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Burial Experiments with Marine Turtle Carcasses and Their Paleocological Significance

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PALAIOS, 1991, V. 6, p. 89-96

Two carapaces of the hawksbill turtle (*Eretmochelys imbricata*) were buried in intertidal calcareous sands in a lagoonal setting of the Seychelles Islands (Indian Ocean). After three weeks, one of the carapaces was still in its original position but decay had resulted in the loss of most marginal plates and all ligaments; reworking of the specimen would have led to complete disarticulation. The second specimen, however, was reworked four days after burial and swept into the subtidal part of the lagoon; complete disarticulation and burial of disintegrated bones occurred within ten days. These taphonomic patterns are compared to similar ones from Upper Jurassic deposits of Central Europe. Additionally, isolated turtle bones were sampled at low tide along three different beach transects; orientation and position to substrate were noted. The accumulation of isolated bones on the beach showed preferred orientation maxima (perpendicular to the shore) and submaxima (parallel to longshore currents).

INTRODUCTION

Studies on the taphonomy of fossil marine invertebrates and terrestrial vertebrates have greatly enhanced our understanding of taphonomic processes (Weigelt, 1927; Behrensmeier

and Hill, 1980; Zangerl and Richardson, 1963). With a few exceptions, however, the taphonomy of marine vertebrates is still poorly understood (Schaefer, 1962; Martill, 1985, 1987). Because taphonomic processes act as selective filters for paleontological information (Behrensmeier and Kidwell, 1988), their understanding is important for the interpretation of fossil "Lagerstätten." The famous Upper Jurassic "Plattenkalk-Lagerstätten" in Solnhofen (Germany) and in Cerin (France) are known for their completely articulated marine turtle skeletons and the 'Solothurn Turtle Limestone' for its unique and dense accumulation of fossil turtle remains (e.g., Lang and Rüttimeyer, 1867; Gaffney, 1976). Until now, data about the quantitative occurrence of whole and disarticulated carapaces were unavailable for all of the mentioned localities. Intact preservation of multi-element skeletons such as echinoderms and vertebrates requires rapid burial (e.g., Schaefer, 1962; Meyer, 1984). To test this hypothesis, I carried out a series of experiments to determine disarticulation rates of modern marine turtle carcasses and their use as current indicators.

MATERIALS AND METHODS

These studies were carried out during a geological survey on La Digue in 1989 (Seychelles, Indian Ocean; Fig. 1A, B). The Seychelles Islands have a tropical, humid climate modified by monsoonal winds. Winter (May to October) is characterized by steady southeast Trade winds that bring cooler, drier and stable weather. For the burial experiments, the dry season was chosen in order to avoid disturbances through heavy fluvial input into the lagoon. The most

important point was to choose a site where occasional tourists wouldn't pass and disturb experiments. Therefore, a site with a difficult beach access was selected. The second point was to find a protected lagoonal setting with a uniform sedimentary environment. The selected site should be bare of coral colonies and have a low density of other benthic faunal elements; this should reduce disturbance of experiments by scavenging benthos or fish to a minimum. The optimal water depth was about 1 m in order to facilitate excavating work with snorkeling equipment.

Locality of Burial Experiments

The experiments were carried out during the entire month of June 1989. The burial site (Fig. 1B, C) lies close to a beach slightly inclined toward the northwest. A small mangrove channel enters to the east, a shallow lagoon, protected by a reef crest, forms the western border of the site. The tidal currents run perpendicular to the shoreline. The strength of surface currents was measured with floating paper chips over a distance of 10 m; 20 runs gave a mean of 0.43 m/sec (measured at midday between tides; during measurements no wind could be detected). The temperature of the water and the surrounding sediment varied from 27 to 30°C.

Burial Experiments

Two complete carapaces of the hawksbill turtle [*Eretmochelys imbricata* (RÜPPEL, 1835)] were obtained from local fisherman. The plastron and the internal soft parts were missing as well as the epidermal scutes, which had previously been removed for jewelry. One carapace (Fig. 2: no. 1) was buried convex side down in the lowermost intertidal zone in 25 cm of medium grained coralline coral sands. The second specimen (Fig. 2: no. 2) was buried convex up in the same sediment and at the same depth (both specimens were put in excavated holes and then covered with sand). To determine the composition of the sediment, more than 500 grains were counted from a 200 g sample (Fig. 2).

