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PALEOENVIRONMENTAL AND PALEOBIOGEOGRAPHICAL IMPLICATIONS OF A MIDDLE PLEISTOCENE MOLLUSC ASSEMBLAGE FROM THE MARINE TERRACES OF BAÍA DAS PIPAS, SOUTHWEST ANGOLA

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ABSTRACT—Quaternary raised marine terraces containing the remains of diverse, shallow water marine invertebrate faunas are widespread across the coast of Angola. These deposits and faunas have not been studied in the same detail as contemporaneous features in northwest and southernmost Africa. We analyzed the fossil assemblages and sedimentology of two closely spaced middle Pleistocene marine terrace deposits in Baía das Pipas, southwest Angola. This revealed 46 gastropod and 29 bivalve species, along with scleractinian corals, encrusting bryozoans, polychaete tubes, barnacles, and echinoids. The fauna is characteristic of intertidal and nearshore rocky substrates and sandy soft-bottom habitats. Sedimentological analysis is consistent with faunal data and indicates an upper shoreface paleoenvironment along a gravel coast. This diverse fauna stands out as a rare example of a marine Pleistocene assemblage from over 6,000 km of the West African coast. The assemblage is dominated by extant tropical West African molluscs, including species from the "Senegalese fauna" that colonized northern Africa and beyond during Pleistocene interstadials. Additionally, as along the modern coast of the Namibe Desert, the influence of the cool-water Benguela Current is apparent in the paleofauna by the occurrence of a few temperate species. The distribution and thermal tolerances of extant species identified in the Pipas fauna indicate that this region experienced similar climatic and oceanographic conditions as that of the present during this interstadial. Seasonal temperature varied between ~20 and 28°C and resulted from upwelling in this tropical setting.

INTRODUCTION

RAISED MARINE terraces are products of tectonic processes and of sea level fluctuations caused by the climatic transitions that drive the waxing and waning of ice-sheets. Because of their sensitivity to temperature and salinity, molluscs found within these coastal remnants are often used to deduce climatic and oceanographic parameters. This is especially true for Pleistocene molluscs, which are typically extant and thus their environmental tolerances can be observed directly, leading to finely resolved reconstructions (e.g., Raffi et al., 1985; Taviani et al., 1991; Noble et al., 1995; Enquist et al., 1995; Aguirre et al., 2005; Bardají et al., 2009; Garilli, 2011), assuming that taxonomic uniformitarianism holds. Perhaps the best examples of molluscs as indicators of past conditions result from work on the thermophilous "Senegalese fauna" (Gignoux, 1913), which today inhabits the West African coast. Dramatic incursions of the Senegalese fauna during Pleistocene interglacials are well documented throughout the Mediterranean and Europe (e.g., Gignoux, 1913; Issel, 1914; Lecointre, 1952; Lecointre et al., 1967; Ruggieri and Buccheri, 1968; Brebion, 1979; Meco and Stearns, 1981; Hearty et al., 1986; Taviani et al., 1991, Bordoni and Valensise, 1999; Callapez and Soares, 2000; Zazo et al., 2003; Ferranti et al., 2006; Nalin et al., 2012), and the thermal tolerances of these species have been used to provide precise temperature estimates for many localities (e.g., Cornu et al., 1993; Ávila et al., 2002; Meco et al., 2002; Bardají et al., 2009; Zazo et al., 2010; Garilli, 2011). While much is known about the Plio-Pleistocene history of the Senegalese fauna outside of West Africa, there has been virtually no study of fossil occurrences from within its current range (Fig. 1).

The lack of an extensive fossil record is especially unfortunate because today the West African coast is home to several marine diversity "hot spots" of fish and invertebrates, including one near the present day Angola-Namibia border (e.g., Le Loeuff and Cosel, 1998). In particular, the modern Angolan mollusc fauna is highly diverse (França 1955a, 1955b, 1960; Gofas et al., 1985; Cosel, 1995, 2006; Rolán and Ryall, 1999). Even more tantalizing from a biogeographic perspective, the Angola-Namibia border region is the southernmost extent of many tropical West African taxa because the warm, southward-flowing Angola Current converges with the cold, northward-flowing Benguela Current to form the Angola-Benguela Front (ABF) (Fig. 1; Nelson, 1992; Shannon and Nelson, 1996; Diester-Haass et al., 2002). The ABF is a strong thermal boundary between the tropical West African province and the temperate South African province (Le Loeuff and Cosel, 1998; Lass et al., 2000; Hardman-Mountford et al., 2003; Spalding et al., 2007). Similar to the areas north of West Africa, this temperate South African province has an extensive Quaternary mollusc fossil record (Fig. 1; e.g., Barnard, 1962; Davies, 1973; Kilburn and Tankard, 1975; Kensley, 1985; Kensley and Pether, 1986; Miller et al., 1995). Thus, the Angola-Namibia border region is of extreme importance for understanding the climatic,

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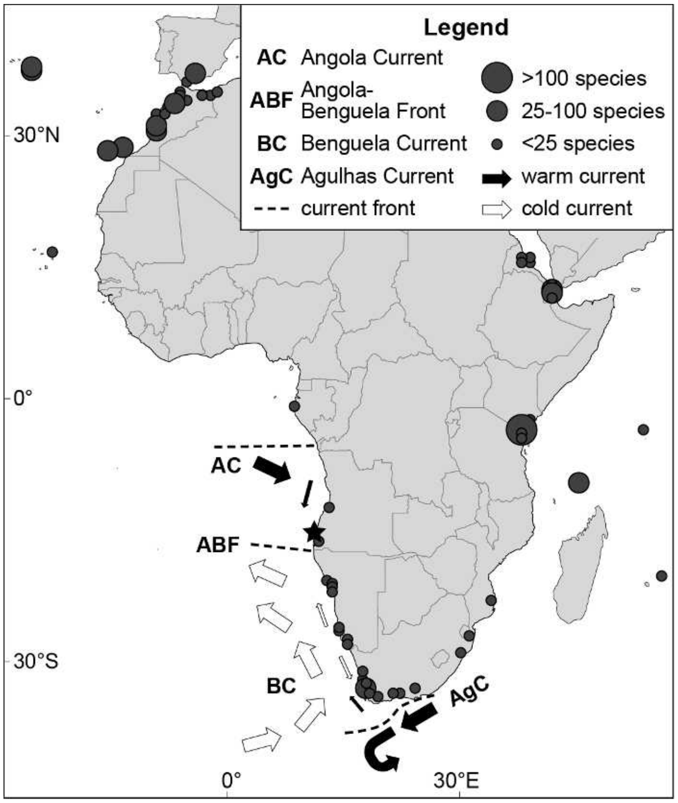

FIGURE *1*—Map of Africa and associated regions, with present day currents indicated for southwestern Africa. Size of arrow indicates current strength. Pleistocene localities with mollusc fossils are plotted as dots, with the size of the dot indicating the number of mollusc species recovered. The studied area of Baía das Pipas, Angola is indicated by the star. Pleistocene occurrence data are derived from: Nardini, 1934, 1937; Abrard, 1942; Lecointre, 1952; Zbyszewski and Ferreira, 1961; Barnard, 1962; Davies, 1973; Kouyoumontzakis and Giresse, 1976; Lecointre et al., 1976; Taylor, 1978; Meco, 1982; Montaggioni, 1982; Bonatti et al., 1983; Giresse et al., 1984; Kensley, 1985; Crame, 1986; Kensley and Penther, 1986; Montaggioni and Hoang, 1988; Callapez and Soares, 2000; Tawadros, 2001; Ávila et al., 2002, 2009; El-Sorogy, 2002, 2008; Bruggemann et al., 2004; Vera-Peláez et al., 2004; Johnson and Baarli, 2005; Zazo et al., 2007; Accordi, et al., 2010.

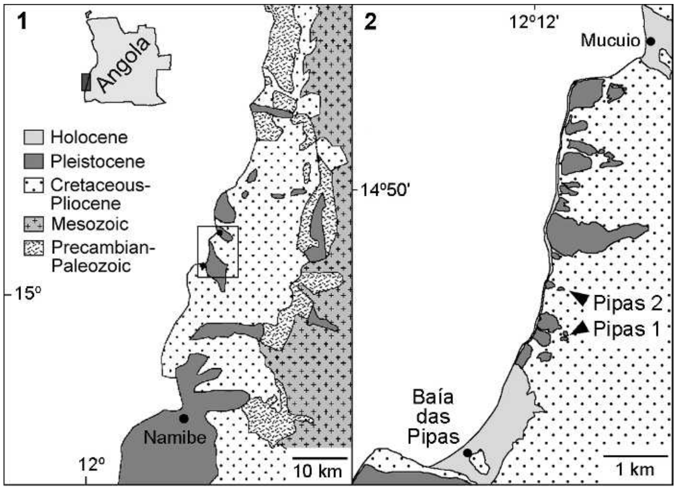

FIGURE *2*—*1*, generalized geological map of the coast of the Namibe province of Angola, modified from Carvalho (1980), indicating the location of the inset map; *2*, inset map showing location of the Pleistocene marine terrace deposits, labeled Pipas 1 and Pipas 2, in the studied area.

oceanographic, and biotic evolution of the East Atlantic Ocean in the Southern Hemisphere.

Here, we present the first thorough documentation of a Pleistocene marine invertebrate fauna from West Africa. Lying along the northernmost Namib Desert coast, the area around Baía das Pipas (Pipas Bay), Angola, is an excellent region in southwestern Africa to study Quaternary terrace deposits (Fig. 2). Some of these raised terraces are highly fossiliferous, but almost none of their molluscan fauna have been identified, especially to genus or species level (see cursory mention in Kouyoumontzakis and Giresse [1976] and Giresse et al. [1984]). The remoteness of this desert region and many years of political instability in Angola explain why these faunas have not been studied in the same detail as the well-known Pleistocene deposits to the north and south. The Pleistocene geological history of the region and particularly its fossil invertebrate faunas were last investigated during Angola's colonial period (Carvalho, 1961), except for a few works primarily concerned with stratigraphy and archeology (Ervedosa, 1980; Giresse et al., 1984; Gutierrez et al., 2001). Additionally, early works were by Portuguese geologists and published in national journals, and thus are not widely known to non-Portuguese speakers (for full references see Carvalho [1961], Ervedosa [1980], and Feio [1981]). These works were more concerned with the morphologic, sedimentologic, and stratigraphic aspects of the raised marine terraces, and only mention the most relevant taxa found in these deposits, if any. Since the 1980s, there have been no field-based studies of the geomorphology or the Quaternary history of southern Angola.

The well-documented present-day mollusc assemblage of Angola is in marked contrast to what is known about its Pleistocene assemblages. This limits the understanding of biogeographic patterns of molluscs, as well as of past sea level and environmental fluctuations of the region. The following description and biogeographic analysis of the molluscan fauna of Baía das Pipas is a significant step towards an improved West African inventory of Pleistocene species. We use the present-day distribution and thermal tolerances of the molluscs found within the terrace deposits to provide an estimate of the climatic conditions they experienced. In turn, when combined with previous studies, this fauna provides insight into the evolving biogeographic, climatic, and oceanographic conditions of the East Atlantic Ocean during part of the Quaternary.

OCEANOGRAPHIC AND CLIMATIC PATTERNS ALONG THE WEST AFRICAN COAST

The tropical West African biogeographic province ranges from Cape Blanc, Mauritania to Cape Frio, Namibia (Le Loeuff and Cosel, 1998; Spalding et al., 2007 and references therein). This marine province is subdivided into regions that are delineated by oceanic currents and the resulting hydroclimatic boundaries. The study area is within the present-day Southern Alternance Region (SAR) of Le Loeuff and Cosel (1998) that ranges from Cape Lopez, Gabon to Cape Frio, Namibia (see also Spalding et al., 2007). The ABF forms the southern boundary of the West African province and the SAR, and is a permanent oceanographic front that seasonally migrates between S 14° and S 16° (Meeuwis and Lutjeharms, 1990; Hardman-Mountford et al., 2003). Mean monthly sea surface temperatures for the SAR range from 20° to 27–28°C (Le Loeuff and Cosel, 1998; Boyer et al., 2006). An important feature of the SAR is the upwelling of cool water, which creates a larger range of temperature through a year (~8 °C) than is typical of tropical regions (Le Loeuff and Cosel, 1998). Thus, taxa that are within the SAR are

