in Carchi Province and one locality in Chimborazo Province allowed concluding that this fauna went extinct during the Last Glacial Maximum and excluded humans as a possible cause of megafauna extinction in these areas. Also, from the early nineties, marine fossil assemblages from the Pliocene Onzole Formation (Esmeraldas Province) were described by Bianucci *et al.* (1993), reporting mainly fish remains including otoliths and teeth.

Some of the fossil mammals from Ecuador are shown in Figure 2, and a complete summary of the orders, families, genera and species of fossil vertebrates of the country is presented in Table 1.

Invertebrate paleontology. One of the first studies mentioning and describing fossil invertebrates from Ecuador was published by Dall and Ochsner (1928), reporting Pliocene–Pleistocene mollusks from Galápagos Islands. Years later, freshwater fossil gastropods from Cañar and Azuay provinces were described by Marshall and Bowles (1932), including a new species: *Ecuadorea bibliana*. Several new species of gastropods and bivalves, all potentially from the Miocene, were also reported from Cañar and Azuay provinces by Palmer (1941). The same year, Pliocene mollusks from western Ecuador (Esmeraldas and Manabí provinces) were reported and described by Pilsbry and Olsson (1941), including several new species of gastropods and bivalves. Robert Hoffstetter, the famous vertebrate paleontologist, also contributed to invertebrate paleontology in Ecuador by reporting Pleistocene mollusks from Santa Elena Province (Hoffstetter, 1948b, 1954a, 1954b, 1954c). In the same years, the first records of Paleozoic invertebrates were reported and listed by Tschopp (1953), including mainly brachiopods, bryozoans, corals and crinoids from Morona Santiago Province.

A very peculiar ichnofossil known as the Cangahua balls, the result of dung beetles activity in Pleistocene ash layers, was described as *Coprinisphaera ecuadoriensis* by Sauer (1955). Decades later, Lindsey Groves reviewed the fossil record of Neogene gastropods from northwestern Ecuador and described a few new species (Groves, 1997).

Some of the fossil invertebrates from Ecuador are shown in Figure 3, and a complete summary of the families of fossil invertebrates of the country is presented in Table 2.

Paleobotany. The first paleobotanical contribution in Ecuador described an important number of Pliocene fossil leaves from Loja Province (Berry, 1929a). The same author described potentially Eocene fossil fruits from Santa Elena Province, including new species such as *Vantanea sheppardi* (Berry, 1929b). Years later, Berry (1933) described a new species of fossil fern, *i.e.*, *Lygodium bifidum*, from Neogene deposits in Loja Province. Several decades later, the first Lower Cretaceous (Aptian–Albian), fossil plants from Ecuador were described by Shoemaker (1982). These came from Loja and El Oro provinces and included mainly gymnosperm fossil leaves and wood from the famous petrified forest of Puyango assigned to *Araucarioxylon*. Almost by the end of the 20th century, a new species of winged fruit, *Tipuana ecuatoriana*, was described by Burnham (1995), based on specimens coming from Miocene rocks in Loja and Azuay provinces.

A summary of the families with fossil plants from Ecuador is presented in Table 3.

Micropaleontology-palynology. The first work describing microfossils from Ecuador was published by Vaughan in 1926, reporting Eocene foraminifera from the west coast of the country, particularly from Guayas and the Santa Elena provinces. However, the first extensive study of foraminifera from the Pacific coast of Ecuador was made by Galloway and Morrey (1929), who described several new species from Manabí Province. Barker (1932) described large foraminifera from the Eocene of Santa Elena Province, including *Discocyclina sheppardi* and *D. anconensis*. A very complete and illustrated guide of the large Tertiary foraminifera from Ecuador was presented years later in the classic work "The Geology of Southwestern Ecuador" (Sheppard, 1937). A summary of the literature on microfossils from Ecuador of the first half of the century was discussed by Thalmann (1945), including some unpublished comments and notes. Cushman and Stevenson (1948) described early Miocene foraminifera from Ecuador, including new species such as *Planularia ecuadorana* and *Planularia charapotoa* from Manabí Province and mentioning the similarity of some of these microfossils with those described from the Miocene of California, USA. The biostratigraphical and chronological importance of the

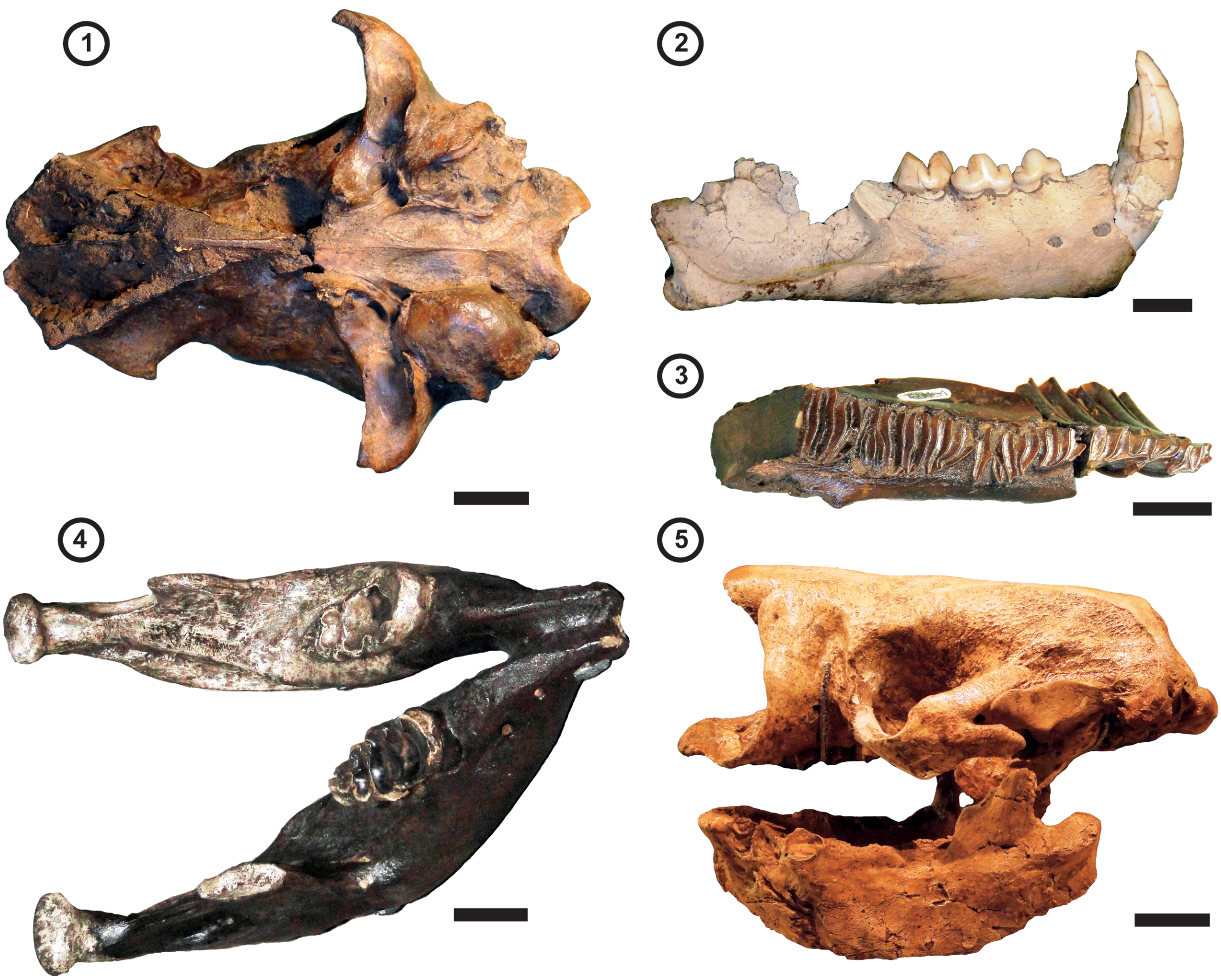

Figure 2. Selected fossil mammals from Ecuador. **1,** Holotype of ***Dusicyon sechurae elenensis*** Hoffstetter, 1952, skull in ventral view, figured in Montellano-Ballesteros and Román-Carrión, 2011 (fig. 4, color version), scale bar= 1 cm; **2,** Holotype of ***Panthera*** (***Jaguarius***) ***onca andina*** Hoffstetter, 1952, lower jaw in lateral view, figured in Montellano-Ballesteros and Román-Carrión, 2011 (fig. 6, color version), scale bar= 2 cm; **3,** Paratype of ***Prohydrochoerus*** (***Neochoerus***) ***sirasakae*** (Spillmann, 1941), lower jaw in dorsal view, figured in Montellano-Ballesteros and Román-Carrión, 2011 (fig. 3, color version), scale bar= 2 cm; **4,** Holotype of ***Notiomastodon*** (***Haplomastodon***) ***guayasensis*** Hoffstetter, 1952, lower jaw in dorsolateral view, scale bar= 5 cm; **5,** Neotype of ***Glossotherium*** (***Oreomylodon***) ***wegneri*** (Spillmann, 1931), skull and lower jaw (cast) in lateral view, figured in Montellano-Ballesteros and Román-Carrión, 2011 (fig. 2, color version), scale bar= 5 cm.