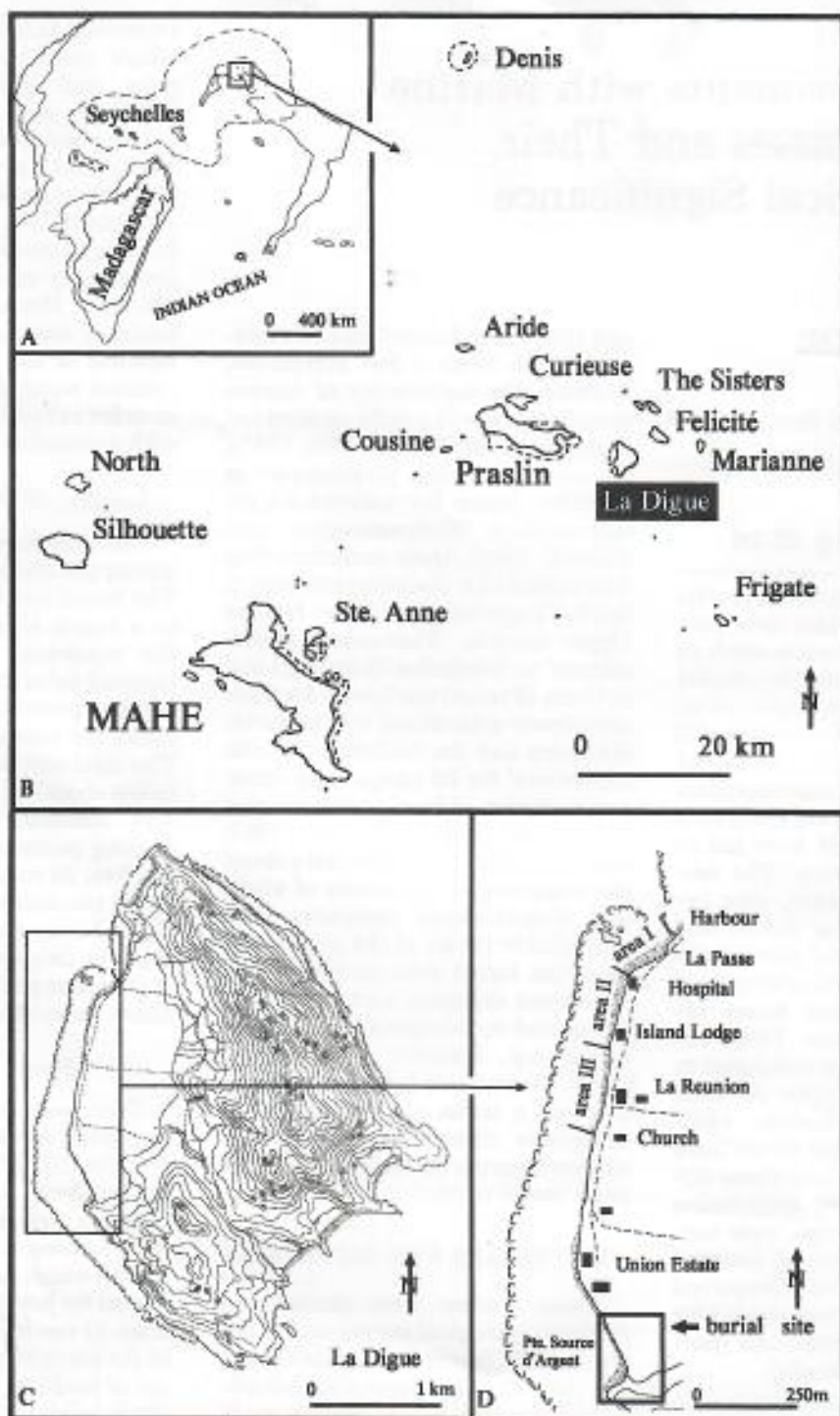


FIGURE 1—Location of the study area. A) Map of a part of the Indian Ocean with the territory of the Seychelles Islands. B) Map of the inner Seychelles Islands. C) Map of La Digue. D) Detailed map of La Digue with the location of the burial site and the collecting sites.