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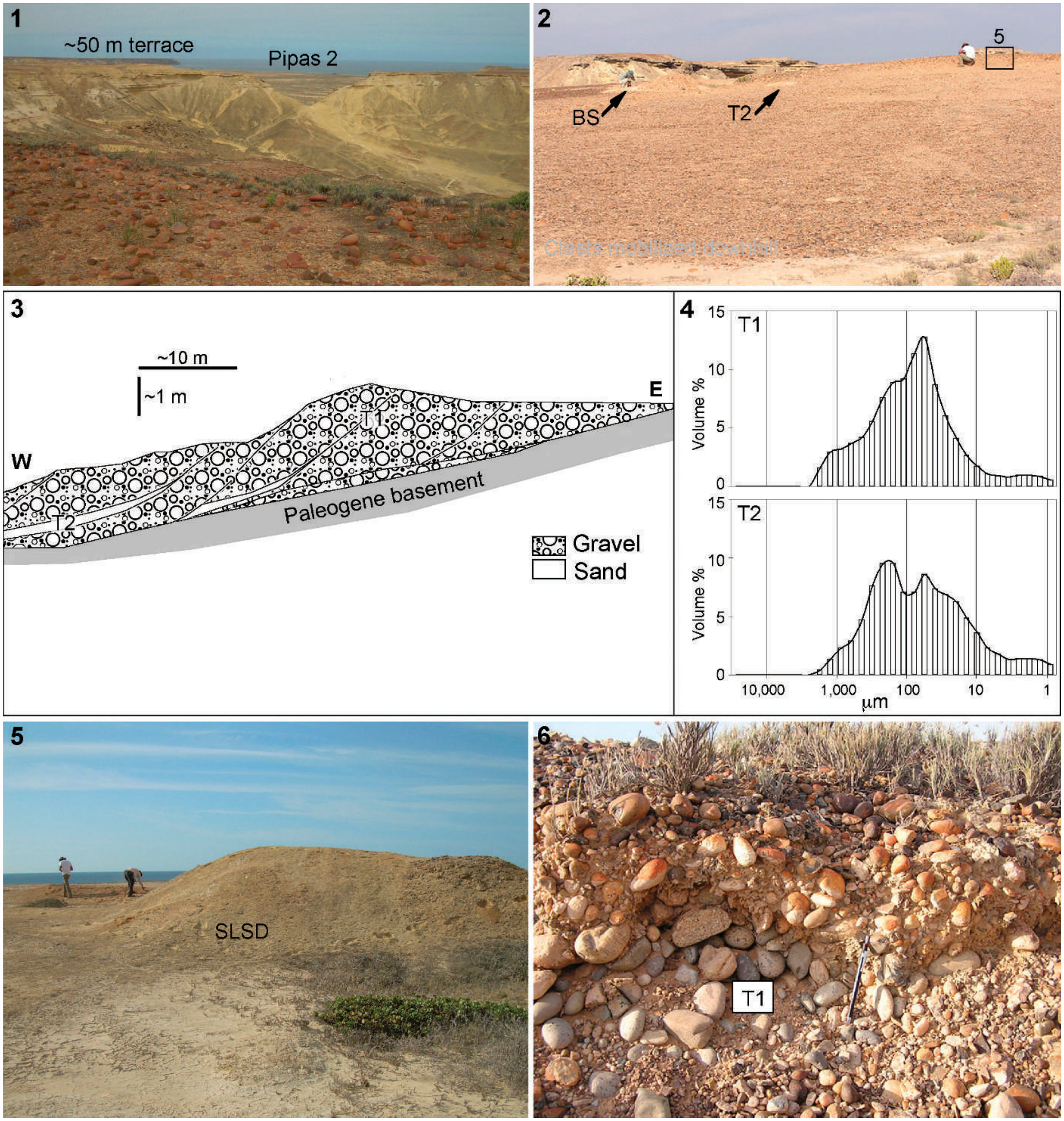

FIGURE *3*—The studied Pleistocene raised beach deposits of Baía das Pipas with sampling locations indicated: T1=grain-size sample; BS=bulk sample; T2: grain-size sample. *1*, panoramic view of Baía das Pipas taken from the highest platform in the area; the location of Pipas 2 terrace is indicated; *2*, landward view of the Pipas 1 terrace, with a gravel pavement of clasts mobilized downhill from the raised beach and the in situ deposit at the top of the hill; *3*, diagrammatic cross section of the Pipas 1 deposit, note the thin sand lenses, including T1 and T2, intercalated within westward-dipping gravel beds; *4*, grain-size distribution curves of samples T1 and T2; *5*, seaward view of the Pipas 1 deposit; a sandy layer with a concentration of shell debris (SLSD) occurs at the bottom of the deposit; *6*, close-up of a Pipas 1 fossiliferous conglomeratic layer with imbricated clasts of metamorphic and igneous basement rocks.

predominately thermophilous, but not solely so; temperate taxa also are present (Le Loeuff and Cosel, 1998).

BIOGEOGRAPHIC PATTERNS AND EVOLUTION ALONG THE WEST AFRICAN COAST

Today, the south Angolan coast hosts a unique assemblage of molluscs: amphi-Atlantic and endemic species, geographically wide spread tropical taxa, and a few temperate-cold water "guests" from Namibia and South Africa are all found within these waters (Kilburn and Rippey, 1982; Le Loeuff and Cosel, 1998; Rolán and Ryall, 1999). Nevertheless, as is expected from its low latitude, molluscs with tropical affinities are dominant. Similar to Cape Verde and the equatorial area from Senegal to Gabon (Burnay and Monteiro, 1977; Bouchet, 1982; Bernard,

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1984; Cosel, 1995; Ardovini and Cossignani, 2004) many of these molluscs are endemic. This pattern of endemism, and in general the composition of marine mollusc faunas from Africa, is thought to result from a complex heritage of responses to paleoclimatic changes since the Miocene (e.g., Bouchet, 1981; Raffi et al., 1985; Vermeij, 1989a, 1989b, 1992, 2012; Harzhauser et al., 2007). The lack of an extensive fossil record from West Africa has meant that these studies have inferred faunal migrations rather than tracked them.

Miocene Namibian and South African coastal waters were warmer than they are today; climatic conditions began to deteriorate during the Pliocene (Tankard and Rogers, 1978; Raymo, 1994; deMenocal, 1995, 2004). The Benguela Current and associated upwelling system was initiated during the Miocene (Shannon and Nelson, 1996; Diester-Haass et al., 2002), further influencing the distribution of taxa, as, of course, did glaciations and interglacial stages. The establishment of the Benguela Current implies that SAR conditions and the ABF also commenced during the Miocene; both fundamentally influence species distributions today. The faunal response to these oceanographic and climatic changes today results in a different faunal province in southern Angola and northernmost Namibia as compared to South Africa, which has many more temperate and cold-water taxa and its own endemics (e.g., Pether, 1994; Le Loeuff and Cosel, 1998; Spalding et al., 2007). Similarly, northern Africa and the Mediterranean Sea today represent a different biogeographic province than tropical West Africa (e.g., Le Loeuff and Cosel, 1998; Spalding et al., 2007; Vermeij, 2012). The lack of Plio-Pleistocene faunal studies from West Africa results in a ~50° latitudinal gap in knowledge (Fig. 1) where the scarcity of taxonomic data biases any attempt to detail biogeographic boundaries.

GEOLOGY AND GEOMORPHOLOGY

The southwest coast of Angola is a long and remote region of rough cliffs and isolated beaches in the northernmost portion of the Namib Desert. The present climate of the Namib Desert is hyperarid to arid; the town of Namibe (formerly Moçamedes) is near to the studied deposits and has an annual precipitation of 42 mm and a mean annual temperature of 20°C (Peel et al., 2007). Similar climatic conditions prevailed throughout much of the Pleistocene in the Namib Desert, with changes in precipitation and aridity occurring during glacial-interglacial cycles (see summaries in Lancaster [2002], deMenocal [2004], and Chase and Meadows [2007]).

The study area of Baía das Pipas is located 25 km north of the town of Namibe, in the Namibe province of Angola (Fig. 2.1). This area contains a staircase of terraces, with altimetric values ranging from present day sea level to at least 150 m high. Some of these platforms are associated with marine terrace deposits, while others constitute erosion surfaces in more resistant basements rocks (Carvalho, 1961). Quaternary raised marine terraces and wave-cut platforms are widespread across this region and to the north, along the western edges of the Benguela and Kwanza basins, as well as to the south, along the coast of Namibia and South Africa (Soares, 1958; Davies, 1959, 1970, 1971, 1972, 1973; Carvalho, 1960, 1961, 1966; Barnard, 1962; Carrington and Kensley, 1969; Giresse et al., 1984; Spaggiari et al., 2006).

Terrace deposits are found on Cretaceous and Paleogene sandstones, limestones, and conglomerates that filled the Namibe Basin, one of the marginal Meso-Cenozoic basins of Angola. These pre-Quaternary units are slightly deformed by open folds and a few normal faults, and their dip is usually lower than 20° (Carvalho, 1961). The southern coastal basins and nearby cratonic interior were uplifted during the early Cenozoic, after the extensional episodes that opened the South Atlantic (Jackson et al., 2005; Guiraud et al., 2010). Several phases of uplift have been proposed for coastal Angola during the Cenozoic (Guiraud et al., 2010).

As a general rule, travel from the interior to the Atlantic Ocean is rather difficult because of coastal cliffs (approximately 40 m high), which are only passable when intercepted by stream valleys. The drainage net includes numerous short streams that are usually dry and just a few kilometers long, with narrow valleys and steep walls that are locally referred to as "damba." The north-south shoreline of the Namibe province contains several small embayments (named Namibe, Pipas, Mucuio, Baba, Mariquita, and Piambo) where these drainages intercept the coast and the cliffs give way to sandy beaches. These embayments show a similar pattern of slightly dipping successions of Upper Cretaceous or Paleogene strata overlain by Pleistocene marine terraces. Some of these deposits are fossiliferous, inviting further research.

MATERIALS AND METHODS

The geology of the Pipas area was investigated in February 2010. Two correlative fossiliferous terraces ("Pipas 1" and "Pipas 2"), about 1 km from each other (Fig. 2.2), were mapped in detail. The geographic coordinates of Pipas 1 are: S 14°56′15.11″, E 12°12′13.86″; Pipas 2 are: S 14°55′51.26″, E 12°12′11.15″. The stratigraphy was documented, and two sediment samples were collected for grain-size analysis from sand lenses within Pipas 1 (Fig. 3). Grain-size distribution was determined by laser diffraction using a Coulter LS 230 instrument. The diffraction data was processed using the Fraunhofer model employed by the Coulter software (LS v3.29). Histogram results were adapted to the ϕ scale (Wentworth, 1922; Krumbein, 1934).

We attempted to collect voucher specimens of all molluscan taxa present within the terraces. Additionally, a 1.0 m long by 0.5 m thick bulk sample was collected from a fossiliferous sandy level near the base of the Pipas 1 terrace (Fig. 3.5). The bulk sample was sieved using a 1 mm mesh screen. All molluscs that remained on the screen were picked and identified to the finest classification possible, which was typically the species level (Appendix 1; Figs. 4–10). Specimens were counted if they retained either an apex (for gastropods) or an umbo (for bivalves). For bivalves, the larger number of disarticulated left or right valves is reported in Table 1; there were no articulated specimens. Modern molluscs along the Namibe province seashore, including the local beach drift at Baía das Pipas, were examined for comparison with this Pleistocene fauna. All mollusc specimens from bulk sampling and surveying are reposited at the Museu Arqueológico de Benguela, Angola (MAB, Angola).

Ecological classification.—Because the mollusc species and/or genera recorded from the Baía das Pipas Pleistocene deposits are extant, we can employ direct observations of these taxa, from the Namibe region and elsewhere, to describe their life habitat and ecology. Taxa are classified with respect to four variables: substrate, tiering, mobility, and feeding mechanism. Substrate reflects the environmental habitat that a species is found in, such as sand or a hard (rocky) substrate. Tiering describes where the animal lives relative to the sediment/water interface. Mobility categorizes the ability of an organism to move under its own power and whether it is attached to a substrate or is free living. Feeding mechanism refers to the way food is acquired by an organism. Descriptions of extant species and genera in the published literature, and the database of Neogene marine biota of tropical America (NMITA; http://eusmilia.geology.uiowa.edu/

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nmita.htm) were the primary sources for categorizing taxa; the Paleobiology Database (http://paleodb.org) and personal observations by PMC were additional resources (Appendix 2). Categorization is based on species and genera; the few cases where higher taxonomic groups were used are noted in the "Data source" column of Appendix 2.

Estimating paleotemperature.—The thermal tolerances of extant species identified in the Pipas paleofauna were used to estimate middle Pleistocene seasonal temperatures. Geographic data for these species in the eastern Atlantic Ocean and Mediterranean Sea were collated from an extensive compilation of references, museum and private collections, and online database resources (sources are provided in online Supplemental Data file 1). The latitude and longitude of these faunal records were determined from either existing ancillary data (e.g., museum catalogs), or by searching place-names in georeferencing software. Only species were used; out of the 75 taxa identified in the Pipas paleofauna, 14 could only be identified to the genus level and six are designated as "cf." or "aff.," and hence were not used in determining paleotemperature.

Temperature and salinity data corresponding to the geographic coordinates in the biogeographic dataset were downloaded from the World Ocean Database 2005 (http://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html; Boyer et al., 2006). This database provides physical and chemical measurements taken at the sea surface (0 m depth) and commonly at deeper depths as well. For a given set of coordinates, the day, month, and year are usually reported, and there are typically many measurements available from different months and years, permitting the delineation of seasonal fluctuations. Temperature values from 0 to up to 50 m depth were averaged together for individual geographic coordinates, reflecting that the depth of collection in the biogeographic dataset is not always precisely known, but is restricted to shallow waters. Values from a small area of less than 1° latitude were used to determine the seasonal variability of that small area. The resulting temperature estimates are shown in Figure 11; the temperature data are provided in online Supplemental Data file 2.