Table 1 – Summary of vertebrate fossils from Ecuador. Abbreviations for references in "Redescription-observations column" 1. Spillman, 1938; 2. Hoffsteter, 1952; 3. Alberdi and Prado, 1992; 4. Montellano-Ballesteros and Román-Carrión, 2011; 5. Costa, 2011; 6. Campbell, 1976; 7. Pujos, 2000; 8. Ficcarelli et al., 1995; 9. Ferretti, 2010; 10. Román-Carrión, 2012d; 11. Cantalamessa et al., 2001; 12. Lindsey and López, 2015; 13. Edmund, 1965; 14. Kurtén & Werdelin, 1990; 15. Cadena et al., 2017

Order	Family	Species	Age/Province	Original reference	Redescription-observations
Mammalia					
Rodentia	Dinomyidae	Drytomomys aequatorialis	Pleistocene/Azuay	Anthony, 1922	
	Caviidae	Prohydrochoerus (Neochoerus) sirasakae	Pleistocene/Santa Elena	Spillmann, 1941	4
	Cricetidae	Copemyodon ecuadorensis	Pleistocene/Carchi	Fejfar, 1996	
Carnivora	Canidae	Lycalopex (Dusicyon) sechurae elenensis	Pleistocene/Santa Elena	Hoffstetter, 1952	4
		Protocyon orcesi	Pleistocene/Santa Elena	Hoffstetter,1952	4
	Felidae	Panthera (Jaguarius) onca andina	Pleistocene/Santa Elena	Hoffstetter,1952	4
		Smilodon fatalis	Pleistocene/Santa Elena	Leidy,1868	14
Perissodactyla	Equidae	Equus(Amerhippus) andium	Quaternary/Chimborazo	Branco, 1883	1, 2, 3, 4, 12
		Equus (Amerhippus) santaeelenae	Quaternary/Santa Elena	Spillmann ,1938	2, 3, 4
		Equus (Amerhippus) insulatus	Quaternary/Tungurahua	Spillmann, 1938	2, 3, 4
Pilosa	Megatheriidae	Eremotherium laurillardi	Pleistocene/Guayas, Santa Elena	Spillmann, 1948	2, 4, 12
		Eremotherium elenense	Pleistocene/Santa Elena	Spillmann, 1948	2, 4
	Mylodontidae	Glossotherium (Oreomylodon) wegneri	Quaternary/Pichincha	Spilmann, 1931	4
		Glossotherium tropicorum	Pleistocene/Santa Elena	Hoffstetter, 1952	4, 12
		Scelidotherium (*?* Scelidodon) reyesi	Pleistocene/Santa Elena	Hoffstetter, 1952	4, 7
Cingulata	Pampatheridae	Holmesina occidentalis	Pleistocene/Santa Elena	Hoffstetter, 1952	4, 12
	Dasypodidae	Anadasypus hondanus	Late Miocene/Azuay	Carlini et al., 2013	
Proboscidea	Gomphotheriidae	Haplomastodon chimborazi	Pleistocene/Santa Elena, Manabí, Carchi, Chimborazo	Proaño, 1984	8, 9, 10
		cf. Notiomastodon	Pleistocene/Santa Elena	Lindsey and López, 2015	
Artiodactyla	Camelidae	Palaeolama aequatorialis	Pleistocene/Santa Elena	Hoffstetter, 1952	4
		Palaeolama crassa	Pleistocene/Santa Elena	Hoffstetter, 1952	4
	Cervidae	Odoccoiles *cf.* salinae	Pleistocene/Santa Elena	Edmund, 1965	
		cf. Odocoileus	Pleistocene/Santa Elena	Lindsey and López, 2015	
Cetacea	Ziphiidae	*Indet.*	Miocene/Esmeraldas	Bianucci et al., 2005	
	Plantanistoidea	Urkudelphis chawpipacha	Oligocene/Manabi	Tanaka et al., 2017	
Teleosti					
Cyprinodon-tiformes	Cyprinodontidae	Carrionellus diumortuus	Lower Miocene/Loja	White, 1927	5
Characiformes	Anostomidae, Characidae, Curimatidae, Erythrinidae and Parodontidae	Hoplias, Leporinus, Parodon *and many other genera, see the original reference for the total list of genera and species*	Miocene/Cuenca	Roberts, 1975	
Several orders	Several families	*See the original reference for the total list of genera and species*	Late Pliocene/Manabí	Landini et al., 2002	
Testudines					
Cryptodira	Testudinidae	Chelonoidis (Geochelone) *sp.*	Pleistocene/Santa Elena	Hoffstetter, 1952	11, 13, 15
	Geoemydidae	Rhinoclemmys (Geomyda) *sp.*	Pleistocene/Santa Elena	Edmund, 1965	15
	Chelydridae	Chelydra *sp.*	Pleistocene/Santa Elena	Cadena et al., 2017	
	Kinosternidae	Kinosternon *sp.*	Pleistocene/Santa Elena	Cadena et al., 2017	
	Pan-Cheloniidae	*Indet.*	Oligocene/Manabi	Cadena et al., 2018a	
Squamata					
Ophidia	Palaeophiidae	Pterosphenus sheppardi	Eocene/Santa Elena	Hoffstetter, 1958	
Aves					
Psittaciformes	Psittacidae	Protoconurus (Aratinga) roosevelti	Pleistocene/Santa Elena	Spilman, 1942	6
Anseriformes	Anatidae	Archeoquerquedula lambrechti	Pleistocene/Santa Elena	Spilman, 1942	6

Eocene and Miocene microfaunas of Ecuador was initially explored and discussed by Stainforth (1948), who noticed differences between the timing of events in the Pacific and the Caribbean and discussed the problems related to this. Years later, the biostratigraphy of the Eocene foraminifera from Ecuador was published by Cushman and Stainforth (1951), a work that was revised and updated by Hofker in 1956. Almost simultaneously Tschopp (1953) reported and listed Paleozoic foraminifera and ostracods from the Macuma Formation, Morona-Santiago Province, attributing to them a Carboniferous age. A new sampling of several Cenozoic localities and new information from wells produced a description and revised morphology of the early Oligocene and early Miocene foraminifera from the west coast of Ecuador (Hofker, 1968).

The work of the French micropaleontologist J. Sigal during the sixties and seventies culminated in at least three important publications in which the microfossils and the biostratigraphy of Ecuador were discussed, including new illustrations of microfossils, this time using Scanning Electron Microscopy (SEM) (Sigal, 1968, 1969, 1972). Another aspect of the micropaleontological record of Ecuador that we summarized here deals with the exploration of the fossil record of coccolithophorids (nannofossils). In particular, one of the first studies explored Pleistocene cores taken offshore from both sides of the Carnegie ridge, showing not only recovery of nannofossils but also discussing their climatic and biostratigraphic implications (Zurita, 1987).

At the beginning of the eighties, the oil exploration boom in Ecuador triggered the need of a permanent biostratigraphy laboratory. It was set up in Guayaquil by Petroecuador and in particular by the Corporación Estatal Petrolera Ecuatoriana (CEPE, Subgerencia Regional Guayaquil) with support provided by BELCO company. This biostratigraphy lab started with a team dominated mostly by Ecuadorian researchers, including Martha Ordóñez and Nelson Jiménez, who during the eighties and nineties presented an important number of internal reports for Petroecuador, as well as occasional works in Geological and Petroleum meetings. One of the published studies described the middle Eocene radiolarian zones from the Ancón Group, Santa Elena Province (Ordóñez, 1995).

The exploration of the palynological-limnological fossil record of Ecuador started during the seventies and eighties with the study of some lakes in the Galápagos Islands and in the Andes and the Amazon lowlands, including the lakes Yaguarcocha, Cunro, Ayauch and Yambo; these studies mentioned the recovery of Pleistocene and Holocene palynomorphs (Colinvaux, 1972; Colinvaux *et al.*, 1988; Bush and Colinvaux, 1988). More localities with Pleistocene palynomorphs, mainly from the Ecuadorian Amazon basin, were studied and included in paleoclimatic reconstructions by Liu and Colinvaux (1985) and Bush *et al.* (1990), particularly the Mera and San Juan Bosco localities from the Napo basin. Holocene diatoms and their implications for reconstructing the most recent paleoclimate of the Ecuadorian Andes were reported from Yambo Lake by Steinitz-Kannan *et al.* (1993).

