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SEQUENCE STRATIGRAPHIC CONTROL ON PRESERVATION OF LATE EOCENE WHALES AND OTHER VERTEBRATES AT WADI AL-HITAN, EGYPT

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ABSTRACT

Biological and physical factors govern the distribution of fossils, but it is not always clear which is more important. The preservation of late Eocene vertebrates at the UNESCO World Heritage site of Wadi Al-Hitan, Western Desert of Egypt, is controlled primarily by the physical processes responsible for sequence stratigraphic architecture on a siliciclastic shelf. Three types of stratigraphic surface, each characterized by a taxonomically and taphonomically distinct fossil assemblage, yield most of the known vertebrate fossils. Complete, partially articulated whale skeletons, primarily *Basilosaurus isis*, are abundant in offshore marine flooding surfaces (MFS) in the late transgressive systems tract (TST) of the first Priabonian sequence (TA4.1), where low net sedimentation rates and environmental averaging in offshore environments promoted the accumulation of carcasses on traceable stratigraphic surfaces. Complete, well-articulated whales, primarily *Dorudon atrox*, are more widely scattered on minor erosion surfaces in rapidly accumulating shoreface sediments of the overlying falling stage systems tract. Fragmented and abraded vertebrate remains are abundant and diverse in a discontinuous conglomerate that marks the first sequence boundary above the base of the Priabonian (Pr-2), which has not been previously recognized in Egypt, but which formed incised valleys with at least 45 m of total relief. Fossils in this variably thick lag conglomerate include skeletal elements reworked by rivers from underlying marine deposits and bones of terrestrial animals living in the fluvial environment. Marginal marine vertebrates, primarily dugongs, occur on shelly marine ravinement surfaces above Pr-2, in the early TST of the second Priabonian sequence. Most vertebrate remains in Wadi Al-Hitan occur in condensed stratigraphic intervals and taxonomic composition changes with sequence position, both important considerations in interpretation of paleobiological patterns.

INTRODUCTION

Sedimentation and fossil preservation are both influenced by the balance between sediment supply and the formation and destruction of sediment accommodation. For this reason, the processes that control sequence stratigraphic architecture often determine apparent timings of biological origination and extinction in the fossil record (Holland, 1995; Brett, 1998; Holland and Patzkowsky, 1999), as well as the abundance, distribution, composition, and taphonomy of fossils within individual stratigraphic sections and sequences. Although a number of field studies and conceptual literature reviews have examined the relationship between sedimentary processes and the preservation and character of shelly marine macroinvertebrates (e.g., Kidwell, 1985, 1991, 1997; Banerjee and Kidwell, 1991; Rogers 1994; Brett, 1995; Courville and Collin, 2002; Scarponi and Kowalewski, 2004; Crampton et al., 2006), few studies have explored marine vertebrate preservation in the context of sequence stratigraphy (Rogers and Kidwell, 2000). The extent to which processes that govern macroinvertebrate preservation can be extrapolated to vertebrates is uncertain because shelly macroinvertebrates differ substantially from marine vertebrates in chemical composition, size, and skeletal durability, as well as in life history modes and standing population sizes.

Here we document sequence stratigraphic architecture and the preservation of marine and terrestrial vertebrates in Priabonian (late Eocene) siliciclastic deposits at Wadi Al-Hitan, Valley of the Whales, in the Western Desert of Egypt (Fig. 1). Archaeocete whales and other fossil vertebrates were first documented from Wadi Al-Hitan more than a century ago (Beadnell, 1905), but the full extent and importance of this site has only recently come to light. An ongoing program of mapping and study initiated in 1983 (Gingerich, 1992) has documented more than 1,400 complete or partial vertebrate skeletons from an area of $\sim$200 km^2. Whale fossils found in Wadi Al-Hitan, including *Basilosaurus isis*, *Dorudon atrox*, and other recently described and related taxa (e.g., Gingerich, 2007), are fully aquatic but retain external hind limbs, providing anatomical evidence that helps to chronicle a profound land-to-sea evolutionary transition (Gingerich et al., 1990; Uhen, 2004). Wadi Al-Hitan was designated a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage site in 2005 in recognition of its paleontological importance and natural desert beauty.

Ongoing GPS mapping of traceable stratigraphic beds and fossil sites in Wadi Al-Hitan demonstrates that vertebrate remains are most abundant in discrete stratigraphic intervals (Gingerich, 1992). Several questions arise from this observation. Is the prevalence of vertebrate remains in certain stratigraphic horizons indicative of such biological events as mass mortality driven by environmental perturbation (e.g., Hogler, 1992), or is vertebrate fossil preservation controlled primarily by such physical factors as sedimentological processes that might also be reflected in sequence architecture? If under physical control, what sedimentary processes are most important in determining the distribution and preservation of vertebrate fossils in Wadi Al-Hitan, and how do these processes compare to those that have been shown to influence the fossil record of shelly marine macroinvertebrates?

GEOLOGIC CONTEXT

The principal synthesis of Eocene stratigraphy and paleogeography in northern Egypt is provided by Salem (1976), who recognized that Ypresian-middle Bartonian strata are dominated by nummulite-bearing carbonates deposited on a complicated and irregular structural topography generated primarily during Late Cretaceous tectonic shortening (Guiraud and Bosworth, 1999). The overlying late Bartonian and Priabonian strata consist primarily of fine-grained siliciclastics deposited at the edge of a northwestward-prograding shoreline. Continental, fluvio-lacustrine strata of Oligocene age are exposed west of the study area. Thus, the Eocene-Oligocene interval in the western desert of Egypt records an overall regressive sedimentary succession, from a time of maximum transgression

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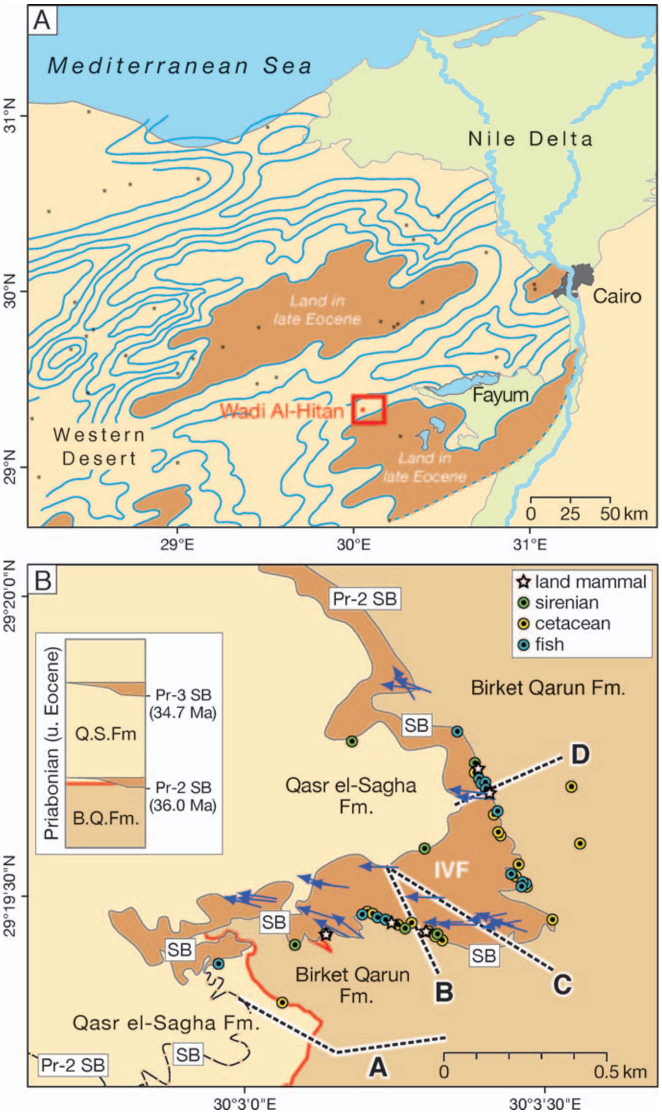

FIGURE 1—Late Eocene paleogeography of northern Egypt and map of study area. A) Paleogeography and paleobathymetry of northern Egypt in the late Bartonian–Priabonian (from Salem, 1976). Red box shows Wadi Al-Hitan World Heritage Site; contours show 50-m isopachs on late Bartonian and Priabonian strata; asterisk = location of cores used by Salem (1976) to reconstruct paleogeography. B) Detail of the study area in Wadi Al-Hitan, with measured current directions (blue arrows), fossil vertebrate locations (dots), and stratigraphic boundaries (inset) shown. SB = Pr-2 sequence boundary; IVF = incised valley fill; red line = widely traceable *Carolia* bed marking traditional boundary between Birket Qarun (B.Q.) and Qasr el-Sagha (Q.S.) Formations; dotted lines indicate section traces A–D.

in the middle Eocene to maximum regression in the early Oligocene. This history of relative sea level in Egypt is consistent with published estimates of global second-order (10^7 years) eustatic sea level (Haq et al., 1987; Miller et al., 2005; Müller et al., 2008), suggesting that there may be a strong eustatic component in the second-order Eocene–Oligocene sedimentary record of northern Egypt. Glacio-eustatically driven changes in sea level on both Milankovitch-band and longer wavelengths are expected during this time because the Eocene witnessed the initial buildup of continental Antarctic ice and a corresponding transition from a hothouse to an icehouse world (Katz et al., 2008; Lear et al., 2008).

Priabonian strata in Wadi Al-Hitan are composed of very fine grained sands, silts, muds, and sandy skeletal coquinas traditionally assigned to the lithostratigraphic Gehannam, Birket Qarun, and Qasr el-Sagha formations (Gingerich, 1992). Shell beds, consisting primarily of oysters, gastropods (turritellids), the extinct anomiid bivalve *Carolia*, and large benthic foraminifera (nummulitids), form prominent, carbonate-cemented, sandy coquina ledges that cap some coarsening-upward mudstone-sandstone and very fine grained sandstone packages. Most of the sands in Wadi Al-Hitan are heavily bioturbated, most conspicuously by *Thalassinoides*. These burrows, along with a wide variety of other trace fossils, obscure nearly all of the sedimentary structures in most of the marine deposits in Wadi Al-Hitan; however, ichnology provides important information about paleoenvironments and sedimentary processes (e.g., McIlroy, 2004).

Environmentally, Priabonian strata in the study area represent laterally heterogeneous, offshore shelf to shoreface environments. Water depths ranged from below maximum storm wave base (SWB) to above normal wave base (NWB), and environments ranged from offshore shelves to protected estuaries and embayments, as well as to continental settings. Lateral facies associations, paleocurrent directions within associated fluvial-tidal deposits (Fig. 1B; see below), and borehole data compiled for the whole of northeastern Egypt (Salem, 1976) show that Priabonian shorelines were located near and to the south and east of Wadi Al-Hitan and that the broader region occupied a protected shelf with numerous, smaller embayments (Fig. 1A). An offshore island is thought to have been located ∼50 km to the north of the study area (Fig. 1A; Salem, 1976), which would have contributed to the sheltered, semi-enclosed, and protected character of the Wadi Al-Hitan shelf.

