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Neogene molluscs, shallow marine paleoenvironments, and chronostratigraphy of the Guajira Peninsula, Colombia

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Abstract The Neogene sedimentary fill of the Cocinetas Basin in northern Colombia preserves a rich record of marine invertebrates and can be analyzed in the context of a high-resolution stratigraphy and excellent chronostratigraphy. Molluscan fossils are highly diverse and often well preserved, offering a window into the rapidly changing paleoenvironments and biogeography of northern South America during parts of the Early to Middle Miocene and latest Pliocene to Pleistocene. Before the evolutionary and biogeographic implications of these fossils can be understood, however, their associated depositional environments and geologic ages must be determined. Here, we present preliminary results from paleoenvironmental, biostratigraphic, and strontium isotope chronostratigraphic analyses of sediments and fossils from the Uitpa, Jimol, Castilletes, and Ware formations found in Cocinetas Basin. The basal unit in the Neogene succession, the Uitpa Formation, comprises mudstones redeposited sandstones and molluscs typical of bathyal to outer shelf environments at its base. It is a shallowing-up sequence and is conformable with the overlying Jimol Formation, which comprises coarse-grained lithic calcarenite, coquina, and mudstone that represent a regressive–transgressive–regressive sequence. This sequence includes foreshore and transition zone through lower inner shelf environments, but generally poorly preserved invertebrate assemblages. The conformably overlying Castilletes Formation contains a varied suite of depositional environments with better-developed shell beds and thicker successions of intervening siltstone. A significant unconformity exists between the Castilletes Formation and the overlying Ware Formation, which represents a deltaic to coastal shoreface deposition environment, rich in shallow marine molluscs from a variety of ecotopes. Biostratigraphic assessment and strontium isotopic results from the Jimol and Castilletes formations indicate that these units contain fossils of latest Early Miocene through Middle Miocene age, while those of the Ware are approximately Late Pliocene in age. These results help to place the shallow marine assemblages of Cocinetas Basin into a wider geologic context that aids our understanding of how these faunas relate to the broader evolutionary and biogeographic history of the southern Caribbean during the Neogene. Additionally, the isotope dating and paleoecology of this fauna help to place co-occurring terrestrial and aquatic vertebrate assemblages into a local paleoenvironmental and chronostratigraphic framework.

Keywords Jimol Formation · Castilletes Formation · Ware Formation · Mollusca · Guajira Peninsula · Colombia

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Introduction

Marine invertebrate paleontology of Cenozoic sediments on the Guajira Peninsula of Colombia has received relatively little attention, despite substantial interest in the stratigraphy and tectonic features of the region and the extensive paleontological research that has been conducted in the neighboring sedimentary basins of northern Venezuela (Jung 1965; Landau and Marques da Silva 2010) and southern Caribbean Islands (e.g., Jung 1969). The Cocinetas Basin on the eastern flank of La Guajira Peninsula, northern Colombia (Fig. 1a), provides an extensive and well-exposed sedimentary and paleontological record of the last 30 million years. The only published work that has dealt specifically with fossil marine invertebrate systematics and biostratigraphy of the Guajira region is a short paper on molluscs from the Macarao (Eocene) and Siamana (Oligocene) formations by Olsson and Richards (1961), which had a poor stratigraphic control and geographic accuracy. More comprehensive systematic research was undertaken by Thomas (1972) in the form of an unpublished dissertation, which focused primarily on molluscs, presumably from either the Jimol or Castilletes

Fig. 1 a Location of Cocinetas Basin in the Guajira Peninsula of northern Colombia and other important Early-Middle Miocene (Burdigalian–Langhian) and Late Pliocene units in the southern Caribbean: *1* upper Culebra Formation (Panama), *2* La Rosa Formation (Venezuela), *3* Agua Clara, Querales, and Soccoro formations (Venezuela), *4* Castillo Formation (Venezuela), *5* Cantaure Formation (Venezuela), *6* Brasso and Manzanilla formations (Trinidad and Tobago), *7* Baitoa Formation (Dominican Republic), *8* Cayo Agua Formation (Panama), *9* San Gregorio Formation (Venezuela), *10* Mare and Playa Grande formations (Venezuela), *11* Araya Formation (Venezuela), *12* Bowden Formation (Jamaica), *13* Mao Limestone (Dominican Republic). **b** Map of northern Colombia and Venezuela showing location of Cocinetas Basin in the context of major regional faults

formations. Both Olsson and Richards (1961) and Thomas (1972), as well as Bürgl (1960), Renz (1960) and Rollins (1960, 1965) barely scratch the surface of the tremendous fossil biodiversity captured in the strata of the Guajira Peninsula, and none of these works explored fully the potential of these fossils for biostratigraphic or paleoenvironmental analysis.

The Neogene fossil record in the Cocinetas Basin is particularly well exposed and offers the opportunity to document more fully the biodiversity and biogeography of the southern Caribbean and northern South America during two intervals: the Early to Middle Miocene and the Late Pliocene (Moreno et al. 2015). Similar Miocene faunas (Fig. 1a) include the Culebra Formation of Panama (e.g., Woodring 1957), the very diverse Cantaure Formation on the Paraguana Peninsula (Jung 1965), the La Rosa, Agua Clara, Querales, and Socorro formations in the Falcón Basin (Hodson 1926; Hodson et al. 1927; Hodson and Hodson 1931a, b; Johnson et al. 2009; Quiroz and Jaramillo 2010) in Venezuela, Early Miocene strata of Trinidad (Maury 1912; Jung 1969) and the Baitoa Formation of the Dominican Republic (e.g., Maury 1917; Saunders et al. 1986). Correlated Pliocene faunas (Fig. 1) may be found in the Cayo Agua Formation of Panama (Olsson 1922), San Gregorio Formation of Falcón Basin (Hodson et al. 1927; Hodson and Hodson 1931a, b), Mare and Playa Grande formations of eastern Venezuela (Weisbord 1962, 1964a, b), Araya Formation of Cubagua Island (Landau and Marques da Silva 2010), Bowden Formation of Jamaica (Woodring 1925, 1928), and Mao Limestone of the Dominican Republic (Saunders et al. 1986). Nevertheless, with the exception of the Dominican Republic, none of these faunas have been studied within the context of well-developed stratigraphy and independent chronostratigraphic framework.

Extensive new fieldwork in Cocinetas Basin, including geological mapping, lithofacies description, and extensive and systematic collection of marine and terrestrial invertebrates has been conducted since 2011. The present paper builds on a revised stratigraphy for the Neogene sedimentary fill of Cocinetas Basin by Moreno et al. (2015). We provide a detailed chronostratigraphic framework derived from $^{87}Sr/^{86}Sr$ isotopic analyses and describe the biodiversity, biostratigraphy, and paleoenvironmental significance of nearly 250 field localities (c. 8000 specimens) collected or surveyed during this recent fieldwork and from historic collections.

Geological setting

Cocinetas Basin, located on the southeast Guajira Peninsula (Fig. 1b), is one of many pull-apart sedimentary basins found along the northern margin of South America
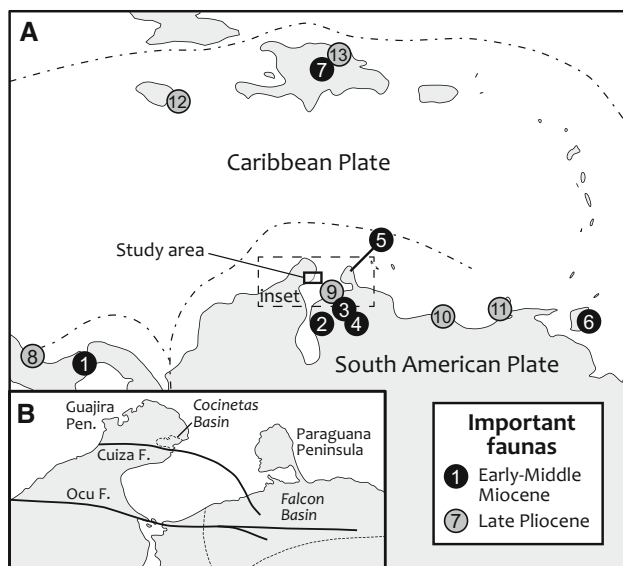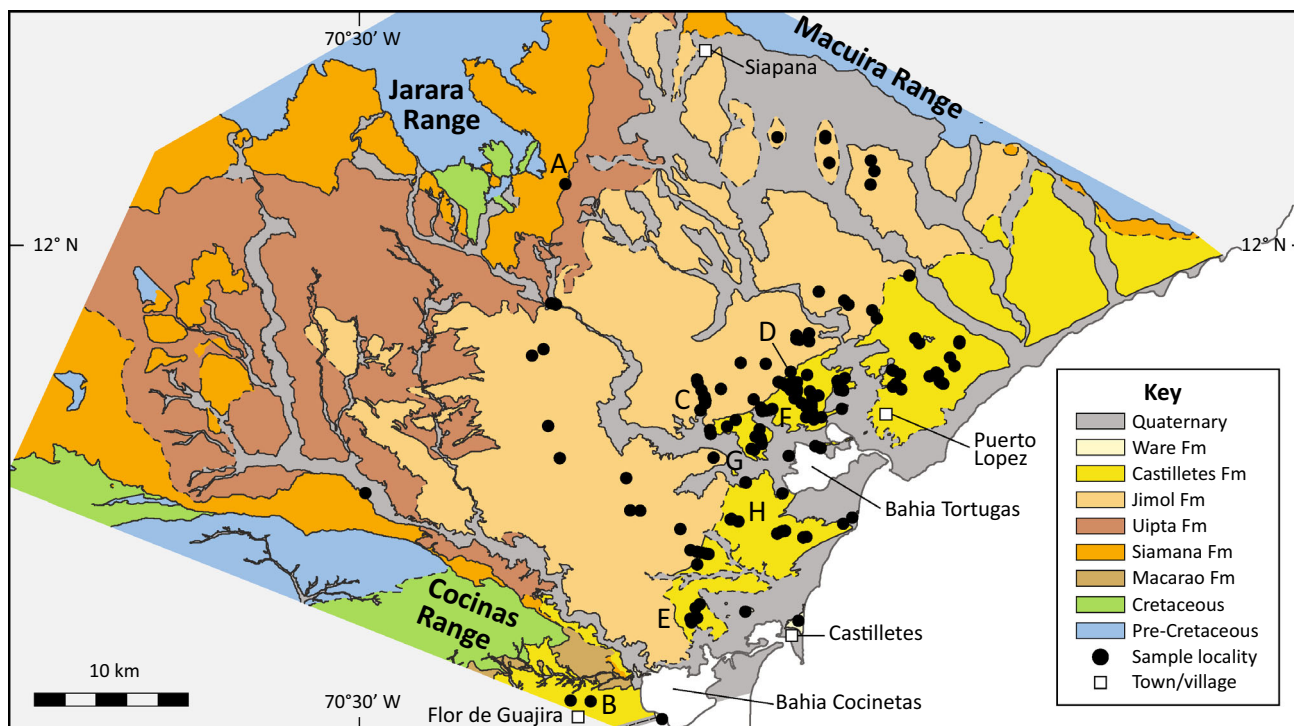
Fig. 2 Geological map of southeastern Cocinetas Basin showing distribution of sedimentary units, sampling localities, and points of interest. These include *a* Arroyo Uipta, *b* Patsúa, *c* Paraguachón, *d* Patajau, *e* Kaitamana, *f* Yotohoro, *g* Bahia Tucacas, *h* Macaraipao

(Muessig 1984; Pindell and Barrett 1990; Macellari 1995). The southern, western, and northern boundaries are delimited by the Cocinas (coincident with Cuiza Fault), Jarara, and Macuira ranges, respectively (Fig. 2). Deposition in the basin began during the Middle to Late Eocene (Macarao Formation), which is overlain by a sequence of conglomerates and thick carbonates of the Siamana Formation (Late Oligocene) (Renz 1960). Overlying the Siamana Formation is the Early Miocene Uitpa Formation, a thick sequence of calcareous mudstone interbedded with lithic sandstones (Renz 1960; Rollins 1965) (Fig. 3). Conformably overlying the Uitpa Formation are the Jimol and Castilletes formations, which have variably been considered Oligocene–Pliocene in age, but are here restricted to the Early to Middle Miocene. In unconformable contact with the Castilletes Formation is the Ware Formation (Late Pliocene), which has been recently erected by Moreno et al. (2015).

In the present study, the Jimol, Castilletes, and Ware formations are of most interest (Fig. 3). The historical definitions, lithostratigraphy, and paleoenvironments of those units are reviewed in Moreno et al. (2015). The Jimol Formation is dominated by coarse detritic and calcareous lithologies with fewer interbedded muddy levels.

The contact between the Jimol and Castilletes formations is very transitional and detailed stratigraphy shows a gradual environmental change between units. The

Fig. 3 Historical lithostratigraphic framework for the Cocinetas Basin, southeastern Guajira Peninsula, Colombia. Epoch and stage definitions follow Gradstein et al. (2012)

overlying Castilletes Formation is dominated by mudstones with uncommon interbedded, thin, calcareous, and coarse detritic levels that form ridges in the landscape. A conspicuous and laterally extensive hard-ground surface at the top of a transgressive calcareous layer provides the basis for a boundary surface between the two formations. The

Ware Formation of Moreno et al. (2015) comprises the sub-horizontal fluvio-deltaic to shallow marine deposits overlying an angular unconformity with the Castilletes Formation. The type section of the Ware Formation is located immediately east of the village of Castilletes, but correlated deposits are distributed along the eastern margin of Cocinetas Basin, cropping out as conspicuous isolated hills with near horizontal strata.

Materials and methods

Samples and data

Data used in biostratigraphic and paleoecological analyses come almost entirely from new field surveys and sampling. Some historic data from Renz (1960), Rollins (1960, 1965), and Thomas (1972) are included where appropriate, but only a few sampling sites of the latter author can be adequately georeferenced and stratigraphically located with sufficient precision to warrant inclusion in diversity and paleoecological analyses. These older collections presently reside at the Academy of Natural Sciences of Drexel University (ANSP), the National Museum of Natural History (USNM), Servicio Geológico Colombiano (SGC), and the Museo Geológico Nacional, Bogota (UN-DG).

Faunal data from the present study comprise laboratory-compiled species lists from samples of handpicked specimens (representative of local species richness), exhaustive field-compiled species lists, semi-quantitative field surveys, and bulk sampled high fossiliferous sediment (5 kg samples). Field surveys or rapid ecological assessments were conducted by placing a 0.25 m^2 quadrat against horizontally exposed bedding planes at randomly placed stations in each location (typically, three replicate surveys per location). All macroscopic taxa observed on the outcrop surface were categorized as abundant, common or rare. In almost all cases, material from the Uitpa, Jimol, and Castilletes formations comprise body fossils, although these specimens may include original (sometimes pristine, sometime leached) or recrystallized shell material. Material from the Ware Formation generally comprised casts or molds, occasionally recrystallized shell material, and rarely original (calcitic) shell material.

In all, data for 233 samples were collected from among 181 localities (Fig. 2) in the Cocinetas Basin, including 4 localities from the Uitpa Formation, 45 localities (65 samples) from the Jimol Formation, 123 localities (154 samples) from the Castilletes Formation, and 9 localities from the Ware Formation (Online Supplement 1). Each locality has been georeferenced using GPS and is reported using Smithsonian Tropical Research Institute (STRI) locality numbers. Stratigraphic heights reported here refer to

the position above or below the contact between the Jimol and Castilletes formations in the basin-wide composite stratigraphy of Moreno et al. (2015). Locality details are recorded in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb). All raw samples, occurrence lists and relative or absolute abundance data are reposited in the Paleobiology Database (http://www.paleobiodb.org), and matrices used in paleoecological analyses are available from Dryad (http://www.datadryad.org). All material is permanently reposited at the Mapuka Museum of Universidad del Norte (MUN-STRI), Colombia (http://www.uninorte.edu.co/web/mapuka).

Taxonomic identifications are largely based on relevant historic works (e.g., Jung 1965; Thomas 1972), but reflect extensive genus-level revisions from Todd (2001), Rosenberg (2009), and Coan and Valentich-Scott (2012), among many other smaller taxonomic works. Formation-level checklists of the taxa reported are provided for each of the formations described in the text.

Age

The biostratigraphic value of macrofossils in the Caribbean and eastern Pacific is greatly diminished by the unrevised nature of much of the available systematic literature for this region. Hodson et al.'s (1926–1927, 1931a, b) series of monographs on Venezuelan molluscs are more than 80 years old and predated the establishment of a lithostratigraphic framework in Venezuela. Many of their records of Oligocene assemblages are in fact Miocene in age, and much of the strata thought to be of Miocene age may well be included in the Pliocene. Likewise, there is doubt regarding the biostratigraphic assignment of many of Olsson's (1928, 1930, 1931, 1932) molluscs from northern Peru. Until these classic faunas are independently dated through absolute means, their usage in biostratigraphic correlation is limited. A number of more modern works on the Neogene successions of the Canal Basin in Panama (Woodring 1957), Paraguana Peninsula in Venezuela (Jung 1965), Trinidad (Jung 1969), and the Dominican Republic (Saunders et al. 1986 and numerous subsequent studies) provide some biostratigraphic control; however, a synthesis utilizing consistent taxonomy and a rigid chronostratigraphy in the southern Caribbean is lacking. Nevertheless, biostratigraphic correlations made here are aided through use of similarity indices, such as the percentage species identified in common and the Jaccard and Simpson similarity measures. Useful biostratigraphic ranges and the likely ages of similar faunas elsewhere in the southern Caribbean are provided in this text.