Collecting of Disintegrated Bones

In addition to the burial experiments, skeletal remains of marine

turtles were collected after every high tide on the shore (high and low tide difference: 1.2–1.5 m) at the high water line. These skeletal remains are most likely parts of turtle carcasses

that have been thrown into the lagoon by local turtle hunters and were swept ashore after disintegration. The shoreline area was divided into three different sampling areas because of

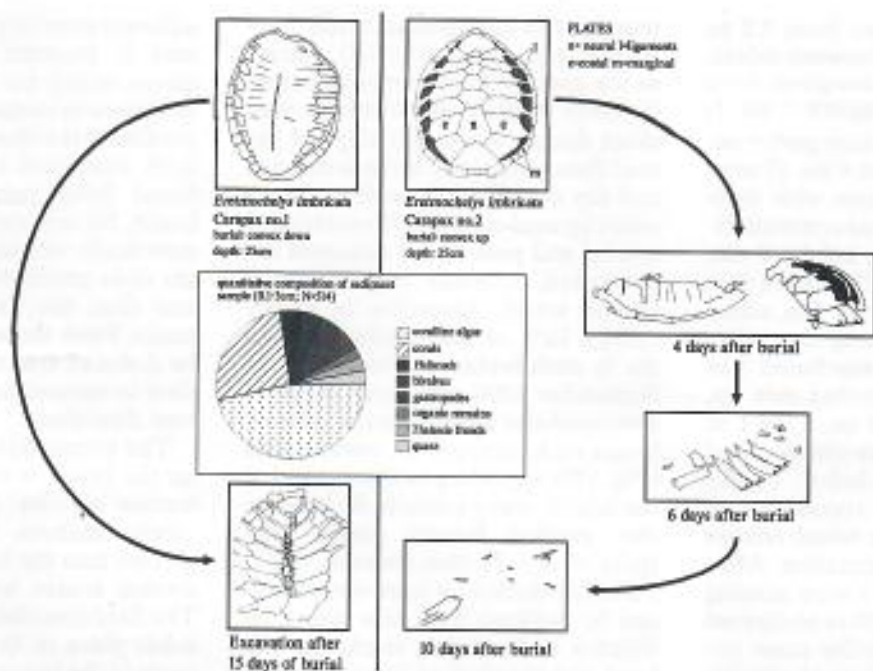


FIGURE 2—Taphonomic patterns of *Eretmochelys imbricata* from La Digue Island (Seychelles) (black areas indicate ligaments).

their different exposure to tidal currents (Fig. 1D). Fortunately, turtle bones are not a conspicuous trophy for shell collectors, therefore minimal disturbance of the collecting sites was assumed. Every bone fragment was photographed, the orientation of its long axis determined by compass, and its anatomical position and outline size and position on the substrate were noted. The orientation data were then analyzed by means of a rose diagram program. In addition, three isolated carapace and plastron elements of *Eretmochelys* were placed in the subtidal part of the lagoon (water depth 2 m) on the surface of *Halimeda* sands. The initial dry weights were noted, and twice a day the declination of the bones was recorded. After removal from the site, their dry weights were measured again.

RESULTS

Decay and Disintegration of Carapaces

Although checks were made twice a day, no changes were seen in carapaces before the sixth day. Six days after burial the first ligaments had become loosened, and the following

day the first detachment of marginals was observed at the sediment/water interface. No other changes were observed until the carapace was excavated after 17 days. The following observations were made after excavation: All bone sutures were open, and the posterior marginals were disconnected. The ligaments of the fontanelles were completely decayed (Fig. 2). Five centimeters of white sand above the carapace had acquired a greyish color and strong smell of H_2S . Beneath the carapace, reducing conditions could only be observed among the neurals. The second carapace (Carapace no. 2; Fig. 2) was buried convex side up. During the first four days it remained buried and no changes were noted. On the fifth day, it was found lying in the lagoon, broken in half. The carapace was broken along the bone sutures of the neurals and some posterior marginals were already missing. It had most likely been excavated during the night by tidal currents and been swept into the lagoon about 50 m along shore to the east of the original burial site. After six days, two neurals, one marginal and one costal plate were found 6 m to the south on the beach. The remaining parts were almost com-

pletely disconnected. Seven costals were still loosely connected, but within an area of about 1 m², one neural and several marginal elements as well as one costal were scattered and covered with a thin layer of calcareous sand. On the following day, five elements (3 costal plates, 2 marginal plates), and parts of loosened ligaments were observed 150 m to the northeast on the opposite shore. Although the area was checked twice a day, the remaining bone material was not found in the area. After ten days, six costals and two marginals were detected by means of snorkeling at the place where the carapace was seen after the 5th day. There it lay under a 2 cm thick cover of sediment, scattered over a surface of 2 m² (Fig. 2).