LITHOFACIES, SEQUENCE STRATIGRAPHY, AND VERTEBRATE TAPHONOMY

Haq et al. (1987) recognized three, third-order (10^6 years) marine sequences in the Priabonian—TA4.1 through TA4.3—defined by four sequence boundaries, Pr-1 through Pr-4 (Fig. 2; Haq et al., 1987; Hardenbol et al., 1998). We find that this same third-order architecture is closely reproduced in the Priabonian of Wadi Al-Hitan, corroborating the eustatic interpretation of Haq et al. (1987). All four sequence boundaries are present at Wadi Al-Hitan, but here we focus on the interval around the second sequence boundary (SB), Pr-2, which separates early Priabonian sequence TA4.1 from middle Priabonian sequence TA4.2 (Fig. 2). Age assignment is based on overall sequence stratigraphy and, more importantly, on calcareous nannofossil biostratigraphy indicative of an NP18 age (see later discussion). Here we focus on sequence stratigraphy and vertebrate preservation in early Priabonian sequence TA4.1 for several reasons: (1) this sequence is exposed at the World Heritage site, (2) a prominent sea-level fall responsible for generating a stratigraphically important surface of subaerial erosion and large-scale fluvial incision (Pr-2; see below) has not previously been recognized in Egypt, and (3) this part of the succession has yielded all of the whale fossils that have been described so far from this World Heritage site. It should be noted, however, that whale fossils are known from underlying carbonate-rich Bartonian strata and that we have also observed whale remains in the younger TA4.2 sequence.

Figure 3 summarizes the measured stratigraphic-section data and our sequence stratigraphic interpretations for the Priabonian strata in Wadi Al-Hitan. Figure 4 provides an outcrop panorama with major stratigraphic features and two measured section traces identified. Each of the major lithofacies, their associated vertebrate remains, and our environmental and sequence stratigraphic interpretations are described below in ascending stratigraphic order.

Mudstone-Sandstone Parasequences of the Late Transgressive Systems Tract (TST)

The base of the measured interval is within the Birket Qarun Formation (Gingerich, 1992) and consists of three, ∼3–5-m-thick mudstone-sandstone packages that coarsen upward from clean, light purplish-gray mudstone with rare body fossils to silty or sandy, brownish, bioturbated mudstone with small nuculid bivalves and gastropods. These silty mudstones coarsen upward and are capped by ledge-forming, tan, burrowed, very fine grained calcareous sandstones that are traceable continuously over the

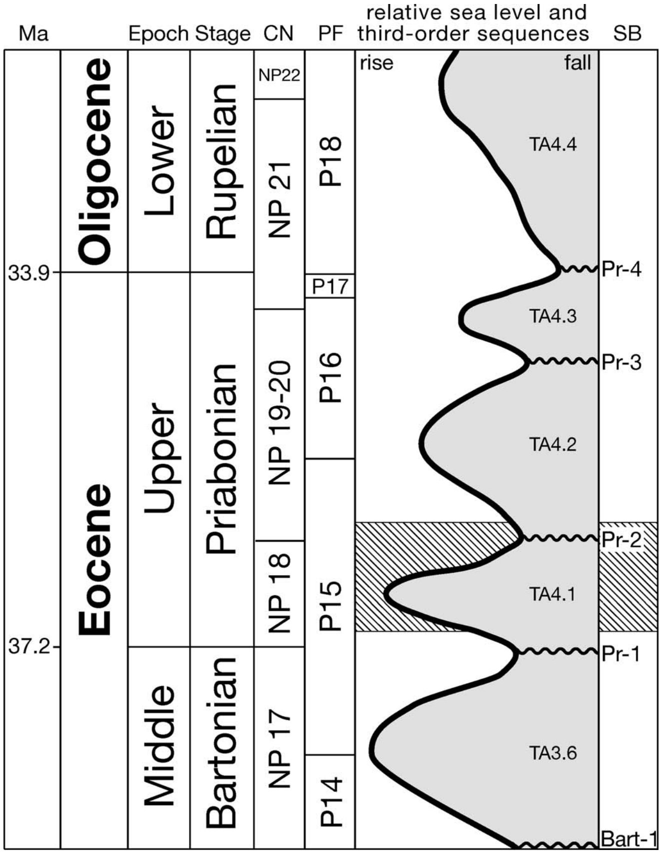

FIGURE 2—Late Eocene–Oligocene timescale, inferred cycles in eustatic sea level, and third-order sequence boundaries (modified from Hardenbol et al., 1998). Studied interval shown (approximately) by hatched area. CN = calcareous nannoplankton zones; PF = planktonic foraminfera zones; SB = sequence boundary.

entire study area (Fig. 1B) and over the greater Wadi Al-Hitan region (~225 km²). Bedding and sedimentary structures in the capping sandstones are obscured by bioturbation and, more problematically, disrupted by late diagenetic gypsum; however, there is evidence for hummocky cross stratification (HCS) and wave ripples at some locations. The sandstone ledges have sharp upper contacts with the light purplish-gray mudstones that constitute the base of each cycle (Fig. 3).

Invertebrate fossils are not prominent anywhere throughout this part of the measured section, but a low-diversity assemblage of small (~1 cm) nuculid bivalves and gastropods is present in the yellowish-tan, calcareous, silty mudstones of each cycle. Calcareous nannoplankton indicative of an NP18 age, including *Discoaster tani nodifer* and *Chiasmolithus oamaruensis*, are abundant and well preserved in calcareous silty mudstones, indicating that the shelf environment was well connected to the open marine system.

Vertebrate fossils in this part of the section consist primarily of *Basilosaurus*, although a few specimens of *Dorudon* have also been recovered (Table 1). Nearly all of the skeletons are found on or within the tops of the coarsening-upward mudstone-sandstone packages. It is difficult to determine the exact position of large whale skeletons located in weathered outcrops—individual vertebrae are up to 35 cm long (Fig. 5)—because the very fine grained sandstones that cap each package are thin (<60 cm). Nevertheless, mapping shows that most of the whale remains are located within 0.5 m of the sharp sandstone-mudstone contact that defines each package boundary. One skeleton has, however, been found in muddy deposits just below the capping sandstone beds, and this specimen appears to be better preserved than most of the whales in this interval. Although whale skeletons are concentrated at the top in each of the three sandstone packages, none of the sandstones can be considered a bone bed because the bones are rather widely scattered. Only 32 vertebrate fossil sites were encountered during the mapping of ~3.6 linear km of nearly continuous exposure of all three packages (Table 1).

Many of the whale skeletons in this part of the section are complete or nearly so (Fig. 5A–C), but skeletons within the same sandstone bed vary in the extent to which they are articulated (i.e., bones located in anatomically correct positions). Most complete specimens clearly preserve the anterior-posterior (AP) axis and the relative positions of major skeletal elements along this axis, even though the AP-axis itself is often curved into a semicircular shape (Fig. 5D). Small bones and bones that are easily transported (e.g., ribs and scapulae) tend to be more widely dispersed about complete skeletons than large or heavy bones such as vertebrae (Fig. 5B). Figure 5A–C shows typical states of preservation for skeletons in this interval. Individual, isolated whale bones have been observed within the sandstone capping beds, but the majority of remains appear to derive from complete or nearly complete skeletons that were disarticulated on the sea floor prior to final burial.

Interpretation.—We interpret this part of the section to represent three shallowing-upward parasequences that record an overall minor deepening during the latest TST of sequence TA4.1 (Fig. 2). Evidence for continued deepening hinges primarily on the thickness and character of the overlying lithofacies (see below), and, given the similarity of these parasequences to each other and to the overlying deposits, it is possible that this part of the section is within the highstand systems tract (HST). Lack of rock exposure in the study area prevented the reliable downward extension of the section, but regional exposures suggest that the base of the measured sections may be within ~20 m of the argillaceous carbonates (marls) and nummulitic limestones of Bartonian sequence TA3.6 (Fig. 2). Water depths in this part of the section are inferred to have ranged from below maximum SWB (mudstone at the base of parasequences) to above average SWB (very fine-grained sandstone at parasequence tops).

The very fine sandstone that caps each parasequence represents amalgamated and winnowed storm deposits that received their final overprint during marine flooding and sediment starvation. Sedimentologic evidence for sediment starvation includes (1) a sharp mudstone-sandstone contact that marks a lithological discontinuity in otherwise rather uniformly coarsening-upward mudstone-sandstone packages; (2) the amalgamation of storm beds in the capping sandstones; and (3) intense bioturbation of capping sandstones that stand in contrast to poorly bioturbated or undisturbed overlying mudstone.

Whale skeletons occur with higher frequencies on the marine flooding surface (MFS) in this part of the section as a result of environmental and temporal condensation during periods of lower net rates of sediment accumulation. Taphonomy and patterns of bone dispersal indicate that storm currents may have played an important role in disarticulating complete whale skeletons and dispersing bones on the sea floor, although scavenging by sharks and other whales is also likely to have been an important disarticulation and dispersal mechanism. We have not yet observed any direct evidence for the scavenging of whale carcasses. Whale skeletons on the MFS vary in their degree of disarticulation, and this may reflect differential arrival times of carcasses to the sea floor and resultant variation in exposure times, which is consistent with sedimentological evidence for low net rates of sediment accumulation. It is somewhat surprising that no direct evidence for colonization of whale bones by epibenthic organisms has been observed (e.g., Allison et al., 1991), although an exhaustive, targeted search for such remains has not yet been conducted. The general paucity of macroinvertebrates in this part of the section does not make the absence of colonizing macroinvertebrates particularly unusual when observing whale remains in the field.