Biostratigraphic age estimates are corroborated by a $^{87}Sr/^{86}Sr$ isotopic chronostratigraphy from the Cocinetas Basin stratigraphy. The $^{87}Sr/^{86}Sr$ isotopic ratios of marine

calcareous shells and marine calcareous sediment can be compared to global ratios of $^{87}Sr/^{86}Sr$ through geologic time to estimate a geological age (Burke et al. 1982; McArthur 1994; Peterman et al. 1970). The most pristine and thick calcareous shells were sampled at various levels through the Jimol, Castilletes, and Ware formations, although sampling was concentrated in intervals of perceived geochronological interest. Following sampling and analytical protocols used in Kirby et al. (2007, 2008), a portion of the surface layer of each shell specimen was ground off to reduce possible contamination, avoiding areas showing chalkiness or other signs of diagenetic alteration. Powdered samples of approximately 0.01–0.03 g were then drilled from the shell using a hand-held Dremel tool. These powdered aragonite and calcite samples were then dissolved in 100 μl of 3.5 N HNO_3 and then loaded onto cation exchange columns packed with strontium-selective crown ether resin to separate Sr from other ions (Pin and Bassin 1992). Isotope analyses were performed on a Micromass Sector 54 Thermal Ionization Mass Spectrometer equipped with seven Faraday collectors and one Daly detector in the Department of Geological Sciences at the University of Florida. Strontium was loaded onto oxidized tungsten single filaments and run in triple collector dynamic mode. Data were acquired at a beam intensity of about 1.5 V for Sr, with corrections for instrumental discrimination made assuming $^{86}Sr/^{88}Sr = 0.1194$. Errors in measured $^{87}Sr/^{86}Sr$ are better than ±0.00002 (2 sigma), based on long-term reproducibility of NBS 987 ($^{87}Sr/^{86}Sr = 0.71024$). Age estimates were determined using the Miocene and Pliocene portions of Look-Up Table Version 4:08/03 (Howarth and McArthur 1997; McArthur et al. 2001) associated with the strontium isotopic age. We fit the age estimates and basin-wide (composite) stratigraphic height using a linear least-squares regression following McArthur et al. (2000, 2007).

Paleoenvironment analysis

General paleoenvironmental interpretations provided here rely on identifying those species in Guajira assemblages that seem to be conspecific with or at least closely related to extant species for which ecological data (bathymetric and salinity preferences) are available (e.g., Keen 1971; Abbott 1974; Rosenberg 2009; Coan and Valentich-Scott 2012). These may be aided by the recognition of associations of taxa in assemblages, which are inferred, to correspond to present-day communities. The paleoecology of macrofossils in the Caribbean and eastern Pacific are therefore fairly well understood for most Neogene paleoenvironments. Species paleoecology is represented here by quantitative data (following Hendy 2013; Online Supplement 2), whereby each species is assigned to a benthic

zone [0 = freshwater, 1 = estuarine, 2 = shoreface (0–5 m), 3 = nearshore (5–15 m), 4 = lower inner shelf (15–50 m), 5 = mid-outer shelf (50–200 m), 6 = bathyal (>200 m)]. A mean benthic zone score for each sample was calculated as an average of the benthic zone scores assigned to all of the species present in that sample, with lower values indicating a shallower depositional environment. All taxa were also assigned to salinity preference (0 = non-marine, 1 = tolerant of reduced salinity, 2 = fully marine).

For a general analysis of the Early to Middle Miocene paleoenvironmental gradient observed in Cocinetas Basin, a dataset containing samples from the Jimol and Castilletes formations was constructed. After culling small samples (<5 species) and rare taxa (<2 occurrences), this matrix comprised 121 samples and 111 species. This matrix was analyzed with Q-mode cluster analysis to broadly define biofacies, using the Bray–Curtis distance measure and unweighted pair group method with arithmetic averaging (UPGMA), and ordinated using detrended correspondence analysis (DCA) to illustrate ecological gradients. The computer package PC-ORD 5.0 (McCune and Mefford 1997) was used for both analyses.

Uitpa Formation

Overview

The Uitpa Formation is not extensively studied at this time, and few comments can be made about the complete biodiversity of the unit. Preservation of aragonitic material is very poor, with most taxa being represented by moldic fossils. Calcitic material is fairly well preserved and should be useful for isotope stratigraphy.

Previous work

Rollins (1965, p. 53) listed: *Pecten* sp., *Flabellipecten fraterculus avaticus* COMBALUZIER, 1939, *Ostrea costaricensis* OLSSON 1922, *Ostrea alvarezii* D'ORBIGNY, 1842, *Turritella gatunensis* CONRAD, 1857, *and Scutellaster interlineatus* (STIMPSON, 1856). The identification of *Flabellipecten fraterculus avaticus*, a pectinid from the Late Miocene of western Europe, is possibly the same as records of *Flabellipecten duplex* COOKE, 1919 from the underlying Sillamana Formation (Olsson and Richards 1961), and both can be referred to *Leopecten*. It is difficult to establish which species of pectinid *Pecten* sp. may refer to, although if not the *Leopecten* mentioned above it is possibly *Mimachlamys canalis* (BROWN & PILSBRY, 1913), which is the most commonly found (redeposited) pectinid in offshore facies of the Uitpa Formation. The record of *Ostrea costaricensis*, which is known from the Early Pliocene of

the Limon Basin in Costa Rica and the Late Pliocene of Jamaica, is not likely to be a correct identification. *Ostrea alvarezii* [=*Cubitostrea alvarezii* (D'ORBIGNY, 1842)] is known from the Late Miocene of Argentina and is also not likely to be a valid identification. Nevertheless, abraded and fragmented specimens of an undifferentiated representative of "*Ostrea*" are present (redeposited) in offshore facies of the Uitpa Formation. The record of *Turritella gatunensis* is probably in reference to one of a number of *Turritella* sp. that can be observed in the underlying Siamana Formation (e.g., *Turritella* sp. cf. *chira* OLSSON, 1928) or overlying Jimol Formation.

Age

Few fossils are presently identified (Table 1) that would permit the biostratigraphic dating or biogeographic correlation of this unit. The presence of *Mimachlamys canalis* would point to an Early Miocene or Middle Miocene age (Waller 2011). Identification of *Orthaulax* also indicates an age no younger than earliest Middle Miocene (Vokes and Vokes 1968), but more likely the Early Miocene. An Early Miocene to earliest Middle Miocene age is therefore

Table 1 Checklist of invertebrate fossils from the Uitpa Formation (this study only)

Species
Gastropoda
Turritella sp.
Xenophora sp.
Architectonica nobilis Röding, 1798
Glossaulax sp.
Orthaulax sp.
Gorgasina sp.
Turridae indet.
Bivalvia
Adrana sp.
Saccella sp.
Limopsis sp.
Mimachlamys canalis (Brown & Pilsbry, 1913)
Cyclopecten sp.
Propeamussium sp.
Ostrea sp.
Pteria sp.
Lucinoma sp.
Psammacoma sp.
Chionopsis sp.
Scaphopoda
Antalis sp.
Fissidentalium sp.

assigned to the Uitpa Formation on the basis of limited macrofaunal data and stratigraphic relations.

Paleoecology and paleoenvironmental analysis

Five principal assemblages were investigated. The first, near Arroyo Uitpa itself (STRI 290070 and 290410) is situated at the base of the Uitpa Formation, immediately overlying the uppermost sandstones of the Siamana Formation (Fig. 4a). This assemblage is deep water in depositional environment, containing numerous *Fissidentalium*, *Antalis*, *Cyclopecten*, *Propeamussium*, *Lucinoma*, *Limopsis*, *Adrana*, *Saccella*, undetermined Turridae, and occasional very small shark teeth. These taxa are clearly offshore in nature, probably living in the outer shelf to upper bathyal water depths (100–250 m). Typical taxa of the Siamana Formation, such as *Mimachlamys canalis* and *Ostrea,* are occasionally collected from this locality, but are typically fragmented and abraded, suggesting redeposition downslope from contemporaneous (Siamana Formation-like) shelfal habitats. An additional assemblage of the Uitpa Formation was sampled near Sillamana (STRI 290410), and like the previous site also accumulated in deeper water. The assemblage is a mixture of shallow marine taxa, such as *Turritella* and *Orthaulax* (<50 m), but also contains more eurytopic forms, including *Xenophora* and *Fissidentalium*. Rather curiously, the common specimens of *Xenophora* are oriented "upside-down", suggesting deposition out of suspension (as opposed to through current winnowing), as might occur in a turbidity current. Nevertheless the fauna is not as deep as that discussed for STRI 290070 and 290410. A fourth site (STRI 290431), somewhat closer to the top of the formation, has not been adequately surveyed at this time, but appears to contain similar facies to Sillamana, and a shallow-water fauna. Assemblages at the very top of the Uitpa Formation are considerably shallower in nature than those at the base. An assemblage some 50 m below the base of the Uitpa Formation at Shirrua (STRI 290600) contained poorly preserved specimens of *Saccella*, *Pteria*, *Psammacoma*, *Chionopsis*, *Glossaulax*, *Architectonica*, and *Gorgasina*.

Jimol Formation

Overview

An estimated 118 species of molluscs (59 bivalves, 68 gastropods, and 1 scaphopod) have been identified from the formation (Table 2; Fig. 5). Dominant taxa of the Jimol Formation include *Potamides suprasulcatus* (GABB, 1873), *Turritella* (*Turritella*) *cocoditana* HODSON, 1926, and *Turritella* (*Turritella*) *matarucana* HODSON, 1926), *Anadara* (*Cunearca*) sp. cf. *zuliana* (HODSON, 1927), *Crassostrea* sp.,
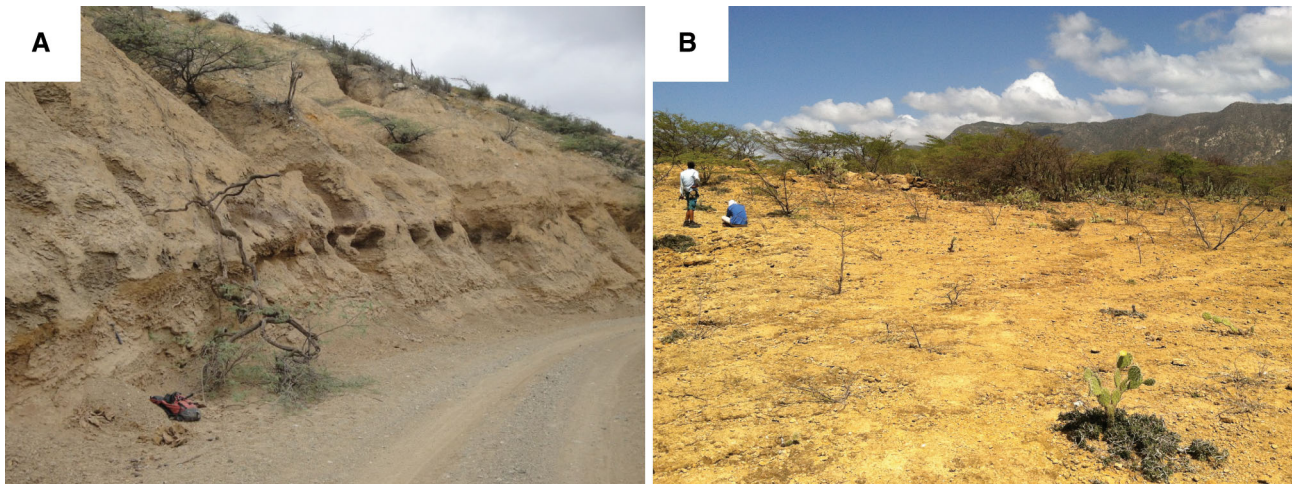
Fig. 4 Outcrop photographs of **a** soft intercalated sandstone of the Uitpa Formation at Arroyo Uitpa (STRI 290410) and **b** cemented shelly sandstone of the Jimol Formation near Siapana (STRI 290817)

Macrocallista sp. aff. *maculata* (LINNAEUS, 1758), and *Panchione* n. sp. Other common taxa include *Turritella machapoorensis* HODSON, 1926, *Glossaulax paraguanensis* (HODSON, 1926), *Muracypraea* sp. cf. *hyaena* SCHILDER, 1939, *Melongena consors* (SOWERBY, 1850), *Turbinella falconensis* (HODSON, 1931), *Conus talis* JUNG, 1965, *Anadara* (*Rasia*) sp. cf. *cornellana* (HODSON, 1927), *Tucetona democraciana* (HODSON & HODSON, 1927), *Lindapecten* sp. cf. *buchivacoanus* (HODSON & HODSON, 1927), *Apiocardia* sp., *Glyptoactis paraguanensis* (HODSON, 1931), *Eucrassatella* (*Hybolophus*) *venezuelana* (HODSON, 1927), *Dallocardia* sp. cf. *sanctidavidsi* (MAURY, 1925)*, Caryocorbula fortis* (JUNG, 1965), and *Dentalium* sp. (Figs. 6, 7). Preservation is variable throughout the Jimol Formation, with most aragonitic taxa being represented by recrystallized and heavily weathered shells in the more cemented horizons of the lower and middle parts of the formation (Fig. 4b). Preservation of macrofossils is improved in the upper part of the formation, and preservation of original aragonitic shell material is common. Originally, calcitic material (e.g., oysters) has often undergone diagenesis; in nearly all cases, it has a black metallic luster.

Previous work

Rollins (1960, p. 91) listed: *Clementia dariena* (CONRAD, 1855), *Cardium gatunense* TOULA, 1909, *Arca chiriquiensis bolivari* WEISBORD, 1928, *Arca grandis colombiensis* WEISBORD, 1928, *Turritella* sp. aff. *supraconcava* HANNA AND ISRAELSKY, 1925, *Turritella* sp., *Cardium* sp., *Ostrea* sp., and *Pecten* sp. It is curious that Renz (1960) did not list any macroinvertebrates from the Jimol Formation, given their frequent occurrence. It is likely that Loc. no. 39 (13 km NW of Castilletes) of Thomas (1972) is within the

distribution of the Jimol Formation. From this site, Thomas recorded *Turritella* (*Turritella*) *curamichatensis* HODSON, 1926, *Turritella* (*Turritella*) *matarucana*, *Cirsotrema* sp. cf. *undulatum* JUNG, 1965, and *Architectonica nobilis* RÖDING, 1798.

Cardium gatunense is a synonym of *Dallocardia dominicense* (GABB), although the Jimol representative that is common throughout the Jimol and Castilletes formations is more likely an undescribed species of *Dallocardia* related to *Dallocardia sanctidavidsi*. Both *Arca chiriquiensis bolivari* and *Arca grandis colombiensis* have been synonymized with *Anadara* (*Grandiarca*) *chiriquiensis* (GABB, 1861), which is uncommonly found in this study. *Turritella* sp. aff. *supraconcava* is a synonym of *Turritella abrupta* (SPIEKER, 1922), which has not been recorded from the field area, but might be confused from large specimens of *Turritella* (*Turritella*) *cocoditana*, which is common through the Jimol Formation and lower Castilletes Formation. *Turritella* sp. of Rollins (1960) likely represents one of several frequently occurring species in the Jimol Formation, which include *Turritella* (*Bactrospira*) sp. cf. *altilira* CONRAD, 1857, *Turritella* (*Turritella*) *cocoditana*, *Turritella* (*Turritella*) *machapoorensis*, and *Turritella* (*Turritella*) *matarucana*. It is unclear what *Cardium* sp. may refer to, although the previous mention of *Cardium gatunense* suggests that it represents a distinct taxon; the only other frequently occurring cardiid is an undescribed species of *Apiocardia*. While a number of species of Ostreidae are recorded from the Jimol Formation, it is likely that the *Ostrea* sp. of Rollins (1960) was in reference to the commonly encountered *Crassostrea* sp. It is unclear what Rollins' (1960) record of *Pecten* sp. may refer to, as a number of pectinids occur infrequently in the formation (e.g., *Leopecten*, *Lindapecten*, and "*Paraleptopecten*").