Taphonomy of Disarticulated Bones

In order to test abrasion rate and orientation of turtle bones in a subtidal setting, three individual elements were placed on the surface of rippled *Halimeda* sands at 1.8 m water depth (low tide); they had been collected as isolated elements on the shore. Measured bottom currents at low tide were negligible whereas tide

surface currents ranged from 0.2 to 0.5 m/sec (measured between tides). The specimens (one marginal from the lateral part of carapace = no. 1; one marginal from anterior part = no. 2; one plastron element = no. 3) were placed convex side down with their long axes parallel to main current direction (S to N; ripple height: 5 cm; wave length: 30 cm). After half a day, the orientation was still the same, whereas on the following day, after one tidal cycle, no. 1 was found 3 m to the west, buried convex side up, no. 2 was missing and no. 3 lay 1 m to the west in the same position and orientation as the day before. On the third day, no. 3 had travelled 1 m further west and was found convex down in the same orientation. After four days, nos. 1 and 3 were missing but no. 2 reappeared 10 m southwest of the original site in the same position and orientation as at the beginning. This marginal was removed and its dry weight noted. Although no abrasion could be seen, the sample lost 20% of its original weight (12 g instead of 15 g).

DISCUSSION

Death and Mortality of Modern Marine Turtles

The main danger for modern marine turtles is surely human impact: either by active catchment of live specimens for turtle soup (e.g., green turtle), jewelry (e.g., hawksbill turtle) and nest poaching or by destruction of potential nesting sites (e.g., touristic development, e.g., Frazier, 1980) and pollution (Fretey, 1981). These main causes for death and disappearance of modern marine turtles are surely not applicable to the fossil record. Fretey's (1981) observations in Guyana seem more interesting. Here, dead mangrove rootstocks are piled up by currents to form submarine barriers several meters in height. Marine turtles that land for nesting at high tide will easily pass, but they cannot find a passage back to the open ocean at low tide and get stuck in the piles of roots and dried out by the sun. This is particularly

true for the leatherback turtle *Dermochelys coriacea* (LINNE), whereas the green turtle is more agile and is rarely trapped in rootstocks. Another danger is the soft clays of the mud flats where they become trapped and dry out. Here the soft parts are eaten by mud crabs (*Callinectes*) and cranial and postcranial elements are dislocated, whereas the carapaces remain intact. According to Fretey (1981), 12% of the nesting females die in such instances every year. In September 1990, two dead males of *Eretmochelys* were observed lying on beach-rock outcrops of Cousin Island (Fig. 1B); according to the warden of the island, many animals die because they swallow floating plastic bags (pers. comm.: Robbie Bresson, 1990). Direct predation by large vertebrates can be deduced from bite marks on flippers and scratch marks on the head and the shell of living animals. Furthermore, stomach contents of *Orcinus orca* in the Lesser Antilles revealed fragments of *Dermochelys*. Fretey (1981) noted predation upon both *Dermochelys* and *Eretmochelys* by tiger sharks (*Galeocerdo cuvieri*) from Guyana.

Accumulation of Disintegrated Turtle Bones

The composition of bone samples shows a high percentage of robust bone plates (Fig. 3). These skeletal remains are most likely disintegrated parts of turtle carcasses that have been thrown into the lagoon by local turtle hunters and were swept ashore after disintegration. Costals, marginal and plastron elements vary between 75% and 94% of the sample, whereas neural-plates, cranial and postcranial elements form only a minor part. In area I, the orientation diagram shows a distinctive butterfly pattern. All anatomical categories display maxima perpendicular to shore and submaxima that are due to shore parallel tidal currents; although the rose diagrams of the marginals have the greatest variance of readings. These relatively dispersed patterns might be related to the close proximity of the reef crest and the

adjacent granitic cliffs in this area. In area II, plastron and marginal elements, which are mainly rectangular to square in outline, were embedded parallel to the shore. Costals with distinct elongated shape were mainly found lying perpendicular to the beach. No orientation measurements were made within area III because of the close proximity of a tourist hotel and thus the likelihood of disturbance. From these observations it can be deduced that turtle bones can be used to reconstruct at least local current directions.

The accumulation of turtle bones on the beach is surely an artifact of human activity. According to local turtle catchers, the carapaces are thrown into the lagoon after the epidermal scutes have been removed. The final disarticulation of carapaces takes place in the shallow, subtidal parts of the lagoon. Here they remain for some time, before they are transported ashore. This can be deduced from the frequent gnawing traces of sea urchins (in this case: *Tripneustes gratilla*) found on some costal plates; most likely they feed upon marine algae growing on these elements.