Thick Mudstone-Sandstone Parasequence of HST

The upper sandstone ledge of the late TST, described above (Fig. 3) contains disarticulated whale remains and has a sharp contact with a thick, overlying purplish-gray mudstone that is mostly devoid of body and trace

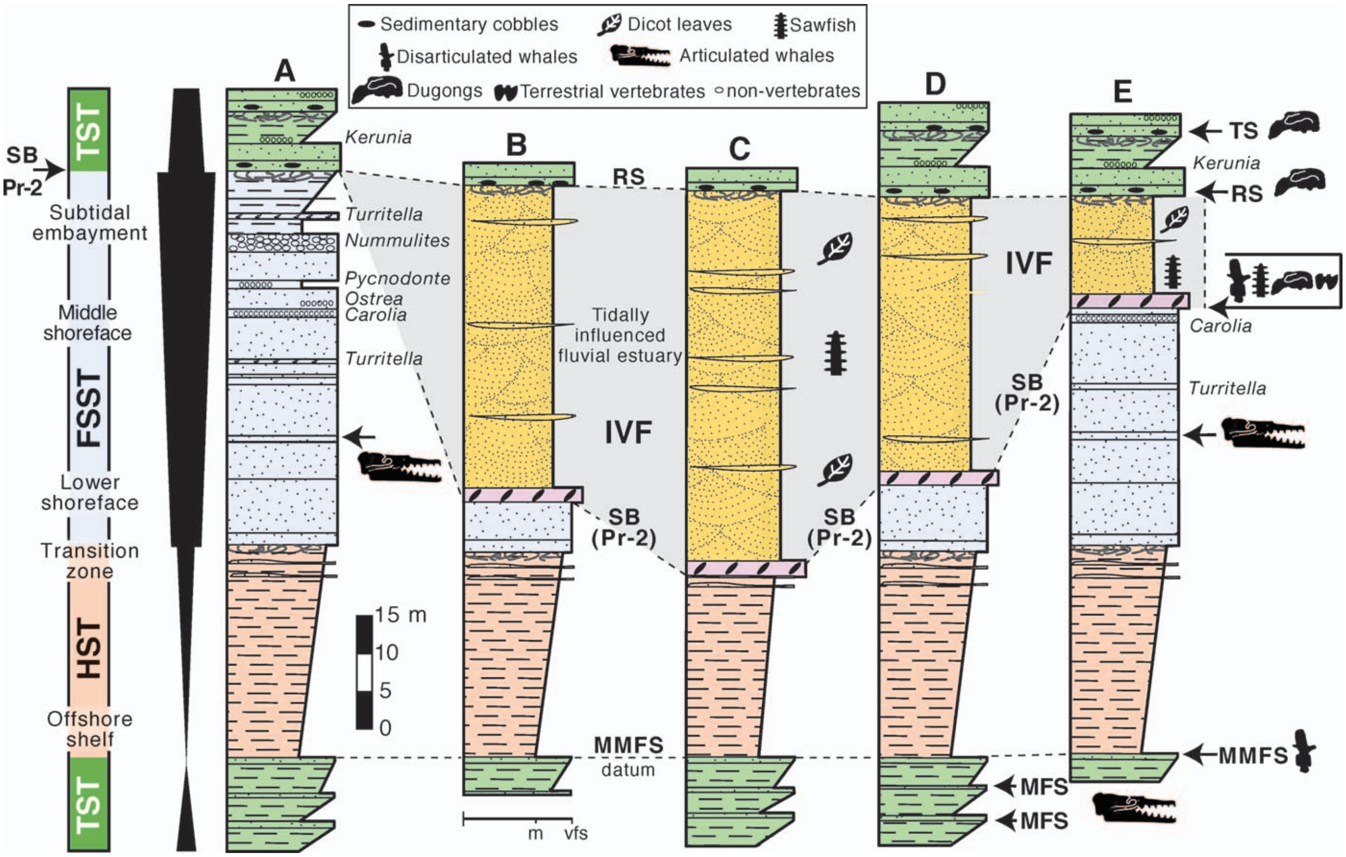

FIGURE 3—Measured stratigraphic sections, stratigraphic position of vertebrate remains, and sequence stratigraphic interpretation of study area. Location of section traces A–D is shown in Fig. 1B. Section trace E is located 1.2 km north of area shown in 1B. Note that lenticular bedforms indicated within sections contained by the shaded area (labeled IVF) represent clinoforms. Inclined cobbles indicate weak imbrication. SB = sequence boundary Pr-2; HST = highstand systems tract; MMFS = maximum marine flooding surface; MFS = marine flooding surface; TS = transgressive surface; TST = transgressive systems tract; FFST = falling stage systems tract; IVF = incised valley fill.

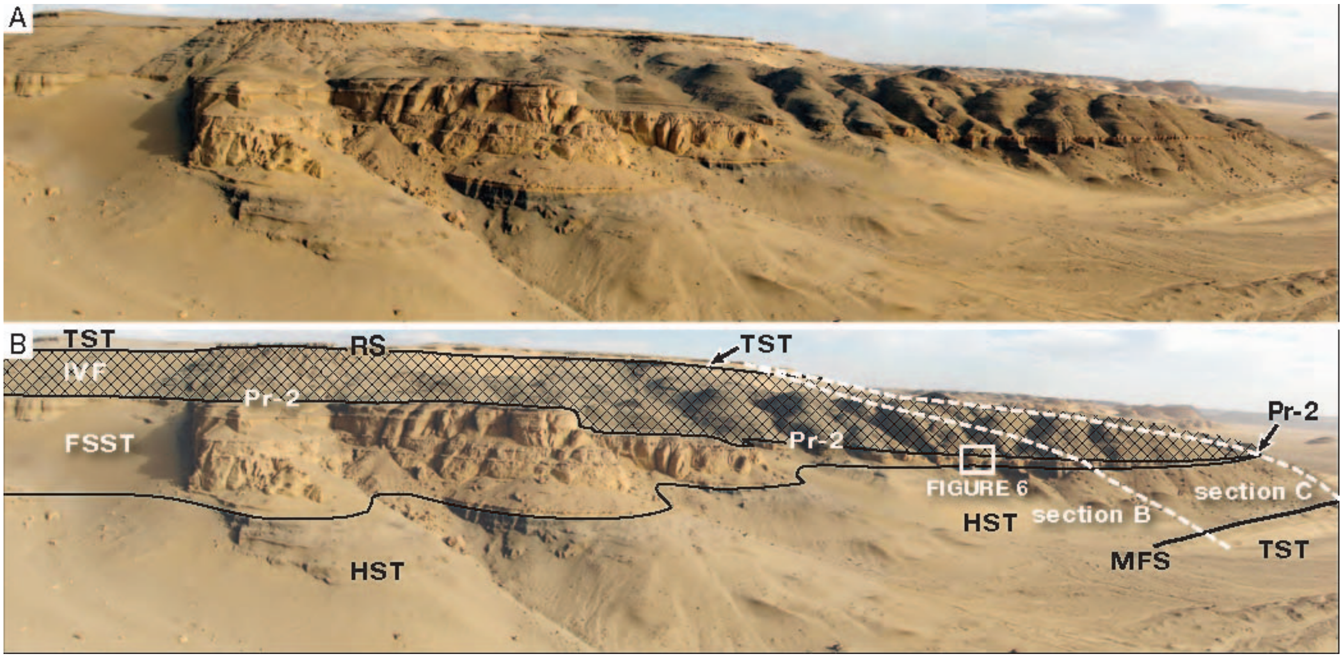

FIGURE 4—Outcrop panorama of Birket Qarun and Qasr el-Sagha formations. A) Original image mosaic. B) Image mosaic with important stratigraphic features labeled; section traces for Section B and Section C (Fig. 3) are shown by white dashed lines and location of Figure 6 indicated by box. Abbreviations as in Fig. 3.

TABLE 1—Vertebrate taphonomy and abundance in relation to stratigraphic position. Each value shows the number of mapped fossil sites. Average taphonomic condition of the vertebrate fossils at each of these sites is summarized by the row titled typical preservation. Average number of sites per linear distance surveyed is given by sites per km, which provides an indication of the approximate absolute abundance and relative abundance of vertebrates in each stratigraphic position. Here, a vertebrate site (specimen) constitutes an occurrence of taxonomically identifiable vertebrate remains, excluding shark and ray teeth.

	Sequence TA4.1		Sequence TA4.2	
	L-TST PS† (3.6 km)#	FSST (4.6 km)#	SB Pr-2 (1.6 km)#	E-TST PS§ (1.2 km)#
Discontinuity	marine flooding surface: offshore mudstone on offshore-transition zone sandstone (n = 3)	marine erosion surface: shoreface sandstone on shoreface sandstone (n = 15)	basal scour: fluvial channel on shoreface to offshore sandstone and mudstones (n = 1)	marine flooding surface: shoreface sandstone on estuary mudstone or shoreface sandstone (n = 2)
Fossils*				
Barytherium	-	-	3	-
Basilosaurus	29	2	3	-
Crocodilian	-	-	2	-
Dorudon	3	4	11	-
Dugong	-	-	6	3
Sawfish	-	-	2	1
Sea Snake	-	-	4	-
Turtle	-	-	2	-
Invertebrates	rare to absent	common to abundant	rare	abundant
Vertebrate taphonomy				
Sites per km	8.9	1.3	20.6	3.3
Typical preservation	Complete disarticulated unfragmented	Complete articulated unfragmented	Incomplete isolated fragmented	Variable disarticulated variable

* Number of mapped sites (specimen); shark and ray teeth are abundant in SB Pr-2, some FSST PS, and the E-TST but were not counted; macroinvertebrates were not mapped so abundances are qualitative.

† Late TST located below Pr-2, including maximum MFS (Fig. 3).

§ Early TST above Pr-2, including ravinement surface (Fig. 3).

Approximate linear outcrop distance traversed to map vertebrate fossil sites.

fossils. This thick, muddy interval, also assignable to the lithostratigraphic Birket Qarun Formation (Gingerich, 1992), is lithologically similar to the thinner, muddy intervals that form the base of each parasequence in the underlying TST. Like the underlying parasequences, this muddy interval coarsens upward, becoming noticeably silty at ~5 m above the base. Scattered, reddish brown, sideritic nodules are present throughout the lower two-thirds of the interval and a low-diversity assemblage of small nuculid bivalves and gastropods, similar to those found in the underlying calcareous mudstones of the late TST, occurs beginning several meters above the basal mudstone-sandstone contact.

The most important sedimentological features in this thick, dark, muddy interval are thin (1–30 cm) interbeds of poorly cemented, very fine grained, white sandstone (Fig. 6A). These prominent sandstone beds, most of which vary in thickness laterally, have sharp upper and lower contacts, are absent in the lower two-thirds of the unit, and become thicker and more closely spaced up-section. The majority of the sandstone beds exhibits well-preserved and unambiguous hummocky cross stratification (HCS; Fig. 6B) or wave ripples. Gutter casts filled by laminated, very fine grained sandstone are also present at the base of some of the HCS sandstone beds or occur as isolated sandy stringers. A minority of the sandy interbeds lack sedimentary structures because they have been completely homogenized by bioturbation with the surrounding mudstone, primarily by *Thalassinoides*.