Age of the studied deposits.—Namibe province Quaternary terraces that occupy platforms above 20 m above sea level (asl) have been attributed to the "Tyrrhenian" faunal stage (Feio, 1946; Carvalho, 1960, 1961). Since its designation by Gignoux (1913) and Issel (1914), the Tyrrhenian has been widely used to name the Pleistocene sedimentary strata with thermophilous taxa from the "Senegalese fauna" that preceded the Holocene in the Mediterranean. Following current Quaternary stratigraphy, the Tyrrhenian may be regarded as equivalent to the MIS 5e highstand or to lie between the MIS 2 and MIS 5 (Cita Sironi et al., 2005). The latter usage implies that the Tyrrhenian includes cold stages, whereas mid-twentieth century geologists considered the Tyrrhenian a warm period, implying a probable MIS 5e usage for our deposits.

We attempted the determination of an absolute age through the analysis of $^{87}Sr/^{86}Sr$ isotope ratios on carbonate sampled from bivalve and gastropod shells. However, specimens yielded ratios that indicated diagenetic overprinting from the granitic catchment geology (D. Jones, personal commun.). Unfortunately, corals were only observed in the field, not collected, preventing U-series analysis at the present.

Work on nearby Namibe province terraces provides constraints on the age of the Pipas terraces. Using U-series dating on mollusc shells, Giresse et al. (1984) found that Namibe terraces from 8 to 20 m asl were between 133,000±10,000 and 174,000±80,000 yr old, and a terrace at 40 m asl was >170,000 to 300,000 yr old. Although U-series dating of mollusc shells is not ideal because they are susceptible to post-depositional U uptake (Kaufman et al., 1971, 1996), these results indicate that the intervening 25 m asl Pipas terraces are likely correlative with MIS 7 (191–244,000 yr ago) or MIS 5e (125,000 yr ago; MIS ages from Lisiecki and Raymo, 2005). These ages are consistent with estimates derived from uplift rates for West Africa (western Morocco through Angola) by Pedoja et al. (2011). Assuming an uplift rate of 0.1 to 0.2 mm/year (Pedoja et al., 2011), the age of the 25 m asl Pipas terraces falls between ~125,000 (MIS 5e) and ~250,000 yr old, which is older than MIS 7. Middle, or, possibly, middle/late, Pleistocene is the most plausible age from the available evidence.

RESULTS AND DISCUSSION

Terrace morphology and sedimentology.—The studied deposits are small outcrops about 500–600 m from the coastline (Fig. 2.2). Both reach 26 m above sea level (asl), with a basal surface that varies between 22 and 24 m asl. The underlying substrate consists of Paleogene marls and sandstones (Carvalho, 1961). The terraces are very dissected and it is not possible to follow a flat upper surface. Several platforms of limited lateral continuity occur between 5 and 20 m asl, sometimes covered by non-fossiliferous terrace deposits. Platforms also occur at ~40 and 80 m asl, and are usually covered by gravel pavements. All platforms dip gently to the sea.

The studied terrace deposits are composed of gravel beds with occasional sand lenses (Fig. 3). Although it is difficult to generalize bed thickness because of limited lateral exposure and lenticular geometry, the gravel beds are about 0.7 m thick, while sand lenses never exceeded 0.1 m in thickness. In Pipas 1, the sand lenses appear to dip seaward and wedge out landward. In both deposits the gravel beds are clast-supported and heterolithic, with a diverse composition of quartzite, quartz, granite, porphyritic igneous rocks, limestone, sandstone and other lithic fragments. Possible source rocks for these clasts are nearby basement units (Carvalho, 1981) and local sedimentary Namibe Basin infill. Many limestone clasts are densely perforated by burrows. Clasts include a mixture of coarse particles that can reach up to 10 cm and pebbles of 1–2 cm, all of which are usually

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FIGURE 4—*1a–b*, *Barbatia* sp.; *2a–b, 3a–b*, *Senilia senilis* (Linnaeus, 1758); *4a–b*, *Acar* cf. *plicata* (Dillwyn, 1817); *5a–b*, *Barbatia complanata* (Bruguière, 1789); *6*, *Arcopsis afra* (Gmelin, 1791); *7a–b*, *Noetiella congoensis* Thiele and Jaeckel, 1931; *8a–b*, *Ostrea stentina* (Payraudeau, 1826); *9a–b*, *Glycymeris concentrica* (Dunker, 1853); *10a–b*, *Anomia* sp.; *11, 12*, *Loripes* sp.; *13a–b*, *Parahyotissa* cf. *rosea* (Gmelin, 1791). Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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FIGURE 5—*1a–b*, *Cardita senegalensis* (Reeve, 1843); *2a–b*, *Hinnites corallinus* Sowerby, 1827; *3a–b*, *Striostrea denticulata* Born, 1778; *4a–b*, *Ungulina cuneata* (Spengler, 1798); *5*, *Pseudochama gryphina* (Lamarck, 1819); *6a–b*, *7a–b*, *Chama crenulata* Lamarck, 1819; *8–10*, *Cardiocardita lacunosa* Reeve, 1843; *11a–b*, *Dosinia lupinus afra* (Gmelin, 1791); *12a–b*, *13a–b*, *Ctena eburnea* (Gmelin, 1791); *14a–b*, *Cardita senegalensis* (Reeve, 1843); *15a–b*, *Cardium* cf. *indicum* Lamarck, 1819. Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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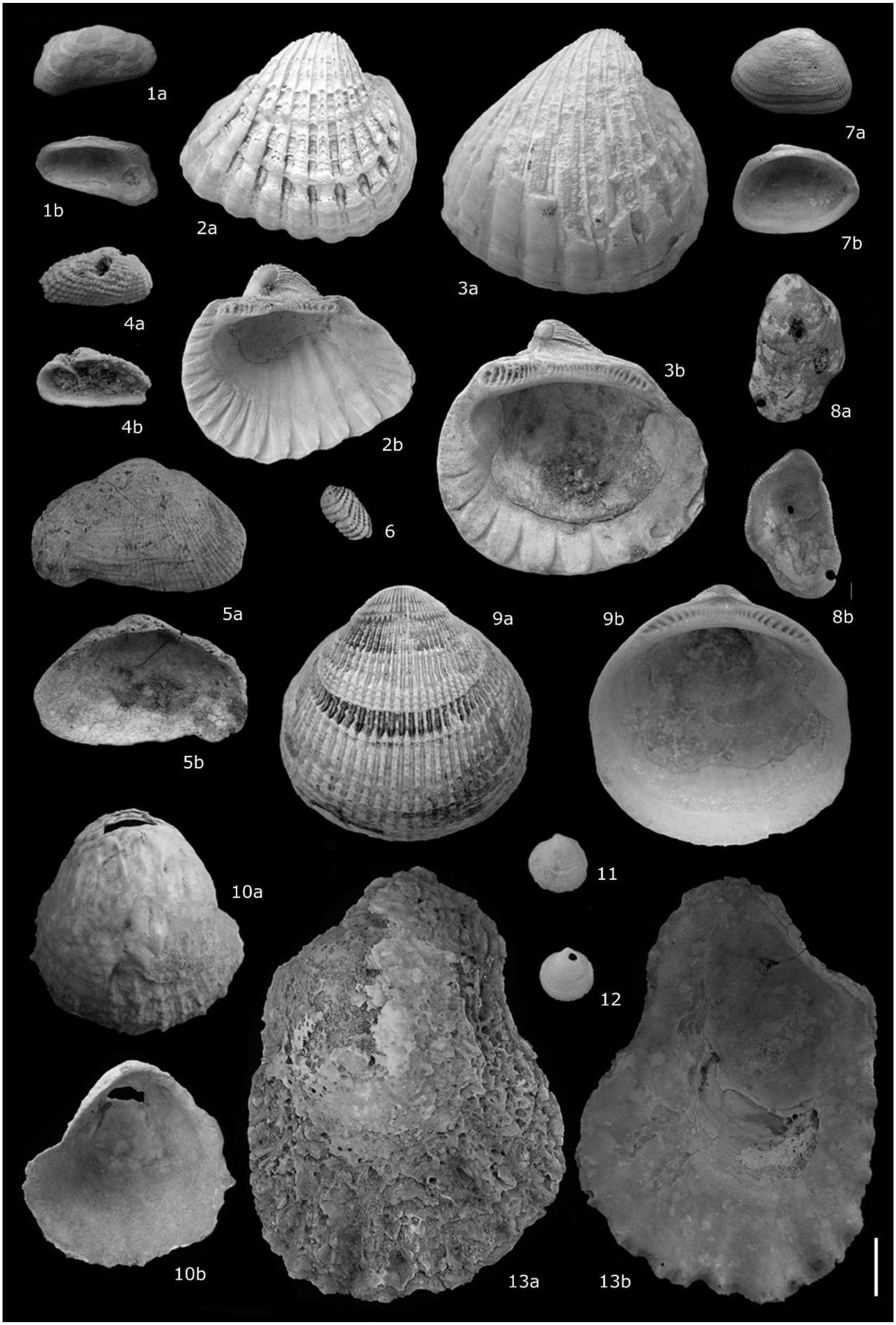

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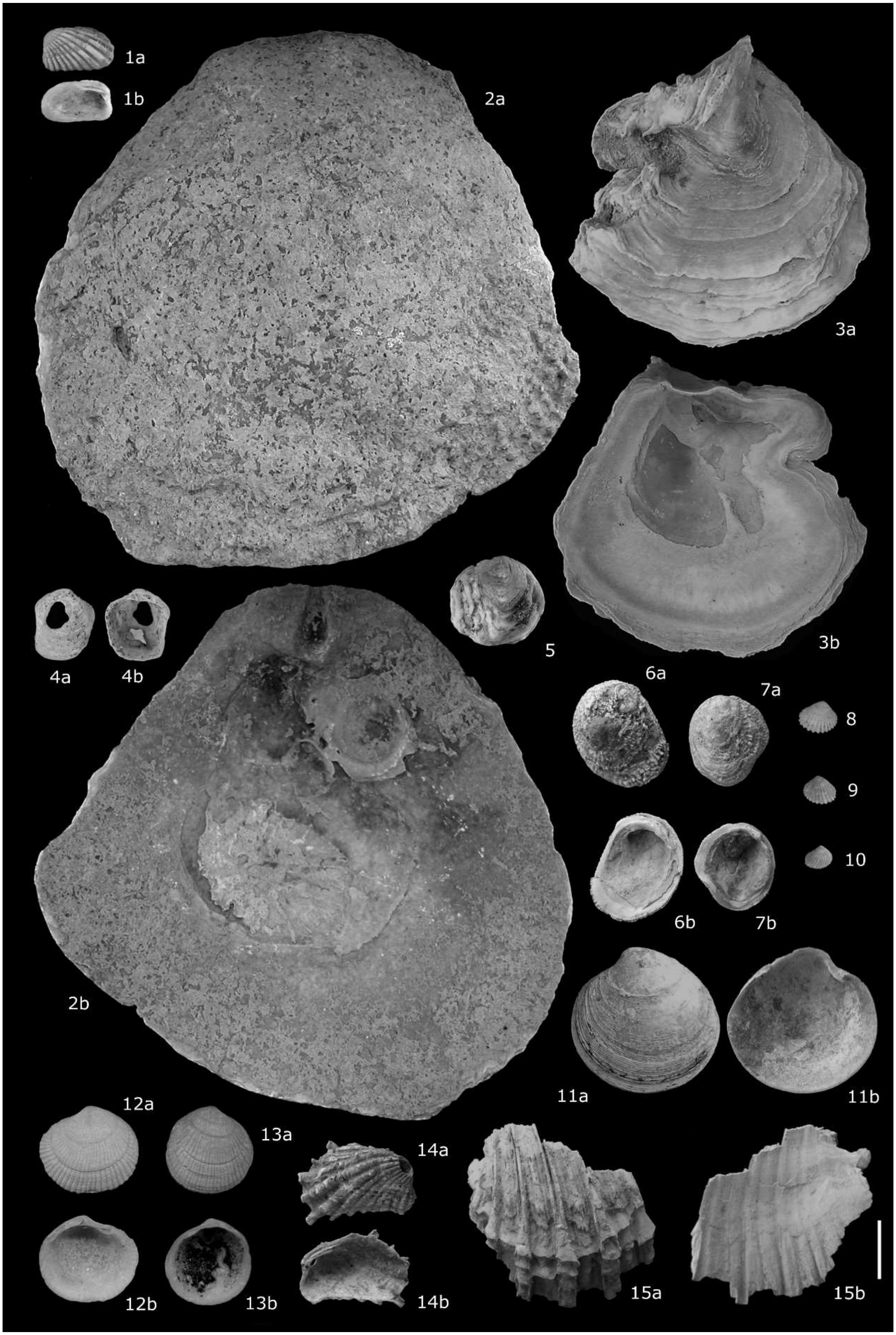

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well- to moderately-rounded. In places inverse grading is apparent. Clast imbrication is highly variable; clasts with seaward, landward, high-angle, and sub-horizontal dips all were found. Imbrication in the upper part of the deposits is more consistent, with clasts usually dipping seaward. The gravel beds contain a moderately sorted sand-silt matrix with a distinct modal size-class of 31–45 μm (Fig. 3.4). Secondary size populations of clay (~1–2 μm) and very fine sand (63–125 μm) are apparent in the grain-size distribution curve. The sand lenses have a polymodal size-distribution, with populations of fine sand (modal size at 90–180 μm mode), coarse silt (modal size at 31–45 μm), and clay (modal size at 1–2 μm) (Fig. 3.4).