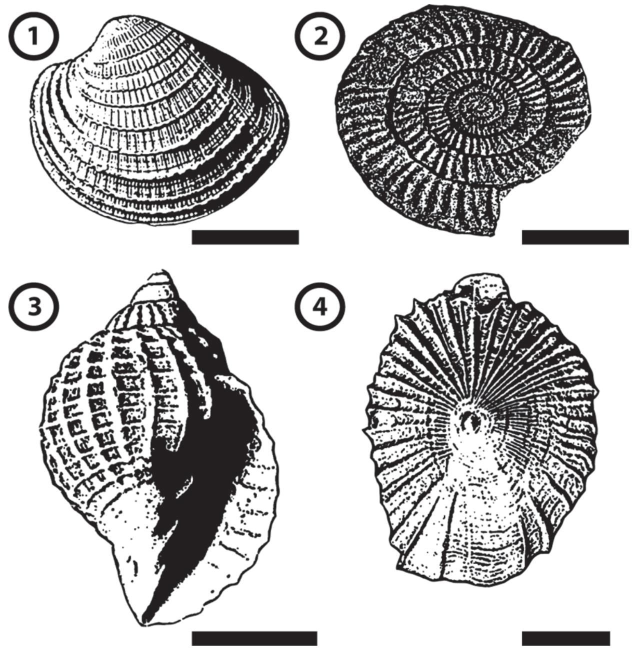

Figure 3. Selected fossil invertebrates from Ecuador. **1,** ***Chione manabia*** (bivalve) from the Pliocene, Pacific Region (Pilsbry and Olsson, 1941; plate 16.1); **2,** ***Orthechioceras* cf. *pauper*** (ammonite) from the Jurassic, Amazon Region (Dommergues *et al.*, 2004; plate 1.8); **3,** ***Clathrodrillia noventa*** (gastropod) from the Pliocene, Pacific Region (Pilsbry and Olsson, 1941; plate 2.5); **4,** ***Crucibulum alloglyptum*** (gastropod), from Pliocene, Pacific Region (Pilsbry and Olsson, 1941; plate 7.5). Original photographs were redrawn in Adobe Illustrator using the option sketch-stamp. Scale bars= 2 cm (**1, 3–4**); 3 cm (**2**).

Paleontology of Ecuador from 2000 to present

Vertebrate paleontology. Over the past seventeen years, vertebrate paleontology in Ecuador has seen important contributions in terms of the discovery of new fossil localities as well as the revision of some important fossils collected and

TABLE 2 – Summary of invertebrate families with fossil occurrences from Ecuador as originally were identified or reported. For complete list of the genera and species see the original reference

Families	*Age/Province*	*Original reference*
	Gastropoda	
Conidae, Fasciolariidae, Nassariidae, Neritidae, Strombidae, Terebridae, Turbinidae, Trochidae	*Pliocene-Pleistocene/ Galápagos*	*Dall and Ochsner, 1928*
Calyptraeidae, Capuliidae, Columbellidae, Epitoniidae, Fissurellidae, Mitridae, Muricidae, Nassariidae, Olivellidae, Terebridae, Triviidae	*Pliocene-Pleistocene/ Galápagos*	*Ragaini* et al., *2002*
Acteocinidae, Buccinidae, Bulimulidae, Bursidae, Caecidae, Cancellariidae, Calyptraeidae, Cassididae, Cerithidae, Columbellidae, Conidae, Cymatiidae, Cypraeidae, Epitoniidae, Fasciolariidae, Ficidae, Marginellidae, Melanellidae, Mitridae, Muricidae, Nassariidae, Naticidae, Olividae, Pyramidellidae, Rissoidae, Solariidae, Terebridae, Tonnidae, Trochidae, Turbinidae, Turritellidae, Turritidae, Vitrinellidae.	*Pliocene-Holocene/ Santa Elena*	*Pilsbry and Olsson, 1941*
Buccinidae, Bullidae, Conidae, Columbellidae, Ellobiidae, Fasciolariidae, Mitridae, Naticidae, Nassariidae, Olividae, Terebridae, Turridae.	*Quaternay/ Santa Elena*	*Hoffstetter, 1954a*
Cypraeidae, Ovulidae, Triviidae	*Neogene/Esmeraldas*	*Groves, 1997*
Buccinidae, Bursidae, Caecidae, Calliostomatidae, Calyptraeidae, Cancellariidae, Clathurellidae, Columbellidae, Conidae, Cylichnidae, Cystiscidae, Epitoniidae, Eulimidae, Fissurellidae, Mangeliidae, Marginellidae, Modulidae, Muricidae, Naticidae, Nidulariaceae, Olividae, Rissoidae, Phasianellidae, Pyramidellidae, Terebridae, Tonnidae, Tornidae, Triviidae, Turritellidae, Vermetidae	*Late Pliocene/ Santa Elena*	*Di Celma* et al., *2010*
Architectonicidae, Acteocinidae, Buccinidae, Bursidae, Caecidae, Calliostomatidae, Calyptraeidae, Cancellariidae, Clathurellidae, Columbellidae, Conidae, Cylichnidae, Cypraeidae, Epitoniidae, Eulimidae, Ficidae, Fissurellidae, Mangeliidae, Marginellidae, Mitridae, Muricidae, Naticidae, Nassariidae, Nidulariaceae, Olividae, Phasianellidae, Pyramidellidae, Terebridae, Tonnidae, Tornidae, Triviidae, Turbinidae, Turritellidae, Rissoidae	*Late Pliocene/Manabí*	*Landini* et al., *2002*
Acteocinidae, Architectonicidae, Buccinidae, Bursidae, Calliostomatidae, Calyptraeidae, Cassidae, Epitoniidae, Marginellidae, Melongenidae, Muricidae, Naticidae, Ringiculidae, Skeneopsidae, Terebridae, Tornidae, Triviidae, Turritellidae	*Early Pleistocene/Manabí*	*Cantalamessa* et al., *2005*
?Amnicolidae, Ampullariidae, Hydrobiidae, Thiaridae	*?Miocene/Cañar, Azuay*	*Marshall and Bowles, 1932*
Neritidae,	*?Miocene/Cañar, Azuay*	*Palmer, 1941*
	Bivalvia	
Anomiidae, Arcidae, Cardiidae, Corbulidae, Crassatellidae (Hiatellidae), Donacidae, Lucinidae, Mactridae, Mytilidae, Nuculanidae, Nuculidae, Ostreidae, Pectinidae, Periplomatidae, Psammobiidae, Semelidae, Spondylidae, Tellinidae, Veneridae.	*Pliocene-Holocene/Santa Elena*	*Pilsbry and Olsson, 1941*
Anomiidae, Arcidae, Cardiidae, Carditidae, Chamidae, Corbulidae, Crasstellidae, Cultellidae, Cyrenidae, Diplodontidae, Donacidae, Garidae, Glycymeridae, Leptonidae, Lucinidae, Mactridae, Mytilidae, Nuculanidae, Nuculidae, Ostreidae, Pectinidae, Petricolidae, Pholadidae, Pinnidae, Semelidae, Solenidae, Spondylidae, Sportellidae, Tellinidae, Veneridae	*Quaternary/Santa Elena*	*Hoffstetter, 1948, 1954b, 1954c.*
Anomiidae, Arcidae, Cardiidae, Cardiniidae, Carditidae, Corbulidae, Crassatellidae, Donacidae, Glycymerididae, Hiatellidae, Isognomiidae, Kelliidae, Lasaeidae, Lucinidae, Mactracidae, Mactridae, Mytilidae, Noetiidae, Nuculanidae, Ostreidea, Pectinidae, Petricolidae, Plicatulidae, Semelidae, Solenidae, Solecurtidae, Sportellidae, Tellinidae, Veneridae	*Late Pliocene/Santa Elena*	*Di Celma* et al., *2002*
Anomiidae, Arcidae, Cardiidae, Corbulidae, Crassatellidae, Donacidae, Glycymerididae, Hiatellidae, Lasaeidae, Lucinidae, Mactridae, Mytilidae, Noetiidae, Nuculidae, Nuculanidae, Ostreidae, Semelidae, Solecurtidae, Solenidae, Sportellidae, Pectinidae, Petricolidae, Pinnidae, Plicatulidae, Tellinidae, Thraciidae, Veneridae, Verticordiidae	*Late Pliocene/Manabí*	*Landini* et al., *2002*
Anomiidae, Arcidae, Cardiidae, Carditidae, Corbulidae, Cuspidariidae, Galeommatidae, Hiatellidae, Mactridae, Montacutidae, Noetiidae, Nuculidae, Kelliidae, Lasaidae, Lucinidae, Pandoridae, Pectinidae, Pholadidae, Psammobiidae, Semelidae, Solecurtidae, Solenidae, Tellinidae, Thraciidae, Veneridae, Yoldiidae	*Early Pleistocene/Manabí*	*Cantalamessa* et al., *2005*
Anomiidae, Arcidae, Basterotiidae, Cardiidae, Glycymerididae, Limidae, Lucinidae, Mytilidae, Noetiidae, Ostreidae, Pectinidae, Tellinidae, Ungulinidae, Veneridae	*Pliocene-Pleistocene/ Galápagos*	*Ragaini* et al., *2002*
Hyriidae	*?Miocene/Cañar, Azuay*	*Marshall and Bowles, 1932*
Cyrenidae, Mutelidae	*?Miocene/Cañar, Azuay*	*Palmer, 1941*
Mycetopodidae	*Miocene/Imbabura*	*Cadena* et al., *2018b*