Outcrop characteristics produced by the overlying thick mudstone typically include a broad, flat contact between the mudstone and underlying sandstone ledge of the TST that bears whale remains (Fig. 3). This broad surface has favored the accumulation of modern, massive caliche rinds and desert pavements, thereby making reliable estimates of vertebrate abundance difficult. No vertebrate remains have been recovered from the thick mudstone itself, although some weathered bones with concretionary rinds have been found in float. Some of these remains may derive from the scattered concretions that occur in the lower half of the mudstone.

Interpretation.—The base of the thick, coarsening-upward, widely traceable mudstone that overlies the last parasequence of the late TST is interpreted to represent the time of maximum sediment accommodation and an expanded parasequence within the HST of sequence TA4.1 (Fig. 3). The maximum MFS is interpreted to occur just above the last sandy parasequence of the underlying TST, but there is little evidence that this surface experienced significantly more sediment starvation or environmental condensation than the three flooding surfaces in the underlying TST. Instead, a slowing rate of sea-level rise and the release of abundant sediment from shoreface sediment traps appear to have resulted in the accumulation of a thick parasequence or parasequence set on the maximum MFS.

The HST mudstone was initially deposited below maximum SWB in hypoxic bottom waters, as evidenced by relatively clean, purplish mudstone that lacks body fossils or prominent bioturbation. During the deposition of this mud, the sea floor was located below the wind-mixed surface layer and bottom circulation may have been restricted by a pycnocline. Water depth appears to decrease uniformly up-section, with storm-deposited, very fine grained sandstone interbeds providing a clear indication of an overall shallowing from below to above maximum SWB. It is also possible that sandy interbeds interpreted here to represent single storm events (Fig. 6B) might also cap parasequence-scale, shallowing-upward cycles that have relatively cryptic signatures within the surrounding mudstones. A minority of the storms responsible for the interbedded HCS sands appears to have resulted in the temporary oxygenation of offshore bottom waters and the transient colonization of the sea floor by crustaceans that subsequently bioturbated the sandy storm beds, possibly as doomed pioneers (*sensu* Grimm and Foellmi, 1994). Net sediment accumulation rates were high enough and water depths great enough to prevent the amalgamation of most storm deposits.

Whale remains are preserved on the maximum MFS, but there is a paucity of vertebrate fossils in the HST muddy interval. This is attributed to a large increase in average rates of sediment accumulation (i.e., to a dilution effect) and to the lack of sedimentologically well-defined MFS that would have resulted in a greater degree of temporal and spatial averaging. It is also possible that whales were less frequent in the most

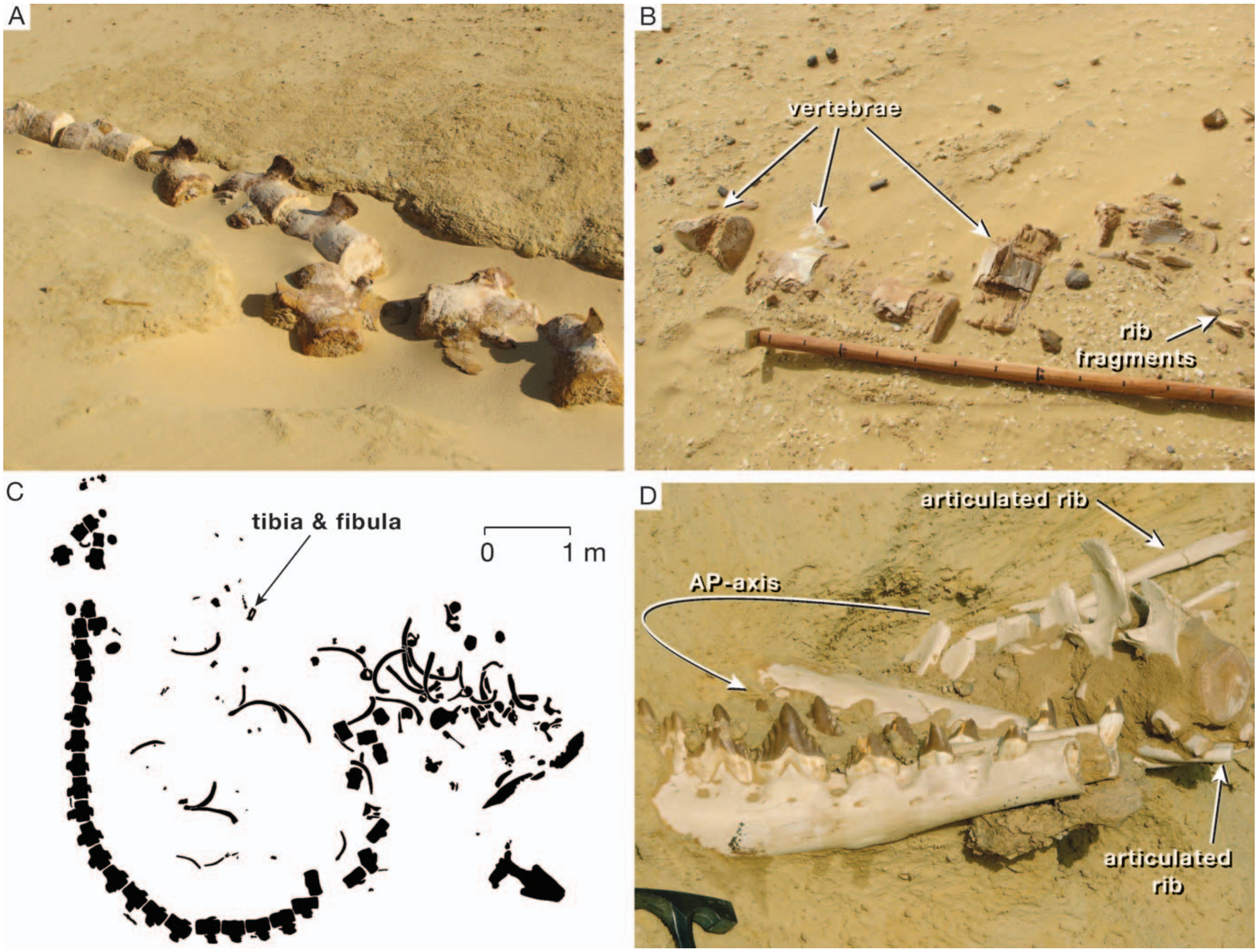

FIGURE 5—*In situ* whale remains in Birket Qarun Formation. A) *Basilosaurus* vertebral column within sandy parasequence top of TST; scale nearly the same as in B. B) As in A, but showing semi-articulated rib fragments; skeleton abraded by wind-blown sands; scale bar shows 10-cm increments.C) Map view of complete *Basilosaurus* from a parasequence top in TST. D) Complete and articulated *Dorudon* from within the very fine grained sandstone of FSST. Many of the articulated *Dorudon* skeletons in Wadi Al-Hitan have a strongly curved anterior-posterior (AP) axis; this specimen has its head juxtaposed against the posterior thorax.

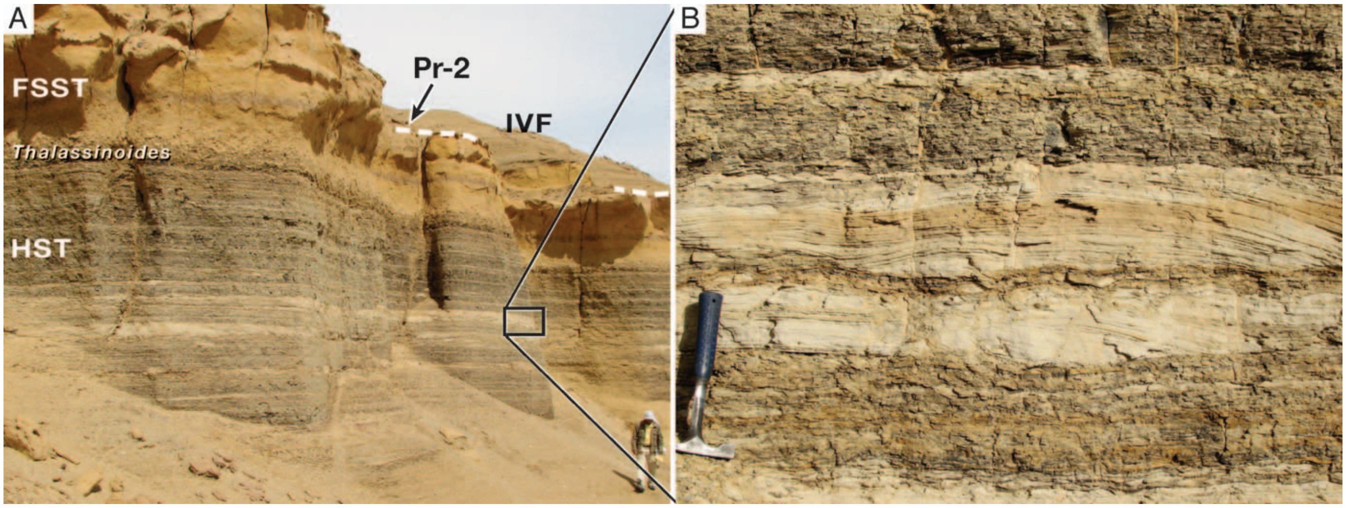

FIGURE 6—Contact between HST mudstone and FSST very fine grained sandstone in Birket Qarun Formation. A) Contact between upper part of purplish-gray silty mudstone and FSST yellowish-tan sandstone; SB Pr-2 and overlying IVF are visible near the top of the photograph. B) Large convex-up hummock of very fine sand within the top of the HST mudstone; see Fig. 4 for photo location.

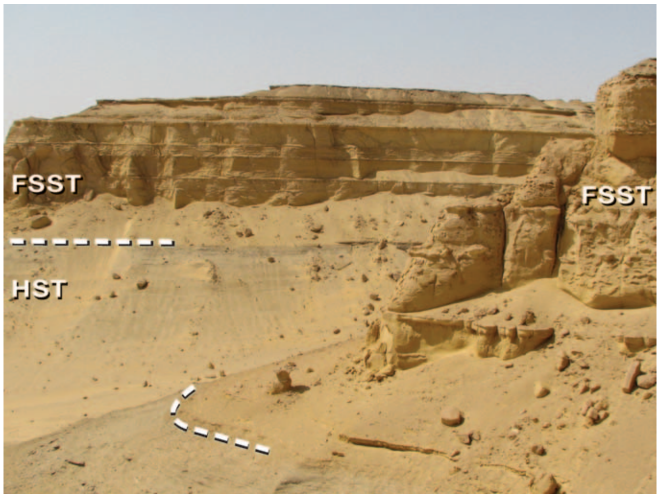

FIGURE 7—Outcrop view of FSST and underlying slopes of HST mudstone in Birket Qarun Formation. Note laterally continuous ledges in FSST sandstone. Break in slope near top of cliff reflects increasing mud content up-section and is within the Qasr el-Sagha Formation.

offshore environments preserved in Wadi Al-Hitan and that the flux of whale carcasses to the sea floor was much lower in these offshore environments than it was in the shallower water environments represented by the rest of the section.