Table 2 Checklist of invertebrate fossils from the Jimol and Castilletes formations

Species	Jimol	Castilletes
Gastropoda		
Calliostoma sp.	•	•
Turbo sp.	•	
Arene sp.		•
Nerita cf. *fulgurans* Gmelin, 1791		•
Neritina n. sp. aff. *woodwadi* (Guppy, 1866)		•
Modulus tamanensis (Maury, 1925)	•	•
Turritella (*Bactrospira*) sp. cf. *altilira* Conrad, 1857	•	•
Turritella (*Turritella*) *cocoditana* Hodson, 1926	•	•
Turritella (*Turritella*) *machapoorensis* Hodson, 1931	•	•
Turritella (*Turritella*) *matarucana* Hodson, 1926	•	•
Architectonica (*Architectonica*) *nobilis* Röding, 1798	•	•
Bittium sp.		•
Rhinoclavis (*Ochetoclava*) *venada* (Maury, 1925)	•	•
Potamides suprasulcatus (Gabb, 1873)	•	•
Terebralia dentilabris (Gabb, 1873)	•	•
Petaloconchus sculpturatus (Lea, 1846)	•	•
Cirsotrema undulatum Jung, 1965	•	
Bostrycapulus sp.		•
Crepidula cantaurana Hodson, 1931	•	•
Crepidula insculpta (Jung, 1965)	•	•
Crepidula plana Say, 1822	•	•
Calyptraea sp. cf. *centralis* Conrad, 1841	•	•
Crucibulum (*Dispotaea*) sp. cf. *springvaleense* Rutsch, 1942	•	•
Trochita trochiformis (Born, 1778)	•	
Aylacostoma n. sp.		•
Charadreon n. sp.	•	•
Doryssa n. sp.		•
Sheppardiconcha n. sp.		•
Natica sp.	•	•
Naticarius sp.	•	•
Glossaulax paraguanensis (Hodson, 1927)	•	•
Polinices sp. cf. *nelsoni* Olsson, 1932	•	•
Sinum gabbi (Brown & Pilsbry, 1913)	•	•
Stigmaulax sp.	•	•
Pachycrommium sp.	•	
Orthaulax sp.	•	
Strombus sp.	•	•
Malea sp.		•
Bursa rugosa (Sowerby II, 1835)		•
Ranellidae indet.		•
Ficus sp. cf. *carbasea* (Guppy, 1865)	•	•

Table 2 continued

Species	Jimol	Castilletes
Distorsio sp.		•
Luria sp.	•	•
Muracypraea sp. cf. *hyaena* Schilder, 1939	•	•
Calotrophon sp. cf. *gatunensis* (Brown & Pilsbry, 1911)	•	•
Chicoreus (*Triplex*) sp. cf. *cornurectus* (Guppy, 1866)		•
Chicoreus (*Triplex*) *corrigendum* Vokes, 1989		•
Cymia cocoditana Hodson, 1931	•	•
Eupleura kugleri Jung, 1965	•	•
Hesperisternia sp.		•
Phyllonotus n. sp.		•
Siphonochelus (*Laevityphis*) cf. *sawkinsi* (Mansfield, 1925)	•	•
Siratus cf. *denegatus* (Jung, 1965)	•	•
Vokesimurex sp. cf. *gilli* (Maury, 1910)	•	•
Antillophos sp. cf. *gatunensis* (Toula, 1909)	•	•
Antillophos sp.		•
Cymatophos cocoditana (Hodson, 1931)	•	•
Cymatophos paraguanensis (Hodson, 1931)	•	•
Gordanops sp. cf. *baranoanus* (Anderson, 1929)		•
Pallacera maracaibensis (Weisbord, 1929)		•
Solenosteira sp.	•	•
Buccinidae indet.		•
Granolaria sp. cf. *gorgasiana* (Brown & Pilsbry, 1913)		•
Latirus sp.	•	•
Vasum quirosense Hodson, 1931	•	
Nassarius sp.		•
Turbinella falconensis (Hodson, 1931)	•	•
Melongena consors (Sowerby, 1850)	•	•
Anachis sp.	•	•
Sincola sp.		•
Strombina sp.	•	•
Persicula venezuelana (Hodson, 1927)	•	•
Prunum quirosense (Hodson, 1931)	•	•
Conomitra sp.	•	
Agaronia sp. aff. *testacea* Lamarck, 1811		•
Eburna sp.	•	
Oliva sp. A	•	•
Oliva sp. B	•	•
Olivella sp.	•	
Aphera sp.		•
Bivetiella sp. cf. *gabbiana* (Pilsbry & Johnson, 1917)	•	•
Euclia sp. cf. *dinota* (Woodring, 1970)		•
Euclia werenfelsi (Jung, 1965)	•	•
Narona sp.		•

Table 2 continued

Species	Jimol	Castilletes
Trigonostoma woodringi Jung, 1965		•
Conus sp. cf. *chipolanus* Dall, 1896	•	•
Conus sp. aff. *jaspideus* Gmelin, 1791		•
Conus sp. cf. *molis* Brown & Pilsbry, 1911	•	•
Conus talis	•	•
Conus sp.		•
Strioterebrum ulloa (Olsson, 1932)	•	•
Terebra (*Paraterebra*) *sulcifera* Sowerby, 1849	•	•
Agladrillia sp.		•
Clathrodrillia sp.	•	•
Crassispira conica Jung, 1965		•
Cruziturricula sp.	•	•
Fusiturricula sp.		•
Gemmula vaningeni (Brown & Pilsbry, 1913)		•
Glyphostoma dentiferum Gabb, 1872		•
Hindsiclava henekeni (Sowerby, 1850)	•	•
Knefastia sp.	•	•
Polystira sp.	•	•
Paraborsonia cantaurana (Jung, 1965)		•
Turridae indet.	•	•
Bulla sp.		•
Polyplacophora		
"*Chiton*" sp.		•
Bivalvia		
Adrana sp.	•	•
Politoleda forcati (Jung, 1965)	•	•
Saccella gracillima (Jung, 1965)	•	
Saccella gnomon (Jung, 1965)		•
Noetia dauleana Marks, 1951		•
Anadara (*Cunearca*) *zuliana* (Hodson, 1927)	•	•
Anadara (*Grandiarca*) *chiriquiensis* (Gabb, 1861)	•	•
Anadara (*Potiarca*) *inutilis* (Jung, 1965)	•	•
Anadara (*Rasia*) sp. cf. *cornellana* (Hodson, 1927)	•	•
Anadara (*Rasia*) *democraciana* (Hodson, 1927)		•
Anadara (*Rasia*) *tirantensis* (Hodson, 1927)		•
Anadara (*Tosarca*) sp. cf. *veatchi* (Olsson, 1922)	•	•
Glycymeris sp.	•	
Tucetona sp. cf. *democraciana* (Hodson & Hodson, 1927)	•	•
Crenella sp.		•
Mytilus sp. cf. *canoasensis* Olsson, 1931	•	•
Brachidontes sp.		•
Atrina sp.		•
Amusium aguaclarense (Hodson, 1927)	•	
Argopecten sp.	•	•

Table 2 continued

Species	Jimol	Castilletes
Leopecten sp.	•	•
Paraleptopecten quirosensis (Harris, 1927)	•	
Lindapecten buchivacoanus (Hodson & Hodson, 1927)	•	•
Pectinidae indet.		•
Crassostrea sp.	•	•
Dendostrea democraciana (Hodson, 1927)	•	•
Hyotissa sp.	•	
Plicatula sp.	•	•
Anomia peruviana d'Orbigny, 1846		•
Spondylus sp.	•	
Unioidae indet.		•
Sphaeriidae indet.		•
Anodontia sp.	•	•
Cavilinga sp.		•
Lucina sp. cf. *pensylvanica* Linnaeus, 1758	•	•
Lucinisca mirandana (Hodson, 1931)		•
Phacoides sp. cf. *pectinatus* (Gmelin, 1791)	•	•
Diplodonta sp.		•
Sportellidae indet.		•
Glyptoactis paraguanensis (Hodson, 1931)	•	•
Arcinella yaquensis (Maury, 1917)	•	•
Chama berjadinensis Hodson, 1927	•	•
Pseudochama quirosana (Hodson, 1927)	•	
Dallocardia sp. cf. *sanctidavidis* (Maury, 1925)	•	•
Trachycardium sp.	•	
Apiocardia n. sp. aff. *aminensis* (Olsson, 1932)	•	•
Crassinella sp.	•	•
Eucrassatella (*Hybolophus*) *venezuelana* (Hodson, 1927)	•	•
Harvella elegans (Sowerby, 1825)		•
Micromactra maracaibensis (Hodson, 1927)	•	•
Mulinia sp.	•	
Raeta sp.		•
Angulus sp.		•
Eurytellina paraguanensis (Hodson et al., 1931)	•	•
?*Macoma* sp.		•
Psammacoma falconensis (Hodson, 1927)	•	•
Psammotreta hadra Woodring, 1982	•	•
Strigilla sp.		•
Tellinidae indet.		•
Donax sp.	•	•
Tagelus (*Mesopleura*) n. sp. aff. *divisus* (Spengler, 1794)	•	•
Solecurtus sp.	•	•
Solena sp.	•	•
Abra sp.	•	•

Table 2 continued

Species	Jimol	Castilletes
Semele sp.	•	•
Agriopoma (*Pitarella*) *paraguanensis* (H. Hodson, 1927)		•
Anomalocardia sp.	•	
Chione sp.	•	•
Chionopsis paraguanensis (Hodson, 1927)	•	•
Clementia dariena (Conrad, 1855)	•	•
Cyclinella venezuelana Hodson, 1927	•	•
Dosinia sp.	•	•
Globivenus palmeri (Hodson, 1927)	•	
Hysteroconcha sp.		•
Lamelliconcha labreana (Maury, 1912)	•	•
Leukoma sp.		•
Lirophora quirosensis (Hodson, 1927)	•	•
Macrocallista n. sp. aff. *maculata* (Linnaeus, 1758)	•	•
Panchione n. sp. aff. *macrtropsis* (Conrad, 1855)	•	•
Pitar sp.		•
Transennella sp.		•
Veneridae indet.	•	•
Caryocorbula fortis (Jung, 1965)	•	•
Caryocorbula quirosana (Hodson, 1927)	•	•
Hexacorbula cruziana (Olsson, 1932)	•	•
Tenuicorbula n. sp. aff. *lupina* (Olsson, 1932)		•
Scaphopoda		
Dentalium sp.	•	•
Echinodermata		
Cidaroida indet.	•	
Echinoida indet.	•	
Arthropoda		
Callianassidae indet.	•	•
Portunidae indet.		•
Balanidae indet.	•	•

Age

The fauna of the Jimol Formation share similarities with other early through Middle Miocene stratigraphic units in the southern Caribbean and isthmian region (Table 3). A vast majority of the taxa in the Jimol Formation can be found in the overlying Castilletes Formation (71 shared species), reflecting a similar age, their conformable contact, and comparable deposition environments. Beyond Cocinetas Basin, 44 species are found in the Cantaure Formation (Burdigalian), 12 species from the Caujarao Formation (Serravallian–Tortonian), and 8 species from the less well-known La Rosa Formation (?Early Miocene), each of which outcrop in Venezuela. A further 12 are known from the Culebra Formation (Aquitanian–Burdigalian) of Panama. A large number of species (30) are also shared with the very diverse Gatun Formation (Tortonian) of Panama, but many of these are long-lived forms, with less biostratigraphic significance.

Among specific taxa identified from the formation many that are identified to species level are indicative of the latest Early Miocene [e.g., *Anadara* (*Cunearca*) sp. cf. *zuliana*, *Tucetona democraciana*, "*Paraleptopecten*" *quirosensis* (HARRIS, 1927), *Cyclinella venezuelana* HODSON, 1927, *Turritella* (*Turritella*) *cocoditana*, *Turritella* (*Turritella*) *machapoorensis*, and *Conus* sp. cf. *chipolanus* DALL, 1896], or more widely ranging through the early to Late Miocene [e.g., *Lindapecten* cf. *buchivacoanus*, *Modulus tamanensis* (MAURY, 1925), *Turritella* (*Turritella*) *matarucana*, *Turbinella falconensis*]. Perhaps, the most significant taxon that places age constraints on the Jimol Formation is *Orthaulax*. Numerous specimens are recorded from Shirrua (STRI 290412-4 and 290421), Rio Topio Norte (STRI 290817), and a similar specimen is collected from beds overlying the Siamana Formation at Patsuá (STRI 290472). The genus was widespread in the western Atlantic during the latest Oligocene and Early Miocene

Table 3 Comparison of the Jimol assemblage with other Atlantic and eastern Pacific Early–Late Miocene faunules at the species level

Formation/age	Country	#SpA	#SpC	%SpC	Jaccard	Simpson
Castilletes Fm (M. Mioc.)	Colombia	95	71	74.7	0.69	0.90
Cantaure Fm (E. Mioc.)	Venezuela	176	44	25.0	0.21	0.56
La Rosa Fm (E. Mioc.)	Venezuela	38	8	21.1	0.07	0.21
Caujarao Fm (M.-L. Mioc.)	Venezuela	139	18	12.9	0.09	0.23
Tuira Fm (11.2–9.2 Ma)	Panama	69	8	11.6	0.06	0.12
Culebra Fm (21–19 Ma)	Panama	116	12	10.3	0.07	0.15
Springvale Fm (L. Mioc.)	Trinidad	133	10	7.5	0.05	0.13
Gatun Fm (11.6–8.5 Ma)	Panama	385	24	6.2	0.05	0.30
Baitoa Fm (17.5–14.5 Ma)	Dom. Rep.	105	6	5.7	0.03	0.08
Zorritos Fm (M. Mioc.)	Peru	134	7	5.2	0.03	0.09

#SpA number of species known from the assemblage, *#SpC* number of species in common with the Jimol Formation, *%SpC* percentage of Jimol taxa present in the assemblage; analyses restricted to named species (*n* = 79 species), *Dom. Rep.* Dominican Republic

Table 4 Strontium isotope data and age estimates from the Jimol Formation

Locality (STRI)	Height (m)	Sample (MUN-STRI)	Taxon	$^{87}86/^{86}Sr$	Age (Ma)	Age range (Ma)
290819	−118	38108	*Tucetona democraciana*	0.708654	17.13	17.02–17.25
290820	−117	38114	*Antigona* sp.	0.708654	17.13	17.02–17.25
290816	−103	38014	*Tucetona democraciana*	0.708679	*16.71*	*16.60–16.83*
290427	−60	16895	*Crassostrea* sp.	0.708649	17.19	17.08–17.31
290427	−60	16895	*Crassostrea* sp.	0.708633	17.45	17.34–17.55
290428	−55	16883	*Crassostrea* sp.	0.708658	17.05	16.93–17.15
290430	−42	17068	*Anadara* sp. cf. *zuliana*	0.708641	17.33	16.96–17.65
290430	−42	17068	*Anadara* sp. cf. *zuliana*	0.708633	17.45	17.10–17.75
290476	−42	17068	?	0.708696	*16.39*	*16.29–16.51*
290476	−42	17068	?	0.708713	*16.01*	*16.01–16.21*
290436	0	16882	*Turritella matarucana*	0.708629	*17.51*	*17.16–17.80*
290436	0	16882	*Turritella matarucana*	0.708668	16.89	16.48–17.27

Ages in italic indicate unreliability relative to replicate samples from same horizon or stratigraphic position

Specimens are reposited at the Mapuka Museum of Universidad del Norte (MUN-STRI), Colombia. Locality numbers can be searched in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb)

strata (Vokes and Vokes 1968), but has only been doubtfully recorded in the Middle Miocene. The genus probably occupied the tropical eastern Pacific during the Late Eocene and was represented by the species named *Oostrombus chiraensis* OLSSON, 1931 of the Chira Formation of Peru and Gatuncillo Formation in Panama. During the Miocene, the genus ranged from Florida through the central Caribbean and Brazil. This is the first Neogene record from Colombia or Venezuela and almost certainly the youngest record of the genus.

Due to the poor preservation of shell material in the lower and middle parts of the Jimol Formation, $^{87}Sr/^{86}Sr$ isotope analyses were only conducted from horizons in the upper part of the formation (Table 4). The oldest $^{87}Sr/^{86}Sr$ isotope ages were 17.45 (STRI 290430) and 17.51 Ma (STRI 290436), near the top of the Jimol Formation. Oysters from slightly lower levels (STRI 290427 and 290428) were dated at 17.05, 17.19, and 17.45 Ma. A series of slightly younger ages from the lowest horizons with well-preserved aragonite that are thought to lie near the middle of the Jimol Formation (STRI 290819, 290820 and 290816) yielded ages of 17.13, 17.13, and 16.71 Ma, respectively. On the basis of $^{87}Sr/^{86}Sr$ ratio, a mean age of 17.0 Ma (range of 16.1–17.51 Ma) is calculated for beds northwest of the village of Paraguachón at the top of the formation (Table 4).

Paleoecology and paleoenvironmental analysis

Much of the Jimol Formation accumulated in very shallow sheltered marine or marginal marine paleoenvironments. Evidence for marginal marine settings includes *Crassostrea* (oyster) bioherms, and assemblages dominated by *Potamides suprasulcatus*, *Anadara* (*Cunearca*) *zuliana*,

and *Chione* sp. The presence of taxa such as *Donax* and *Mulinia* at STRI 290416 (Shirrua) indicates a sheltered nearshore (<5 m) sandy soft-bottom environment. Other localities contain fully marine, although sheltered and shallow subtidal assemblages of *Turritella* spp., *Turbinella falconensis*, *Tucetona democraciana*, *Eucrassatella* (*Hybolophus*) *venezuelana*, *Dallocardia* sp. cf. *sanctidavidsi*, and *Macrocallista* sp. aff. *maculata*. Assemblages typical of deeper, albeit inner shelf waters are rare.