TABLE 2 – Continuation

Families	*Age/Province*	*Original reference*
	Scaphopoda	
Dentaliidae, Siphonodentaliidae	*Pliocene-Holocene/Santa Elena*	*Pilsbry and Olsson, 1941*
Dentaliidae, Gadilidae	*Late Pliocene/Santa Elena*	*Di Celma* et al., *2002*
Dentaliidae, Gadilidae	*Late Pliocene/Manabí*	*Landini* et al., *2002*
Dentaliidae, Gadilidae	*Early Pleistocene/Manabí*	*Cantalamessa* et al., *2005*
	Cephalopoda (Ammonoidea)	
Arietitidae, Echioceratidae, Schlotheimidae	*Early Jurassic/ Morona-Santiago*	*Dommergues* et al., *2004*
Brancoceratidae, Lyelliceratidae	*Late Albian/Napo, Pastaza*	*Bulot* et al., *2005*
	Brachiopoda	
Disciniidae, Productidae	*Carboniferous/ Morona-Santiago*	*Tschopp, 1953*
	Echinodermata	
Arbaciidae	*Late Pliocene/Santa Elena*	*Di Celma* et al., *2002*
Crinoidea, indeterminate families	*Carboniferous/Morona-Santiago*	*Tschopp, 1953*
	Coleoptera (beetles)	
Scarabaenidae	*Pleistocene/Pichincha*	*Zunino, 2013*
	Isoptera (termites)	
Rhinotermitidae	*Miocene/Morona-Santiago*	*Engel and Krishna, 2007*

stored in collections for decades. In 2001 a new late Quaternary (probably Pleistocene to early Holocene in age) fossil locality was discovered at Río Cañas (Manabí Province), showing the occurrence of fragmentary material of mammal species previously described, including *Eremotherium* cf. *laurillardi* and *Haplomastodon chimborazi,* as well as an isolated fragment of the giant tortoise *Geochelone* (*Chelonoidis*) (Cantalamessa *et al.*, 2001). A detailed record of the late Pliocene teleostean otoliths from the Canoa Formation was presented by Landini *et al.* (2002). The same year, Tomiati and Abbazzi (2002) described deer faunas from different Pleistocene and Holocene localities in Ecuador. An analysis of the fossil record of the giant Holocene mammals from Ecuador was compiled to propose a model of extinction by Ficcarelli *et al.* (2003); it concluded that three important factors caused their extinction: high aridity, high humidity and geographic factors.

In the first decade of the 21st century, two new fossil localities were discovered along the Pacific coast of Ecuador, the first one showing the occurrence of Miocene cetaceans from Esmeraldas Province (Bianucci *et al.*, 2005), and a second locality in Manabí Province recording the occurrence of Pleistocene remains of the giant sloth *Eremotherium laurillardi* (Tito, 2008). Also during the first decade of 21st century, two studies based on review and reexamination of previously described fossil specimens include the extensive taxonomic reevaluation and phylogenetic analysis of the famous late Pleistocene *Haplomastodon chimborazi* from Carchi Province published by Ferretti (2010) and the revision of the geographical distribution of Pleistocene giant sloths from Ecuador (Román-Carrión, 2007).

Over the last seven years, the number of studies on fossil vertebrates from Ecuador has increased considerably compared to previous decades, including the study of fish remains from the Súa Member, early Pliocene of Esmeraldas Province (Carnevale *et al.*, 2011); the rediscovery of several mammal holotypes thought to be lost, including *Eremotherium elenense*, *Glossotherium tropicorum*, *Scelidotherium* (*? Scelidodon*) *reyesi*, among others by Montellano-Ballesteros and Román-Carrión (2011); the redescription of the

Table 3 – Summary of fossil plants (macrofossils) families from Ecuador as originally were identified or reported. For complete list of the genera and species see the original reference(s)

Families	*Age/Province*	*Original reference(s)*
	Leaves	
Annacardiaceae, Apocynaceae, Bignoniaceae, Bombacaceae, Caesalpiniacea, Capparidaceae, Cyperaceae, Euphorbiaceae, Lauraceae, Lecythidaceae, Loranthacea, Malphighiaceae, Mimosaceae, Moraceae, Myristicaceae, Myrtaceae, Nyctaginaceae, Papillionaceae, Piperaceae, Poaceae, Polypodiacea, Rhamnaceae, Rubiaceae, Sapindaceae, Sterculiaceae, Styracaceae, Tiliaceae, Ulmaceae, Vochysiaceae	*Miocene/Loja*	*Berry, 1929b*
Gymnospermae (Bennettiales indeterminate families, Cycadaceae, Podocarpaceae, Polypodiaceae)	*Aptian-Albian/ Loja- El Oro*	*Shoemaker, 1982*
Cecropiaceae, Clusiaceae, Fabaceae, Rhamnhaceae	*Late Miocene/Azuay*	*Kowalski, 2001*
Lygodiaceae	*Miocene/Loja*	*Berry, 1933*
Indet.	*Miocene/Imbabura*	*Cadena* et al., *2018b*
	Fruits	
Annacardiaceae, Annonaceae, Humiriaceae, Palmaceae, Sapindaceae	*Eocene?/Santa Elena*	*Berry, 1929b*
Leguminosae	*Miocene/Loja-Azuay*	*Burnham, 1995*
Annardiaceae	*Miocene/Loja-Azuay*	*Burnham, 2004*
	Woods	
Araucariaceae	*Aptian-Albian/Loja- El Oro*	*Shoemaker, 1982*

early Miocene freshwater fish *Carrionellus diumortuus* from Loja Province (Costa, 2011); and the summary of the fossil vertebrates of Ecuador presented in the book “Fauna de Vertebrados del Ecuador” (Albuja *et al*., 2012). The same year, several chapters of the Revista Politécnica from the Escuela Politécnica Nacional (EPN) were dedicated to describing new fossil discoveries, including three localities with Pleistocene megafauna in Quito: the Historic Center of the city (Román-Carrión, 2012a), Caraburo, northeast of the city (Román-Carrión, 2012b), and Conocoto, southeast of the city (Román-Carrión, 2012c). A last chapter was dedicated to report the record of *Stegomastodon waringi* from San Vicente, Manabí Province (Román-Carrión 2012d).

Recent descriptions include a new species of Xenarthra *Anadasypus aequatorianus* from the late Miocene of Azuay Province by Carlini *et al.* (2013); new fossils from Quebrada Seca, Santa Elena Province (Ruiz-Sánchez *et al*., 2014); and the late Pleistocene mammals from the new Tanque-Loma locality, also in Santa Elena Province (Lindsey and López, 2015). In a book dedicated to describe the asphalt-preserved biotas of the continent, La Carolina and Tanque-Loma fossil faunas from Santa Elena Province were mentioned and summarized in terms of their composition by Lindsey and Seymour (2015). The most recent publications on fossil mammals from Ecuador include a summary of the fossil record of proboscideans (Mothé *et al*., 2017), the ground sloth *Glossotherium tropicorum* (De Iuliis *et al*., 2017), the report of the shrew genus *Cryptotis* (Moreno-Cárdenas and Román-Carrión, 2017), and the Oligocene dolphin from Montañita/Olón locality at the pacific coast (Tanaka *et al*., 2017).