Sandy Cycles of the Falling Stage Systems Tract (FSST)

The coarsening-upward HST mudstone has a very sharp and widely traceable contact with overlying yellowish-tan, burrow-homogenized, very fine grained sandstone. The contact between the mudstone and the sandstone is riddled with prominent sand-filled *Thalassinoides* that extend up to 50 cm into the underlying silty HST mudstone. A complete succession of this part of the TA4.1 sequence is only preserved at section A (Fig. 3), though portions of the sandstone occurring elsewhere are nearly identical. In the study area, the sandstone consists of ∼3–10-m-thick cycles of homogenous, very fine grained, yellowish-tan sandstone (Fig. 7) with variable amounts of invertebrate shells and shell fragments. Cycle boundaries in the basal 20 m are defined primarily by changes in the style and increases in the intensity of bioturbation and, in the upper 20 m, by both bioturbation and an increase in the abundance of invertebrate fossils and calcite cementation. The latter is due to the dissolution of aragonitic shells and their reprecipitation as porosity-filling calcite. No physical sedimentary structures have been observed in the sandstone due to pervasive bioturbation.

Invertebrate diversity and abundance increase up-section. A prominent, densely packed bed of the anomiid bivalve *Carolia*, marking the traditional boundary between the Birket Qarun and Qasr el-Sagha formations, occurs near the top of the interval (Fig. 1B; Fig. 3, section A and E). In the upper quarter of section A, within the Qasr el-Sagha Formation, greenish-gray and buff-colored mudstone is interbedded with densely packed sandy coquinas consisting primarily of nummulitid foraminifera, turritellid gastropods, and oysters, though individual beds tend to be dominated by one taxon. Some of the muddy and sandy packages near the top of this interval contain localized pycnodontid oyster clusters with articulated, extraordinarily thick-shelled individuals up to 18 cm wide. Large *Thalassinoides* are present throughout the entire interval but are prominent at the basal mudstone-sandstone contact and at cycle bases, where sand-filled and shell-fragment–filled burrows penetrate into underlying strata.

Vertebrate remains are relatively rare in this part of the section (Table 1). The few whale fossils that have been found occur in the yellowish, very fine grained sandstone of the Birket Qarun Formation, and these skeletons are typically complete, articulated, and very well preserved (Fig. 5D). *Dorudon* is the most commonly recovered whale in the sand, though *Basiliosaurus* skeletons have also been found (Table 1). A locality near section A, in FST sands of the Birket Qarun Formation, yielded a complete and articulated *Dorudon atrox* specimen that provided casts now on display in many museums around the world. With few exceptions, vertebrate skeletons are located at the tops of burrow- and shell-defined cycles that form subtle ledges on outcrop (Fig. 7). One *Dorudon* skeleton found within the middle of a sandy cycle is exceptionally pristine, with only minor displacement of loosely articulated bones (Fig. 5D). Only dugongs have been found in the greenish-gray mudstones and sandy skeletal coquinas of the Qasr el-Sagha Formation, in the upper part of this interval (Fig. 3).

Interpretation.—The sharp contact between the silty mud of the HST and the overlying very fine grained sandstone (Fig. 6–7) is interpreted to represent a regressive surface of marine erosion followed by a rapid influx of very fine sand during the initiation of a fall in sea level. The resultant decrease in accommodation prompted the rapid offshore export of very fine grained sandstone and the emplacement of a thick, sandy FSST above offshore HST silty mudstones. Sedimentation rates were comparatively high throughout most of the FSST, particularly in the lower half of the deposit, but shallowing resulted in the oxygenation of bottom waters and the colonization of the sea floor by benthic animals, particularly bioturbators. *Thalassinoides* occurring at the HST-FSST contact may reflect marine erosion of water-saturated mud and the establishment of a firmground on offshore-transition zone mud. Alternatively, the burrows could have originated from a surface within the sands above the mud-sand contact and only penetrate downwards into the mud.

The thickness of the FSST relative to the HST in the study area (Fig. 3) might seem unusual, and in up-dip directions the FSST is expected to be absent. Regional mapping, however, shows that the study area is located just offshore from the slope break formed by the progradational HST clinoform (results not presented in this report). The study area is, therefore, optimally positioned along the shelf to preserve a thick FSST and a comparatively thin HST. Up dip, the FSST amalgamates with a composite surface that marks a SB and the ravinement surface (RS) of the overlying sequence. The FSST in the study area is similar in thickness and in character to FSSTs from the Cretaceous Interior that abruptly juxtapose middle-shoreface sandstones on transition-zone silty mudstones (e.g., Ferron Sandstone; Edwards et al., 2005).

Cycle boundaries within the FSST reflect minor temporal and spatial condensation, probably as a result of forced regression, but this minor condensation was sufficient to permit accumulation of a greater number of invertebrate shells and vertebrate remains than is typically found within the surrounding sediment. Further higher-resolution analysis is required to ascertain the specific environmental signature of the cycle boundaries. The high quality of preservation of vertebrate remains throughout the FSST is attributed to relatively high sedimentation rates overall. Rarity of vertebrate remains in general (Table 1) is attributed to a shift in environment up-section from an offshore shelf to a shallow, protected embayment and to higher rates of sedimentation that resulted in the dilution of skeletal input. The presence of rare but exceptionally well-preserved skeletons within cycles, rather than at cycle tops, provides additional evidence for rapid sediment accumulation and minor condensation along cycle boundaries.

The transition from sand-dominated cycles to mixed mud-sand cycles is interpreted to record the rapid infilling of the basin combined with continued sea-level fall. This sea level fall resulted in ponding, or the formation of a broad, protected shallow embayment with no analogue lower in the section. Continued sea-level fall reduced this remnant seaway further and eventually drained it completely, resulting in subaerial exposure and erosion or nondeposition (discussed in the following section). Falling sea level, thus, did not simply result in the seaward migration of a static shoreface, but it resulted in the development of a qualitatively

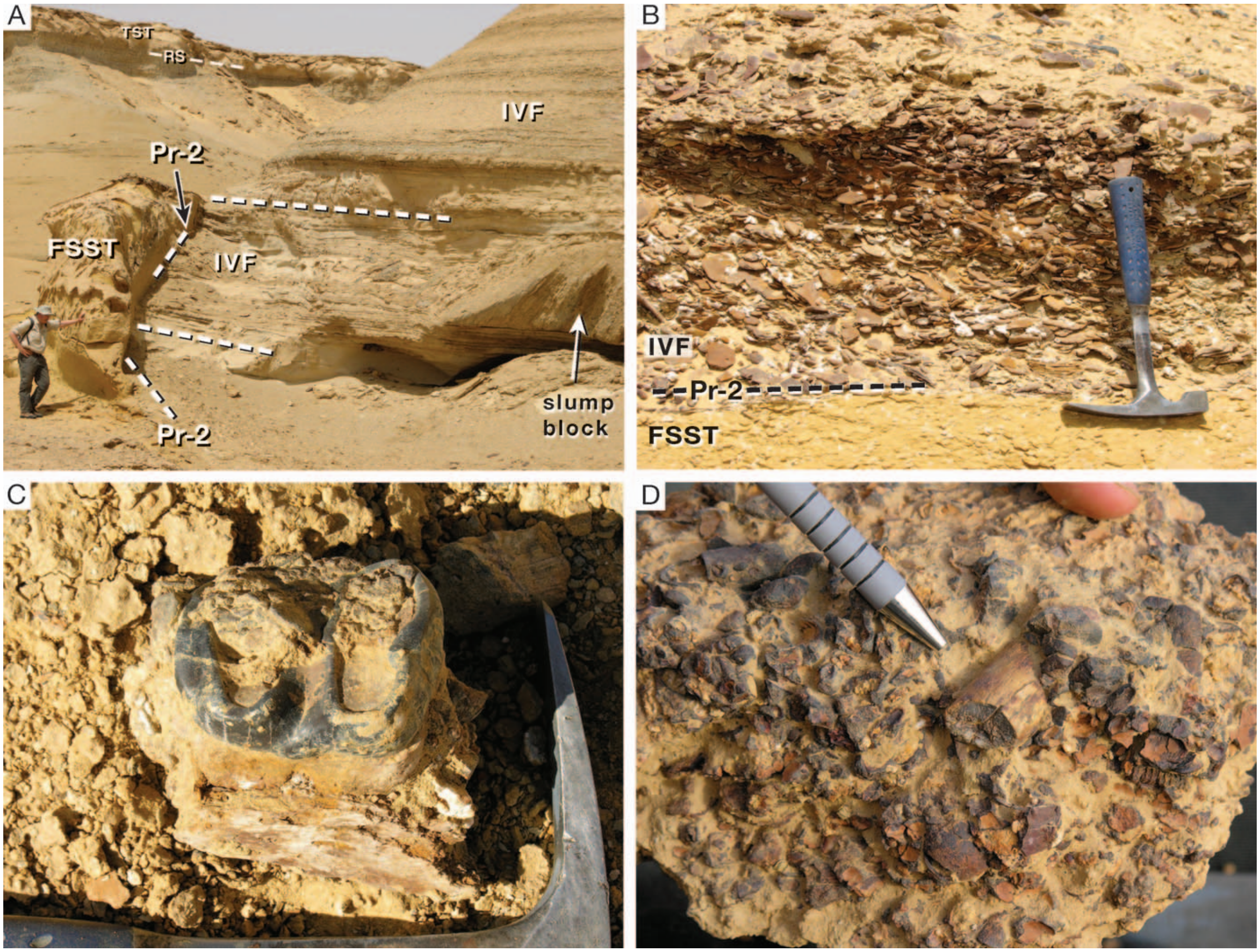

FIGURE 8—SB Pr-2 and IVF in Birket Qarun Formation. A) Cutbank developed on erosional sequence boundary; massive lunate exposure on left, with Gingerich leaning against it, is an erosional remnant of very fine grained sandstone from the FSST; on the right, thinly bedded, ripple-laminated very fine grained sandstone and mudstone abuts concave erosional surface. A large slump block of ripple-laminated sandstone and mudstone has foundered from above the erosional surface and toppled into a scour fill formed within the IVF. B) Imbricated pebble conglomerate developed on the SB. C) Molar tooth and jaw fragment of land mammal *Barytherium* in SB conglomerate. D) Sirenian rib fragment in thin SB conglomerate.

different shelf geomorphology from that characterizing the underlying TST and progradational HST.