As stated above, the accumulation of turtle bones is indirectly due to human "predation"; nesting sites on La Digue were observed within area II (Fig. 1D) in September 1990, according to local fishermen the disturbance of nesting females is minimal. On other Seychelles Islands, for example on Frigate, Cousin and Curieuse (see Fig. 1B), where hawksbill and green turtles are also known to nest (Frazier, 1984, and pers. obs. in October 1989 and September 1990), no bone accumulations were observed; however, turtle hunting does not occur on these islands.

The Decay of Modern Turtle Carapaces

These observations on decay and disintegration of marine turtles give us a first glimpse into the processes that are involved. Nevertheless, it must be stressed that these results may not be directly applicable to the fossil record. In fact, we do not know

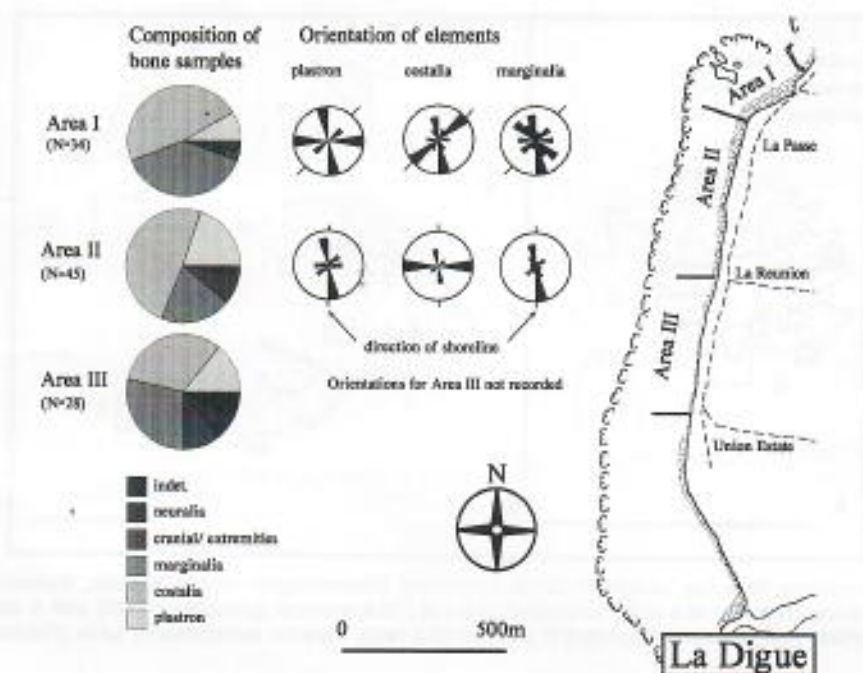


FIGURE 3—Orientation and composition of turtle bone samples from beach transects of La Digue Island (Seychelles).

the role of the epidermal scutes in binding together the carapace, because these were missing in our experiments. The rapid disarticulation of the buried turtle carapaces is probably the result of several processes. First, the high temperature of the water and the surrounding sediment (27°–30° C) increase the bacterial decomposition of binding ligaments. Zangerl and Richardson (1963) observed that fish placed in cages in swampy bayou sediments decay completely within seven days. Wuttke (1983) noted that the rate of decay in anuran skeletons is controlled by temperature. The oxygen content of the surrounding medium is negligible and anaerobic conditions occur everywhere in vertebrate corpses. Chemical reactions that influence the multiplication of microorganisms are strongly temperature dependent. The strength and patterns of local currents contribute greatly to the preservation potential of buried skeletons. The presence or absence of large predators and scavengers (fishes, sea urchins, endobenthic crustaceans) also have a strong influence on the future taphonomic patterns.