The lithology and sedimentary structures of these deposits are compatible with an upper shoreface gravel beach (Massari and Parea, 1988; Hart and Plint, 1989). The inverse grading and seaward imbrication observed in the upper portion of the gravel beds, and the presence of intercalated sand lenses at the base of the deposits, are all common features of gravel beach facies from coastal gullies and interfluves (Felton et al., 2006). The sand lenses are interpreted to result from the settling of particles during fair-weather conditions.

There are multiple lines of evidence for the mixing of sediments from different upper shoreline locations: 1) variable gravel clast sizes of the heterometric layers; 2) multiple imbrication orientations; and 3) the presence of a sand matrix within the gravel beds that is similar to the intervening sand lenses. This interpretation is also supported by the taxonomic and taphonomic data discussed below. Mixing likely occurred from the action of storm events, as observed in modern coastal environments (e.g., Massari and Parea, 1988).

Taxonomy.—Most of the macroinvertebrate fossils collected from the Baía das Pipas terraces are small to moderate-sized (5 to 50 mm) bivalve and gastropod shells (Figs. 4–10). Some large and robust specimens of pectinid, spondylid, ostreid and conid taxa also occur, sometimes reaching more than 200 mm (e.g., *Spondylus senegalensis* in Fig. 7.2). Scleractinian corals, encrusting bryozoans, polychaete tubes, disarticulated cirriped plates, and abundant echinoid radiola were also observed; all commonly preserved invertebrate taxa found in coastal environments are represented in these deposits. We focus on the molluscs because they are by far the most diverse bioclastic component in these assemblages. A taxonomic checklist of the identified mollusc taxa and their systematic hierarchy is provided in Appendix 1.

Monographs and checklists on the recent and Pleistocene faunas of Macaronesia, Western Europe, the Mediterranean Sea, West Africa, and Namibia and South Africa were used for identification and nomenclature. Comparison with Recent molluscs was undertaken primarily using the works of Tebble (1976), Rolán (1984), and Rolán et al. (1990) for Western Europe; Poppe and Goto (1991, 1993), Piani (1980), Aartsen et al. (1984), and Sabelli et al. (1990) for the Mediterranean and northwestern Africa; Rodríguez and Sánchez (1997) and Hernandéz et al. (2011) for Macaronesia; Nicklès (1950), Knudsen (1956), Bouchet (1982), Bernard (1984), Cosel (1995), Ardovini and Cossignani (2004), and Monteiro et al. (2004) for West Africa; Burnay and Monteiro (1977) and Guerreiro and Reiner (2000) for Cape Verde; Rosewater (1975) for Ascension Island; Gofas et al. (1985), Rolán and Ryall (1999), and Rolán and Röckel (2000, 2001) for Angola; and Kensley (1973), Kilburn and Rippey (1982), and Steyn and Lussi (1998) for the Namibian and South African coasts.

For Pleistocene faunas, we referred to: Lecointre (1952), Lecointre et al. (1967), and Brebion (1979) for Northwest Africa; Callapez and Soares (2000) and Ávila et al. (2002) for Macaronesia; Pellerin et al. (1987) for the Mediterranean; Callapez (2000) and Soares et al. (2007) for the Portugal and Western Europe; and Kilburn and Tankard (1975), Kensley (1972, 1985), and Kensley and Pether (1986) for southwest Africa. Taxonomic assignments were updated to be consistent with the World Register of Marine Species (Appeltans et al., 2012).

Taphonomy.—Most of the studied specimens display biostratonomic evidence that suggests condensation and time-averaging in a moderately energetic nearshore environment (Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991), such as disarticulation, fragmentation, encrustation, and bioerosion. Residence time in the taphonomically active zone prior to final burial was long enough for shell damage and destruction to occur, as well as colonization by a variety of bioeroders and epizoans. Shell surfaces reveal varying degrees of abrasion intensity, and some gastropod shells are reduced to the columellar pillar.

Many shells from epifaunal taxa, especially large shells, exhibit dense clionid-like borings (*Entobia*) on their surfaces (e.g., Figs. 4.13, 9.4, 9.5, 10.1). Within the basal conglomerate of the Pipas 1 deposit, pavements of large and heavy shells contain borings and encrustations by epizoans, cryptic taxa (e.g., *Arcopsis, Barbatia*), and cemented and byssate bivalves (e.g., *Chama, Pseudochama*, and *Ostrea*). These organisms occur on both exterior and interior shell surfaces, suggesting that these bioclasts were exposed for prolonged periods in a relatively high-energy, taphonomically active environment (Kidwell, 1991). On the other hand, shells from infaunal taxa known to inhabit soft sands (Table 1), like the tellinids and venerids, do not display borings or encrusters, suggesting that they entered the Pipas deposits soon after disarticulation, without significant time spent in the taphonomically active zone after death.

Paleoecology.—Abundance estimates from the bulk sample indicate a predominance of taxa known to inhabit rocky shorelines and a secondary population of taxa from sandy habitats. The three most abundant species are *Fissurella nubecula* (30%), *Siphonaria capensis* (13%), and *Medusafissurella* aff.

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FIGURE 6—*1a–b*, *2a–b*, *Dosinia lupinus afra* (Gmelin, 1791); *3a–b*, *4a–b*, *Dosinia isocardia* (Dunker, 1845); *5*, *Spondylus senegalensis* (Schreibers, 1793); *6a–b*, *Mactra glabrata* Linnaeus, 1767; *7a–b*, *Lutraria senegalensis* Gray, 1837; *8a–b*, *Tellina madagascariensis* Gmelin, 1791; *9a–b*, *Pholas campechiensis* Gmelin, 1791. Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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FIGURE 7—*1a–b*, *Venus verrucosa* Linnaeus, 1758; *2*, *Spondylus senegalensis* (Schreibers, 1793); *3a–b*, *Patella granularis* Linnaeus, 1758; *4*, *Nerita senegalensis* Gmelin, 1791; *5*, *Diodora* cf. *benguelensis* (Dunker, 1853); *6*, *Diodora menkeana* (Dunker, 1853); *7a–b*, *Circomphalus foliaceolamellosus* (Dillwyn, 1817); *8a–b*, *Bostrycapulus* sp.; *9–12*, *Fissurella nubecula* (Linnaeus, 1758); *13a–b*, *14a–b*, *Turritella bicingulata* (Lamarck, 1822). Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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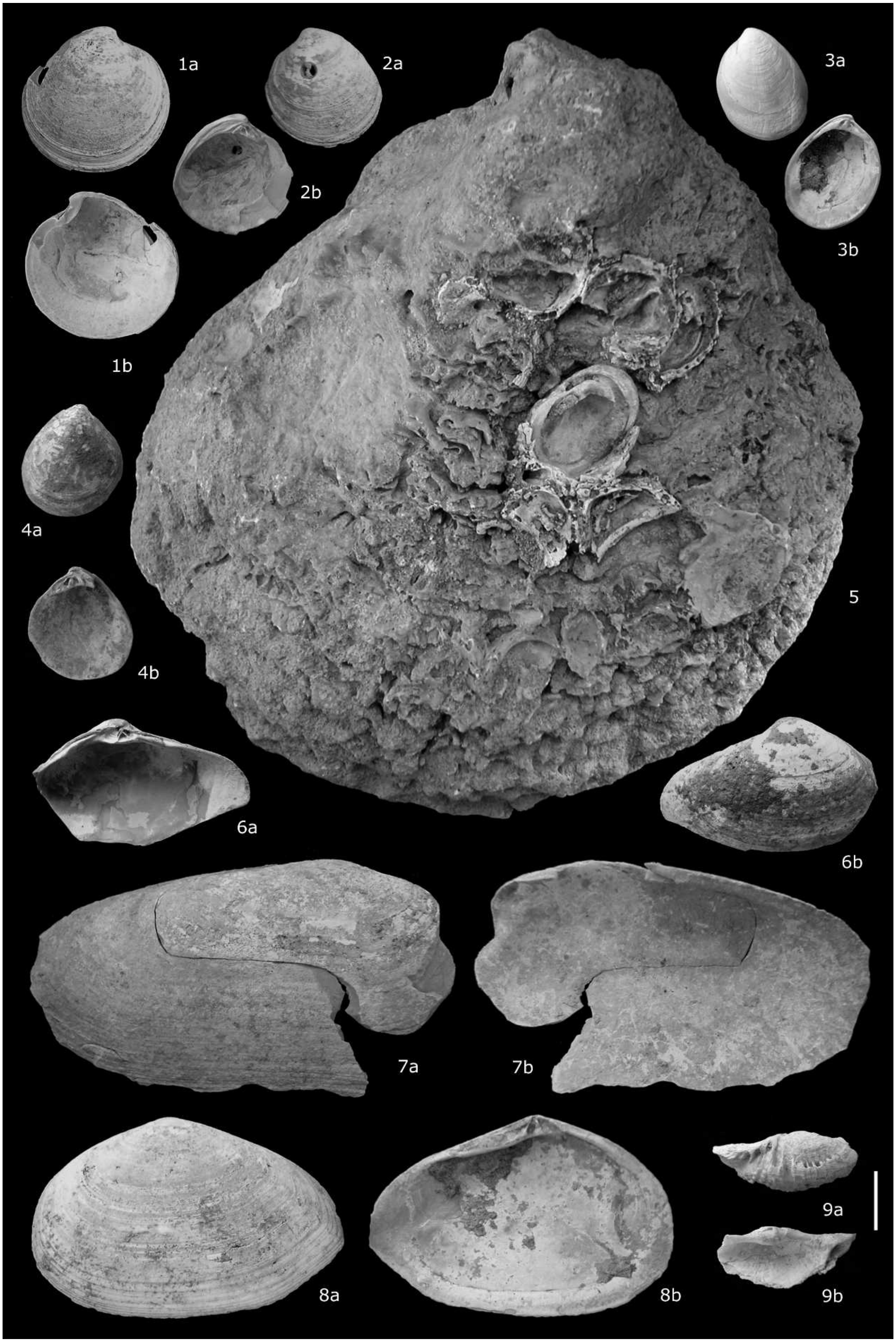

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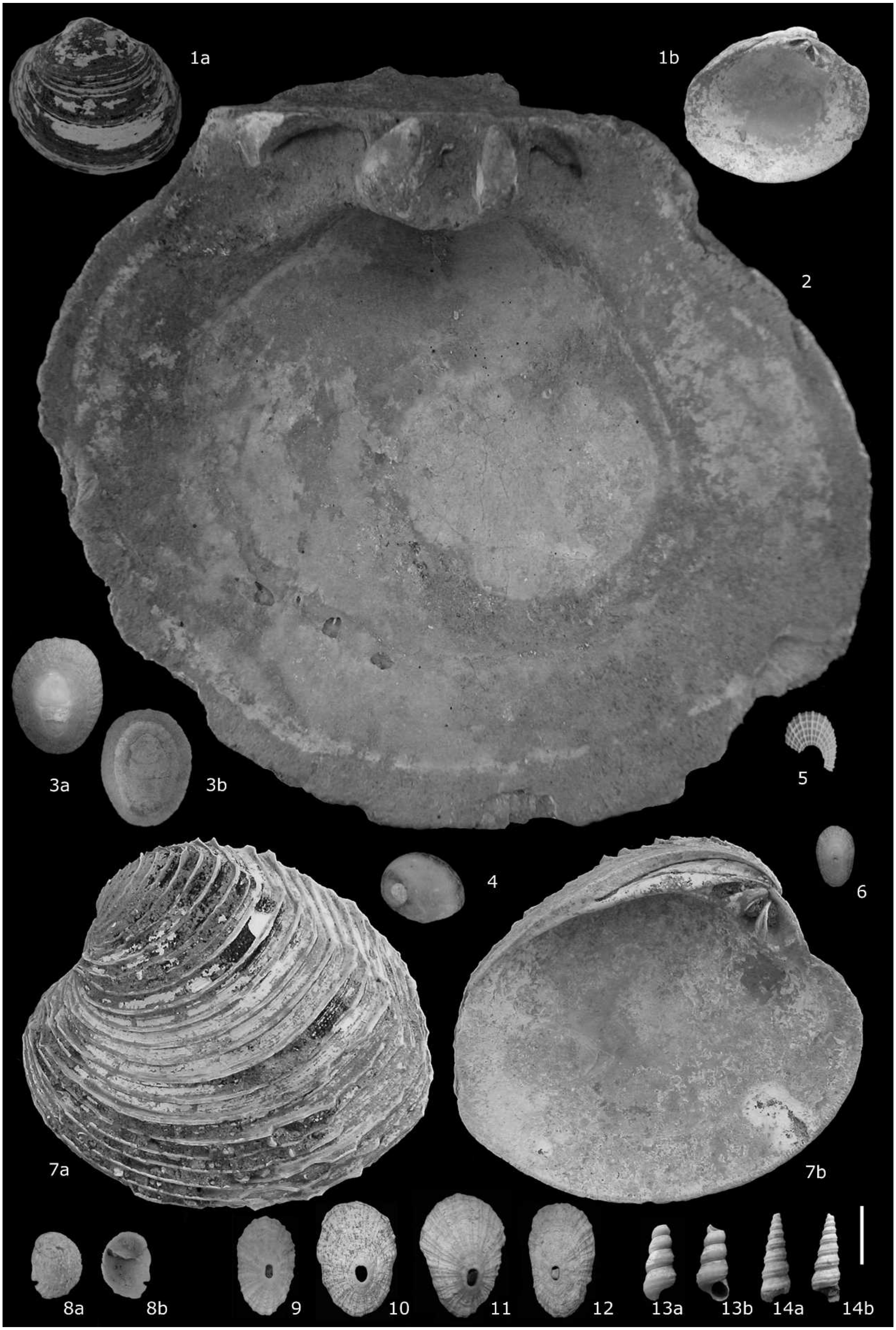

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chemnitzii (11%), epifaunal gastropods known to inhabit lower intertidal and upper infralittoral hard substrates (Table 1), where they feed upon the abundant alga that grows on rocks (Allanson, 1958; Serra et al., 2001; Kawauchi and Giribet, 2011). All three are common to the modern Angolan coast and their shells are abundant in beach drift deposits (personal observation). Additional gastropod species with similar ecologies are *Trimusculus mammillaris* (4%), *Patella granularis* (3%), and *Crepidula porcellana* (2%); and *Nerita senegalensis*, *Diodora* cf. *benguelensis*, *D. menkeana*, and *Bostrycapulus* sp. (Table 1).