Castilletes Formation

Overview

Dominant taxa of the Castilletes Formation include *Potamides suprasulcatus*, the turritellids *Turritella* (*Turritella*) *cocoditana* and *Turritella* (*Turritella*) *matarucana*, *Anadara* (*Cunearca*) sp. cf. *zuliana*, *Crassostrea* sp., and *Panchione* n. sp. Other frequently occurring species include *Turritella* (*Turritella*) *machapoorensis*, *Glossaulax paraguanensis*, *Polinices* sp. cf. *nelsoni* OLSSON, 1932, *Architectonica nobilis*, *Cymia cocoditana* HODSON, 1931, *Cymatophos cocoditoensis* (HODSON, 1931), *Melongena consors*, *Oliva* sp., *Euclia werenfelsi* (JUNG, 1965), *Conus talis*, *Mytilus* sp., *Tucetona democraciana*, *Glyptoactis paraguanensis*, *Dallocardia* sp. cf. *sanctidavidsi*, *Chionopsis paraguanensis* (HODSON, 1927), and *Caryocorbula fortis*. An estimated 173 species of molluscs (96 gastropods, 75 bivalves, one chiton, and one scaphopod), 3 echinoderms, and 4 arthropods are here recorded from the formation (Table 2; Figs. 6, 7). This tally is still far from complete as many collected bulk samples have yet to be fully investigated and appear to contain numerous
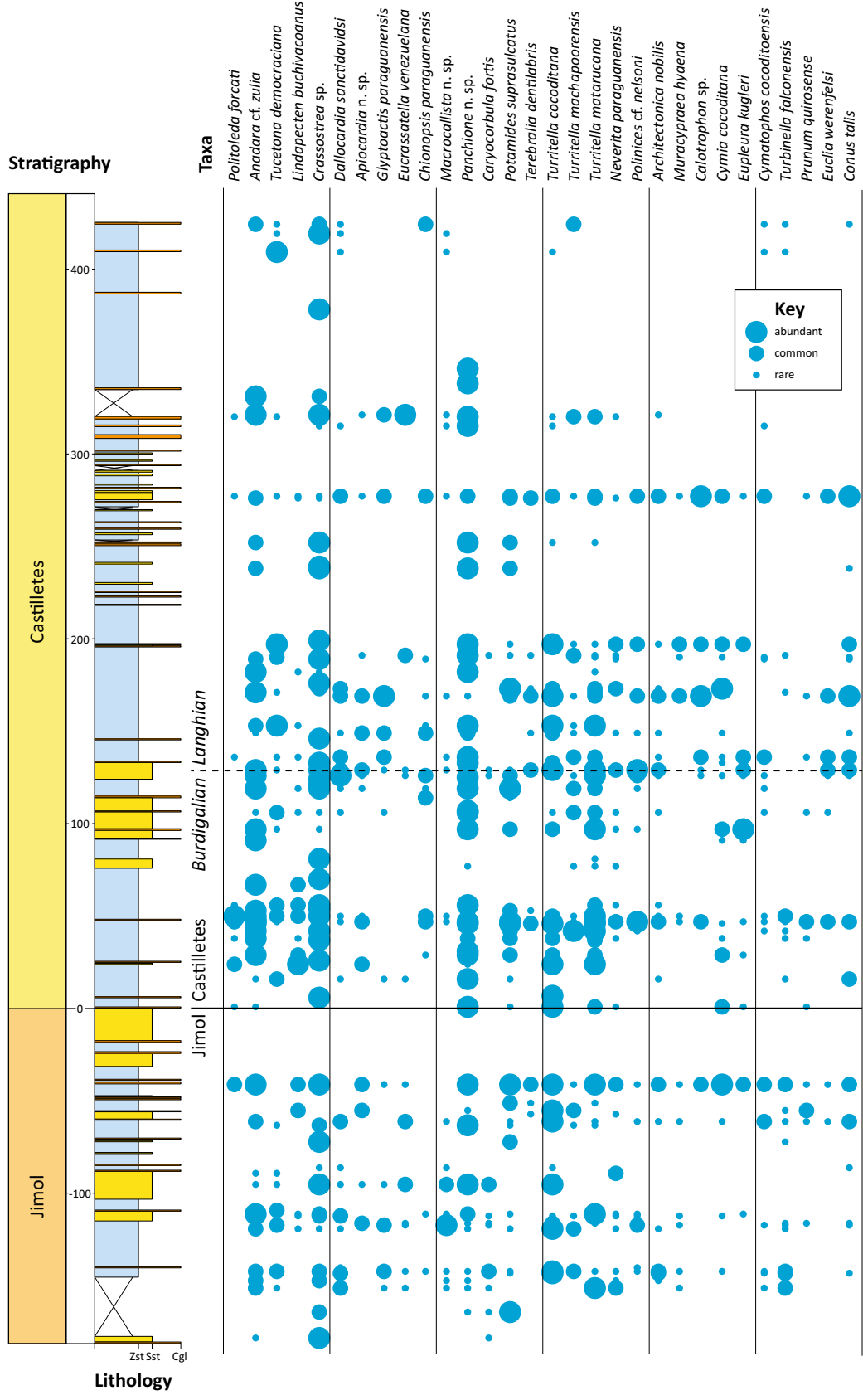
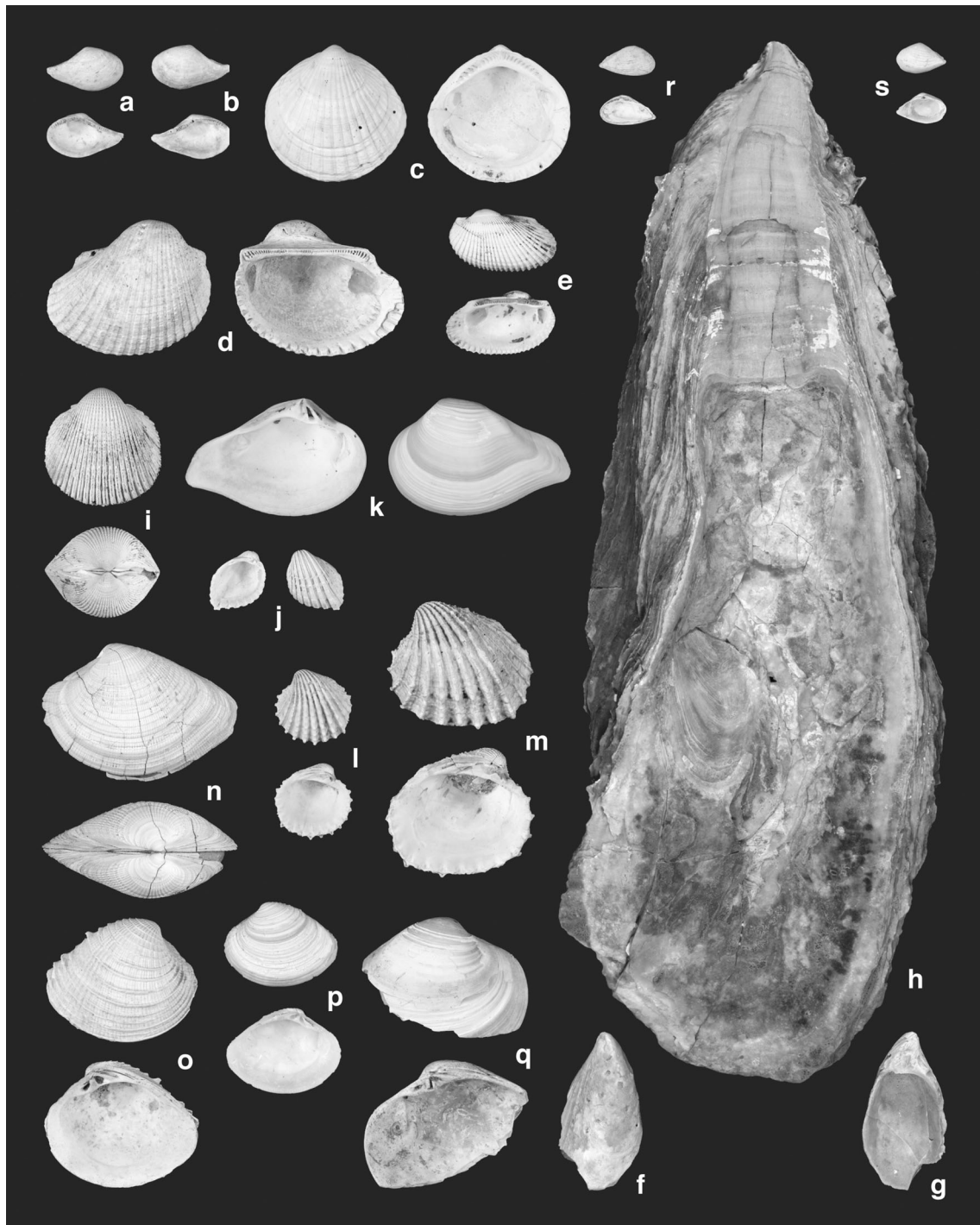**Fig. 5** Relative abundance of frequently occurring molluscan taxa in the Jimol and Castilletes formations

Fig. 6 Frequently occurring bivalves of the Miocene Jimol and Castilletes formations, Cocinetas Basin. **a**, **b** *Saccella gnomon* (**a** MUN-STRI-17093-3, **b** MUN-STRI-17093-2), **c** *Tucetona democraciana* (MUN-STRI-17088-7), **d** *Anadara zuliana* (MUN-STRI-17073-3), **e** *Anadara* sp. cf. *cornellana* (MUN-STRI-16962-2), **f**, **g** *Mytilus* sp. (MUN-STRI-16872-2), **h** *Crassostrea* sp. (MUN-STRI-17083-1; 0.8), **i** *Dallocardia sanctidavidsi* (MUN-STRI-17054-1), **j** *Apiocardia* sp. (MUN-STRI-17068-2), **k** *Eucrassatella venezuelana* (MUN-STRI-17088-8), **l**, **m** *Glyptoactis paraguanensis* (**l** MUN-STRI-17101-1, **m** MUN-STRI-16911-4), **n** *Chionopsis paraguanensis* (MUN-STRI-17101-1), **o** *Chione* sp. (MUN-STRI-17088-1), **p** *Panchione* n. sp. (MUN-STRI-17088-2), **q** *Macrocallista* sp. cf. *maculata* (MUN-STRI-17093-4), **r** *Caryocorbula fortis* (MUN-STRI-17071-7), **q** *Caryocorbula quirosana* (MUN-STRI-17071-6). All specimens are of actual size unless stated
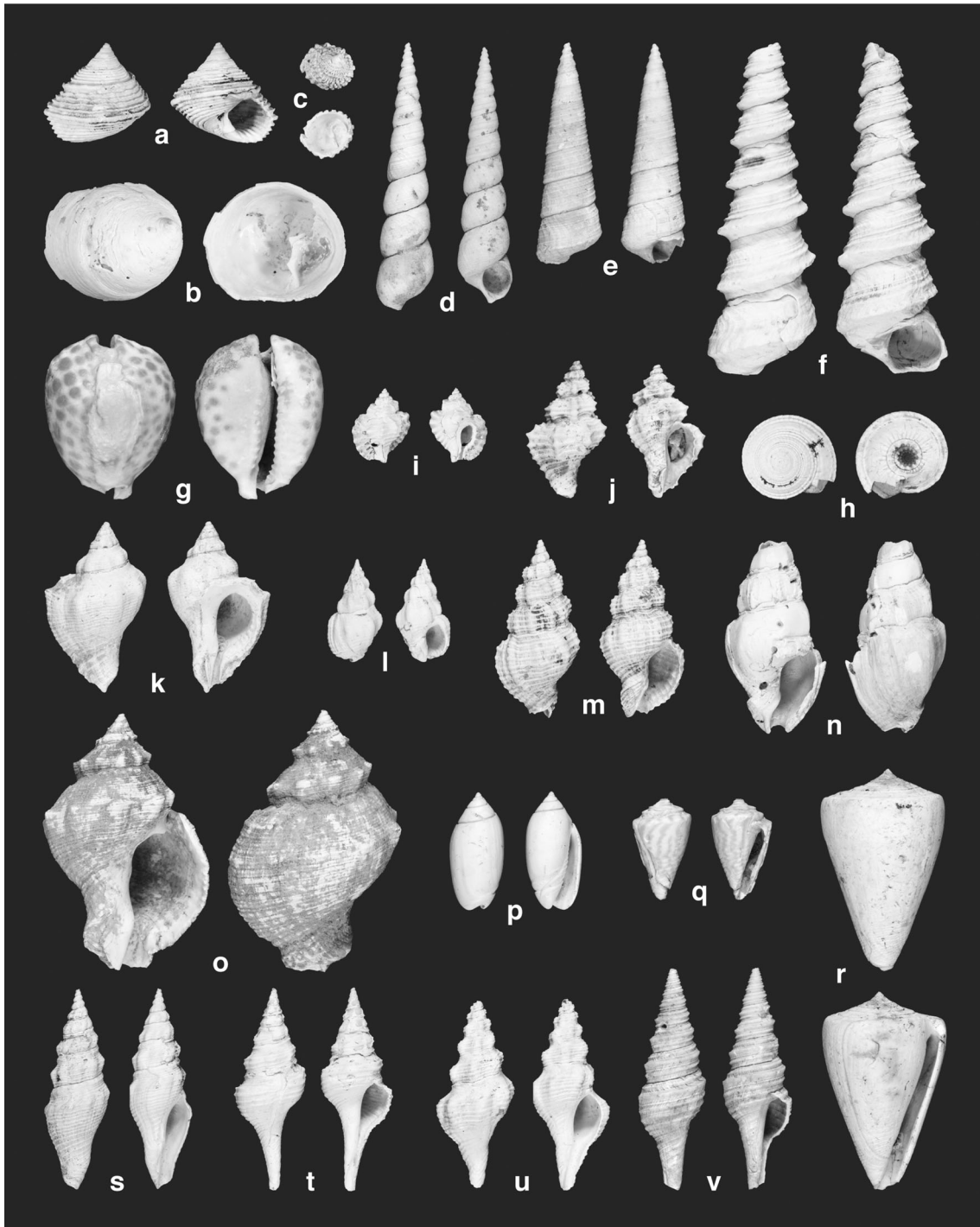
Fig. 7 Frequently occurring gastropods of the Miocene Jimol and Castilletes formations, Cocinetas Basin: **a** *Modulus tamanensis* (MUN-STRI-17088-13), **b** *Crepidula insculpta* (MUN-STRI-16911-3), **c** *Crucibulum* sp. cf. *springvaleense* (MUN-STRI-17068-3), **d** *Turritella matarucana* (MUN-STRI-16882-5), **e** *Turritella machapoorensis* (MUN-STRI-17072-2), **f** *Turritella cocoditana* (MUN-STRI-17070-1), **g** *Muracypraea* sp. cf. *hyaena* (MUN-STRI-17093-6), **h** *Architectonica nobilis* (MUN-STRI-17049-4), **i** *Eupleura kugleri* (MUN-STRI-17088-11), **j** *Calotrophon* sp. cf. *gatunensis* (MUN-STRI-17049-6), **k** *Siratus* sp. cf. *denegatus* (MUN-STRI-17072-3), **l** *Cymatophos cocoditana* (MUN-STRI-17088-17), **m** *Cymatophos paraguanensis* (MUN-STRI-17068-4), **n** *Pallacera maracaibensis* (MUN-STRI-17088-1), **o** *Cymia cocoditana* (MUN-STRI-16882-4), **p** *Oliva* sp. (MUN-STRI-17088-1), **q** *Conus talis* (MUN-STRI-17093-1), **r** *Conus molis* (MUN-STRI-17049-1), **s** *Crassispira conica* (MUN-STRI-17093-3), **t** *Cruziturricula* sp. (MUN-STRI-17088-4), **u** *Knefastia* sp. (MUN-STRI-17088-5), **v** *Polystira* sp. (MUN-STRI-17093-1). All specimens are of natural size unless stated

additional taxa and micromolluscs. The total diversity of molluscs in the Castilletes Formation should exceed 200 species. Aragonitic material has undergone variable diagenesis, varying from pristine to chalk throughout, but more commonly recrystallized in better-cemented beds in the upper part of the formation. Calcitic material is generally well preserved throughout the formation. Most beds can yield fossils appropriate for isotopic analysis.

Previous work

Rollins (1960, p. 94) listed: *Ostrea pulchana* D'ORBIGNY, 1842, *Ostrea* sp., *Chlamys (Aequipecten) plurinomis morantensis* WOODRING, 1925, *Pecten bowdenensis* DALL, 1898, *Chione* sp., *Cardium* sp. Rollins' identification of *Ostrea pulchana* [= *Ostrea puelchana*] is unlikely, as this extant species is restricted to Argentina. Numerous Ostreidae are present in the Castilletes Formation, including *Crassostrea* sp. and *Ostrea* sp., and the correct identification of either *Ostrea pulchana* or *Ostrea* sp. is difficult to assume. *Chlamys (Aequipecten) plurinomis morantensis* [= *Lindapecten morantensis* (WOODRING, 1925)] is known from the Late Pliocene Bowden shell bed of Jamaica. This record more likely refers to the pectinid identified here as *Lindapecten buchivacoanus*. *Pecten bowdenensis* [= *Euvola bowdenensis* (DALL, 1898)] is also known from the Late Pliocene Bowden Shell bed of Jamaica, and again is unlikely to be a correct identification. A number of cardiid bivalves are recognized in the Castilletes Formation, including *Dallocardia*, *Trachycardium*, *Laevicardium*, and *Apiocardia*. It is unclear which of these Bürgl's identification of *Cardium* sp. referred to, although *Dallocardia* sp. cf. *sanctidavidsi* is most frequently encountered.

Age

As discussed for the preceding unit, there is high similarity among the Jimol Formation and the Castilletes Formation, with more than 70 species shared between them. Outside of the Guajira Peninsula, the Castilletes Formation has most taxa in common with the Burdigalian Cantaure Formation of Venezuela (55 species) and the Serravalian–Tortonian Gatun Formation of Panama (30 species). Other units with high similarity include the Early Miocene Culebra of Panama (12 species) and La Rosa of Venezuela (8 species), and the Serravalian–Tortonian Caujarao Formation of Venezuela (21 species). Most stratigraphic units with similar faunas that are listed in Table 5 are of Early or Middle Miocene age.

The biostratigraphic implications of specific taxa that are found in the Castilletes Formation are much the same as the Jimol, given the many species found in common. Among the molluscan taxa identified from the formation are those with latest Early Miocene (e.g., "*Paraleptopecten*" *quirosensis*, *Glyptoactis paraguanensis*, *Cyclinella venezuelana*, *Eupleura kugleri* JUNG, 1965, *Cymatophos cocoditana*, *Euclia werenfelsi*, *Conus* sp. cf. *chipolanus* and *Conus talis*) or Middle to Late Miocene (e.g., *Lindapecten* sp. cf. *buchivacoanus*, *Modulus tamanensis*) age ranges. Notably, the characteristic gastropod *Orthaulax* (see discussion for Jimol Formation) has not been recorded from the Castilletes Formation, consistent with its presently known last appearance during the earliest Middle Miocene.