The Fossil Record of Taphonomic Patterns in Marine Turtles

In the case of the Upper Jurassic Solnhofen limestone, many intact turtle skeletons (primarily eucryptodirans) have been found (Wellnhofer, 1967), but no information on the ratio of intact/disintegrated turtles is known. Judging from figured specimens (Wagner, 1859; Wellnhofer, 1967), it is obvious that they underwent no major physical or biological perturbations prior to burial (but this could also represent a sampling or publication artifact). Their exceptional preservation is due to cyanobacterial sealing which formed in a stratified water body; most vertebrate fossils from this locality apparently were washed in, or died within a short period of time in a submerged, restricted basinal setting (Seilacher et al., 1985). A second case is the turtle-bearing strata from the Kimmeridgian of the Hannover area. Oertel (1924) noted that disintegrated bones are frequent, but intact carapaces are rare; the latter occur in sediments that are thought to have been deposited in brackish water. The

lithographic limestones from Cerin (Kimmeridgian, France) have also yielded a dozen complete turtle specimens. Although new excavations have been undertaken recently, the taphonomy and articulation rate is not known for these lagoonal strata (Barale et al., 1985). The geological record of marine turtles from the 'Solothurn Turtle Limestone' (Kimmeridgian, Switzerland) shows dense accumulations of turtle remains and intact skeletons within a 90 cm thick layer of biotritical wackestones. The common species here is *Plesiochelys etalloni* (Pictet, 1857), a large turtle with a massive carapace (Fig. 4B). Another but small eucryptodiran turtle, *Eurysternum?ignotum* BRÄM 1965, possesses a 'light' carapace with large fontanelles (Fig. 4A) and is very similar to the modern *Eretmochelys imbricata* in the sense of overall morphology. Highest densities of turtle bones in these fossil strata are found near the base (15 counts/m²), decreasing rapidly upward. Here, almost every type of disarticulation can be found, from complete carapaces with associated skulls and postcranial elements to isolated

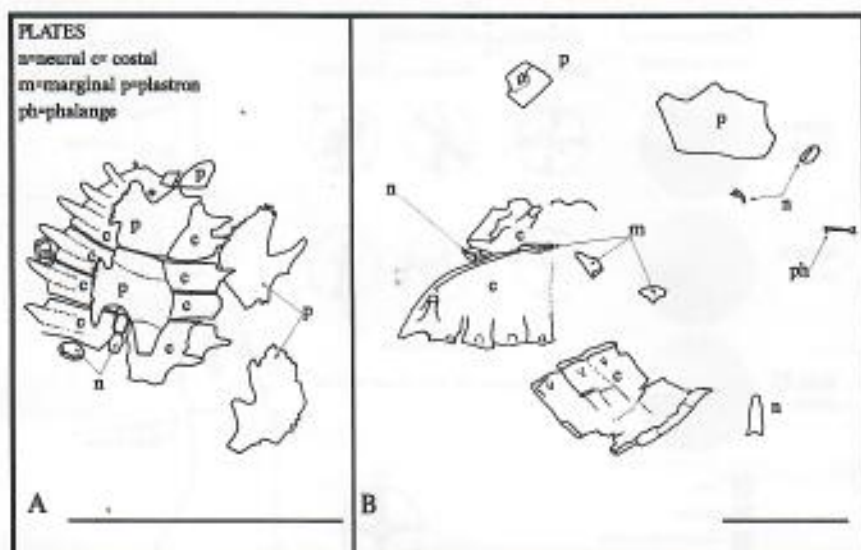


FIGURE 4—Taphonomic patterns from the 'Solothurn Turtle Limestone' (Kimmeridgian; Upper Jurassic, Switzerland; scale bar for both specimens: 30 cm). A) Inverted carapace of a small eucriptodiran turtle (*Eurysternum ignotatum* BRÄM) with a shell morphology similar to that of *E. imbricata*. B) Partially disintegrated carapace and plastron of a large, massive eucriptodiran turtle (*Plesiochelys stalloni* PICTET).

costals or marginals within the same layer (Meyer, 1989). The ratio of complete carapaces/disarticulated bones averages about 1:200. The preserved taphonomic patterns (Fig. 4) are comparable with the results obtained from the present experiments. Some of the fossil specimens show distinct feeding traces of sea urchins (*Gnatichtius pentax*; produced by *Hemicidaris mitra*) and in some cases small encrusting oysters (*Nanogyra*) on the internal part of the plastron. This points at least to extended exposure at the sediment/water interface and therefore to different rates of disintegration. Within this unit we find a mixed taphonomic assemblage of marine turtles that results from rapid burial and subsequent partial reworking of complete carapaces. The sedimentary facies patterns, terrestrial plants and sauropod trackways strongly suggest a lagoonal setting in a tidal-flat environment (Meyer, 1990). Crushed turtle shells showing clear bite marks associated with splintered teeth of mesosuchian crocodiles (*Machimosaurus*) strongly support the hypothesis that the turtle bone accumulation is partially the result of predation by crocodiles. From a morphofunctional approach Krebs (1967) and Buffetaut (1982) suggested that the teleosaurid