Bivalves that are known to inhabit lower intertidal to infralittoral rocky substrates are diverse and moderately abundant in the bulk sample and include the cementing taxa *Chama crenulata* (3%), *Pseudochama gryphina* (1%), *Ostrea stentina* (1%), and *Anomia* sp. (0.5%), and the byssally attached species *Barbatia complanata* (1%), *Arcopsis afra* (0.5%), and *Cardita senegalensis* (0.5%). Rocky shoreline species comprise ~75 percent of individuals in the bulk sample.

Taxa from less energetic intertidal environments are also represented in the Pipas deposits (Table 1). The small gastropod *Olivella millepunctata* (10%) is the forth most abundant taxon in the bulk sample, and, like *Olivella nana* (4%), lives in agitated sands of the shoreface through infralittoral zone (Caetano et al., 2003). Several infaunal bivalves were found, like the lucinids *Ctena eburnea* (4%) and *Loripes* sp. (1%), and the cartitid *Cardiocardita lacunosa* (1%).

We recovered additional infaunal and semi-infaunal taxa by collecting in the upper sand lenses of the Pipas 1 deposit. Here, shell concentrations contained many non-abraded specimens of infaunal and semi-infaunal bivalves, such as the tellinids, venerids, and lucinids, and of numerous semi-infaunal gastropods, like *Olivella* and *Terebra* (Table 1). This association, and the abundance and diversity of semi-infaunal and infaunal taxa in the bulk sample, suggest the existence of sandy soft-bottom habitats in close proximity to the gravel pavements discussed above. In many recent rocky shores, including those we observed in the Namibe province, it is common to find localized sandy areas, protected from the effects of storms and currents by the surrounding rocks. These areas allow the settlement of soft bottom communities with infaunal species like those of the studied deposits, despite proximity to the lower intertidal mark.

The environmental interpretation inferred from the paleontological and sedimentological data indicate that the studied deposits were formed in a fully marine, rather energetic, nearshore paleoenvironment, with a bathymetric range compatible with the intertidal to upper infralittoral zones. A lower energy, sand-dominated habitat was locally transported and mixed with the gravel-dominated environment, possibly by the action of storms.

Paleobiogeography.—The Baía das Pipas paleofauna is dominated by extant species today restricted to Tropical West Africa, along with species that also range into the adjacent temperate regions of southern Africa, Western Europe, and the Mediterranean, and a few cold-water species from South Africa that today do not live northward of the SAR. The bivalves *Venus verrucosa* and *Dosinia lupinus* (Fig. 11), and the gastropods *Fissurella nubecula, Monoplex corrugatus, Bursa scrobilator,* and *Mitra cornea* are eurythermal, ranging from South Africa to the Mediterranean Sea and adjacent Western European coastlines (Aartsen et al., 1984; Sabelli et al., 1990; Poppe and Goto, 1991, 1993; Rodríguez and J. Sánchez, 1997; Hernandéz et al., 2011). We have recorded several amphi-Atlantic species that range across the tropical and warm-temperate areas of the Atlantic Ocean. They include the bivalves *Ostrea stentina* and *Parahyotissa* cf. *rosea,* and the gastropods *Cassis tessellata, Stramonita haemastoma,* and *Siphonaria pectinata*. These taxa are excellent examples of how eurythermic tolerance permits wide distribution and latitudinal range. *Venus verrucosa* and *Dosinia lupinus* (Fig. 11) range from the British Channel waters in the north (Tebble, 1976; Poppe and Goto, 1991) to Walvis Bay, Namibia, in the south (Kensley, 1973; Kilburn and Rippey, 1982; Steyn and Lussi, 1998), where one of us recently observed a large community of *Dosinia lupinus afra*.

Plio-Pleistocene climatic shifts resulted in episodic trans-equatorial connections in the Atlantic Ocean that generated disjunct modern species distributions in Europe and South Africa (e.g., Vermeij, 1992). While many of the species identified within the Pipas deposits are also present along the Angolan coast (e.g., Fig. 11), there are a few notable absences from the terrace deposits that may have resulted from these episodic connections. The well-known invasive brown mussel *Perna perna* has an amphi-Atlantic and Indo-Pacific sub-tropical distribution (Segnini de Bravo et al., 1998), and today is quite common along the Angolan coast (personal observation; Gofas et al., 1985; Rolán and Ryall, 1999). It was not recovered from the Pipas deposits, nor has it been reported from equivalent deposits of southern Africa (Carvalho, 1960, 1961, 1966; Barnard, 1962; Giresse et al., 1984; Kensley, 1985; Kensley and Pether, 1986) to our knowledge or personal observation. Similarly, *Trochita trochiformis* is common along the present day southern Angola coast and Cape Verde (Gofas et al., 1985; Rolán and Ryall, 1999; Rolán, 2005), and was widespread along the Moroccan coastline during the Pleistocene (Lecointre, 1952; Plaziat et al., 2008). It is also absent from the Pipas paleofauna. Since it is difficult to justify these absences by sampling, taphonomic, or environmental reasons, it seems likely that *P. perna* and *T. trochiformis* arrived to the Angolan coast after the middle Pleistocene. This idea could be explored with further study of the Pleistocene of Angola and Namibia.

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FIGURE 8—*1a–b*, *Persististrombus latus* (Gmelin, 1791); *2*, *Cassis tessellata* (Gmelin, 1791); *3a–b*, *Medusafissurella* aff. *chemnitzii* (Sowerby, 1835); *4a–b*, *Haliotis parva* Linnaeus, 1758; *5a–b*, *Medusafissurella* aff. *chemnitzii* (Sowerby, 1835); *6a–b*, *Crepidula porcellana* (Lamarck, 1799); *7a–b*, *Volvarina* sp.; *8–10a–b*, *Trona stercoraria* (Linnaeus, 1758); *11a–b*, *Bursa scrobilator* (Linnaeus, 1767); *12a–b*, *13a–b*, *14a–b*, *Columbella adansoni* Menke, 1853; *15a–b*, *Cancellaria* sp.; *16a–b*, *17*, *Cantharus viverratus* (Kiener, 1834); *18*, ?*Bullia* sp. Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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FIGURE 9—*1a–b*, *Monoplex corrugatus* Lamarck, 1816; *2*, *Mitrella* sp.; *3a–b*, *Stramonita haemastoma* (Linnaeus, 1767); *4a–b*, *Distorsio smithi* (von Maltzan, 1884); *5a–b*, *Hexaplex rosarium* (Röding, 1798); *6a–b*, *7a–b*, *Olivella millepunctata* (Duclos, 1835); *8a–b*, *Mitra cornea* (Gmelin, 1791); *9a–b*, *Marginella* sp.; *10a–b*, *Thais nodosa* (Linnaeus, 1758); *11a–b*, *12a–b*, *Agaronia acuminata* (Lamarck, 1822); *13a–b*, *14a–b*, *15a–b*, *16a–b*, *Olivella nana* (Lamarck, 1811); *17a–b*, *Olivella pulchella* (Duclos, 1835); *18a–b*, *Pseudoliva crassa* (Gmelin, 1791); *19a–b*, *Conus* sp. aff. *C. babaensis* Rolán and Röckel, 2001. Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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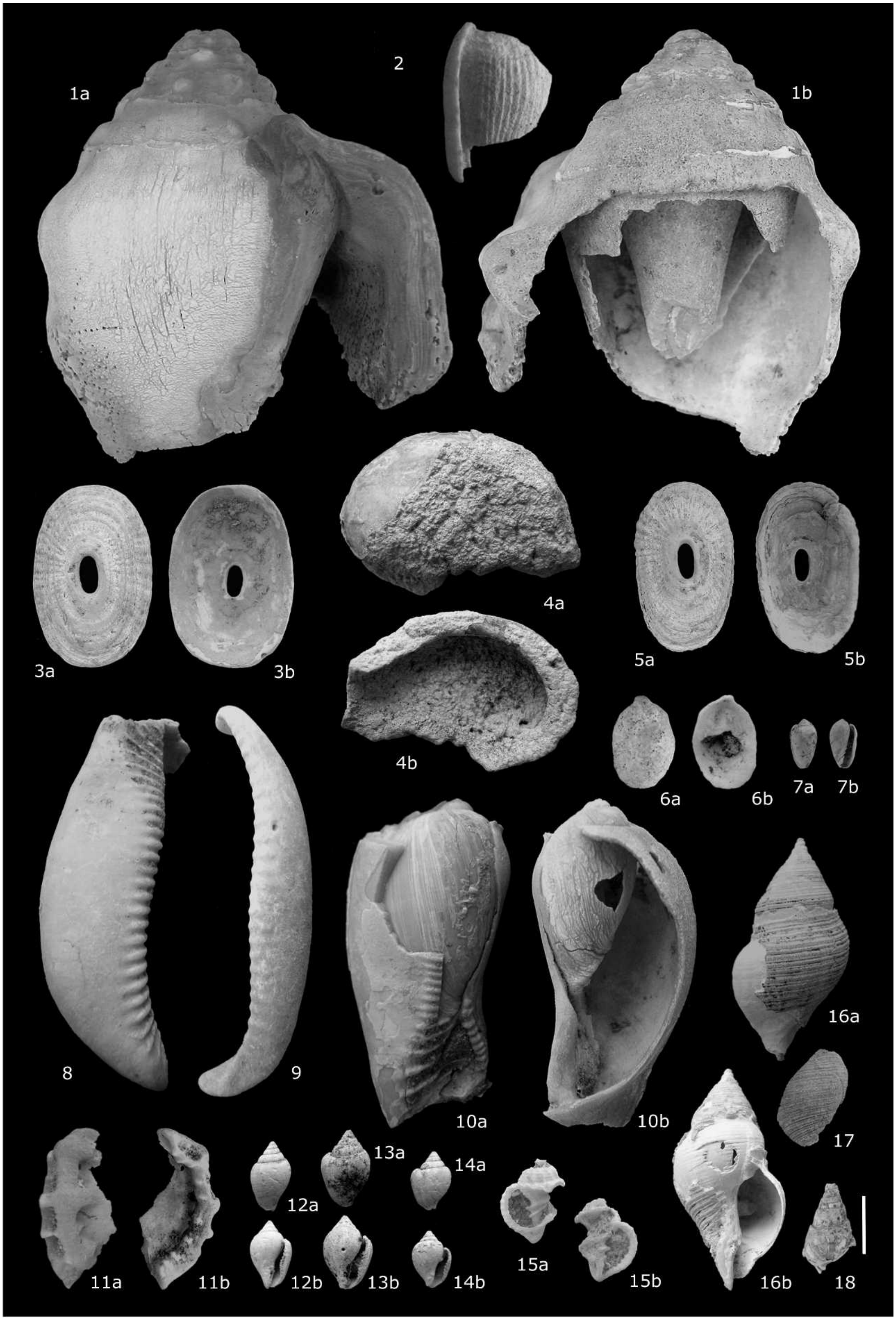