A mean age of 16.2 Ma (range of 16.33–16.07 Ma) is calculated for beds in the Patajau Valley near the base of the formation, on the basis of $^{87}Sr/^{86}Sr$ ratios (Table 6). Further to the south, and east of Paraguachón, the Patajau

Table 5 Comparison of the Castilletes assemblage with other Caribbean Early–Late Miocene faunules at species level

Formation/age	Region	#SpA	#SpC	%SpC	Jaccard	Simpson
Jimol (17.9–16.7 Ma)	Colombia	79	71	89.9	0.69	0.90
Cantaure (E. Mioc.)	Venezuela	176	55	31.3	0.25	0.58
La Rosa (E. Mioc.)	Venezuela	38	8	21.1	0.06	0.21
Caujarao Fm (M.-L. Mioc.)	Venezuela	139	21	15.1	0.10	0.22
Culebra Fm (21–19 Ma)	Panama	116	12	10.3	0.06	0.13
Tuira Fm (11.2–9.2 Ma)	Panama	69	10	14.5	0.06	0.14
Springvale Fm (L. Mioc.)	Trinidad	133	12	9.0	0.06	0.13
Gatun Fm (11.6–8.5 Ma)	Panama	385	30	7.8	0.07	0.32
Baitoa Fm (17.5–14.5 Ma)	Dom. Rep.	105	8	7.6	0.04	0.08
Zorritos Fm (M. Mioc.)	Peru	134	7	5.2	0.03	0.07

#SpA number of species known from the assemblage, *#SpC* number of species in common with the Castilletes Formation, *%SpC* percentage of Castilletes taxa present in the assemblage, analyses restricted to named species (*n* = 95 species), *Dom. Rep.* Dominican Republic

Table 6 Strontium isotope data and age estimates from the Castilletes Formation

Locality (STRI)	Height (m)	Sample (MUN-STRI)	Taxon	$^{87}86/^{86}Sr$	Age (Ma)	Age range (Ma)
290666	41[a]	37193	*Anadara* sp. cf. *zuliana*	0.708713	*16.10*	*16.01–16.21*
290455	45	17073	*Crassostrea* sp.	0.708696	16.33	16.01–16.80
290455	45	17073	*Phacoides* sp.	0.708714	16.07	15.71–16.46
290456	46	17049	*Crassostrea* sp.	0.708701	16.31	15.93–16.71
290456	46	17049	*Anadara* sp. cf. *zuliana*	0.708706	16.22	15.85–16.62
290423	49[b]	16872	*Anadara* sp. cf. *zuliana*	0.708707	16.21	16.10–16.32
290423	49[b]	16872	*Turritella matarucana*	0.708749	*15.52*	*15.43–15.62*
290423	49[b]	16872	?	0.708777	*15.08*	*14.94–15.21*
290423	49[b]	16872	?	0.708757	*15.42*	*15.33–15.51*
290666	52[a]	37192	*Anadara* sp. cf. *zuliana*	0.708667	*16.91*	*16.79–17.02*
290666	55[a]	37191	*Crassostrea* sp.	0.708623	*17.59*	*17.48–17.68*
290469	105	16962	*Anadara* sp. cf. *zuliana*	0.708731	15.82	15.73–15.91
290469	105	16962	*Turritella matarucana*	0.708747	15.57	15.47–15.67
290438	152	17044	*Tucetona democraciana*	0.708735	15.76	15.67–15.85
290438	152	17044	*Panchione* sp.	0.70881	*13.24*	*12.92–13.71*
290446	189	16907	*Anadara* sp. cf. *zuliana*	0.708760	15.37	15.37–15.56
290446	189	16907	*Anadara* sp. cf. *zuliana*	0.70878	15.01	14.86–15.15
290461	275	16918	*Anadara* sp. cf. *zuliana*	0.708774	15.14	14.50–15.51
290461	275	16918	*Anadara* sp. cf. *zuliana*	0.708766	15.29	14.79–15.64
290461	275	16918	*Anadara* sp. cf. *zuliana*	0.708759	15.39	14.97–15.75
290461	275	16918	*Anadara* sp. cf. *zuliana*	0.708767	15.27	14.76–15.62
290463	276	16885	*Glyptoactis paraguana*	0.708756	15.43	15.04–15.79
290463	276	16885	*Glyptoactis paraguana*	0.708703	*16.28*	*16.17–16.39*
290463	276	16885	*Glyptoactis paraguana*	0.708882	*10.12*	*9.93–10.34*
290662	319	37819	*Eucrassatella venezuelanus*	0.708792	14.71	14.41–14.88
290828	386	38133	*Anadara* sp. cf. *zuliana*	0.708844	*11.52*	*11.21–11.95*

[a] Localities correlated to the basin composite stratigraphy with low–moderate accuracy

[b] Possibly faulted block and correlated to the basin composite stratigraphy with low–moderate accuracy; ages in italic indicate unreliability relative to replicate samples from same horizon or stratigraphic context. Specimens are reposited at the Mapuka Museum of Universidad del Norte (MUN-STRI), Colombia. Locality numbers can be searched in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb)

Valley abruptly runs into a fault-bounded block (STRI 290423) that lies adjacent to the top of the Jimol Formation, and samples from here yielded a mean age of 15.6 Ma (range of 16.21–15.08 Ma) indicating possible discontinuity with the surrounding stratigraphy. Another faulted block containing beds roughly correlated with the Patajau Valley still further south at Kaitamana (STRI 290666) yielded ages of 17.59, 16.91 and 16.1 Ma. Beds in the middle part of the formation near Makaraipao yielded mean $^{87}Sr/^{86}Sr$ ratio-derived age of 15.30 Ma (range of 15.14–15.43 Ma) (Table 6). A sample from the upper part of the formation on the southern shore of Bahia Tucacas yielded a $^{87}Sr/^{86}Sr$ ratio-derived age of 14.71 Ma and provides a key tie point for inferring the age of the top of the Castilletes Formation.

Paleoecology and paleoenvironmental analysis

The Castilletes Formation (Figs. 8a–d, 9a–c) predominantly accumulated in sheltered shallow marine, marginal marine, or coastal plain paleoenvironments. Marginal marine assemblages include taxa such as *Potamides suprasulcatus*, *Terebralia dentilabris* (GABB, 1873), *Modulus tamanensis*, *Cerithium* sp., *Anadara* (*Cunearca*) sp. cf. *zuliana*, *Brachidontes* sp., and abundant *Crassostrea* sp., which often form thick monospecific bioherms (Fig. 8d). Somewhat more marine, but nevertheless shallow (5–10 m), assemblages are also common throughout, and comprise *Turritella* spp., *Anadara* (*Cunearca*) sp. cf. *zuliana*, *Turbinella falconensis*, and *Melongena consors*. Occasional horizons in the lower and middle

parts of the formation contain taxa more typical of deeper waters (<25 m) and are characterized by higher diversity, particularly among gastropods such as muricids (e.g., *Calotrophon*, *Phyllonotus*, *Vokesmurex*) and turrids, e.g., *Crassispira*, *Knefastia*, *Polystira*). Freshwater elements (e.g., *Aylacostoma*, *Charadreon*, *Doryssa*, and *Sheppardiconcha*) are infrequently observed (but often in some abundance) reworked within shallow marine beds, although not outside of the lower part of the formation. One remarkable succession in Patajau Valley (STRI 290454-456) contains a transgressive sequence, comprising from bottom to top non-marine mudstone, a bed of in situ unionid clams, a vertebrate-rich (primarily crocodilian and turtle remains) freshwater snail bed (dominated by *Aylacostoma* and *Charadreon*), a marginal marine assemblage [dominated by *Anadara* (*Cunearca*) sp. cf. *zuliana*] and

then a more fully marine assemblage. Numerous paleosols, non-marine fossil invertebrate assemblages, and continental vertebrate faunas indicate that sea-level regularly oscillated between the shallow marine and non-marine realm.

Ware Formation

Overview

The Ware Formation that crops out near the town of Castilletes, at Flor de Guajira, and south into Venezuela, contains a quite distinct invertebrate fauna to underlying units (Figs. 10, 11). Dominant taxa of the Ware Formation include *Argopecten* sp., *Crassostrea rhizophorae* (GUILDING, 1828), *Plicatula gibbosa* (LAMARCK, 1801), and
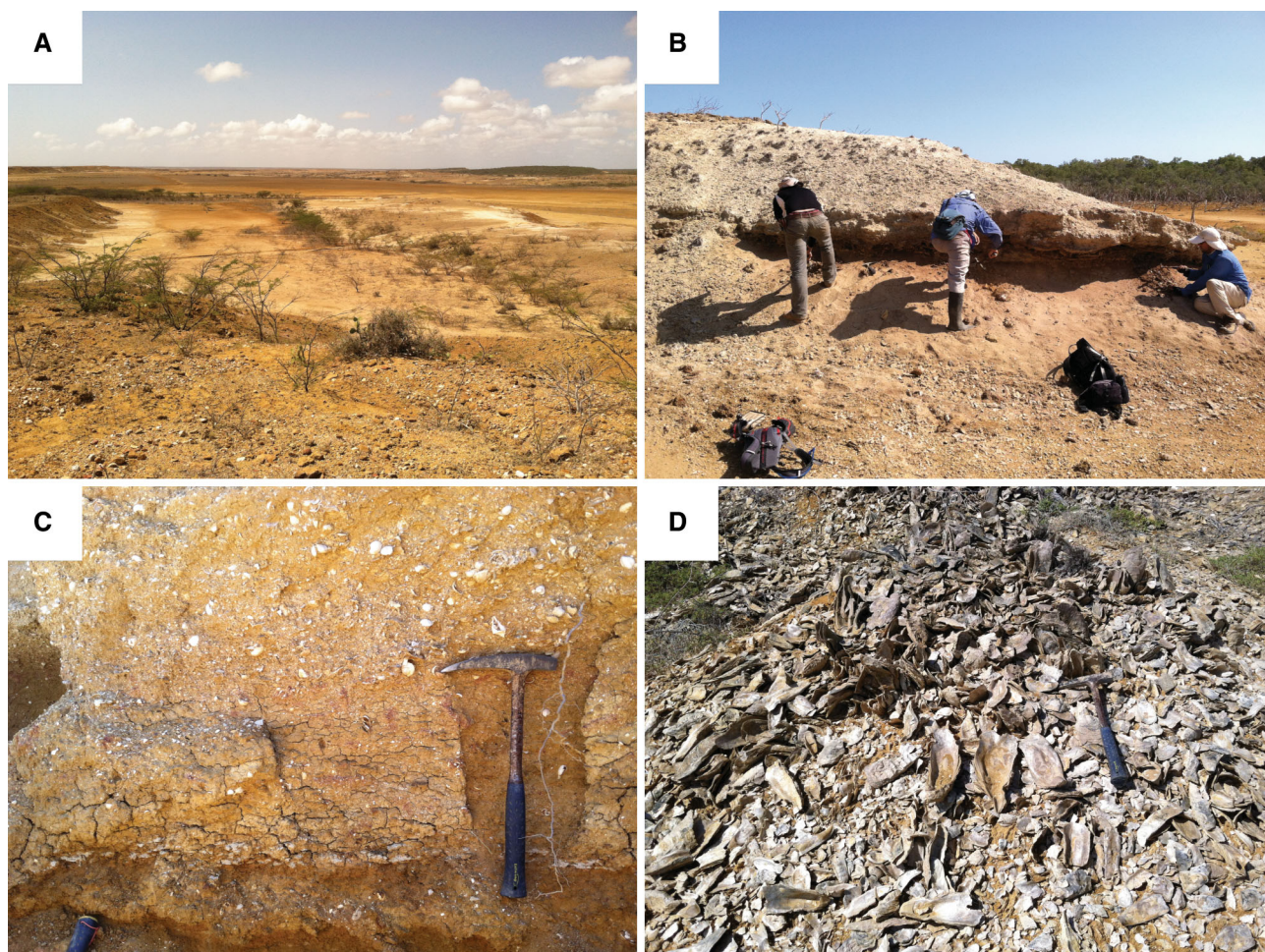

Fig. 8 a Typical surface expression of Castilletes Formation with low relief, gently sloping ridges capped by shell beds bounding recessive intervals of mudstone. **b** Sedimentary succession in upper Castilletes Formation near Bahia Tortugas (STRI 290657), comprising non-marine mudstone and coal (lowstand facies), and overlying marginal marine shell bed (transgressive facies). **c** Close-up of a sequence boundary in middle Castilletes Formation near Patajau (STRI 290849) with lowstand estuarine mudstone with articulated *Phacoides* and scattered *Potamides* overlain by a condensed shell bed of *Anadara* and *Panchione*. **d** *Crassostrea* bioherm in the upper Castilletes Formation near Bahia Tortugas (STRI 290658)
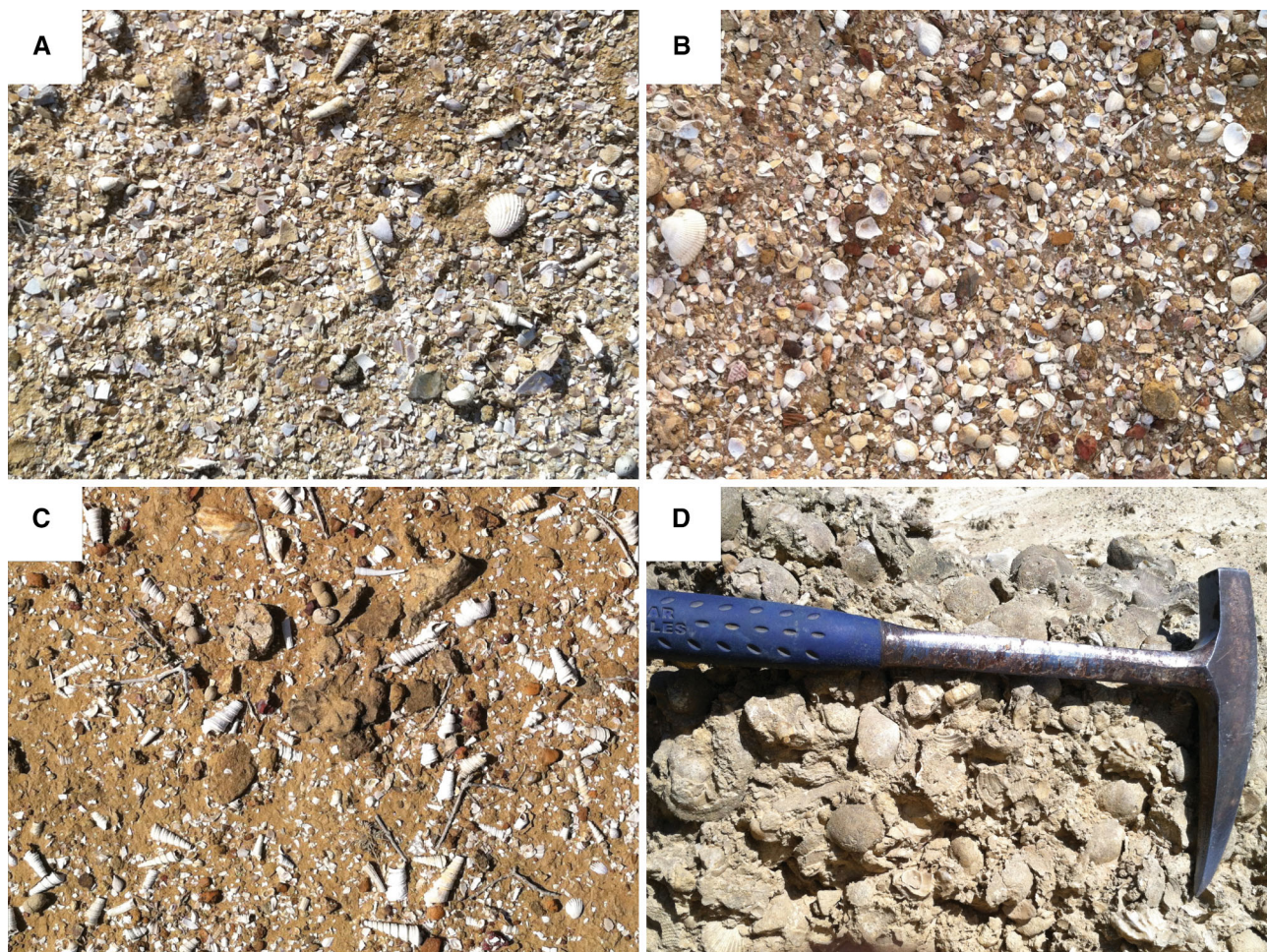
Fig. 9 a Shell bed in upper Jimol Formation near Siapana (STRI 290816) containing *Turritella*, *Polystira*, and *Glyptoactis*. **b** Shell bed with typical marginal marine assemblage of *Panchione* and *Anadara* near Patajau. **c** Shell bed containing *Turritella*, turrids and *Dentalium* in uppermost Jimol Formation near Paraguachón (STRI 290602). **d** Typical preservation of Ware Formation near Puerto Lopéz (STRI 290679), with numerous internal molds of *Anodontia*, *Chione*, and *Macrocallista*

Anodontia n. sp. Other frequently occurring taxa include *Crucibulum* sp., *Strombus* sp., *Naticarius* sp. cf. *canrena* (LINNAEUS, 1758), *Oliva* sp. cf. *tuberaensis* ANDERSON, 1929, *Bulla* sp. cf. *striata* BRUGUIÈRE, 1792, *Anadara* (*Rasia*) *lienosa* (SAY, 1832), *Euvola codercola* (HARRIS, 1927), *Lindapecten* sp., *Codakia orbicularis* (LINNAEUS, 1758), *Dallocardia muricata* (LINNAEUS, 1758), *Laevicardium serratum* (LINNAEUS, 1758), *Mactrellona* sp. cf. *alata* (SPENGLER, 1802), *Chione cancellata* (LINNAEUS, 1767), *Dosinia* sp., *Lirophora* sp., and *Macrocallista maculata* (LINNAEUS, 1758) (Figs. 10, 11). An estimated 61 species of molluscs (21 gastropods and 40 bivalves) and one echinoderm (*Clypeaster rosaceus* LINNAEUS, 1758) are here recorded from the formation (Table 7). With respect to preservation, the assemblage consists of internal molds from which aragonite was completely dissolved (Fig. 9d), although calcitic forms (pectinids, ostreids) are generally well preserved as shells. The

recorded diversity of the Ware Formation is certainly retarded by its poor preservation, although further careful collection and preparation of silicone peels will almost certainly increase this number and the precision of existing identifications.