In terms of fossil reptiles, turtles from at least five new localities near the town of Atahualpa, Santa Elena Province were reported, including geoemydids (*Rhinoclemmys* sp.), kinosternids (*Kinosternon* sp.) and the first fossil record of chelydrids (*Chelydra* sp.) in South America (Cadena *et al*., 2017) (Fig. 4). More recently the first record of Oligocene sea turtles (Pan-Cheloniidae) of South America was re-

Figure 4. Selected fossil turtles from Santa Elena Province, Ecuador. **1,** Costal bone of ***Rhinoclemmys*** **sp**. in dorsal view; **2,** Neural bone of ***Rhinoclemmys*** **sp**. in dorsal view; **3,** Nuchal bone of ***Rhinoclemmys*** **sp.** in dorsal view; **4,** Peripheral bone of ***Kinosternon*** **sp.** in dorsal view; **5–6,** Costal bone fragment of ***Chelydra*** **sp.** in dorsal and ventral view respectively. Fossils figured in Cadena *et al.* (2017). Scale bars= 2 cm.

ported from the Montañita/Olón locality, also from Santa Elena Province (Cadena *et al.*, 2018a).

One of the most recent paleontological studies of Ecuador, reported the occurrence of a partially articulated skull with teeth from a Miocene scombridid fish from Manabí Province (Cadena *et al.*, 2018b).

Invertebrate paleontology. For the invertebrate paleontology field in Ecuador, the 21st century started with a series of studies that beyond describing new taxa used them to answer sedimentological, taphonomical and paleogeographical-ecological questions. That is the case of the paleoecological study of late Pliocene gastropods preserved in turbiditic slope deposits constituting the Onzole Formation, northwestern Ecuador (Walker, 2001); the utility of shell concentrations as tools for sedimentation dynamics, mainly the use of bivalves from the Canoa Formation, late Pliocene of Manabí Province (Di Celma *et al.*, 2002); also from the Canoa Formation, the analysis of the mollusks fauna to correlate it with other Pacific biotic provinces (Landini *et al.*, 2002); from Isabela Island (Galápagos), the paleoecology and paleobiogeography of Pleistocene mollusks (Ragaini *et al.*, 2002), and from the early Pleistocene Jama Formation, an integrated study of shell concentrations for sequence stratigraphy reconstructions (Cantalamessa *et al.*, 2005). Years later, and also from the Jama Formation, the structure, taphonomy and paleoecology of the fossil record of ostreids was studied by Ragaini and Di Celma (2009). Cretaceous bivalves from different localities in eastern Ecuador were reported and described by Dhondt and Jaillard (2005), showing their chronostratigraphic range. Also from the Cretaceous, ammonites from the late middle–early late Albian of eastern Ecuador were studied and described from the Napo Group by Bulot *et al.* (2005); most of these ammonites were initially reported and illustrated by Tschopp (1953) and Aspden and Ivimey-Cook (1992). Ammonites from the Jurassic of the Santiago Formation, including new species such as *Pseudagassiceras equadorensis*, were reported and described by Dommergues *et al.* (2004). Amber also makes up part of the fossil record of Ecuador; in particular, a new species of termite named *Dolichorhinotermes lanciarius* was described by Engel and Krishna (2007) based on material from the Miocene Gualaquiza locality, northeast of Loja, Morona-Santiago Province. Recently, amber without any clear occurrence of trapped fossils was reported from the Cretaceous of the Napo Basin, Napo Province (Cadena *et al.*, 2018b).

Decades after the first report of the Cangahua balls (*Coprinisphaera ecuadoriensis*) in volcaniclastic sequences of Ecuador (Sauer, 1955), remains of the producer of one of these particular ichnofossils (an insect) was found inside, corresponding to a partially but finely preserved dung beetle head, representing a new species described by Zunino (2013) as *Phanaeus violetae* (Fig. 5.1). More recently, a new ichnospecies of Cangahua ball called *Coprinisphaera kitu* (Fig. 5.2) from La Ronda, Quito, Pichincha Province, was described by Sanchéz *et al.* (2013); who also pointed out that *C. ecuadoriensis* is a junior synonym of *C. murguiai* (Fig. 5.3).

Fossil insects from the late Miocene San José Formation, Malacatos Valley in Loja Province were briefly described by Berosa and Román-Carrión (2012) (Fig. 5.4–5), as well as freshwater shrimps from the late Miocene of Cuenca and Loja provinces (Herrera and Román-Carrión, 2012) (Fig. 5.6).

Recently, Miocene freshwater mussels from the Chota Formation were reported and studied from El Refugio locality, Imbabura Province, northern of Ecuador (Cadena *et al.*, 2018b; Cadena and Casado-Ferrer, in press).

Paleobotany. One of the most relevant works in paleobotany, not only for Ecuador but also for all of tropical South America, was the description and analysis of the middle to late Miocene fossil plants from the Nabón Basin (Kowalski, 2001), which not only included new species such as *Gouania andica* (a liana) and *Coussapoa namarina* (a hemi-epiphyte),

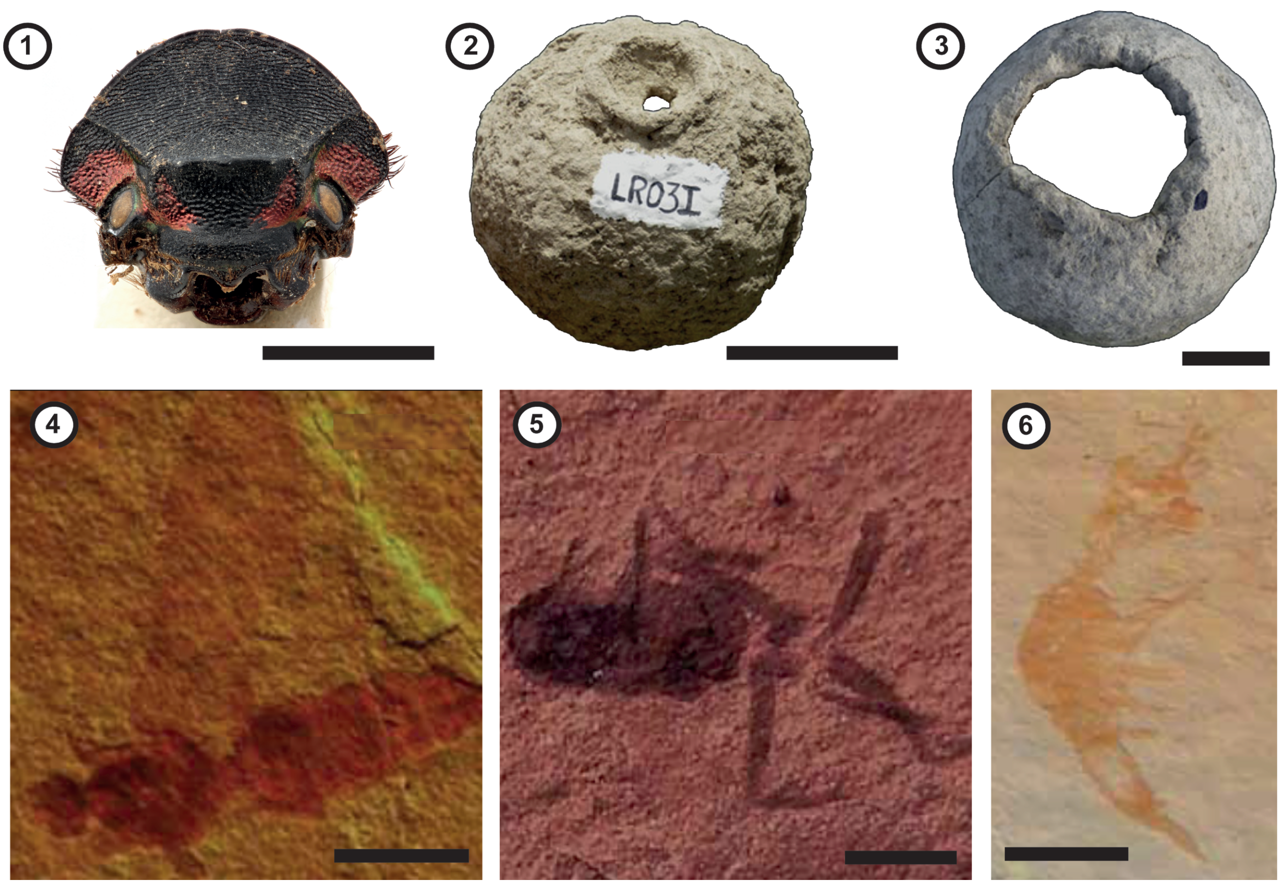

Figure 5. Selected ichnofossils and fossil arthropods from Ecuador. **1,** ***Phanaeus violetae*** Zunino 2013. Head in anterior view (color version and high resolution photo); **2,** Paratype of ***Coprinisphaera kitu*** Sánchez *et al.*, 2013 (Cangahua ball), figured in Sánchez *et al.* (2013, fig. 8L); **3,** Lectotype of ***Coprinisphaera*** **(*ecuadoriensis*)** ***murguiai*** Sauer, 1955, figured in Sanchéz *et al.*, (2013, fig. 8D); **4,** Hymenoptera (Formicidae), figured in Berosa and Román-Carrión (2012, fig. 3); **5,** Insect imprint, figured in Berosa and Román-Carrión (2012, fig. 4); **6,** Fossil freshwater shrimp imprint, figured in Herrera and Román-Carrión (2012, fig. 3). Scale bar= 4 mm (**1**); 3 cm (**2**); 2 cm (**3**); 1 cm (**4**); 5 mm (**5**–**6**). Permission for the use of the photographs was granted to J.L. Román-Carrión.