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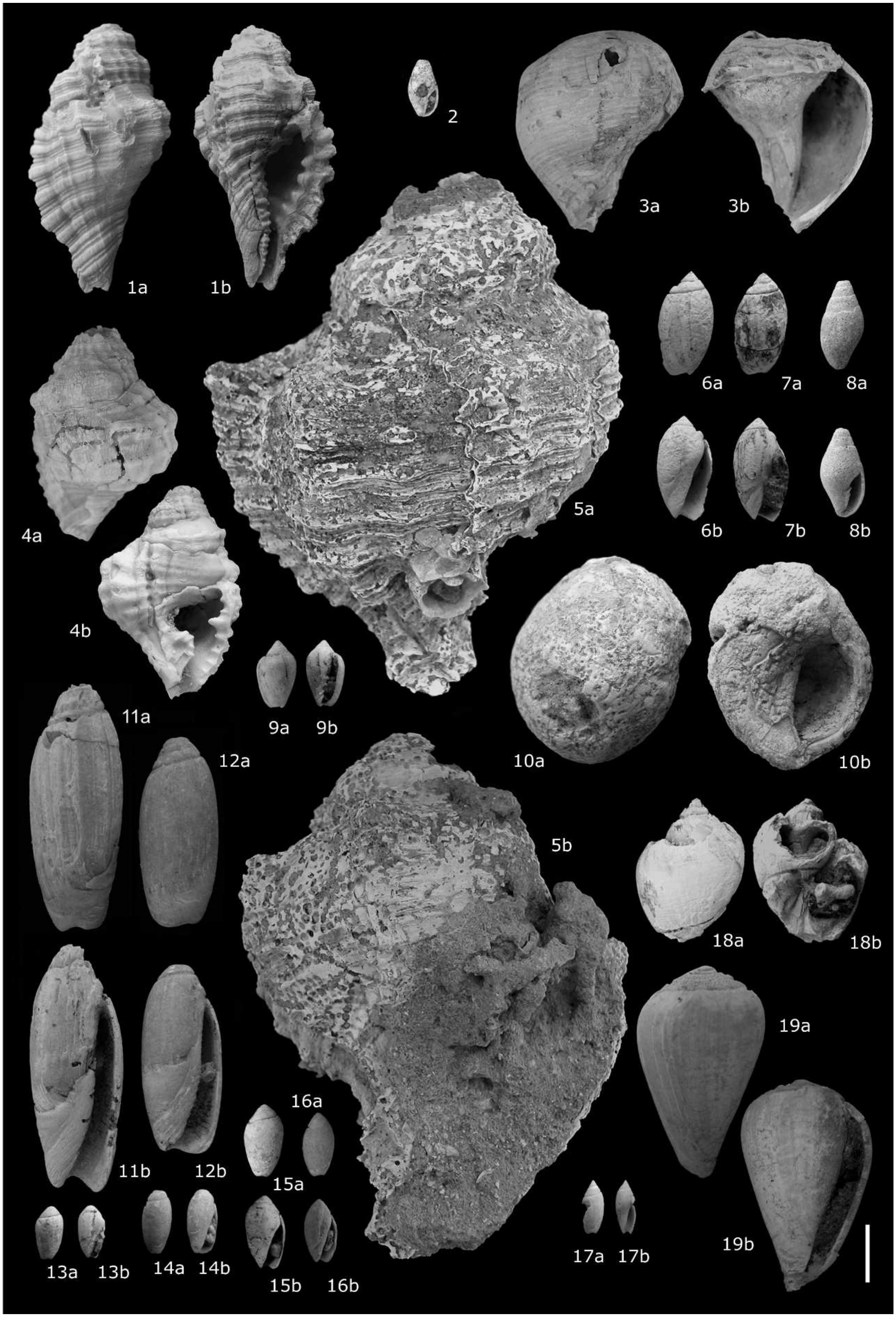

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TABLE *1*—Taxonomic composition and ecology of specimens identified in the Pipas 1 bulk sample and additional taxa recovered from survey of the Pipas 1 and 2 terrace deposits. Abbreviatiions and symbols: *=taxa from the Senegalese fauna; MNI=minimum number of individuals (for bivalve taxa, this is the valve with higher frequency); hard=hard surfaces; Cr=cryptic; Bor =borer; Tier=tiering; Epi=epifaunal; Semi=semi-infaunal; Shallow=shallow infaunal; Deep=deep infaunal; Mob=mobikity; Creep=creeping; Fac un=facultatively mobile, attached; Imm un=immobile, unattached; Imm att=immobile, attached; Feed=feeding; S=suspension feeder; DC=chemosymbiotic deposit feeder; D=deposit feeder; H=herbivore; P=predator/scavenger.

Taxa within the bulk sample	MNI	%	Substrate	Tier	Mob	Feed
Fissurella nubecula	62	30	Hard	Epi	Fac un	H
Siphonaria capensis	27	13	Hard	Epi	Fac un	H
Medusafissurella aff. *chemnitzii*	23	11	Hard	Epi	Fac un	H
Olivella millepunctata	21	10	Sand	Epi	Creep	P
Trimusculus mammillaris	9	4	Sand	Epi	Creep	P
Ctena eburnea	8	4	Sand	Shallow	Fac un	DC
Olivella nana	8	4	Sand	Epi	Creep	P
**Chama crenulata*	7	3	Hard	Epi	Imm att	S
Patella granularis	6	3	Hard	Epi	Fac un	H
Siphonaria pectinata	5	2	Hard	Epi	Fac un	H
Crepidula porcellana	4	2	Hard	Epi	Fac un	S
Ostrea stentina	3	1	Hard	Epi	Imm att	S
Pseudochama gryphina	3	1	Hard	Epi	Imm att	S
Barbatia complanata	2	1	Hard; Cr	Epi	Fac att	S
Loripes sp.	2	1	Sand	Shallow	Fac un	DC
Cardiocardita lacunosa	2	1	Sand	Epi	Fac un	S
Volvarina sp.	2	1	Mixed	Epi	Creep	P
Conus spp. indet.	2	1	Mixed	Epi	Creep	P
Arcopsis afra	1	1	Hard; Cr	Epi	Fac att	S
Anomia sp.	1	1	Hard	Epi	Imm att	S
**Cardita senegalensis*	1	1	Hard; Cr	Epi	Fac un	S
**Lutraria senegalensis*	1	1	Sand	Deep	Fac un	S
Nerita senegalensis	1	1	Hard; Cr	Epi	Creep	H
Diodora cf. *benguelensis*	1	1	Hard	Epi	Fac un	H
Diodora menkeana	1	1	Hard	Epi	Fac un	H
Bostrycapulus sp.	1	1	Hard	Epi	Fac un	S
? *Bullia* sp.	1	1	Sand	Epi	Creep	P
Cancellaria sp.	1	1	Hard	Epi	Creep	P
**Pusionella nifat*	1	1	Mixed	Epi	Creep	P
Hastula lepida	1	1	Sand	Epi	Creep	P
Bulk sample richness=30 taxa	208					
Additional taxa from field survey						
Barbatia sp.			Hard; Cr	Epi	Fac att	S
**Senilia senilis*			Sand	Semi	Fac un	S
Acar cf. *plicata*			Hard; Cr	Epi	Fac att	S
Noetiella congoensis			Hard; Cr	Epi	Fac un	S
Glycymeris concentrica			Sand	Semi	Creep	S
Hinnites corallinus			Hard	Epi	Imm att	S
Spondylus senegalensis			Hard	Epi	Imm att	S
Parhyotissa cf. *rosea*			Hard	Epi	Imm att	S
Striostrea denticulata			Hard	Epi	Imm att	S
Ungulina cuneata			Hard; Cr	Epi	Fac un	S
Cardium cf. *indicum*			Sand	Epi	Fac un	S
Mactra glabrata			Sand	Shallow	Fac un	S
Tellina madagascariensis			Sand	Deep	Creep	D
Venus verrucosa			Sand	Shallow	Fac un	S
Circomphalus foliaceolamellosus			Sand	Shallow	Creep	S
Dosinia isocardia			Sand	Shallow	Creep	S
Dosinia lupinus afra			Sand	Shallow	Creep	S
Pholas campechiensis			Hard; Bor	Epi	Imm un	S
Haliotis parva			Hard	Epi	Fac un	H
Turritella bicingulata			Sand	Epi	Fac un	S
**Persististrombus latus*			Sand	Epi	Creep	H
Trona stercoraria			Hard	Epi	Creep	H
Cassis tessellata			Mixed	Epi	Creep	P
Monoplex corrugatus			Mixed	Epi	Creep	P
Distorsio smithi			Mixed	Epi	Creep	P
Bursa scrobilator			Mixed	Epi	Creep	P
Hexaplex rosarium			Mixed	Epi	Creep	P
Thais (Thais) nodosa			Hard	Epi	Creep	P
Stramonita haemastoma			Hard	Epi	Creep	P
**Cantharus viverratus*			Hard	Epi	Creep	P
Columbella adansoni			Hard	Epi	Creep	H
Mitrella sp.			Hard	Epi	Creep	P
Agaronia acuminata			Sand	Epi	Creep	P
Olivella pulchella			Sand	Epi	Creep	P
Olivella sp.			Sand	Epi	Creep	P
Pseudoliva crassa			Mixed	Epi	Creep	P
Marginella sp.			Mixed	Epi	Creep	P
Mitra cornea			Hard	Epi	Creep	P
**Conus ermineus*			Mixed	Epi	Creep	P
**Conus pulcher*			Mixed	Epi	Creep	P
Conus sp. aff. *C. babaensis*			Mixed	Epi	Creep	P
Clavatula sp. indet.			Mixed	Epi	Creep	P
Pusionella sp. indet.			Mixed	Epi	Creep	P
Terebra senegalensis			Sand	Epi	Creep	P
Hastula sp. indet.			Sand	Epi	Creep	P

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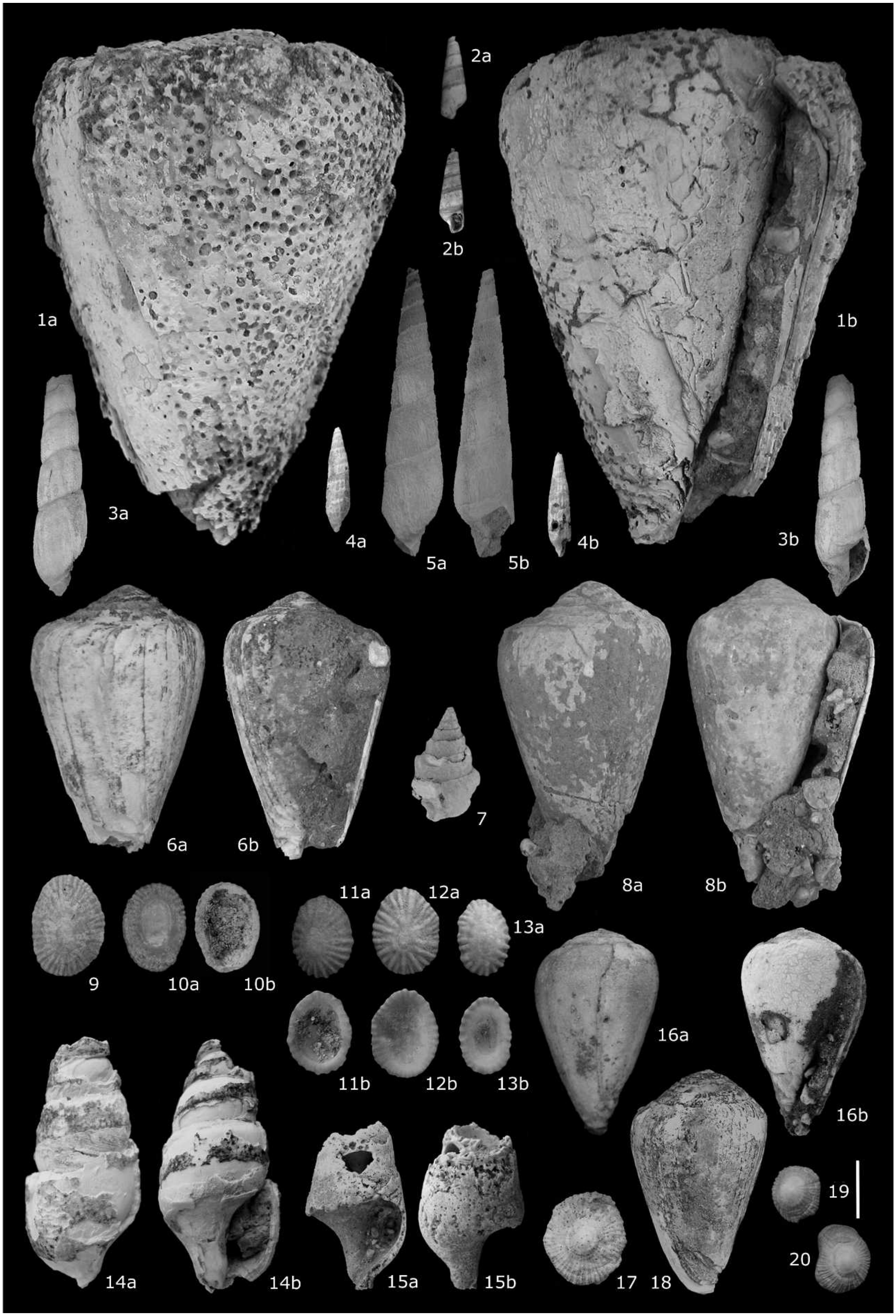

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A number of taxa are reported to be endemic to the present-day Angolan continental shelf. *Hinnites corallinus* is one such species, which only occurs in southern Angola (Gofas et al., 1985; Ardovini and Cossignani, 2004; Fig. 11). The Conidae, noted for their high diversity of geographically restricted species (Duda and Rolán, 2005), are represented by more than 30 species in Angola (Rolán and Röckel, 2000, 2001). Recent monographs (like Monteiro et al., 2004) differentiate many of these *Conus* species based on color patterns, in addition to anatomical and skeletal morphology. While remnants of color can sometimes be recovered in fossil shells by using ultraviolet light to detect patterns (e.g., Dockery, 1980; Swann and Kelley, 1985; Hendricks, 2008; Caze et al., 2010), this method did not reveal distinct patterns on Baía das Pipas *Conus* specimens, most likely because of abrasion. Therefore, we used traditional morphological details such as spire, aperture, and overall shell shape to identify some specimens, and left the remainder in open nomenclature.