Age

The molluscan fauna of the Ware Formation shows much greater similarity with modern assemblages offshore of northern South American than with those of the underlying units in Cocinetas Basin. Nevertheless, few taxa provide finely resolved age constraints for the Ware Formation. Pectinid bivalves such as *Amusium mortoni* (BROWN, 1913) (Early Pliocene to earliest Pleistocene), *Euvola codercola* (latest Miocene-Pliocene), and *Nodipecten arnoldi* (AGUERREVERE, 1925) (Late Pliocene to Early Pleistocene) suggest an age close to the Pliocene–Pleistocene boundary.
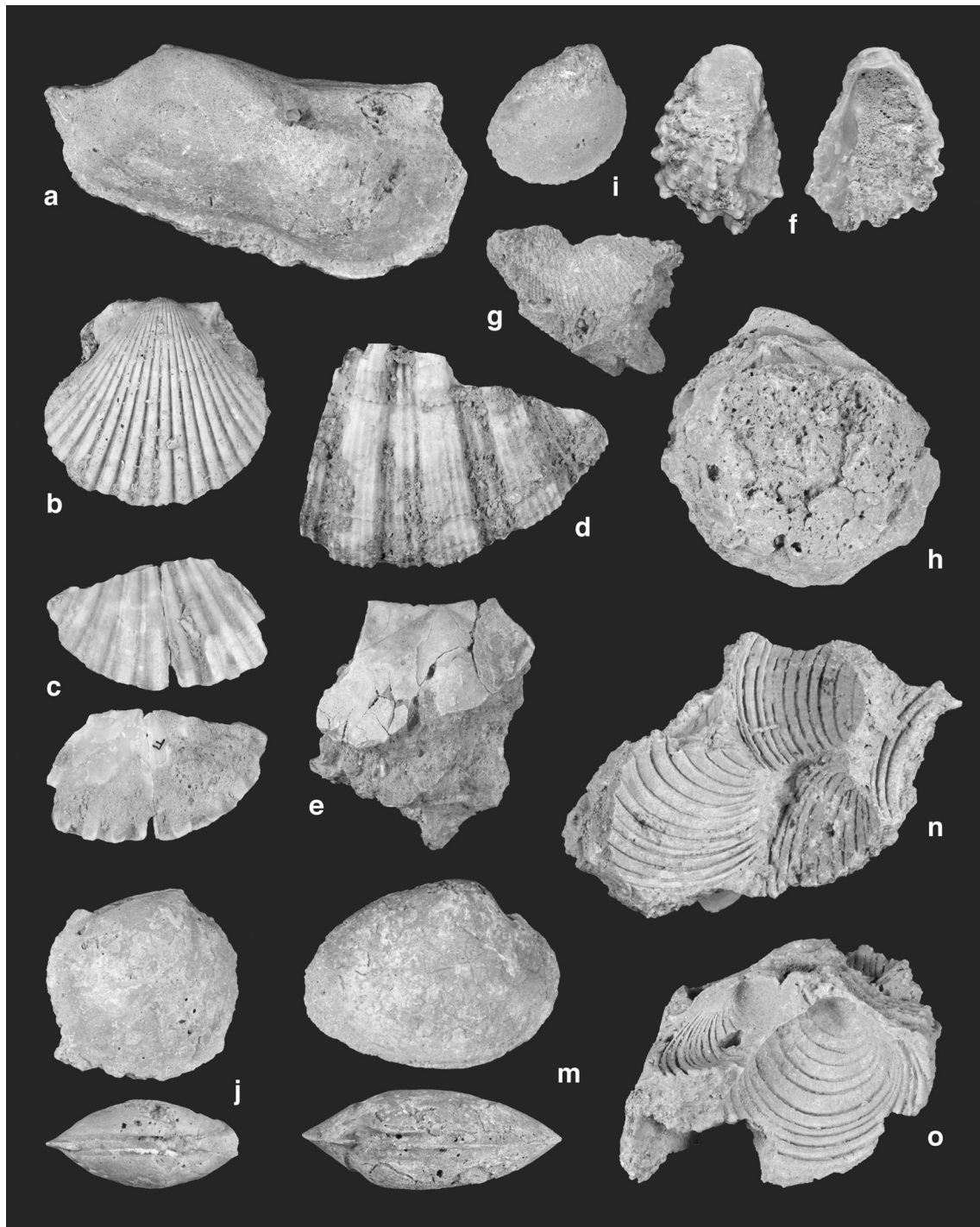
Fig. 10 Frequently occurring bivalves of the Pliocene Ware Formation, Cocinetas Basin: **a** *Arca zebra* (MUN-STRI-10347-2; ×0.8), **b** *Argopecten* sp. (MUN-STRI-11063-1, **c** *Euvola codercola* (MUN-STRI-10347-10), **d** *Nodipecten arnoldi* (MUN-STRI-10347-3), **e** *Amusium toulae* (MUN-STRI-16097-3), **f** *Dendostrea democraciana* (MUN-STRI-10347-4), **g** *Codakia orbicularis* (MUN-STRI-10347- 15), **h** *Dosinia* sp. (MUN-STRI-10347-14), **i** *Laevicardium serratum* (MUN-STRI-10347-9), **j** *Dosinia* sp. (MUN-STRI-10347-13), **m** *Macrocallista maculata* (MUN-STRI-16097-2), **n**, **o** *Chione* sp. (**n** MUN-STRI-10347-7, **o** MUN-STRI-10347-6). All specimens are of actual size unless stated

One of the most curious forms identified from the Ware Formation is *Acrosterigma* sp. cf. *dalli* (HEILPRIN, 1886), which is represented by two articulated internal molds.

This is a very distinctive, smoothly ribbed large cardiid bivalve, whose identification cannot be mistaken for any other species of the genus, fossil or Recent, in the Western
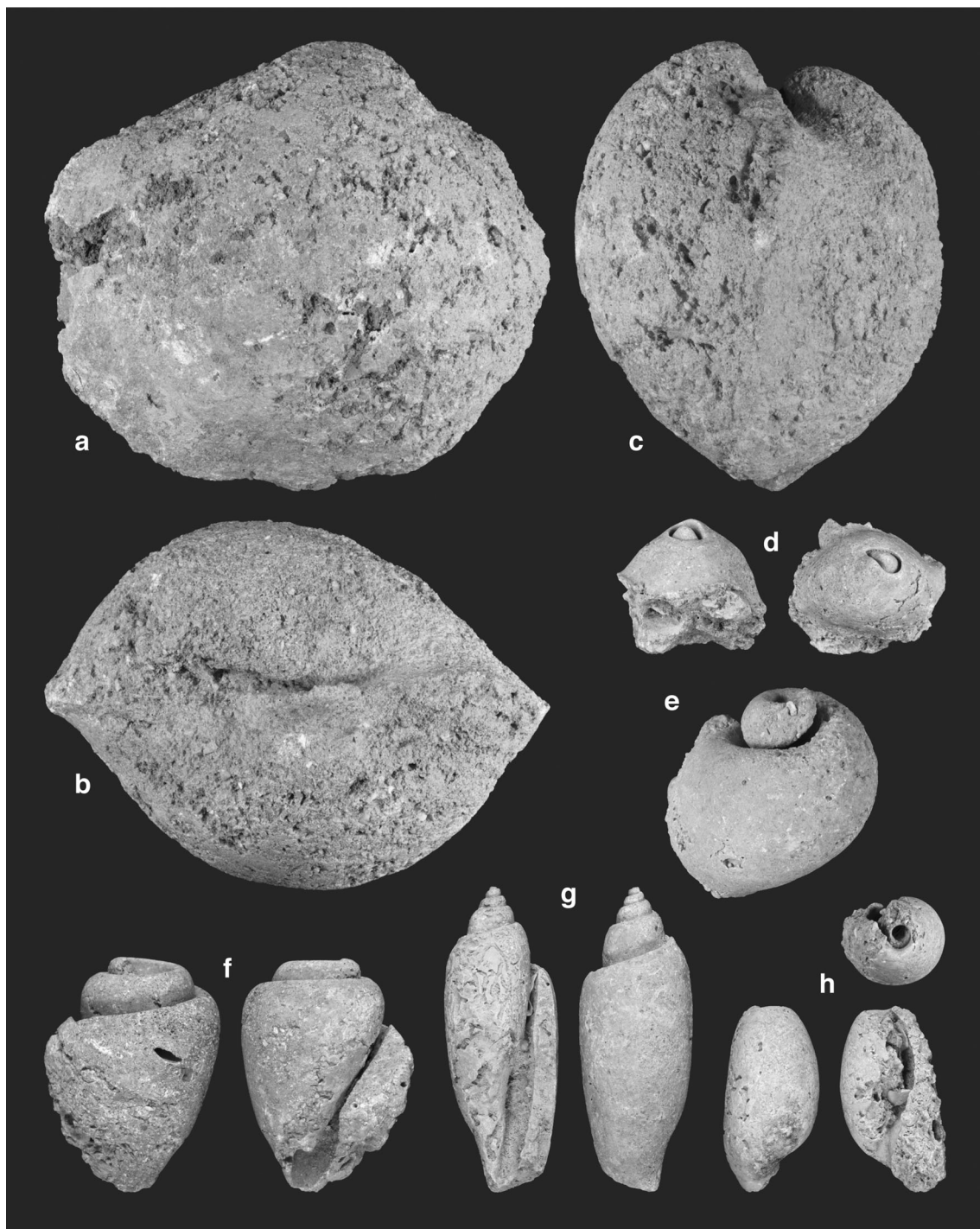
Fig. 11 Frequently occurring bivalves and gastropods of the Pliocene Ware Formation, Cocinetas Basin: **a–c** *Anodontia* n. sp. (MUN-STRI-17060-1; ×0.5), **d** *Crucibulum* sp. (MUN-STRI-16880-2), **e** *Naticarius canrena* (MUN-STRI-16097-1), **f** *Strombus* sp. (MUN-STRI-16880-1), **g** *Oliva* sp. (MUN-STRI-10347-5), **h** *Bulla striata* (MUN-STRI-16880-4). All specimens are of actual size unless stated

Atlantic or eastern Pacific. *Acrosterigma dalli* is only known from the earliest Pleistocene of Florida, although other members of the genus have been noted from the Pliocene and Pleistocene of the Caribbean; however, none of these resemble *Acrosterigma* sp. cf. *dalli* in size or shape. The relatively few species identified to species

resolution (<30 species) in the Ware Formation precludes meaningful comparison with other circum-Caribbean Pliocene and Pleistocene faunules (Table 8).

A mean age of 3.2 Ma (range of 3.40–2.78 Ma) is calculated for the shell bed at the top of the formation from $^{87}Sr/^{86}Sr$ ratios (Table 9). A latest Pliocene (Piacenzian)

Table 7 Checklist of invertebrate fossils from the Ware Formation (this study only)

Species
Gastropoda
Trochidae indet.
Astraea (*Lithopoma*) sp.
Petaloconchus sp. cf. *sculpturatus* (Lea, 1846)
Turritella sp.
Crepidula sp.
Calyptraea sp. cf. *centralis* (Conrad, 1841)
Crucibulum sp.
Naticarius sp. cf. *canrena* (Linnaeus, 1758)
Neverita sp.
Polinices sp.
Malea sp.
Strombus sp.
Ficus sp.
Cypraeidae indet.
Muricidae indet.
Buccinidae indet.
Turbinella sp.
Oliva sp. cf. *tuberaensis* Anderson, 1929
Volutidae indet.
Conus sp.
Bulla sp. cf. *striata* Bruguière, 1792
Bivalvia
Arca imbricata Bruguire, 1789
Arca zebra (Swainson, 1833)
Anadara (*Cunearca*) sp.
Anadara (*Rasia*) *lienosa* (Say, 1832)
Barbatia sp. cf. *mauryae* (Olsson, 1922)
Tucetona sp. cf. *lamyi* (Dall, 1915)
Eontia ponderosa (Say, 1822)
Atrina sp. cf. *serrata* (G. B. Sowerby I, 1825)
Amusium toulae (Brown, 1913)
Argopecten sp.
Euvola codercola (Harris, 1927)
Lindapecten sp.
Nodipecten arnoldi (Aguerrevere, 1925)
Pectinidae indet.
Crassostrea rhizophorae (Guilding, 1828)
Dendostrea democraciana Hodson, 1927
Ostrea sp.
Plicatula gibbosa (Lamarck, 1801)
Anomia simplex d'Orbigny, 1845
Spondylus bostrychites Guppy, 1867
Isognomon sp.
Anodontia n. sp.
Codakia orbicularis (Linnaeus, 1758)
Arcinella arcinella (Linnaeus, 1758)
Chama cf. *corticoraformis* Anderson, 1929
Acrosterigma sp. cf. *dalli* (Heilprin, 1886)
Americardia media (Linnaeus, 1758)
Dallocardia muricata (Linnaeus, 1758)
Dinocardium sp.

Table 7 continued

Species
Laevicardium serratum (Linnaeus, 1758)
Mactrellona sp. cf. *alata* (Spengler, 1802)
Raeta sp.
Psammacoma sp.
Solecurtidae indet.
Chione sp. cf. *cancellata* (Linnaeus, 1767)
Dosinia sp.
Globivenus sp.
Lirophora sp.
Macrocallista maculata (Linnaeus, 1758)
Periglypta sp.
Veneridae indet.
Echinodermata
Clypeaster rosaceus Linnaeus, 1758

age is assigned to the Ware Formation on the basis of macroinvertebrate biostratigraphy and $^{87}Sr/^{86}Sr$ isotope chronostratigraphy. An early Pleistocene age for the highest strata of the formation is also possible, given the high number of extant taxa reported from that part of the stratigraphy.

Paleoecology and paleoenvironmental analysis

The assemblage contains taxa typical of exposed open ocean shoreface and settings, such as *Euvola codercola*, *Nodipecten arnoldi*, *Dosinia* sp., and *Macrocallista maculata*. The presence of species such as *Arca imbricata* Bruguière, 1789 and *Arca zebra* Swainson, 1833, *Arcinella arcinella* (Linnaeus, 1758), *Codakia orbicularis*, *Spondylus bostrychites* Guppy, 1867, *Periglypta* sp., and *Bulla* sp. cf. *striata* suggest proximity to carbonate depositional environments such as subtidal seagrass or patch reef facies. A mixture of taxa from varied habitats such as these is not unexpected in higher energy, shallow marine setting where skeletal assemblages are prone to time averaging (Kidwell and Bosence 1991) and the coastline is often environmentally heterogeneous.

Results and discussion

Paleoecology and paleoenvironments

Paleoecology of the Jimol and Castilletes formations

The fauna of the Jimol and Castilletes formations are typical of tropical Atlantic marginal marine and shallow-water assemblages during the Miocene. Estuarine and lagoonal ecosystems are obvious, with the presence of

Table 8 Comparison of the Ware assemblage with other Caribbean Pliocene-Pleistocene faunules at species level

Formation/age	Region	#SpA	#SpC	%SpC	Jaccard	Simpson
Araya Fm (L. Plioc.)	Venezuela	179	11	6.1	0.06	0.37
Fort Thompson Fm (L. Ple.)	Florida	255	11	4.3	0.04	0.37
Bermont Fm (M. Ple.)	Florida	436	14	3.2	0.03	0.47
Mare Fm (E. Plioc.)	Venezuela	416	12	2.9	0.03	0.40
Caloosahatchee Fm (E. Ple.)	Florida	671	17	2.4	0.02	0.53

#SpA number of species known from the assemblage, *#SpC* number of species in common with the Ware Formation, *%SpC* percentage of Ware taxa present in the assemblage, analyses restricted to named species ($n = 27$ species)

Table 9 Strontium isotope data and age estimates from the Ware Formation

Locality (STRI)	Height (m)	Sample (MUN-STRI)	Taxon	$^{87}86/^{86}Sr$	Age (Ma)	Age range (Ma)
290045	462	10347	*C. rhizophorae*	0.7091014	1.57	1.22–2.24
290045	462	10347	*P. gibbosa*	0.7090639	2.78	1.93–4.82
290045	462	10347	*C. rhizophorae*	0.7090591	3.28	2.12–4.99
290045	462	10347	*E. codercola*	0.7090584	3.4	2.15–5.03
290080	462	11063	*P. gibbosa*	0.709058	3.4	2.15–5.03
290080	462	11063	*Argopecten* sp.	0.7090104	5.71	5.09–6.10

Specimens are reposited at the Mapuka Museum of Universidad del Norte (MUN-STRI), Colombia. Locality numbers can be searched in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb)

characteristic taxa such as oysters and potamid gastropods, occasional crab carapaces and chelae, and freshwater and euryhaline fish otoliths. Shallow subtidal ecosystems are indicated by an increased diversity of taxa, including turritellid and naticid gastropods, cardiid and venerid bivalves, and fish otoliths and ray dental plates. Less commonly encountered are more distal inner shelf (<50 m) fully marine ecosystems, which are indicated by an increased presence of muricid and turrid gastropods, and shark teeth. In situ freshwater ecosystems are represented in only a few stratigraphic layers and may be recognized from abundant thiarid gastropods, unionid bivalves, and aquatic crocodilians and turtle, but transported aquatic invertebrates and vertebrates are frequently reworked in shallow marine assemblages.