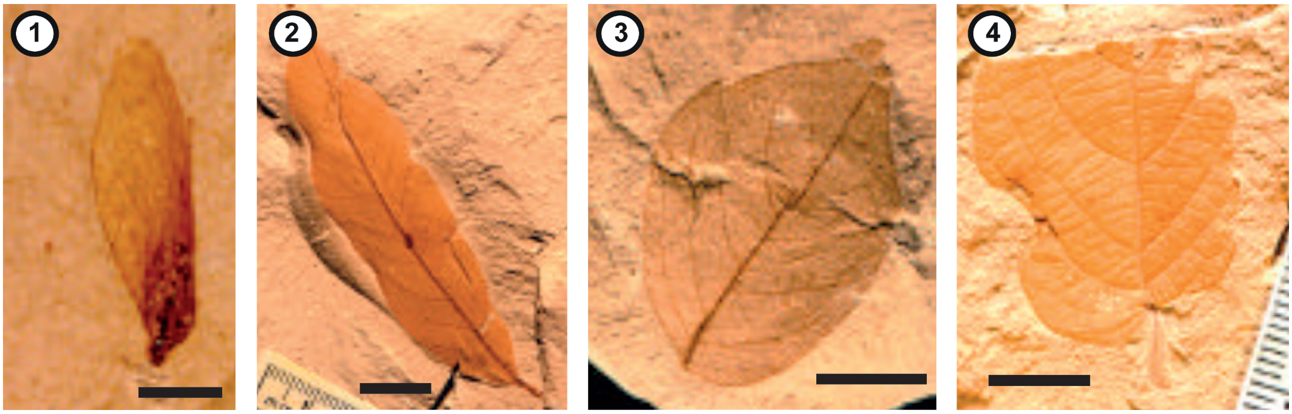

Figure 6. Selected fossil leaves from Ecuador. **1–4,** Different examples of fossil leaves (unknow taxa) from Cuenca, Ecuador. Photographs taken from Burnham, R.J. (2001). Scale bars= 1 cm.

but also explored the utility of fossil leaves as a proxy for paleotemperature-paleoelevation reconstructions. Years later a new fossil species of winged fruit was described from Miocene rocks of the Loja Basin, Loja Province; it was named *Loxopterygium laplayense* by Burnham and Carranco (2004). Most of the fossil plants reported or described from Ecuador were mentioned in a paper on South American paleobotany and the origins of Neotropical rainforests by Burnham and Johnson (2004). Different morphotypes of Miocene fossil leaves and seeds were recently reported from El Refugio locality, Chota Basin, Imbabura Province (Cadena *et al.*, 2018b) and wait for detail studies on their taxonomy and paleobotanical implications.

Some of the fossil plants and seeds from Ecuador are shown in Figure 6, and a complete summary of the families of fossil plants (leaves, fruits and wood) of the country is presented in Table 3.

Micropaleontology-palynology. As for the other fields of paleontology in Ecuador, the initial studies of the 21st century involved more implications and analysis of the fossil record than descriptions or reporting of new localities and species. A study involving benthic foraminifera from the late Pliocene Canoa Formation described their similarities with other foraminifera from the Pacific and the Atlantic (Landini *et al.*, 2002). The most complete micropaleontological work of this century is titled "Micropaleontología Ecuatoriana" and was published by Ordóñez *et al.* (2006). With its sixteen chapters exploring, illustrating and summarizing the knowledge on foraminifera, radiolarian, nannofossils and palynomorphs from Ecuador for each of the most important sedimentary basins and regions, this work constitutes a reference "bible" for anyone interested in micropaleontological-palynological research in the country. Some of the microfossils and palynomorphs of Ecuador are shown in Figure 7.

Palynomorphs and nannofossil biostratigraphy of the Cretaceous Napo Group was published by Vallejo *et al.* (2002) based on the analysis of the Pungarayacu 30 well belonging to Petroproducción Ecuador. Reconstruction of the Pleistocene and Holocene forests of Ecuador, particularly for the Andes and Amazon regions has principally involved the study of palynomorphs in the absence of a good macrofossil record of the vegetation. That is the case of the study of the late Quaternary fossil pollen from the El Tiro Pass, Loja Province, to infer changes in vegetation, climate and fire dynamics (Niemann and Behling, 2008). Palynological studies have also been conducted in the Galápagos Islands, particularly based on the Quaternary record (Collins *et al.*, 2013, Bush *et al.*, 2014). More recently, diatoms were reported from Quaternary paleolake deposits of the Chota Basin, Imbabura Province (Cadena *et al.*, 2018b).

The following is a summary of the microfossil and palynomorph occurrences through time for the three major geographical regions of Ecuador (the Pacific Region including the Galápagos Islands, the Andes Region and the Amazon Region) (see also Figure 8) based on the works from Ordóñez *et al.* (2006), Niemann and Behling (2008), Collins *et al.* (2013), and Bush *et al.* (2014).

Pacific Region. Quaternary: Palynomorphs; Pleistocene: Tablazo Formation (Fm.) (forams, nannofossils and palynomorphs); Pliocene: Puna Fm. (forams); late Miocene–early Pliocene: Onzole Fm. (forams, nannofossils and palynomorphs); middle–late Miocene: Progreso Fm. (forams, nannofossils and palynomorphs), Angostura Fm. (forams and nannofossils); early–middle Miocene: Dos Bocas Fm. (forams and radiolarians), Villingota Fm. (forams, radiolarians and diatoms), Subibaja Fm. (forams and palynomorphs), Tosagua Fm. (forams and nannofossils), Viche Fm. (forams, radiolarians, nannofossils and palynomorphs); Oligocene: Playa Rica Fm. (forams and nannofossils), Pambil Fm. (forams, nannofossils, palynomorphs and radiolarians); Middle–late Eocene: Caliza de las Delicias (forams), Zapallo Fm. (forams and nannofossils), Cerro Fm. (forams, nannofossils and palynomorphs); Eocene: Ancón Group (Gp.) (forams, nannofossils, radiolarians and palynomorphs), San Mateo Fm. (palynomorphs); late Paleocene–early Eocene: San Eduardo Fm. (forams, nannofossils and radiolarians); Paleocene: Azúcar Gp. (forams, nannofossils and palynomorphs); Maastrichtian–Paleocene: Guayaquil Fm. (forams, nannofossils and radiolarians), Santa Elena Fm. (forams, nannofossils and radiolarians); Santonian–Campanian: Cayo Fm. (forams, radiolarians, dinoflagellates and palynomorphs), San Lorenzo Fm. (forams and radiolarians); Coniacian: Calentura Fm. (forams).

Andes Region. Quaternary: Palynomorphs; Paleocene–Eocene: Saquisilí Fm. (forams and palynomorphs), Gallo Rumi Fm. (forams and palynomorphs); Campanian–Maastrichtian: Yunguilla Fm. (forams, palynomorphs and radiolarians), Jadan Fm. (forams and palynomorphs); Coniacian–