Some of the molluscs found within the Baía das Pipas assemblage are part of the "Senegalese fauna" (Gignoux, 1913), a warm, thermally anomalous association found in many Pleistocene deposits of the Mediterranean region where it indicates accentuated climatic changes related to interglacial stages or interstadial episodes (e.g., Brebion, 1979; Bordoni and Valensise, 1999; Zazo et al., 2002, 2003; Nalin et al., 2012). *Persististrombus latus* is a common species on the recent Angolan coast (Gofas et al., 1985; Rolán and Ryall, 1999, and references therein), and the figurehead of the Senegalese fauna. Historically known as *Strombus bubonius,* this thermophilous strombid colonized the Mediterranean during the last interglacial (e.g., Taviani, 2002), where it reached as far as the southeast coast of Spain (Hillaire-Marcel et al., 1986; Cornu et al., 1993; Zazo et al., 2003), southern Italy (Ruggeri and Buccheri, 1968; Nalin et al., 2012), and Cape Verde (Zazo et al., 2010). The buccinid *Cantharus viverratus* is another common element of both the modern rocky shores of Angola (Gofas et al., 1985; Rolán and Ryall, 1999, and references therein) and of the Senegalese fauna. It also reached considerably higher latitudes that its current range during the Pleistocene interglacials, such as the MIS 5e deposits of Santa Maria Island, Azores (Callapez and Soares, 2000; Ávila et al., 2009). Other classic Senegalese fauna that occur in the Baía das Pipas fauna include *Senilia senilis*, *Chama crenulata, Cardita senegalensis, Lutraria senegalensis*, *Conus pulcher* (syn. *Conus prometheus*), *Conus ermineus* (syn. *Conus testudinarius*), and *Pusionella nifat* (Table 1).

Paleoclimatic significance.—The fauna of the Pipas Pleistocene terraces is very similar to that living along the southern Angola coast today (compare our faunal list to Rolán and Ryall [1999]), indicating an overall similarity of climatic and oceanographic parameters. The geographic distributions and thermal tolerances of the extant species within the Pipas terrace deposits were used to estimate the seasonal temperature range of this region in the middle Pleistocene. Out of the 55 species identified within the terraces, 20 would be considered stenotypic, with a geographic range extending between Cape Verde and the Angolan-Namibian border. *Persististrombus latus* is an example of one such species from the Tropical West African province (Fig. 11). These stenotypic species limit the range of temperatures possible for the Pipas climate, and indicate a mean annual temperature of ~23°C, with seasonal limits of ~20°C and 28°C (Fig. 11). This range agrees well with other estimates of the temperature requirements of *Persististrombus latus* singularly and of the Senegalese fauna as a whole (Cornu et al., 1993; Meco et al., 2002; Zazo et al., 2010). In particular, the coldest temperatures possible for the Pipas paleofauna are constrained by these thermophilous species, and sustained 19–20°C temperatures are a distinct, and noted, limit for the Senegalese fauna and other thermophilous species (Cornu et al., 1993; Meco et al., 2002; Zazo et al., 2010; Silva et al., 2011).

The occurrence of the Senegalese fauna and other thermophilous taxa, such as members of the Muricidae, Marginellidae, and Terebridae, are an obvious indication that the middle Pleistocene was warm. On the other hand, some indicators of cooler waters of the South African province are also evident. The taxa *Haliotis parva*, *Patella granularis*, and *Siphonaria capensis* are present in the studied deposits as well as along the modern coast of southern Angola/northern Namibia and the cooler water assemblages that characterize the temperate South African province (personal observation; Kilburn and Rippey, 1982; Rolán and Ryall, 1999; Fig. 11). These taxa live in temperatures that are at the lower end of the thermal tolerances of the Senegalese species, and only co-occur with them in the SAR (Fig. 11). This further indicates the similarity between the present day climate of the Angolan coast and that of the marine terraces, and supports the idea that the Pleistocene Benguela Current System was not significantly different than today, without glacial intensification of cold water flow or increased coastal upwelling (Schneider et al., 1995; Summerhayes et al., 1995; Kirst et al., 1999). This apparent climatic stability also explains why the interglacial Senegalese faunal incursions were so marked in the coastal waters of Morocco, the Canaries, and the western Mediterranean, but not noticeable in southern Africa, where Pleistocene mollusc assemblages contain taxa from temperate/cold areas (Barnard, 1962; Kensley, 1985; Kensley and Pether, 1986).

CONCLUSIONS

Sedimentological and paleontological data presented here from the middle Pleistocene of southern Angola fill a large geographic gap in the Quaternary record of Western Africa. In particular, the fauna collected from the raised terraces of Baía das Pipas is a rare example of a marine Pleistocene assemblage from West Africa. Like the well-studied deposits from Morocco, Cape Verde, and South Africa, the remote Namib Desert coast in southern Angola contains widespread Quaternary raised marine terraces and associated geomorphic features. The sedimentology, taphonomy, and faunal composition of the Pipas terraces indicate a time-averaged, high-energy setting, characteristic of intertidal and nearshore rocky-bottom settings, that was adjacent to sandy soft-bottom habitats. This environmental interpretation is similar to modern coastal environments of the region, which explains in part the similarity of the Pipas fauna to the modern one. Seventy-five mollusc taxa were identified, 29 bivalve and 46 gastropods, all of which are known from recent West African coastal habitats.

←
FIGURE 10—*1a–b*, *Conus pulcher* Lightfoot, 1786; *2a–b*, *Hastula* sp. indet.; *3a–b*, *Terebra senegalensis* Lamarck, 1822; *4a–b*, *Hastula lepida* (Hinds, 1844); *5a–b*, *Terebra senegalensis* Lamarck, 1822; *6a–b*, *Conus ermineus* Born, 1778; *7*, *Pusionella nifat* (Bruguière, 1792); *8a–b*, *Conus ermineus* Born, 1778; *9*, *10a–b*, *Siphonaria pectinata* (Linnaeus, 1758); *11a–b*, *12a–b*, *13a–b*, *Siphonaria capensis* (Quoy and Gaimard, 1833); *14a–b*, *Pusionella* sp. indet.; *15a–b*, *Clavatula* sp. indet.; *16a–b*, *Conus* sp. aff. *C. babaensis* Rolán and Röckel, 2001; *17*, *Trimusculus mammillaris* (Linnaeus, 1758); *18*, *Conus ermineus* Born, 1778; *19*, *20*, *Trimusculus mammillaris* (Linnaeus, 1758). Scale bar=1 cm. Specimens are reposited at MAB, Angola under these figure and specimen numbers.

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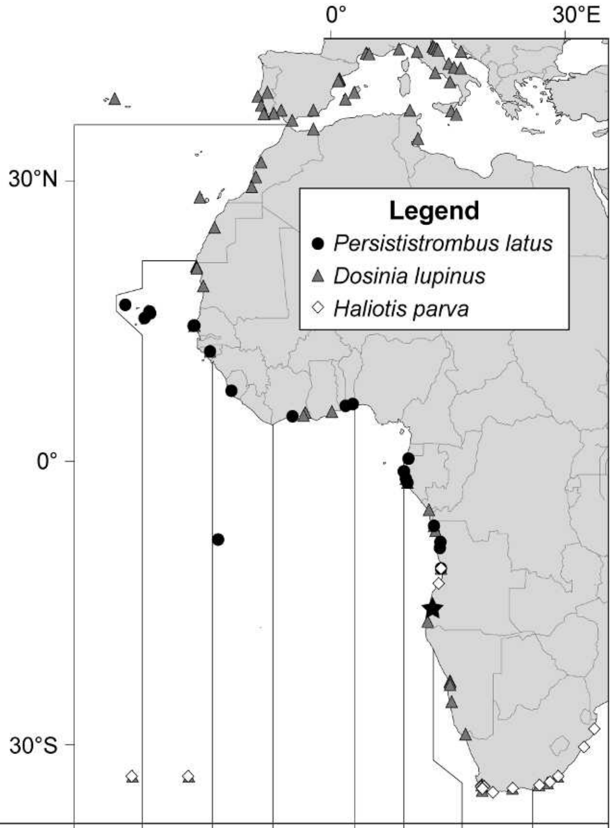

Warmest	26-28	27-29	28	26-27	28.5	**27.5**	18-20	25-27
Coldest	16-18	18-19	26	22-24	25	**19.5**	10-12	20-22
Senilia senilis	●	●	●	●	●	●		
Pusionella nifat	●	●	●	●	●	●		
Cantharus viverratus	●	●	●	●		●		
Hastula lepida	●	●		●		●		
Lutraria senegalensis	●	●				●		
Terebra senegalensis	●	●				●		
Cardita senegalensis		●	●	●		●		
Hexaplex rosarium		●		●	●	●		
Turritella bicingulata		●		●		●		
Thais (Thais) nodosa		●	●	●	●	●		
Hinnites corallinus						●		
Patella granularis						◇	◇	
Siphonaria capensis						◇	◇	◇

FIGURE *11*—Map displaying the present day geographic distribution in the East Atlantic Ocean of a thermophilous species (*P. latus*), a eurythermal species (*D. lupinus*), and a temperate/cold-water species (*H. parva*) found in the Pipas terrace deposits. Present day seasonal temperature ranges for regions along the African coast are plotted and the seasonal temperature range of the study area is in bold. Listed below the map are additional thermophilous and cold-water species from the Pipas deposits, with symbols indicating their present-day distributions. The thermophilous species do not live in regions that are colder than ~20°C for several months of the year, and the only place where they co-occur with the cold-water species is near the Angolan-Namibian border. See online Supplemental Data files 1 and 2, respectively, for full geographic and temperature datasets.

The present day biogeographic ranges and dominance of thermophilous species suggest that the Baía das Pipas Pleistocene fauna lived in relatively warm surface waters. The cool-water Benguela Current extended its influence to the coastline of Namib Desert during the middle Pleistocene, resulting in the occurrence of temperate species that presently have their southernmost range along the coast of South Africa. The thermal tolerances of the molluscs found in Pipas assemblage imply that during the middle Pleistocene interstadial, climate was similar to today, ranging from ~20° to 27–28°C. As in the modern, proximity to the Benguela Current and associated upwelling resulted in a diverse fossil fauna.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.qf4sj.

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APPENDIX 1

Taxonomic list of species found in the middle Pleistocene marine terrace deposits of Baía das Pipas, Angola.

Class Bivalvia Linnaeus, 1758
Family Arcidae Lamarck, 1809
Genus Senilia Gray, 1842

Senilia senilis (Linnaeus, 1758) Figures 4.2a–b, 4.3a–b

Genus Acar Gray, 1847

Acar cf. *plicata* (Dillwyn, 1817) Figure 4.4a–b

Genus Barbatia Gray, 1842

Barbatia complanata (Bruguière, 1789) Figure 4.5a–b
Barbatia sp. Figure 4.1a–b

Family Noetiidae Stewart, 1930
Genus Arcopsis Köenen, 1885

Arcopsis afra (Gmelin, 1791) Figure 4.6

Genus Noetiella Thiele and Jaeckel, 1931

Noetiella congoensis Thiele and Jaeckel, 1931 Figure 4.7a–b

Family Glycymerididae Dall, 1908
Genus Glycymeris Da Costa, 1778

Glycymeris concentrica (Dunker, 1853) Figure 4.9a–b

Family Pectinidae Rafinesque, 1815
Genus Hinnites Defrance, 1821

Hinnites corallinus Sowerby, 1827 Figure 5.2a–b

Family Spondylidae Gray, 1826
Genus Spondylus Linnaeus, 1758

Spondylus senegalensis (Schreibers, 1793) Figures 6.5, 7.2

Family Anomiidae Rafinesque, 1815
Genus Anomia Linnaeus, 1758

Anomia sp. Figure 4.10a–b

Family Gryphaeidae Vialov, 1936
Genus Parahyotissa Harry, 1985

Parhyotissa cf. *rosea* (Gmelin, 1791) Figure 4.13a–b

Family Ostreidae Rafinesque, 1815
Genus Ostrea Linnaeus, 1758

Ostrea stentina (Payraudeau, 1826) Figure 4.8a–b

Genus Striostrea Vialov, 1936

Striostrea denticulata Born, 1778 Figure 5.3a–b

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Family Lucinidae Fleming, 1828
Genus Ctena Mörch, 1860

Ctena eburnea (Gmelin, 1791) Figures 5.12a–b, 5.13a–b

Genus Loripes Poli, 1791

Loripes sp. Figures 4.11, 4.12

Family Ungulinidae Gray, 1854
Genus Ungulina Bosc, 1801

Ungulina cuneata (Spengler, 1798) Figure 5.4a–b

Family Chamidae Lamarck, 1809
Genus Chama Linnaeus, 1758

Chama crenulata Lamarck, 1819 Figures 5.6a–b, 5.7a–b

Genus Pseudochama Odhner, 1917

Pseudochama gryphina (Lamarck, 1819) Figure 5.5

Family Carditidae Férussac, 1822
Genus Cardita Bruguière, 1792

Cardita senegalensis (Reeve, 1843) Figures 5.1a–b, 5.14a–b

Genus Cardiocardita Anton, 1838

Cardiocardita lacunosa Reeve, 1843 Figures 5.8, 5.9, 5.10

Family Cardiidae Lamarck, 1809
Genus Cardium Linnaeus, 1758

Cardium cf. *indicum* Lamarck, 1819 Figure 5.15a–b

Family Mactridae Lamarck, 1809
Genus Mactra Linnaeus, 1767

Mactra glabrata Linnaeus, 1767 Figure 6.6a–b

Genus Lutraria Lamarck, 1799

Lutraria senegalensis Gray, 1837 Figure 6.7a–b

Family Tellinidae Blainville, 1814
Genus Tellina Linnaeus, 1758

Tellina madagascariensis Gmelin, 1791 Figure 6.8a–b

Family Veneridae Rafinesque, 1815
Genus Venus Linnaeus, 1758

Venus verrucosa Linnaeus, 1758 Figure 7.1a–b

Genus Circomphalus Klein *in* Mörch, 1853

Circomphalus foliaceolamellosus (Dillwyn, 1817) Figure 7.7a–b

Genus Dosinia Scopoli, 1777

Dosinia isocardia (Dunker, 1845) Figures 6.3a–b, 6.4a–b
Dosinia lupinus afra (Gmelin, 1791) Figures 5.11a–b, 6.1a–b, 6.2a–b