Fluvial Conglomerate on SB Pr-2 (LST)

The most important stratigraphic feature in Wadi Al-Hitan is a discontinuous, variably thick (0–70 cm) conglomerate consisting of pebbles and cobbles of platy, limonite-goethite–cemented, very fine grained sandstone (Fig. 8). Where the conglomerate is thick, the platy sandstone cobbles are typically imbricated and indicate current flow to the west-northwest (Fig. 8B). The contact between the conglomerate and the underlying strata is always very sharp and exhibits considerable relief that truncates horizontal bedding in underlying marine strata on many different scales (Fig. 3, 8A). All of the beds below the conglomerate are laterally continuous in the study area, except where they are interrupted by the conglomerate-bearing surface. For example, the prominent *Carolia* bed, marking the traditional boundary between the lithostratigraphic Birket Qarun and Qasr el-Sagha formations, occurs at the same height above the MFS in sections A and E but is absent in sections B–D where the conglomerate occurs lower in the section. In some places (e.g., near section C), the sandstones of the thick FSST are completely absent, but sand-filled *Thalassinoides* characteristic of the HST-FSST contact remain in the few centimeters beneath the conglomerate, thereby providing conclusive evidence that the FSST sandstone previously existed below the conglomerate but was removed by erosion.

Continuous physical tracing and measured sections (Fig. 3) demonstrate that the conglomerate surface has more than 45 m of vertical relief over the entire study area and up to 3 m of relief at the scale of individual exposures. For example, Figure 8A shows a vertically oriented contact between the conglomerate surface and flat-lying FSST sands. This contact can be traced continuously over ~10 m into a sharp horizontal contact with a thick, imbricated pebble conglomerate bed (Fig. 8B). Such topographically irregular contacts (Fig. 8A) are common on this surface, which is often characterized by a discontinuous iron oxide rind.

Vertebrate remains are abundant and highly diverse in the conglomerate (Table 1, Fig. 1), but they consist of isolated bones and teeth, most of which are fragmented and abraded to various degrees (Fig. 8D). *Dorudon* vertebrae are the most common whale remains, but isolated bones of *Basilosaurus*, dugongs, crocodilians, turtles, and a variety of other vertebrates have also been recovered (Table 1). Shark and ray teeth are also very abundant in this conglomerate. Most notable among the fossils found in the conglomerate are several specimens of the semi-aquatic, but entirely continental, proboscidians *Moeritherium* and *Barytherium*. Remains of *Barytherium*, which have not been found at any other stratigraphic level in Wadi Al-Hitan, include a tooth and jaw fragment (Fig. 8C), as

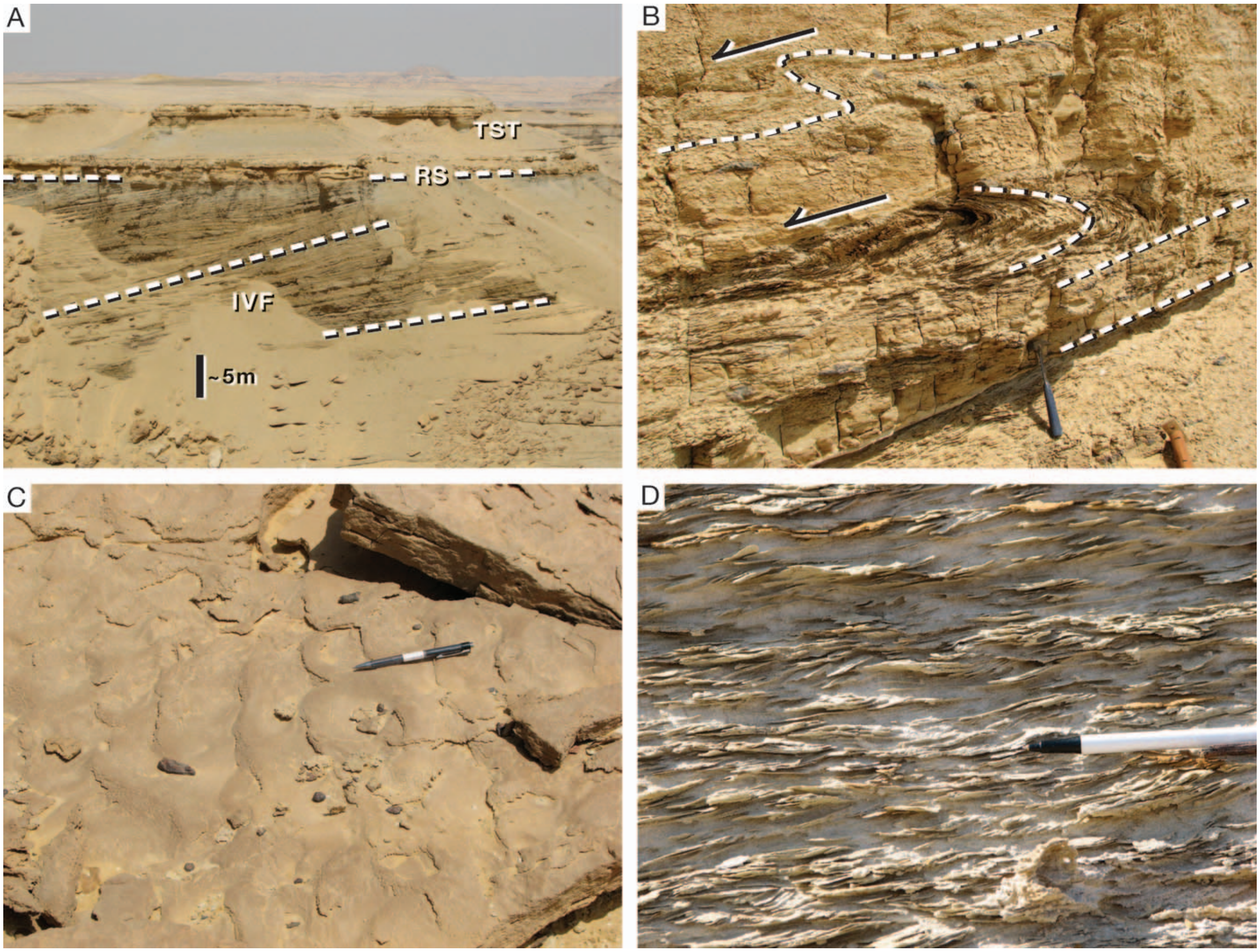

FIGURE 9—IVF and transgressive RS. A) Outcrop view showing large clinoforms (bedding along inclined dashed lines) truncated by RS; the first parasequence of the TST in sequence TA4.2 (Fig. 2) is within the sandy ledge above the IVF; the second parasequence is thicker and has greenish-gray mudstone at its base. B) Down-dip slump folds on a clinoform within the IVF. C) Asymmetric, out of phase linguloid ripples in an unusually well cemented, fine-grained sandstone within the IVF; beds were measured for current directions in Fig. 1B, D) Climbing, flaser-bedded ripples in IVF.

well as a partially articulated lower hind limb. The partial *Barytherium* limb is the only semi-articulated fossil recovered from the conglomerate.

Interpretation.—We interpret the thin, discontinuous, imbricated conglomerate and associated vertebrate remains to indicate fluvial incision and physical reworking of FSST and HST marine sediments during a fall in sea level that resulted in subaerial exposure. The resultant surface of fluvial erosion constitutes a SB interpreted to be correlative to Pr-2 (Fig. 2) of Haq et al. (1987), based on calcareous nannoplankton biostratigraphy and large-scale sequence architecture in the Wadi Al-Hitan region. The irregular paleotopography developed on the SB, including clearly defined erosion surfaces within FSST marine sandstones (Fig. 8A), indicates exhumation of underlying marine deposits and the development of an incised river system that indicates a minimum base level fall of 45 m. The conglomerate and underlying SB can be continuously traced into an interfluve in section A. Although we would expect the development of paleosols on the interfluve, the SB in section A is cryptic because all evidence of subaerial exposure has been scavenged during subsequent marine transgression (explained later).

Most of the vertebrate remains in the conglomerate were eroded from marine deposits and transported short distances as sedimentary clasts in the fluvial system. The marine remains are, thus, allochthonous and represent reworked and eroded fossils left behind as erosional lags at the base of fluvial channels. Continental vertebrate remains derive directly from animals that lived in and adjacent to the fluvial system and were, therefore, subject to less taphonomic and diagenetic modification than marine remains. Platy, iron-cemented sandstone cobbles were similarly derived from the exhumation and reworking of *Thalassinoides*, which tend to be better cemented by iron oxides than the surrounding FSST sandstones. The iron cementation prevalent in the sandstone clasts, and locally on the SB itself, may indicate subaerial exposure and meteoric diagenesis during subaerial exposure.

Flaser-Bedded and Rippled Sand of Incised Valley Fill (IVF) of Initial TST

A succession of flaser-bedded, cross-laminated, very fine grained to fine-grained, white, poorly cemented sandstone with thin, greenish-gray mud interbeds (Fig. 9) overlies the imbricated pebble conglomerate wherever it is found. This flaser-bedded interval is lens-shaped in large-scale geometry (Fig. 3). It is, however, remarkably homogeneous lithologically. Ripples within the flaser-bedded sand consist primarily of asymmetric, out-of-phase, linguoid sand waves (Fig. 9C) that are often climbing and that typically have thin laminae consisting of alternating mud-sand couplets (Fig. 9B). Measurement of the mean transport direction on 22 well-exposed bedding planes indicates a consistent west-northwest direction across the study area (Fig. 1B). This transport vector is similar to the flow direction indicated by imbricated cobbles in the underlying Pr-2 conglomerate.

Large-scale clinoforms more than 8-m high are clearly visible within the flaser-bedded interval (Fig. 4, 9A). The beds within these clinoforms consist of finely ripple-laminated and flaser-bedded sand that indicate similar transport vectors regardless of dip direction, which is variable, but generally west of north-south. Decimeter-scale, ripple-laminated horizons within the clinoforms show evidence of down-dip, bedding-parallel slippage and soft sediment deformation (Fig. 9B), and growth faults have been observed. Broad (5–10-m-wide), low-angle scours are common within the flaser-bedded sandstone and are filled with either tabular cross-bedded, very fine grained, white sandstone or flaser-bedded sandstone similar to those found throughout the rest of the interval. The subaqueous erosive channels responsible for the broad scour-and-fill structures reworked the flaser-bedded sand, as evidenced by greenish-gray mud rip-up clasts and by foundered, large blocks of flaser-bedded sandstone (Fig. 8A).

Bioturbation and invertebrate body fossils are rare in this interval. The rostra of two sawfish, which are known to swim far upstream in modern rivers, are the only vertebrates known, and no invertebrate fossils have been recovered. Well-preserved, whole dicot plant leaves are abundant in finer-grained beds throughout the interval. Organic-rich beds with abundant plant debris are also present.