Data from field observations and bulk samples are used here to quantitatively describe this gradient of marginal marine through fully marine ecosystems and aid in the description of depositional paleoenvironments in the Jimol and Castilletes formations. Two multivariate techniques, DCA and Q-mode cluster analysis, are employed to reveal compositional relationships among the samples observed and collected from the Jimol and Castilletes formations. The Q-mode cluster analysis (Fig. 12a) provides a basis for classification of biofacies from these units. Three biofacies may be distinguished at a fairly coarse scale. One of these comprises essentially monospecific assemblages of *Crassostrea* sp., which in the field are

Fig. 12 Quantitative paleoecological analyses of the Jimol and ▶ Castilletes formations. **a** Q-mode cluster analysis, with samples coded by lithostratigraphic position (= strat.), salinity score, and benthic zone score (= depth); see Key for explanation. **b** DCA of species, with taxa coded by salinity preference. DCA of samples coded by benthic zone score (**c**), salinity score (**d**), and lithostratigraphic position (**e**)

manifested as either dramatic, large mound-shaped oyster bioherms or as thinner laterally extensive shell beds. The *Crassostrea* biofacies is largely restricted to the Castilletes Formation, and is suggestive of reduced salinity and sometimes estuarine conditions. A second biofacies (*Panchione–Anadara*) is characterized by frequent *Anadara* (*Cunearca*) *zuliana*, *Crassostrea*, *Panchione*, *Potamides*, and *Turritella* (*Turritella*) *matarucana*. The biofacies is found throughout both the Jimol and Castilletes formations and comprises taxa common to both reduced and fully marine conditions, ranging from estuarine to nearshore depositional environments. A turritellid-dominated biofacies is distinguished by *Turritella* (*Turritella*) *cocoditana*, *Turritella* (*Turritella*) *matarucana*, *Anadara* (*Cunearca*) *zuliana*, *Melongena*, *Dallocardia*, *Potamides*, *Panchione*, and *Conus talis*. This biofacies is found throughout both formations, in typically fully marine and nearshore depositional environments.

DCA calculates taxon scores simultaneously with sample scores and plots them on the same axes and scales (Fig. 12b–e) permitting easy interpretation of underlying
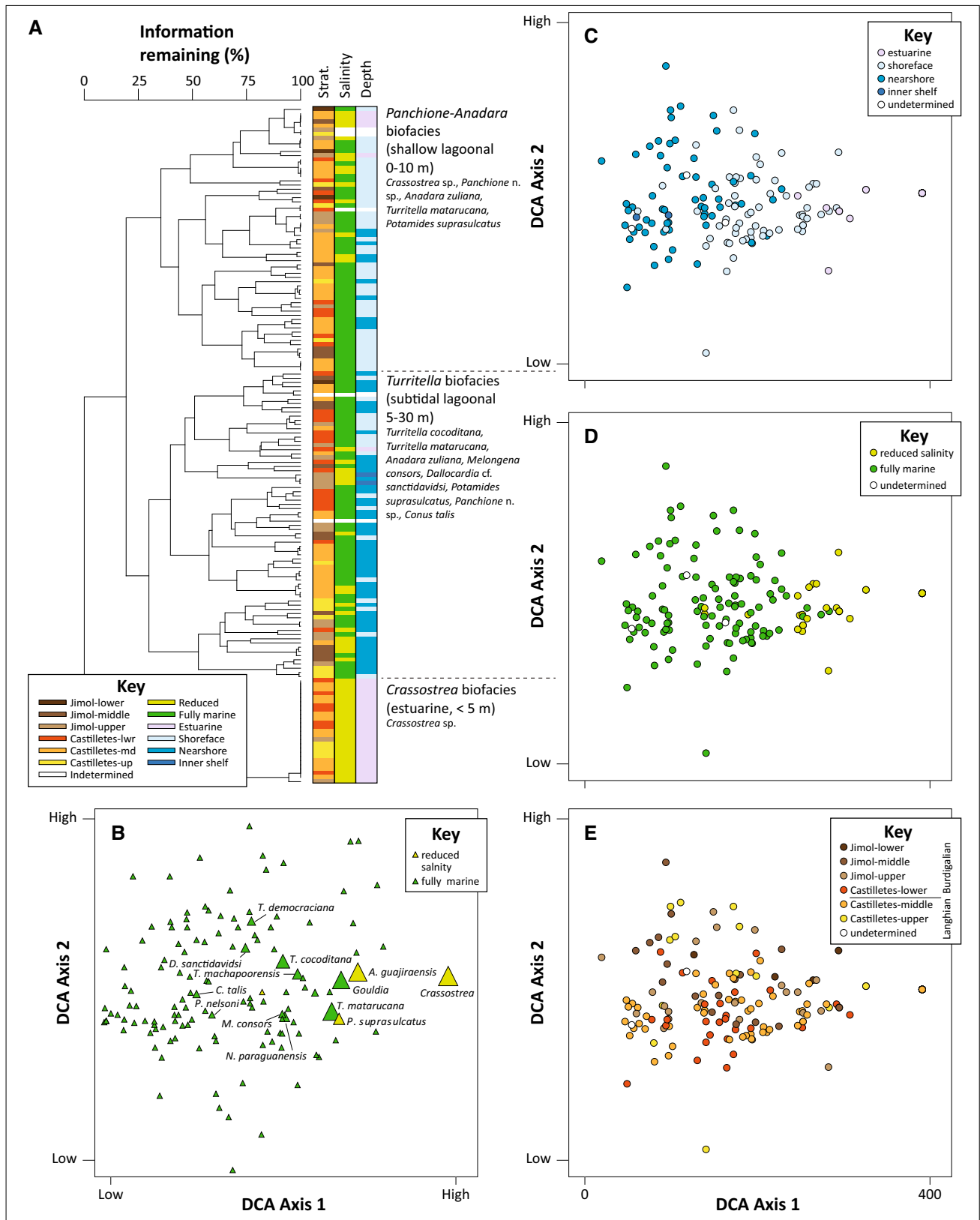
paleoenvironmental gradients. The taxon DCA of Fig. 12b indicates the presence of three important taxa [*Crassostrea*, *Anadara* (*Cunearca*) sp. cf. *zuliana*, and *Potamides*] that inhabit reduced salinity environments on the right hand side of the plot, with relatively high DCA axis 1 scores. All taxa on the left hand side of the plot, with relatively low DCA axis 1 scores, have preferences for fully marine conditions and include the relatively common *Tucetona*, *Dallocardia*, *Turritella* (*Turritella*) *cocoditana* and *Turritella* (*Turritella*) *machapoorensis*, *Glossaulax*, *Polinices*, *Melongena*, and *Conus talis*.

Samples are plotted in Fig. 12c–e. When the benthic score of individual samples are overlain (Fig. 12c) a very clear depth gradient is exhibited parallel to DCA axis 1, with the deepest samples bearing low DCA axis 1 values and the shallowest samples showing high DCA axis 1 values. Likewise, when salinity scores of samples are overlain (Fig. 12d), samples frequented by taxa typical of reduced salinity conditions have high DCA axis 1 values, while those that are fully marine have low DCA axis 1 values. A salinity (fully marine to reduced salinity) or depth gradient (offshore to estuarine) is therefore reproduced by the ordination. An overlay of lithostratigraphic assignment of samples indicates no differentiation by stratigraphic position within the ordination. The community composition along the paleoenvironmental gradient recognized in Fig. 12b–d is likely maintained throughout the study interval.

Paleoenvironmental history

While the sedimentary fill of Cocinetas Basin includes strata of Eocene (Macarao Formation) and Oligocene (Siamana Formation), the Neogene stratigraphic record is particularly extensive, well exposed, and now well studied (see Moreno et al. 2015). The stratigraphic framework that has been developed now permits an interpretation of changing paleoenvironments and fossil faunas over the last 20 million years.

The Uitpa Formation (?Aquitainian–Burdigalian) records a basin-wide drowning of the shallow marine carbonates of the Siamana Formation (Chattian–Aquitanian). Near its base, macrofossils suggest that the Uitpa Formation accumulated in upper bathyal to outer shelf depths. This is consistent with previous interpretations by Becker and Dusenbury (1958) who suggested deposition occurred in depths greater than 150 m, Rollins (1965), who indicated a neritic to deep marine environment, and Thomas (1972), who observed radiolarians indicative of deep water. Shallow marine molluscs near the top of the formation indicate a regression leading up to the contact with the Jimol Formation.

The Jimol Formation (Burdigalian) marks a shift to consistently shallow marine or terrestrial conditions through the top of the Castilletes Formation (Fig. 13). The base of the Jimol Formation comprises well-cemented sandstone with occasional fossiliferous horizons of nearshore and marginal marine taxa that accumulated in foreshore or shoreface environments. This corroborates the study by Rollins (1965), which interpreted the Jimol Formation to have accumulated in a shallow marine environment where beach conditions prevailed during most of the interval. Nevertheless, the middle parts of the formation comprise thicker successions of mudstone with scarce marine macrofossils, suggesting a shift toward deeper shelf paleoenvironments. Shell beds become more frequent and thicker in the top of the formation and include the marginal marine *Crassostrea* and shallow subtidal *Panchione–Anadara* biofacies. These broad facies changes likely reflect a formation-wide transgressive–regressive cycle.

The Castilletes Formation (Burdigalian–Langhian) is defined by a minor, but seemingly extensive transgression, as recorded by an extensive burrowed sandstone and cemented skeletal-rich sandstone that is capped by a mineralized hard-ground surface. The macrofaunal assemblages overlying this surface are much the same as those in the upper Jimol Formation (Figs. 5, 13) and represent the *Crassostrea* and *Panchione–Anadara* biofacies (Fig. 12). Nevertheless, fine-grained siliciclastic packages become thicker, forming large valleys that follow the strike of these recessive sediments. These are punctuated by thicker shell beds that in places are more cemented and provide laterally extensive, resistant ridges. For the most part, the faunas of these shell beds represent nearshore (<15 m) water depths, and a habitat that is protected from considerable wave and current action. Oyster bioherms and shell beds are occasionally encountered in the lower Castilletes Formation, indicating possible deposition in intertidal or shallow subtidal and reduced salinity conditions. Freshwater invertebrate assemblages are also observed in the lower part of the formation and are associated with a diversity of aquatic vertebrates such as turtles and crocodilians.

Oyster bioherms become increasingly frequent in the middle and upper parts of the Castilletes Formation (Fig. 13) and are clustered spatially and stratigraphically, perhaps associated with subtidal channels across the protected shallow bay or lagoon. Shell beds also increase in diversity, including many more forms associated with deeper water, and some of the formation's most offshore assemblages. Nevertheless, these assemblages are unlikely to have accumulated in excess of 50 m of water depth and additionally do not exhibit the effects of considerable wave or current energy, suggesting deposition continued within the confines of a protected embayment. Freshwater taxa are less common in the middle part of the formation and are absent from the upper part, which is exposed further east, and more distal from the likely source areas of riverine
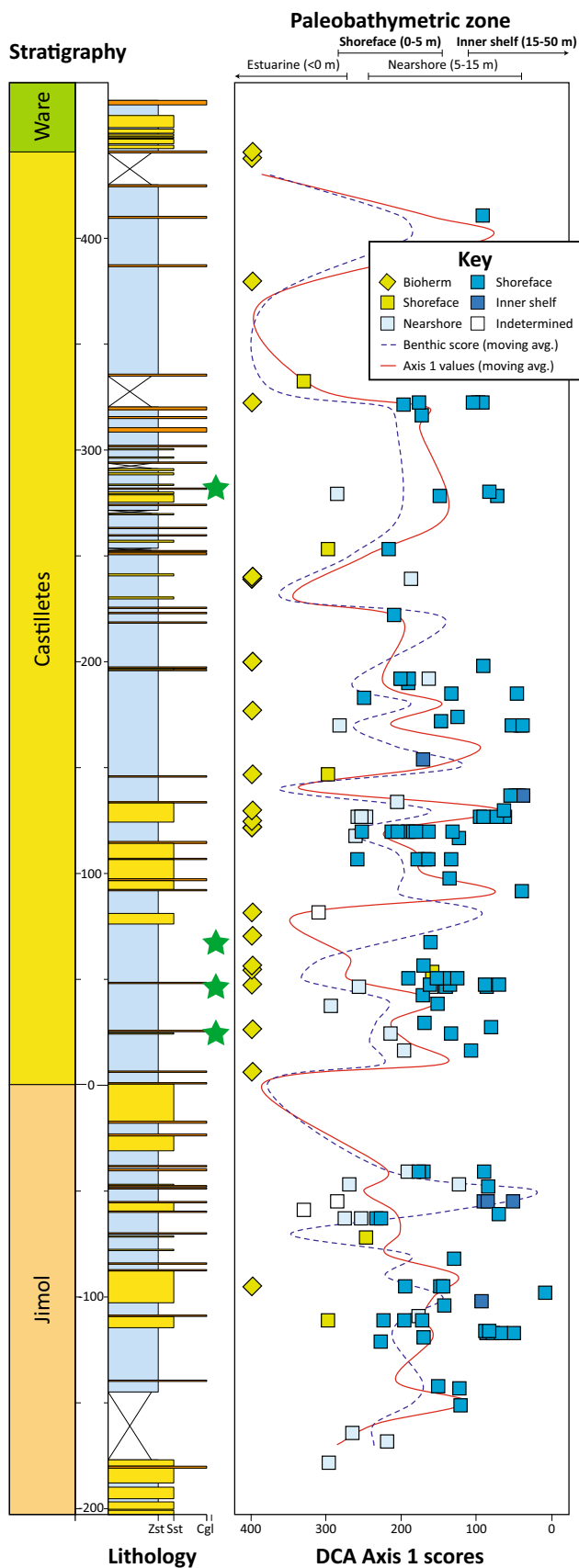
◄**Fig. 13** DCA axis 1 scores plotted by stratigraphic position within Jimol and Castilletes formations. Moving average curves (3 point) for both mean benthic scores and DCA axis 1 scores reveal paleobathymetric trends. *Green stars* indicate key terrestrial vertebrate assemblages (see Moreno et al. 2015)

input between the Cocinas, Jarara, and Macuira ranges. Marine vertebrates, including turtles, crocodilians, and Cetacea, are frequent toward the base of the middle part of the formation. The upper part of the formation appears to comprise coarser sediments and more tightly packed shell beds and in general is more cemented. These shell beds are generally of nearshore origin.

In summary, paleoenvironments fluctuate fairly regularly within the Castilletes Formation (Fig. 13), and particular parts contain deeper water faunas than others. This interpretation is consistent, albeit more complex, with that of Rollins (1965) who viewed the Castilletes Formation as a shallow marine environment, similar to that just offshore of present-day Guajira Peninsula.

An unconformity of approximately 11 million years separates the upper Castilletes Formation from the overlying Ware Formation (Piacenzian–Gelasian). The Ware is not a particularly thick unit, and is preserved as small remnants across what would have been a much more widespread distribution through the coastal Cocinetas Basin. The most complete exposures near the town of Castilletes record as many as two partial cycles of sea-level oscillation. A minor transgressive lag is exposed at the base of the section, with highly fragmented and abraded oyster and scallop fossils, edge-rounded bone fragments, and coarse siliciclastic clasts. The overlying stratigraphy includes mudstone and siltstone, which give way to thicker beds of fine sandstone with planar and trough cross-bedding. The top of the formation is marked by a much thicker transgressive horizon, comprising extremely fossiliferous (albeit largely moldic) conglomeratic biosparite. The lower sequence of the Ware Formation is interpreted to have been deposited in a fluvio-deltaic environment, while the horizon at the top of the unit accumulated in a more exposed open ocean shoreface and nearshore setting, perhaps proximal to coral reef or seagrass habitats.