Machimosaurus most likely fed on turtles. A comparable case is the Upper Cretaceous of Romania where Nopsca (1902) discovered large concentrations of broken dinosaur bones with teeth marks, turtle remains and only the teeth of crocodiles. He interpreted these limnic deposits as a site where crocodiles fed on corpses of dinosaurs and turtles. The youngest known occurrence of subfossil marine turtles comes from Aldabra (Seychelles). In the Aldabra limestone ($118-136 \pm 9$ ka; Braithwaite et al., 1973, fig. 33, p. 323) complete carapaces of *?Eretmochelys* sp. were found in sand cay deposits. Here, carapaces lay buried upside down in calcarenites, plastron elements are missing (or weathered) and some loosely connected marginals are present. On the whole, these turtle occurrences display similar taphonomic patterns to those observed in the present experiment (Carapace no. 1; Fig. 2) and in the 'Solothurn Turtle Limestone' (Fig. 4A).

In the Upper Jurassic of Europe surface water temperature was probably similar to temperatures on the Seychelles today, although the results of oxygen isotope studies are still in debate (e.g., Hallam, 1984). For example, Irwin et al. (1977) calculated the bottom water temperatures for

the Lower Kimmeridge clay at 15°C and for the Upper Kimmeridge clay at $15-20^{\circ}\text{C}$, whereas Donn (1982) estimated the surface water temperature between $20-30^{\circ}\text{C}$. From these data and the discussion about abrupt climatic changes during the Upper Jurassic (see Wignall and Ruffell, 1990) it seems possible that the rate of decomposition of binding ligaments by bacteria may have occurred at much lower rates than I actually suggest.

CONCLUSIONS

1. Disarticulation of modern marine turtles can occur within a few days to a few weeks, this is consistent with observations made on anurans (Wuttke, 1983) and fishes (Zangerl and Richardson, 1963) under stagnant conditions. It must be kept in mind that in our experiments epidermal scutes were missing, so the effective disarticulation rate may be somewhat longer.
2. Orientation of disintegrated bones shows preferred maxima and submaxima that can be used in reconstructing shore line and current directions. Isolated turtle bones rapidly lose weight through reworking by tidal currents.

Whether the weight loss was due to abrasion could not be determined. Due to the small sample size a significant conclusion is impossible.

3. Occurrence of dense accumulations of Jurassic turtle bones and carapaces in different stages of disintegration is due to rapid burial of intact specimens and subsequent partial reworking and/or predation impact by large predators such as mesosuchian crocodiles.
4. Based upon the reported occurrences, the taphonomic patterns in marine turtles display no great temporal variability since the Upper Jurassic. Although variations in taphonomic patterns may be related to different depositional environments (e.g., from estuarine/brackish to lagoonal and more open, basinal settings) they display similar taphonomic patterns.

Furthermore, it is interesting to note that most fossil and subfossil occurrences of articulated marine turtle carcasses are within lagoonal or coral-reef environments (see above), only a few are known from brackish water deposits (e.g., Nessov, 1987). In the Upper Jurassic, the accumulation of turtle remains was only partly due to predation by mesosuchian crocodiles, especially in the case of the 'Solothurn Turtle Limestone'. Today, however, the accumulation of turtle bones on the beach of La Digue represents the product of hunting by man.

ACKNOWLEDGMENTS

We express our sincere thanks to Ericson Larsen and Charles Louis from La Digue (Seychelles) for the turtle material and the Government of the Republic of Seychelles for the permission to carry out research on their territory. Colin Braithwaite (Dundee) provided photographs of subfossil turtles from Aldabra and Peter Mozley (Bern) and Carole Gee (Zurich) corrected the English version of this manuscript. Rene Herb (Bern) gave valuable comments; due to his critical remarks, Martin Sander (Bonn) substantially improved an

earlier draft of this paper. Two anonymous reviewers made valuable suggestions and comments. This study would not have been possible without the financial support of the Swiss Academy of Natural Sciences, Zetter Enterprises (Solothurn), Steinbruch AG (Egerkingen) and the Atelier Imhof (Olten). Special thanks go to Julia's 'Gondwana trust' who sponsored this field work in a substantial manner.

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ACCEPTED DECEMBER 21, 1990