Family Pholadidae Lamarck, 1809
Genus Pholas Linnaeus, 1758

Pholas campechiensis Gmelin, 1791 Figure 6.9a–b

Class Gastropoda Cuvier, 1795
Family Fissurellidae Fleming, 1822
Genus Diodora Gray, 1821

Diodora cf. *benguelensis* (Dunker, 1853) Figure 7.5

Diodora menkeana (Dunker, 1853) Figure 7.6

Genus Fissurella Bruguière, 1789

Fissurella nubecula (Linnaeus, 1758) Figures 7.9, 7.10, 7.11, 7.12

Genus Medusafissurella McLean and Kilburn, 1986

Medusafissurella aff. *chemnitzii* (Sowerby, 1835) Figures 8.3a–b, 8.5a–b

Family Haliotidae Rafinesque, 1815
Genus Haliotis Linnaeus, 1758

Haliotis parva Linnaeus, 1758 Figure 8.4a–b

Family Patellidae Rafinesque, 1815
Genus Patella Linnaeus, 1758

Patella granularis Linnaeus, 1758 Figure 7.3a–b

Family Neritidae Rafinesque, 1815
Genus Nerita Linnaeus, 1758

Nerita senegalensis Gmelin, 1791 Figure 7.4

Family Turritellidae Lovén, 1847
Genus Turritella Lamarck, 1799

Turritella bicingulata (Lamarck, 1822) Figures 7.13a–b, 7.14a–b

Family Strombidae Rafinesque, 1815
Genus Persististrombus Kronenberg and Lee, 2007

Persististrombus latus (Gmelin, 1791) Figure 8.1a–b

Family Calyptraeidae Lamarck, 1809
Genus Crepidula Lamarck, 1799

Crepidula porcellana (Lamarck, 1799) Figure 8.6a–b

Genus Bostrycapulus Olsson and Harbison, 1953

Bostrycapulus sp. Figure 7.8a–b

Family Cypraeidae Rafinesque, 1815
Genus Trona Jousseaume, 1884

Trona stercoraria (Linnaeus, 1758) Figures 8.8, 8.9, 8.10a–b

Family Cassidae Latreille, 1825
Genus Cassis Scopoli, 1777

Cassis tessellata (Gmelin, 1791) Figure 8.2

Family Ranellidae Gray, 1854
Genus Monoplex Perry, 1811

Monoplex corrugatus (Lamarck, 1816) Figure 9.1a–b

Family Personidae Gray, 1854
Genus Distorsio Röding, 1798

Distorsio smithi (von Maltzan, 1884) Figure 9.4a–b

Family Bursidae Thiele, 19258
Genus Bursa Röding, 1798

Bursa scrobilator (Linnaeus, 1767) Figure 8.11a–b

Family Muricidae Rafinesque, 1815
Genus Hexaplex Perry, 1811

Hexaplex rosarium (Röding, 1798) Figure 9.5a–b

Genus Thais Röding, 1798

Thais (*Thais*) *nodosa* (Linnaeus, 1758) Figure 9.10a–b

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Genus Stramonita Schumacher, 1817

Stramonita haemastoma (Linnaeus, 1767) Figure 9.3a–b

Family Buccinidae Rafinesque, 1815
Genus Cantharus Röding, 1798

Cantharus viverratus (Kiener, 1834) Figures 8.16a–b, 8.17

Family Columbellidae Swainson, 1840
Genus Columbella Lamarck, 1799

Columbella adansoni Menke, 1853 Figures 8.12a–b, 8.13a–b, 8.14a–b

Genus Mitrella Risso, 1826

Mitrella sp. Figure 9.2

Family Nassariidae Iredale, 1916 (1835)
Genus *Bullia* Gray *in* Griffith and Pidgeon, 1834

? *Bullia* sp. Figure 8.18

Family Olividae Latreille, 1825
Genus Agaronia Gray, 1839

Agaronia acuminata (Lamarck, 1822) Figures 9.11a–b, 9.12a–b

Genus Olivella Swainson, 1831

Olivella millepunctata (Duclos, 1835) Figures 9.6a–b, 9.7a–b
Olivella nana (Lamarck, 1811) Figures 9.13a–b, 9.14a–b, 9.15a–b, 9.16a–b
Olivella pulchella (Duclos, 1835) Figure 9.17a–b
Olivella sp.

Genus Pseudoliva Swainson, 1840

Pseudoliva crassa (Gmelin, 1791) Figure 9.18a–b

Family Marginellidae Fleming, 1828
Genus Marginella Lamarck, 1799

Marginella sp. Figure 9.9a–b

Genus Volvarina Hinds, 1844

Volvarina sp. Figure 8.7a–b

Family Mitridae Swainson, 1829
Genus Mitra Lamarck, 1798

Mitra cornea (Gmelin, 1791) Figure 9.8a–b

Family Cancellariidae Forbes and Hanley, 1851
Genus Cancellaria Lamarck, 1799

Cancellaria sp. Figure 8.15a–b

Family Conidae Fleming, 1822
Genus Conus Linnaeus, 1758

Conus pulcher Lightfoot, 1786 Figure 10.1a–b
Conus ermineus Born, 1778 Figures 10.6a–b, 10.8a–b, 10.18
Conus sp. aff. *C. babaensis* Rolán and Röckel, 2001 Figures 9.19a–b, 10.16a–b
Conus spp. indet.

Family Clavatulidae Gray, 1853
Genus Clavatula Lamarck, 1801

Clavatula sp. indet. Figure 10.15a–b

Genus Pusionella Gray, 1847

Pusionella nifat (Bruguière, 1792) Figure 10.7
Pusionella sp. indet. Figure 10.14a–b

Family Terebridae Mörch, 1852
Genus Terebra Bruguière, 1789

Terebra senegalensis Lamarck, 1822 Figures 10.3a–b, 10.5a–b

Genus Hastula H. Adams and A. Adams, 1853

Hastula lepida (Hinds, 1844) Figure 10.4a–b
Hastula sp. indet. Figure 10.2a–b

Family Siphonariidae Gray, 1827
Genus Siphonaria Sowerby, 1823

Siphonaria capensis (Quoy & Gaimard, 1833) Figures 10.11a–b, 10.12a–b, 10.13a–b
Siphonaria pectinata (Linnaeus, 1758) Figures 10.9, 10.10a–b

Family Trimusculidae J.Q. Burch, 1945 (1840)
Genus Trimusculus Schmidt, 1818

Trimusculus mammillaris (Linnaeus, 1758) Figures 10.17, 10.19, 10.20

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APPENDIX *2*—Sources used for the ecological characterization of taxa in Table 1. Categorization is based on extant genera; the few cases where higher taxonomic groups were used are noted in the "Data source" column. For classifications from the Paleobiology Database (PaleoDB), the specific reference(s) are also listed; NMITA=Neogene Marine Biota of Tropical America; personal obs.=personal observation by Pedro M. Callapez.

Taxa within the bulk sample	Data source
Fissurella nubecula (Linnaeus, 1758)	NMITA; Serra et al., 2001
Siphonaria capensis (Quoy and Gaimard, 1833)	NMITA; Allanson, 1958
Medusafissurella aff. *chemnitzii* (Sowerby, 1835)	NMITA; Serra et al., 2001; McLean and Kilburn, 1986
Olivella millepunctata (Duclos, 1835)	NMITA; Caetano et al., 2003
Trimusculus mammillaris (Linnaeus, 1758)	NMITA
Ctena eburnea (Gmelin, 1791)	NMITA
Olivella nana (Lamarck, 1811)	NMITA
Chama crenulata Lamarck, 1819	NMITA
Patella granularis Linnaeus, 1758	personal obs.; PaleoDB, family: Kiessling, 2004; Hendy et al., 2009
Siphonaria pectinata (Linnaeus, 1758)	NMITA; Allanson, 1958; Kawauchi and Giribet, 2011
Crepidula porcellana (Lamarck, 1799)	NMITA
Ostrea stentina (Payraudeau, 1826)	NMITA
Pseudochama gryphina (Lamarck, 1819)	NMITA
Barbatia complanata (Bruguière, 1789)	NMITA
Loripes sp.	NMITA, family
Cardiocardita lacunosa Reeve, 1843	NMITA
Volvarina sp.	NMITA
Conus spp. indet.	NMITA
Arcopsis afra (Gmelin, 1791)	NMITA
Anomia sp.	NMITA
Cardita senegalensis (Reeve, 1843)	NMITA
Lutraria senegalensis Gray, 1837	personal obs.; PaleoDB, genus: Aberhan et al., 2004; Sanchez, 1926
Nerita senegalensis Gmelin, 1791	personal obs.; NMITA; Oyenekan and Olufowobi, 1987
Diodora cf. *benguelensis* (Dunker, 1853)	NMITA
Diodora menkeana (Dunker, 1853)	NMITA
Bostrycapulus sp.	NMITA; Collin, 2005
? *Bullia* sp.	NMITA, family
Cancellaria sp.	NMITA
Pusionella nifat (Bruguière, 1792)	NMITA, family
Hastula lepida (Hinds, 1844)	NMITA
Additional taxa from census collection	
Barbatia sp.	NMITA
Senilia senilis (Linnaeus, 1758)	subfamily: Mikkelsen and Bieler, 2008
Acar cf. *plicata* (Dillwyn, 1817)	NMITA
Noetiella congoensis Thiele and Jaeckel, 1931	personal obs.
Glycymeris concentrica (Dunker, 1853)	NMITA, family
Hinnites corallinus Sowerby, 1827	PaleoDB, genus: Kiessling, 2004; Hendy et al., 2009
Spondylus senegalensis (Schreibers, 1793)	NMITA
Parhyotissa cf. *rosea* (Gmelin, 1791)	NMITA
Striostrea denticulata Born, 1778	NMITA
Ungulina cuneata (Spengler, 1798)	PaleoDB, family: Sanchez, 1926; Aberhan et al., 2004
Cardium cf. *indicum* Lamarck, 1819	NMITA, family
Mactra glabrata Linnaeus, 1767	NMITA
Tellina madagascariensis Gmelin, 1791	NMITA
Venus verrucosa Linnaeus, 1758	NMITA, family; PaleoDB, family: Kiessling, 2004; Aberhan et al., 2004
Circomphalus foliaceolamellosus (Dillwyn, 1817)	NMITA
Dosinia isocardia (Dunker, 1845)	NMITA
Dosinia lupinus afra (Gmelin, 1791)	NMITA
Pholas campechiensis Gmelin, 1791	NMITA
Haliotis parva Linnaeus, 1758	personal obs.; PaleoDB, genus: Kiessling, 2004; Hendy et al., 2009
Turritella bicingulata (Lamarck, 1822)	NMITA, family
Persististrombus latus (Gmelin, 1791)	NMITA
Trona stercoraria (Linnaeus, 1758)	NMITA; Bernard, 1984
Cassis tessellata (Gmelin, 1791)	NMITA
Monoplex corrugatus Lamarck, 1816	NMITA
Distorsio smithi (von Maltzan, 1884)	NMITA
Bursa scrobilator (Linnaeus, 1767)	NMITA
Hexaplex rosarium (Röding, 1798)	NMITA
Thais (*Thais*) *nodosa* (Linnaeus, 1758)	NMITA
Stramonita haemastoma (Linnaeus, 1767)	NMITA
Cantharus viverratus (Kiener, 1834)	NMITA
Columbella adansoni Menke, 1853	NMITA; Oliverio, 1995
Mitrella sp.	NMITA
Agaronia acuminata (Lamarck, 1822)	NMITA
Olivella pulchella (Duclos, 1835)	NMITA
Olivella sp.	NMITA
Pseudoliva crassa (Gmelin, 1791)	PaleoDB, family: Kiessling, 2004; Hendy et al., 2009
Marginella sp.	NMITA
Mitra cornea (Gmelin, 1791)	NMITA; Harasewych, 2009
Conus ermineus Born, 1778	NMITA
Conus pulcher Lightfoot, 1786	NMITA
Conus aff. *babaensis* Rolán and Röckel, 2001	NMITA
Clavatula sp.	PaleoDB, family: Kiessling, 2004, Hendy et al., 2009
Pusionella sp. indet.	NMITA, family
Terebra senegalensis Lamarck, 1822	NMITA
Hastula sp. indet.	NMITA

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