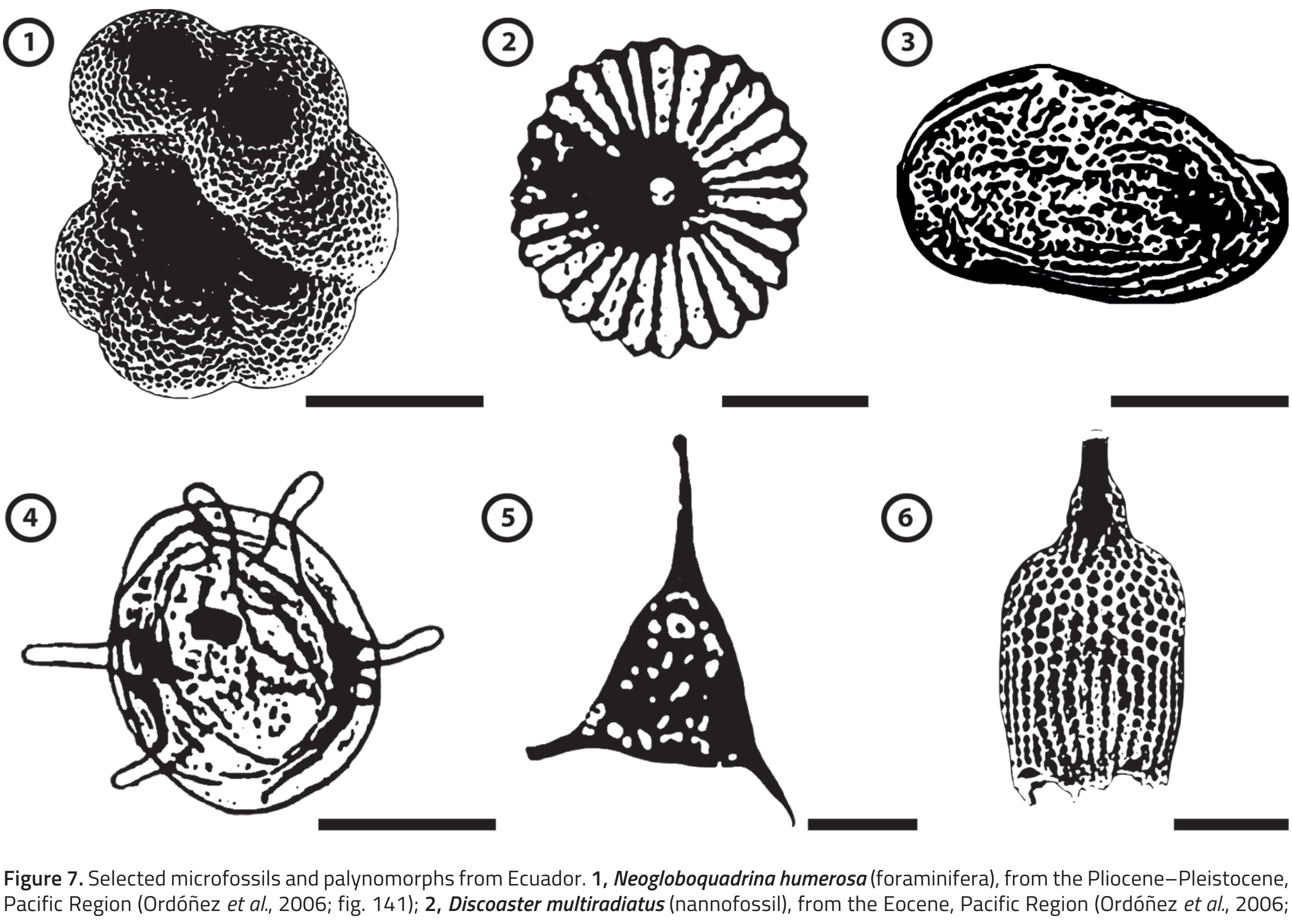

Figure 7. Selected microfossils and palynomorphs from Ecuador. **1,** ***Neogloboquadrina humerosa*** (foraminifera), from the Pliocene–Pleistocene, Pacific Region (Ordóñez *et al*., 2006; fig. 141); **2,** ***Discoaster multiradiatus*** (nannofossil), from the Eocene, Pacific Region (Ordóñez *et al*., 2006; fig. 225); **3,** ***Cytheretta* sp.** (ostracod), from the Miocene, Pacific Region (Ordóñez *et al*., 2006; fig. 2.4); **4,** ***Elaterosporites klaszi*** (pollen), from the Early Cretaceous, Amazon Region (Ordóñez *et al*., 2006; fig. 11.13); **5,** ***Veryhachium trispinosum*** (acritarch), from the Devonian, Amazon Region (Ordóñez *et al*., 2006; fig. 11.2); **6,** ***Calocycletta virginis*** (radiolarian), from the Miocene, Pacific Region (Ordóñez *et al*., 2006; fig. 183). Original photographs were redrawn in Adobe Illustrator using the option sketch-stamp. Scale bar= 2 mm (**1**); 10 µm (**2**); 0.5 mm (**3, 5**); 1 mm (**4, 6**).

Maastrichtian: Casanga Fm. (forams and palynomorphs); Turonian–Campanian: Alamor Fm. (forams and nannofossils), El Naranjo Fm. (forams and nannofossils); Aptian–Albian: Cazaderos Fm. (forams, nannofossils, ostracods and palynomorphs).

Amazon Region. Quaternary: Palynomorphs; middle–late Miocene: Arajuno Fm. (forams, palynomorphs and ostracods); Miocene: Chalcana Fm. (palynomorphs and ostracods); late Eocene–Oligocene: Orteguaza Fm. (forams and palynomorphs); Eocene: Tiyuyacu Fm. (forams and palynomorphs); Coniacian–Santonian: Napo Superior Fm. (forams, nannofossils, palynomorphs and ostracods); middle Turonian–Coniacian: Napo Medio Fm. (forams, nannofossils and paly- nomorphs); late Albian–early Cenomanian: Napo Inferior Fm. (forams, nannofossils and palynomorphs); late Albian: Napo Basal Fm. (forams, nannofossils and palynomorphs); middle–late Albian: Hollin Fm. (forams and palynomorphs); Jurassic–Early Cretaceous: Chapiza Fm. (forams, palynomorphs and ostracods); Middle–Upper Devonian: Pumbuiza Fm. (acritarchs).

FOSSIL RECORD BIAS ACCORDING TO AGE, SAMPLING, AND STUDIES

Paleozoic

The Paleozoic is poorly represented in Ecuador, with only a few outcrops in Morona-Santiago and Zamora Chinchipe provinces, according to the Geologic Map of Ecuador (Inigemm, 2016) (Fig. 1.1), the stratigraphic guide of Bristow and Hoffstetter (1977) and the geological summary of Vera (2013); it is mainly restricted to Carboniferous rocks of the Isimanchi Unit and Macuma Formation. Invertebrates and microfossils reported from the Macuma Formation (Tschopp, 1953) remain poorly known. At the same time, these sections have not been revisited or explored by any scientists in decades, suggesting that the potential for new and better findings is a matter of increasing sampling and exploration. Besides the Carboniferous reports, the only other Paleozoic fossils are the Devonian acritarchs reported from wells drilled in the Amazon region (Ordóñez *et al*., 2006). Currently, J.L Román-Carrión and some of his students are conducting new fieldwork expeditions in the eastern region of Ecuador, finding new fossils that are expected to be described in the near future.

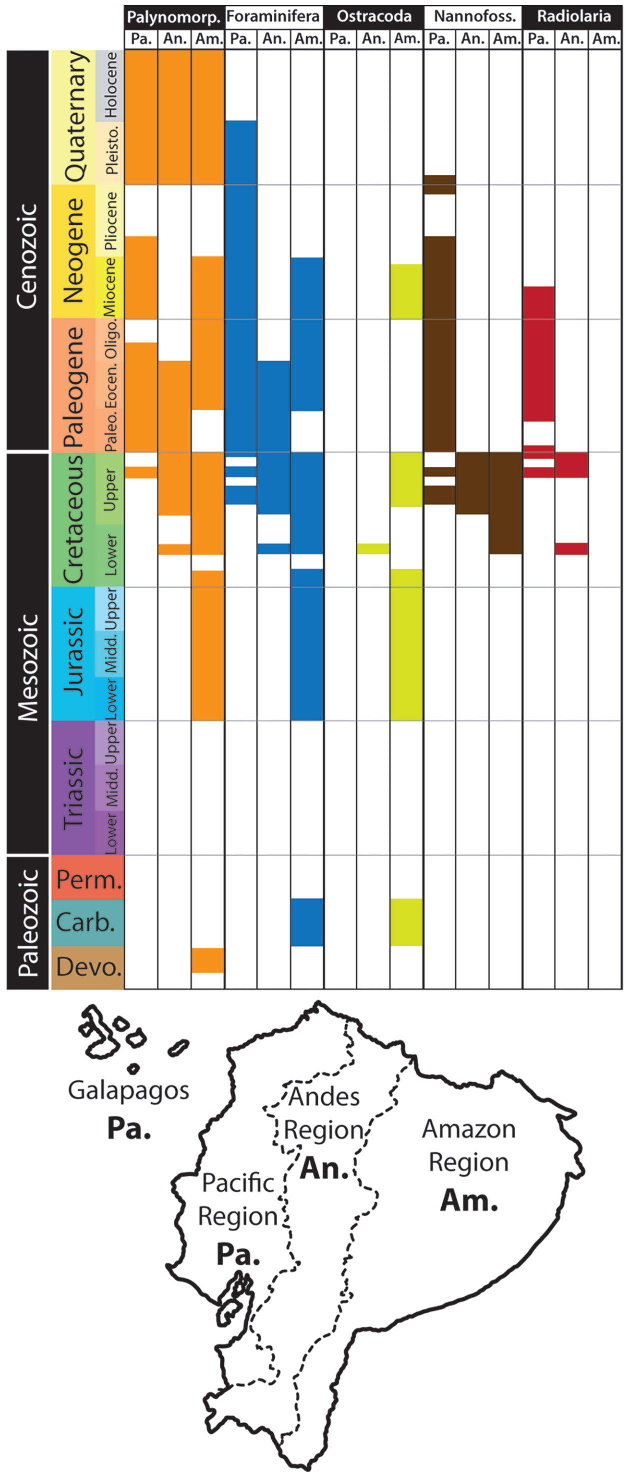

Figure 8. Chronologic distribution of microfossils and palynomorphs of Ecuador, principally from Ordóñez *et al.* (2006). For the Jurassic occurrences, the whole range of the taxa were considered following Ordóñez *et al.* (2006). *Abbreviations:* **Am.** Amazon Region; **An.** Andes Region; **Carb.** Carboniferous; **Devo.** Devonian; **Eocen.** Eocene; **Midd.** Middle; **Oligo.** Oligocene; **Pa.** Pacific Region; **Paleo.** Paleocene; **Perm.** Permian; **Pleisto.** Pleistocene. The three major regions (Amazon, Andes, and Pacific) are shown in the map, bottom of the figure.