Lithostratigraphic definitions for the Birket Qarun and Qasr el-Sagha formations have not satisfactorily accounted for this unit, and it has, therefore, been inconsistently assigned to both formations, primarily based on its variable stratigraphic position relative to the oldest *Carolia* bed in a given section (Fig. 1, 3).

Interpretation.—We interpret the flaser-bedded sandstone interval to represent infilling of an incised river valley during the initial shift in the balance between sediment supply and the formation of accommodation, probably during the initial transgressive phase of sequence TA4.2 (Fig. 2). Bundling of mudstone-sandstone packages at the scale of ripple laminations (Fig. 9D) and decimeter-scale bundles (visible in Fig. 9A-B) are interpreted as tidally generated rhythmites. The sandstones and thin mudstone drapes in this IVF are, thus, thought to have been deposited in a river-dominated estuary that experienced variation in the magnitude of unidirectional flow due to ebb-flood and spring-neap tidal cycles. The large clinoforms, which appear to lack a consistent orientation, are interpreted to represent rapidly building, broad, subaqueous sediment lobes or kinematic waves that formed in response to rapid deposition and aggradation of river transported sediment. Accommodation formed quickly as a result of sea level rise and was closely matched or slightly exceeded by sediment delivery, resulting in rapid aggradation.

Rapid sediment buildup during the deposition of the IVF resulted in the development of subaqeous distributary-tidal channel systems that scavenged the flaser-bedded sandstone. The lack of bioturbation, an abundance of well-preserved plant fossils, some of which are indicative of fresh or brackish water, the presence of sawfish, and the prevalence of asymmetric ripples yielding unimodal current orientations (Fig. 1B) in a lenticular sand body (Fig. 3–4), all indicate rapid sedimentation in a fluvial-dominated, fresh- or slightly brackish-water tidal estuary. The apparent lack of any significant aggradation of a fully fluvial system during the initial stages of sea-level rise is somewhat surprising given the evidence for high sediment supply. This may provide evidence for a very rapid initial sea-level rise that abruptly transitioned a fluvial system into an estuary. Isolated evidence for fluvial channels, however, occurs near the base of the IVF (Fig. 8D) and may reflect minor aggradation of the fluvial system during initial transgression.

Conglomerates and Mudstone-Coquina Parasequences of Early TST

The top of the IVF, including the tops of steeply dipping clinoforms, is truncated (Fig. 9A) by a thin (<5 cm), matrix-supported conglomerate with abundant pebbles and cobbles of very fine grained sandstone as well as shark teeth and fragmented vertebrate bones, primarily from dugongs, and marine macroinvertebrates (Table 1). The conglomerate is continuous in thickness and in character over the entire study interval, including where the IVF is absent (section A, Fig. 3). The conglomerate is overlain by a ~3-m-thick, widely traceable, very fine grained, tan sandstone that contains abundant, fragmented marine invertebrate shells indicative of normal-marine conditions, including oysters, gastropods, corals, echinoids, and crustaceans. These sandstones are thoroughly bioturbated, and *Thalassinoides* boxworks penetrate down into the top 1–1.5 m of the underlying IVF. Locally, large-scale (1–3 m) ball-and-pillow structures with clear dish and pillar structures are present in the sandstone immediately overlying the conglomerate, which is often injected vertically between the pillows.

The top of the shelly sandstone that overlies the conglomerate is unique in having small scleractinian coral colonies and a great abundance of the enigmatic calcareous fossil *Kerunia*, which occurs nowhere else in the section (Fig. 3). The shelly sand bed is overlain by a ~4-m thick, greenish-gray mudstone that coarsens upward to silty, lighter greenish-gray mudstone (Fig. 3; Fig. 9A). This mudstone is overlain by a thin conglomerate and skeletal coquina that is similar to the sandy bed that caps the underlying IVF, but with larger, more complete invertebrate shells and abundant *Carolia*. Dugong skeletons are present near the top of the second skeletal bed (Table 1), which is complex and exhibits evidence for scour-and-fill structures to form broad (6 m), shallow troughs. The measured sections are capped by a densely packed ostreiid oyster bed that contains rare dugong skeletons. Traditional lithostratigraphic definitions place the entire interval within the Qasr el-Sagha Formation.

Vertebrates in this part of the section, albeit rare in the upper quarter of the underlying upper FSST, are consistently located on two shelly, conglomeratic surfaces. No whales have been found in this interval, but dugongs, sharks, and sawfish are present (Table 1). Skeletons vary in their degree of articulation and completeness, with remains on the first RS being mostly incomplete and fragmentary and remains on the second surface being better preserved, on average.

Interpretation.—The top of the IVF is erosively truncated by a marine RS that resulted in the formation of a thin, widely traceable transgressive lag of matrix-supported conglomerate that consists of sedimentary clasts (iron-cemented, very fine grained sand, probably *Thalassinoides* burrow fills) and vertebrate remains, primarily from dugongs and sharks. Normal marine conditions were established during the initial transgression, as evidenced by the presence of fragmented corals and echinoids in a condensed transgressive sandstone overlying the RS. The lower 1.5 m of the early TST in sequence TA4.2 appears to be condensed, but localized, large-scale ball-and-pillow structures that deform the RS conglomerate suggest sediment destabilization, possibly during a single storm that rapidly deposited sand over the newly created, broad shelf.

Another marine flooding in the early TST, ~2.8 m above the initial RS, resulted in the formation of a clear-water, normal marine, shallow shelf that permitted scleractinian corals and abundant *Kerunia* to colonize a sandy skeletal seafloor. The overlying parasequence of the early TST is thicker, contains greenish-gray mudstone at its base, and records continuing transgression during the TST. An erosive marine RS with *Thalassinoides*; a conglomerate; and a densely packed, sandy skeletal lag dominated by oysters and anomiid bivalve *Carolia* also caps this coarsening-upward parasequence. This ravinement is very similar to the conglomerate developed on the underlying RS, but the invertebrate shells and vertebrate remains are typically less fragmented. The early TST, thus, records at least two episodes of prominent marine ravinement during an overall deepening succession.

The mudstone, sandy coquinas, and densely packed oyster bed that caps these sections record the formation of a broad, muddy shelf or embayment similar to the embayment that existed during the late stages of the underlying FSST at section A. On the interfluve (section A), deposits above and below the Pr-2 SB are, therefore, lithologically and environmentally similar, despite the fact that they are from different third-order sequences. Without the aid of a clearly exposed incised valley and an easily traceable RS, the Pr-2 sequence boundary, which represents a ≥45-m-fall in sea level and subaerial exposure of the region, would be cryptic and is very easily overlooked at section A. The lack of clear evidence for subaerial exposure within the interfluve at section A appears to be the result of substantial erosion during the formation of the first RS in sequence TA4.2.

DISCUSSION

Relationship to Previous Stratigraphic Research in Egypt

Several kilometers northwest of the study area, and higher in the Qasr el-Sagha Formation, a flaser-bedded, ripple-laminated sand with large-scale clinoforms overlies a vertebrate-bearing conglomerate. This interval constitutes the cross-bedded siltstone and shale with gypsum and carbonaceous shale from 163–172 m in Gingerich's (1992) Minqar Abyad section, and it is lithologically very similar to IVF and basal conglomerate described here on top of the Pr-2 sequence boundary. We interpret this up-section repetition of a lithofacies assemblage that is diagnostic of the IVF of Pr-2 to mark the overlying SB, Pr-3 (Fig. 2). The IVF above SB Pr-3 is overlain by a shelly sandstone that is nearly identical to the transgressive RS described here in the TA4.2 sequence, including the occurrence of *Kerunia*. Both the Pr-2 and the Pr-3 sequence boundaries in the Wadi Al-Hitan region are, thus, represented by conspicuous and similar facies assemblages that formed in response to subaerial exposure and subsequent transgressive ravinement. The Eocene-Oligocene boundary in the Wadi Al-Hitan region is characterized by the permanent withdrawal of the sea and a transition to fully continental sedimentation. This final Eocene sea-level fall marks the Pr-4 SB (Fig. 2).

The flaser-bedded sandstone facies that constitutes the IVF of sequence TA4.3 at Wadi Al-Hitan is the westward and basinward extension of the interbedded claystone, siltstone, and quartz sandstone facies (Vondra, 1974) as well as the giant, cross-bedded sandstone (Bown and Kraus, 1988) described near Qasr el-Sagha, some 60 km east-northeast of Wadi Al-Hitan. Vondra (1974) interpreted this conspicuous, upper, cross-bedded unit as a prograding delta front, whereas Bown and Kraus (1988) thought it represented lateral accretion deposits formed within stream channels. Given the more proximal, landward location of these previously described sections (Fig. 1), we would expect the IVFs to have a more fluvial character than the IVF in Wadi Al-Hitan.

The lower part of the Qasr el-Sagha Formation is less well exposed near Qasr el-Sagha, but it is probable that the Pr-2 SB and overlying IVF is also present southeast of Qasr el-Sagha. For example, Seiffert et al. (2008) report fragmentary remains of the proboscideans *Moeritherium* and *Barytherium*, as well as sirenians, whales, and an associated BQ-2 fauna of terrestrial micromammals, from the Umm Rigl Member of the Birket Qarun or Qasr el-Sagha Formation. The precise stratigraphic position of BQ-2 and its correlation to strata in Wadi Al-Hitan is uncertain at this time because the section at BQ-2 is comparatively poorly exposed. The Pr-2 IVF that we describe at Wadi Al-Hitan, however, provides the earliest evidence of land mammals (*Moeritherium* and *Barytherium*) in the Wadi Al-Hitan section, the stratigraphic setting below Pr-3 is similar, and the Pr-2 IVF is probably correlative with the BQ-2 terrestrial mammal locality.

Implications for Vertebrate Taphonomy and Ecology

In the absence of a sequence stratigraphic framework, it would be tempting to interpret the prevalence of complete whale skeletons in a few stratigraphic intervals as evidence for episodic mass mortality during breeding periods, biotic responses to environmental change, or some other unusual biological events. The consistent occurrence of whales and other vertebrates on distinct stratigraphic surfaces that are expected to have experienced enhanced environmental and temporal averaging, however, suggests that such interpretations are unjustified. Instead, the distribution of whale skeletons in Wadi Al-Hitan is consistent with a relatively steady flux of carcasses to the sea floor, with periods of reduced sedimentation and environmental averaging during marine flooding, affording greater opportunity for remains to accumulate on widely traceable stratigraphic surfaces. There is often little transport or loss of remains following the emplacement of vertebrate remains on active depositional surfaces because they have large, durable bones that can eventually act as large sedimentary clasts (Fig. 5) in relatively low-energy marine environments. Rapid burial is, thus, not required in order for marine vertebrates to occur as complete and semi-articulated to articulated skeletons on traceable stratigraphic surfaces.