Sea-level oscillations

The sedimentary record of the Castilletes and the upper part of the Jimol Formation is clearly overprinted by rapid oscillations of base level. Condensed skeletal deposits, which vary between 10 cm and 1 m in thickness, regularly punctuate the thick siliciclastic successions of both formations. These accumulations exhibit characteristics of

Fig. 14 Idealized local paleogeography of Cocinetas Basin during **a** sea-level highstand and **b** sea-level lowstand conditions
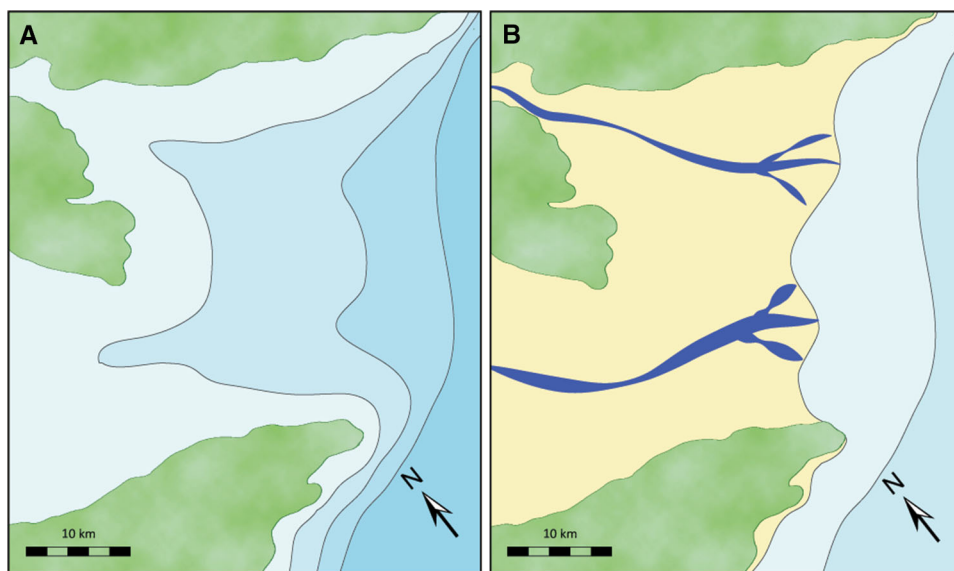
time averaging often associated with rapid marine transgressions, such as their thickness, mixing of communities from locally derived habitats, and the disarticulation and fragmentation of skeletal elements. These often overlay paleosols or assemblages dominated by continental vertebrates and invertebrates, which indicate that sea-level fluctuations regularly brought the basin into the non-marine domain. While each shell bed is presently represented by a narrow band exposed along strike, they likely were laterally extensive (presently eroded up-dip, and buried down-dip) across the basin, recording a basin-wide transgression (Fig. 14a). More than 40 shell beds are observed throughout the Castilletes Formation. However, some of these are thin and appear laterally discontinuous, particularly among the thicker sections of fine-siliciclastic sediments (recessive), and hence this tally is likely an underestimate. Over the extrapolated 2.5 million years of deposition for the Castilletes Formation, these shellbed-bound sedimentary packages could easily have accumulated consistent with the periodicity estimated for sixth-order or 41-kilo year Milankovitch-scale obliquity cycles (Hays et al. 1976). While eccentricity (100 kilo year) cyclicity was dominant during the Early Miocene (Zachos et al. 2001), Shevenell et al. (2004) reported that the Middle Miocene was a time dominated by obliquity cycles. Indeed, fine examples of obliquity-induced sea-level cycles have been reported from uplifted shallow marine Middle Miocene sediments, including Aswan and Ozawa (2005). Even in Amazonian lakes, a strong signal of obliquity cyclicity can be observed in lacustrine deposits of Middle Miocene age (Wesselingh et al. 2006a). Certainly, delta progradation played an important role in the accumulation of the Jimol and Castilletes formations. Riverine input likely originated from valleys between the highland areas

represented by today's Cocinas, Jarara, and Macuira ranges, and would have deposited sediment during lowstand conditions across Cocinetas Basin (Fig. 14b). Nevertheless, the regular concentrations of shells, the thickness of shell beds, and evidence of sea-level rise upward through the stratigraphy of these shell beds are more likely the result of reduced sedimentation rate and condensation associated with high-frequency marine transgressions (e.g., Kidwell 1989; Brett 1995; Hendy et al. 2006; Brett et al. 2011).

Geochronology

Strontium isotope dating

The oldest $^{87}Sr/^{86}Sr$ isotope ages from the Jimol Formation of 17.51 and 17.45 Ma were recorded near the top of the Jimol Formation (Figs. 15, 16). $^{87}Sr/^{86}Sr$ isotope analyses could not be conducted from the lower and middle parts of the Jimol Formation due to poor preservation of shell material. With this in mind, the age of the base of the unit might well exceed these dates. An even older age of 17.59 Ma was recorded from a poorly constrained (faulted) section within the overlying Castilletes Formation, but could not corroborated by samples from adjacent stratigraphic horizons. The youngest reliable $^{87}Sr/^{86}Sr$ isotope age from the Castilletes was from the upper part of the formation. The horizon that yielded an age of 14.71 ± 0.30 Ma (Fig. 15, 16) is still of some thickness below the top of the unit, and it is likely that the top of the unit is even younger. Somewhat younger ages (10–13 Ma) can be discounted given their stratigraphic position and the ages of replicate samples, and therefore they are of little value in establishing age control in the Jimol and Castilletes formations.
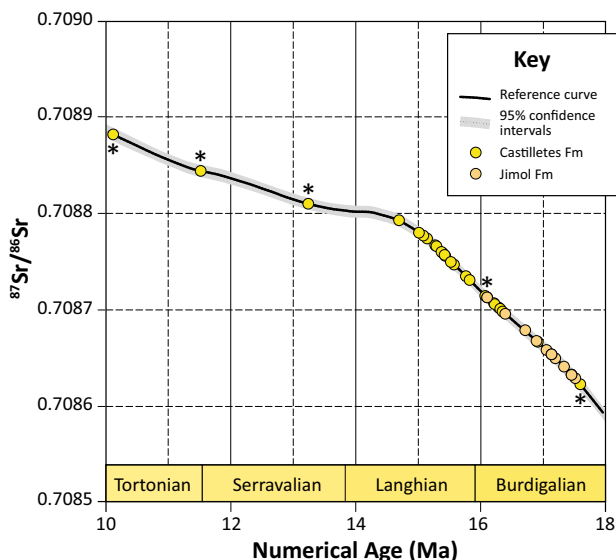
Fig. 15 Reference curve of Howarth and McArthur ([1997](#)) for the Early and Middle Miocene (18–12 Ma) overlain by $^{87}Sr/^{86}Sr$ isotope ratios from this study. Confidence intervals of the mean line are drawn at 95 % confidence interval. *Asterisk* samples not analyzed in this study

Fig. 16 Least-squares linear regression of $^{87}Sr/^{86}Sr$ with stratigraphic ▶ height measured in meters from datum, which is taken as 0 m at the base of the Castilletes Formation. Symbols distinguish data used in each regression (*blue*) and those excluded (*red*) due to concerns about their stratigraphic placement or their anomalous values. The function for deriving the regression is $y = -0.0058x + 16.722$ ($r^2 = 0.89$, $n = 21$) (color figure online)

An age model for the Jimol and Castilletes formations

Given the importance of understanding stratigraphic changes in biodiversity and paleoenvironments through the thickness of the Jimol and Castilletes formations, it is useful to develop an age model for dating individual horizons. We apportion time to the strata of the Jimol and Castilletes formations using a linear regression of the stratigraphic position and $^{87}Sr/^{86}Sr$ isotope ages. When extrapolated, the regression line implies that the base of the Jimol Formation is at approximately 17.9 Ma and that top of the Castilletes Formation would be around 14.2 Ma (Fig. 16). The contact between the Jimol and Castilletes formations at the datum level of 0 m would be approximately 16.7 Ma. This matches well with those samples confidently correlated with the lower 50 m of the Castilletes Formation, which has a mean value of 16.23 Ma ($n = 4$, range of 16.07–16.33 m), and those samples from the upper 50 m of the Jimol Formation, which has a mean value of 16.95 Ma ($n = 6$, range of 16.10–17.51 Ma). Those samples from the fault-bounded block at STRI 290423, which has been tentatively correlated at around
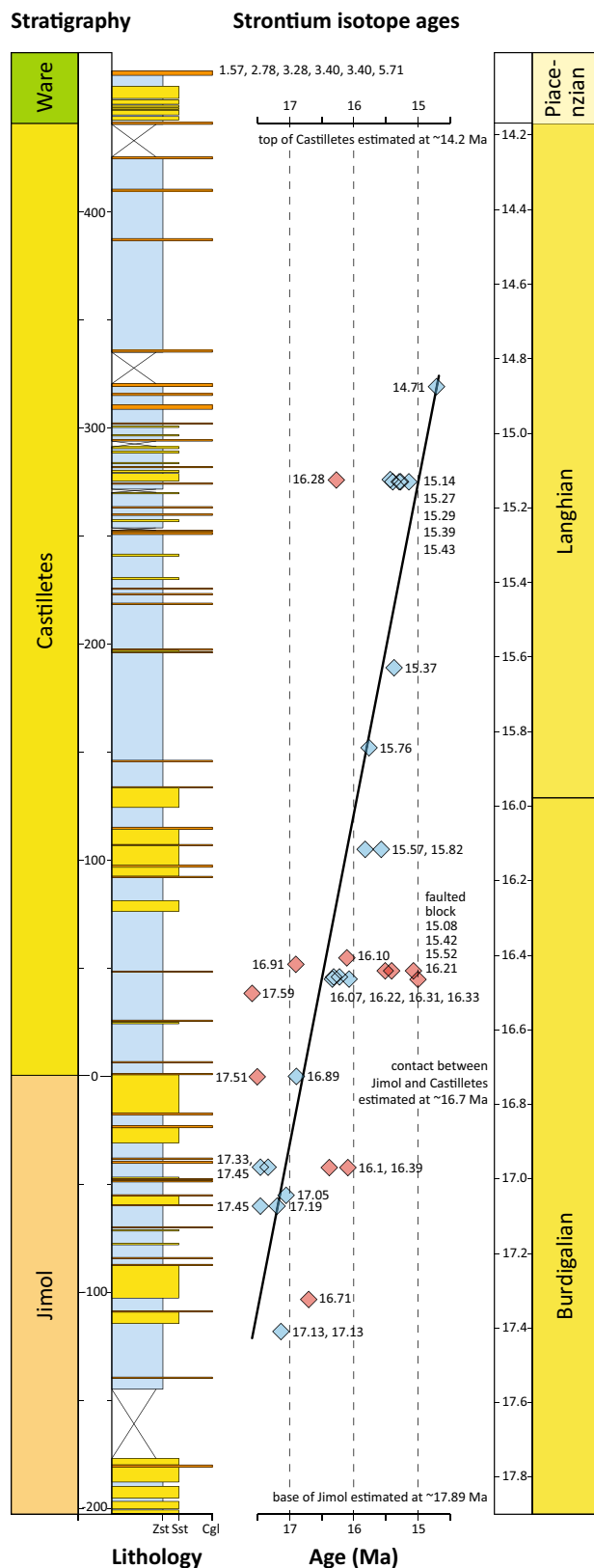
40–50 m above the Jimol–Castilletes contact, have a mean value of 15.56 ($n = 4$, range of 15.07–16.21) and quite possibly remain out of sequence.

Chronological position of vertebrate-bearing horizons

The Jimol–Castilletes succession clearly encompasses a continuous record through the Upper Burdigalian and Lower Langhian stages of the early and Middle Miocene (Fig. 17). Not only does the Cocinetas Basin therefore preserve an exceptional record of marine invertebrates for this interval, but it also contains a number of important marine, aquatic, and continental vertebrate assemblages. This is significant in that this succession can be very precisely and independently correlated with the biochronology that is applied through South America, known as South American Land Mammal Ages (SALMAs) (Flynn and Swisher III 1995). It should be noted, however, that knowledge of terrestrial biodiversity and faunal turnover in South America is largely based on better sampled continental assemblages from temperate regions where the SALMA biochronology has largely been established. The ^{87}Sr/^{86}Sr isotope dating of the Jimol Formation indicates that it is equivalent to the Santacrucian, while the Castilletes Formation overlaps with the highest Santacrucian, a gap in the existing SALMA biochronology, and the Colloncuran Mammal Age (Fig. 17). The precise ages of key vertebrate-bearing assemblages in the Jimol and Castilletes formations, as established from direct ^{87}Sr/^{86}Sr isotope ages or derived from the age model, are provided in Table 10.

The molluscan zones of Wesselingh et al. (2006b) offer further potential for developing not only a basin-scale biostratigraphy, but also region-wide correlations. As many as 12 mollusc zones have been introduced for the Early through Middle Miocene of Amazonia, based on a combination of occurrence data from different taxa and lineages. Their resolution is fine, with the upper 11 zones covering a time interval of approximately 7 million years. It is yet to be determined whether freshwater species from the Jimol and Castilletes formations can be related to this biostratigraphic framework (Fig. 16). Nevertheless, preliminary comparisons with Wesselingh (2006) suggest that the Castilletes Formation gastropod *Aylacostoma* sp. may be most closely related with *Aylacostoma browni* (ETHERIDGE, 1879), which is found in MZ6–MZ9, and specimens of *Charadreon* are superficially similar to *Charadreon eucosmius* (PILSBRY & OLSSON, 1935), which is limited to MZ1–MZ7. On the basis of ^{87}Sr^{86}Sr isotope data, the Jimol–Castilletes succession is equivalent to the lowest six molluscan zones of Wesselingh (2006).

Lastly, it should be noted that the Jimol and Castilletes formations span the entirety of the Middle Miocene climatic optimum (warming event) and the Middle Miocene disruption (cooling event) (Zachos et al. 2001). Establishing a correlation between fossil assemblages in the Jimol–Castilletes succession and these critical events will permit a
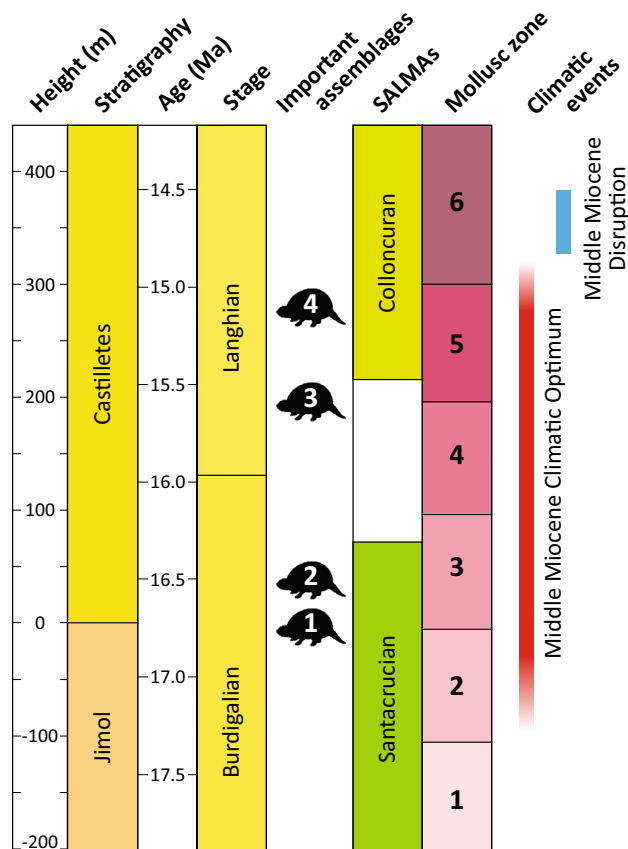

Fig. 17 Chronological position of Jimol and Castilletes vertebrate and invertebrate assemblages relative to South American Land Mammal Ages (SALMAs), molluscan zones of Wesselingh et al. (2006b), and major oceanographic and paleoclimatic events (Zachos et al. 2001). Key to important assemblages: *1* Patajau Norte (lower), *2* Patajau (middle), *3* Yotojoro, *4* Macaraipao; see Table 10 and Moreno et al. (2015) for additional details

better understanding of how significant global paleoenvironmental changes were manifested in tropical ecosystems of South America.

Conclusions

The Uitpa, Jimol, Castilletes, and Ware formations preserve a rich marine invertebrate fossil record that documents paleoenvironmental change through the Neogene. This succession shows a broad pattern of changing depositional environments associated with the tectonic history of Cocinetas Basin. In the context of a high-resolution stratigraphy, more rapid paleoenvironmental fluctuations may be observed, with depositional environments ranging between non-marine or estuarine and offshore shelf habitats within a few meters of stratigraphy. A major unconformity exists between the Castilletes and Ware formations, indicating an end to basin subsidence during

Table 10 Estimated age of principal vertebrate-bearing assemblages in the Jimol and Castilletes formations

Assemblage	Section	Locality	Height (m)	Extrapolated age (Ma)	Direct ages (Ma)
Paraguachón (lower)	290432	390091	−55	17.0	17.05 (same level)
					17.19, 17.45 (5 m below)
Paraguachón (middle)	290432	390092	−32	16.9	17.33, 17.45 (10 m below)
Patajau Norte (lower)	430103	470058	25	16.6	n/a
Patajau Norte (middle)	430103	470066	46	16.5	16.07, 16.22, 16.31, 16.33 (2 m above)
Kaitamana	430118	290666, 290085, 430053	41–55[a]	n/a	16.10, 16.91 (approx. level)
Paraguachón (upper)	290423	390090, 470065	46–49[a]	n/a	15.08, 15.42, 15.52, 16.21 (same level)
Patajau Norte (upper)	430103	290612	78	16.3	n/a
Yotojoro	430203	490006	128	16.0	n/a
Macaraipao	170514	390093	279	15.1	15.14, 15.27, 15.29, 15.39, 15.43 (3–4 m below)

Extrapolated ages are derived from the calibrated age model (where sections are confidently correlated with composite stratigraphy). Direct ages include ^{87}Sr/^{86}Sr isotope dates from horizons <10 m above or below vertebrate assemblage

[a] Faulted blocks within Cocinetas Basin that are only approximately correlated to the composite stratigraphic column; ages are therefore not extrapolated on the basis of stratigraphic height. Section and locality numbers are detailed in Moreno et al. (2015) and can be searched in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb)

the Middle Miocene before resuming sedimentary accumulation in the Pliocene. Biostratigraphic assessment of molluscan taxa from the Jimol and Castilletes formations indicate that these units are latest Early Miocene through Middle Miocene age, while those of the Ware Formation are approximately Late Pliocene in age. Strontium isotope analysis of macrofossils from the Neogene sequence in Cocinetas Basin show that the oldest group of samples (17.45–17.51 Ma) obtained from the upper part of the Jimol Formation correlate with the Burdigalian stage (latest Early Miocene). A younger group of samples (14.7–15.43 Ma) obtained from the upper part of the Castilletes Formation correlate with the Langhian stage (earliest Middle Miocene). Strontium isotope analysis of calcitic molluscs in the Ware Formation are more variable (5.7–1.6 Ma), but cluster within the Piacenzian stage (Late Pliocene). An age calibration of the Jimol–Castilletes succession has important implications for the dating of major vertebrate paleontological finds in the Castilletes Formation. These data also suggest that the contact between the Jimol and Castilletes formations would occur around 16.7 Ma, within the late Burdigalian. These data provide a high-resolution paleoenvironmental and chronostratigraphic framework for aiding interpretation of how co-occurring terrestrial and aquatic vertebrate assemblages relate to the broader evolutionary and biogeographic history of northern and Central America during the Neogene.

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