Mesozoic

The Mesozoic in Ecuador is mostly represented by Jurassic and Cretaceous rocks, with some small Triassic outcrops in the Zamora-Chinchipe province (Egüez *et al.*, 2017; Vera, 2013) (Fig. 1.2). The fossil record is still restricted to invertebrates, plant remains and microfossils (including palynomorphs) as described above, lacking, for example, well-preserved and taxonomically identifiable vertebrates, which are abundant in other Mesozoic sequences of northern South America, mostly in Colombia and Venezuela (Barrett *et al.*, 2008; Cadena and Parham, 2015; Langer *et al.*, 2014). It seems to us that this in part is due to a lack of specific paleontological fieldwork searching for this type of fossils because most of the lithologies of the Ecuadorian Mesozoic formations are similar to those in which vertebrates from Colombia and Venezuela have been found (shales, mudstones, limestones, and calcareous sandstones).

Cenozoic

Almost 80% of the sedimentary rocks outcroppings in Ecuador are Cenozoic (Fig. 1.3–4) and, as described above, they exhibit most of the fossil record and localities of the country, including a diverse and abundant record of invertebrates, vertebrates, plants and microfossils-palynomorphs. However, most of these fossils require updated information on their current physical locations in museums or institutions and collections in Ecuador and in other countries, something that, for example, has been completed for some of the vertebrates (Montellano-Ballesteros and Román-Carrión, 2011).

Most of the Cenozoic fossils need revision and taxonomic updating, as well as their inclusion in recent phylogenetic studies of South American and global Cenozoic faunas. One case is, for example, the fossil record of tortoises from the famous La Carolina site and other nearby sites in Santa Elena Province, a work currently conducted by a student of the Pontificia Universidad Católica del Ecuador. Additionally, most of the published works have been mainly limited to descriptions of fossils, lacking more advanced paleoecological and paleophysiological studies using state of the art techniques, such as microcomputer tomography, isotopes, bone histology and molecular paleontology, as well as biomechanical models and evo-devo analyses, among others.

THE CURRENT AND NEAR FUTURE STATUS AND CHALLENGES FOR ECUADORIAN PALEONTOLOGY

One of the major limitations in the advancement of any field of science is not only the lack of investment in infrastructure-equipment, research itself, and qualified professionals, but also the lack of continuity and updating of all these aspects. The lack of some or all these aspects together have dominated the paleontological activity in Ecuador during the last three centuries, *e.g.*, the lack of active paleontologists at universities and government institutions that can constantly conduct expeditions as well as develop research, educational activities and publishing. Part of this is reflected in the fact that almost 90% of the paleontological publications mentioned or discussed in this paper have been led or completed mainly by foreign researchers and institutions that had come to Ecuador to work only for a couple of years or months or even for shorter terms, such as in the case of researchers completing PhD or MSc theses. Currently, the number of active paleontologists in Ecuador working for universities, museums or government institutions is no higher than five (including the two authors of this paper), and none of the universities' geosciences schools or departments offer postgraduate programs directly involving paleontology or any related aspects of it.

In terms of infrastructure dedicated to house and exhibit the fossil record of Ecuador, there are only a few small museums and collections that house some of the most relevant fossils. In Quito, these include: the Museo de Historia Natural Gustavo Orcés V (**MHNGOV**) (the largest natural history museum in the country, preserving some of the holotypes of the Neogene megafauna) run by the Escuela Politécnica Nacional, the collections at the Museo Ecuatoriano de Ciencias Naturales run by the Instituto Nacional de Biodiversidad, some fossil collections at the Universidad Central de Ecuador, and the Museo Antropológico del Colegio Mejía. On the Pacific coast, the Museo Paleontológico Megaterio of the Universidad Estatal de la Península de Santa Elena (**UPSE**), located in La Libertad, Santa Elena Province, preserving the fossil record of this region, and in the North, the Museo Paleontológico de Bolivar, located in Bolivar, Carchi Province, does the same for the fossils of its region, but always with limited budgets, maintenance, and without on-line catalogues that can be accessed by the scientific community. Other minor collections and fossil displays are located at the Universidad Técnica Particular de Loja, Loja Province; the Puyango petrified forest fossil site, El Oro Province; Quebrada Chalán fossil site, Chimborazo Province; and the Casa de la Cultura in Lago Agrio, Sucumbios Province.

In terms of infrastructure for the preparation and proper curation of fossil material, only the MHNGOV in Quito has a basic laboratory for mechanical preparation and casting of fossils, but detailed preparation of macrofossils or deeper studies of the material show important limitations. However, a brand-new university in Ecuador, Yachay Tech, located in San Miguel de Urcuquí, Imbabura Province, is building a state-of-the-art facility for the preparation and study of fossils, including the first computer tomography equipment exclusively dedicated for research in northern South America.

The near future of paleontology in Ecuador seems to be very promising, considering that currently at least three institutions (MHNGOV, UPSE and Yachay Tech) have active paleontologists who, in cooperation with local and international institutions, are promoting the exploration and recovery of new fossils, revisiting previous localities as well as discovering new ones and at the same time training the first generation of paleontologists educated in Ecuador.

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Appendix 1. Summary of relevant paleontological unpublished works for the last 20 years, including principally undergraduate and graduate theses on paleontology or fossils from Ecuador, and other technical reports.

Undergraduate theses

Lasluisa, R., and Moreno K. 2018. La Formación Macuma en la cordillera de Cutucú al sureste de Ecuador: Paleontología y Estratigrafía. Escuela Politécnica Nacional, 89 pp.

Mantilla-Lucero, G.E. 2017. Análisis comparativo de los moluscos Plio-Cuaternarios de la Costa y Galápagos: Revisión y caracterización de la colección de fósiles del Museo Petrográfico. Escuela Politécnica Nacional, 75 pp.

Macas, P. 2013. Fósiles de aves del Pleistoceno superior de las tierras impregnadas de brea de la Península de Santa Elena-Ecuador y sus implicaciones paleoambientales. Universidad Central del Ecuador, 101 pp.

Mesías, A. 2012. Registro y distribución de roedores fósiles pertenecientes al Pleistoceno del Ecuador. Universidad Central del Ecuador, 85 pp.

Román-Carrión, J.L. 2005. Distribución geográfica de los perezosos gigantes (Superorden Xenarthra, Orden Tardigrada) del Pleistoceno del Ecuador. Universidad Central del Ecuador, 68 pp.

Romero-Carrasco, A.I. 2017. Marcas de Herbivoría en hojas fósiles de las cuencas miocénicas del sur de Ecuador. Universidad Central del Ecuador, 89 pp.

Torres-Chiriboga, F. 2016. Bone histology of Pleistocene giant tortoises (Testudinidae) from continental Ecuador, with comments on the origin of Galápagos tortoises. Pontifícia Universidad Católica de Ecuador, 95 pp.

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Román-Carrión, J.L. 2009. Informe de diagnóstico de flora y fauna fósil en la Cuenca Occidental del Río Nangarita y la Cordillera del Cóndor, Provincia de Zamora Chinchipe. Fase 1: Concesión La Zarza, 46 pp.

Román-Carrión, J.L. 2011. Biodiversidad terrestre actual y pasada de los últimos remanentes de vegetación de los valles secos interandinos del Ecuador. Componente Paleontológica, 22 pp.

Román-Carrión, J.L. 2014. Informe de prospección paleontólogica a la vía de ingreso a la casa de máquinas del proyecto Coca-codo-Sinclair, 39 pp.

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Van Hemelryk, I. 2009. Excavación en la Quebrada de Chalán cerca de Punín, 86 pp.