Superimposed on variation in the concentration and state of preservation of vertebrate remains in Wadi Al-Hitan is a shift in the dominant taxon from *Basilosaurus* at the base of the section to *Dorudon* remains in the middle, and to dugong-dominated assemblages at the top (Table 1). It is unlikely that taphonomic processes in subtidal marine environments studied here have strongly biased the relative abundance of vertebrates, based on a study of a modern beach with marine vertebrate bones that accurately reflect local community composition (Liebig et al., 2003). The vertical succession in relative abundance observed in Wadi Al-Hitan, however, may not be indicative of a true temporal biological trend. Instead, this up-section change in dominant taxa (Table 1) could be controlled by a sea-level-forced environmental stacking pattern (Fig. 3) that resulted in the vertical stratigraphic juxtaposition of an original onshore-offshore faunal gradient (i.e., habitat tracking; Brett, 1998). Specifically, the stratigraphic distribution of remains suggest that *Basilosaurus*, the largest-bodied whale in Wadi Al-Hitan, may have been more prevalent than *Dorudon* in deeper water, offshore environments, even though both whales occur across the same range of environments (Table 1). The dominance of dugong remains in shoreface and embayment environments (Table 1) is consistent with their subsistence on sea grasses, which have been found as fossils in dugong-bearing strata in Wadi Al-Hitan.

The possibility of an onshore-offshore gradient in faunal dominance, with *Basilosaurus* dominant in the deeper water, transgressive phase of sequence TA4.1, does not support the hypothesis that *Basilosaurus* was a shallow marine specialist. Instead, *Basilosaurus* may have been generally adapted to the expansive, epeiric sea environments in which whales first evolved (Gingerich, 1983). A sea-level fall, through the elimination or modification of shallow shelf habitats, could cause a true decline in the abundance of *Basilosaurus* as well as a coordinated environmental trend up-section. Our observations do not allow this common-cause mechanism to be adequately tested at this time, but they do constrain the range of biological hypotheses that should be entertained and provide the necessary stratigraphic framework for further consideration of a common cause hypothesis. For example, the results of this study indicate that stratigraphic patterning is important in determining the stratigraphic distribution of vertebrate fossils, but they also suggest that there are qualitative differences in coastal geomorphology and shallow shelf environments between transgressive and regressive phases that could have evolutionary and ecological consequences. Such effects might cause elevated rates of morphological evolution or extinction and cladogenesis during inflection points in relative sea level that transcend those expected by sampling effects imposed by sequence stratigraphy (e.g., Holland, 1995; Brett, 1998; Hannisdal, 2006).

Notwithstanding the possible evolutionary consequences of rising and falling sea level, sedimentary processes operating within a third-order sequence exert a dominant control on vertebrate preservation and taphonomy in Wadi Al-Hitan. It is, therefore, probable that physical sedimentological processes similarly structure other marine vertebrate assemblages. Insofar as eustatic sea level is an important component, sequence stratigraphic control on marine vertebrate preservation could be useful in more precisely correlating distant fossil localities. For example, the ≥45 m sea-level fall recorded by the Pr-2 SB in Wadi Al-Hitan is identified elsewhere (Haq et al., 1987) and does not appear to be under local tectonic control. We, therefore, anticipate that eustatic sea-level changes, in conjunction with the bio- or chemostratigraphic control necessary to align sequence stratigraphic records, will prove useful for correlating whale fossils globally and locally, and that sequence stratigraphy will provide additional control on the timing and environmental context of the land-to-sea transition in whale evolution.

As a tangible example of the potential of sequence stratigraphy as an additional correlation tool for whale fossils, *Basilosaurus isis* in Egypt is found principally in the Birket Qarun Formation, below SB Pr-2, in lower Priabonian sequence TA4.1 (Fig. 2). In North America, a closely related whale species, *Basilosaurus cetoides*, is found in the Pachuta Marl and Shubuta Marl members of the Yazoo Formation of Alabama (and correlative strata in nearby states). The Pachuta Marl contains SB Pr-3, and virtually all *B. cetoides* are found in the Pachuta and Shubuta members in upper Priabonian sequence TA4.3 (Miller et al., 2008). On the basis of sequence stratigraphy, *B. isis* in Egypt (c. 36.5 Myr) is, thus, expected to be on the order of 2.5 million years older than *B. cetoides* in Alabama (c. 34 Myr). In this case, calcareous nannofossil biostratigraphy provides the temporal constraints necessary to properly align a sequence-stratigraphy–based correlation scheme, but enhanced resolution within individual biostratigraphic zones may be facilitated by eustatically controlled SBs (Fig. 2), both within and between sedimentary basins.

Comparison to Other Skeletal-rich Marine Records

In terms of vertebrate preservation, one of the studies that is most closely related to the present is that of Rogers and Kidwell (2000), which documented the sequence stratigraphic distribution of vertebrates along an onshore-offshore transect in the Cretaceous of Montana. In that area, no consistent relationship was found between the inferred durations of erosional-omissional hiatuses and the degree of concentration or state of preservation of vertebrate remains. Instead, vertebrate-rich beds occurred as lag concentrations, with taxonomic composition and skeletal abundance controlled primarily by the fossil contents of facies that underlie and that are adjacent to ravinements and fluvial channels. In Wadi Al-Hitan, a similar example of a vertebrate lag concentration occurs on the Pr-2 SB within the incised valley. In this case, terrestrial animals living near the active fluvial environment contributed a minority of remains, but a majority were reworking from underlying FSST mudstone and sandstone. Despite the prevalence of macroinvertebrates in the reworked sediments, only limited numbers of the most durable (primarily ostreiid oysters) occur as fragments in this lag. The abundance of bone is the direct result of differences in hard-part durability between macroinvertebrates and vertebrates.

The stratigraphic distribution and taphonomy of marine macroinvertebrates has been well documented for third- and fourth-order sequences throughout the Phanerozoic (e.g., Kidwell, 1991, 1993; Brett and Baird, 1993). For example, Kidwell (1989) examined shell concentrations associated with *Thalassinoides*-burrowed, transgressive surfaces that are either merged with an underlying SB or separated from it by an IVF. Taxonomically diverse and internally complicated coquinas overlie these transgressive surfaces and consist of shells that were produced locally during deepening. The taphonomic signatures of these concentrations are typically commensurate with the duration of the inferred hiatus (Kidwell, 1993). Very similar patterns of macroinvertebrate skeletal accumulation occur in association with MFSs in Wadi Al-Hitan, particularly in the early TST of sequence TA4.2. Outside of the incised valley, the distribution and taphonomic conditions of vertebrates closely follow the expectations of hiatal concentrations developed on the basis of marine macroinvertebrates (Kidwell, 1991, 1993).

Despite notable similarities between the marine vertebrate and macroinvertebrate fossil records, there are several important differences. First, fossils of marine vertebrates are much less common than those of macroinvertebrates and, with the possible exception of locally rich lag concentrations on the Pr-2 SB, no horizon in Wadi Al-Hitan can be considered a true bone bed, even though skeletons are unambiguously associated with MFS. The widely scattered nature of vertebrate remains in Wadi Al-Hitan is probably due both to comparatively high rates of net sedimentation—average accumulation rate is ~100 m/Myr, or within the moderate subsidence range of Kidwell (1993)—and to a comparatively low flux of skeletal material to the sea floor. For these reasons, the accumulation of marine vertebrates in Wadi Al-Hitan did not change the physical properties of the sea floor during the formation of a hiatus, as macroinvertebrates often do. The second difference is that marine vertebrate bones and teeth are much more durable and less easily transported than most macroinvertebrates. Complete skeletons can, therefore, remain articulated even when they are exposed on the sea floor for long periods of time. In contrast to the typical situation for macroinvertebrates, articulation, therefore, need not indicate rapid burial. Nevertheless, more detailed aspects of quality of preservation do appear to vary with inferred hiatal durations (Table 1).

CONCLUSIONS

1. Strata at Wadi Al-Hitan record the transgressive and regressive phases of third-order Priabonian sequence TA4.1, as well as the initial transgressive phase of Priabonian sequence TA4.2. Environments at Wadi Al-Hitan spanned a range of water depths—from below SWB in a muddy, hypoxic offshore shelf, to above NWB in a sandy shoreface, and to protected, muddy-bottomed embayments with oyster shoals and nummulitid banks.
2. A fall in sea level of at least 45 m resulted in the subaerial exposure of the Wadi Al-Hitan shelf, and the formation of incised river valleys. An imbricated fluvial conglomerate characterizes the Pr-2 SB in the incised valley and is overlain by flaser-bedded and ripple-laminated, tidal estuary sandstones with a multi-km lenticular geometry. Subsequent marine transgression likely resulted in the erosion of continental soils or sediments on interfluves and the formation of a cryptic SB, merged with a marine RS, that juxtaposes regressive marine strata of sequence TA4.1 on transgressive marine strata of sequence TA4.2.
3. Second- and third-order sequence stratigraphy in Wadi Al-Hitan is consistent with Haq et al. (1987), suggesting a eustatic sea level component to late Eocene sedimentation in the western desert of Egypt. Eustatic sea level may have been driven by the initiation of widespread Antarctic glaciation at the end of the Eocene. The overall thickness of the Priabonian section in Wadi Al-Hitan (~110 m) also suggests an important role for passive margin subsidence.
4. The preservation of vertebrates at Wadi Al-Hitan is closely linked to sequence stratigraphic architecture. The majority of vertebrate remains are found as complete, articulated to semi-articulated skeletons on MFSs or as fragmented, isolated elements in an erosional lag concentration on the Pr-2 SB. Terrestrial mammals, the oldest known from Egypt, are also found in the Pr-2 lag. There is no direct evidence for biological events as fossil concentration mechanisms at Wadi Al-Hitan. The general abundance of whale remains in the Wadi Al-Hitan region may, however, reflect ecologically favorable conditions within a protected shelf setting. The scarcity of whales in the most-offshore marine environments in Wadi Al-Hitan may indicate the preferential congregation of whales in shallower water environments.
5. *Basilosaurus* is the most common whale in the deepest-water environments at Wadi Al-Hitan, and *Dorudon*, a smaller-bodied archaeocete whale, is most abundant in lower to middle shoreface environments, though both whales occur across the same spectrum of shelf settings. Dugong remains predominate in the shallowest water environments, such as protected embayments at the top of sequence TA4.1 and in the early transgressive shelf environments of sequence TA4.2. The elimination of broad, shallow shelves during eustatic sea level fall, as well as correlated

changes in coastal-shelf geomorphology, may have influenced marine vertebrate ecology and evolution during the late Eocene transition to an icehouse world.

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