Taphonomy of the Recent molluscs of Bahia la Choya (Gulf of California, Sonora, Mexico)

By

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With 24 figures in the text and 6 plates

ABSTRACT

The "target genera" *Protothaca, Chione, Dosinia, Tagelus, Cerithium, Cerithidea* and *Encope* have been used to study taphonomic differences between the subenvironments of a sandy tidal flat at Bahia la Choya near the head of the Gulf of California. The most important taphonomic agents (e. g. physical abrasion, bioerosion, encrustation) are identified and briefly discussed. The degree of taphonomic alteration of shells expressed by loss of ornament, loss of color, fragmentation, encrustation, boring, shell solution, and sorting was cal-culated semi-quantitatively for each target genus and each subenvironment (outer, mid, inner flat, outer, mid, and salt marsh channel). Because taphonomic features vary between various subenvironments, taphofacies, corresponding to sub-environments can be distinguished.

Applying the taphonomic approach to subrecent shell banks, shelly beachrock, and shelly Pleistocene rocks, we demonstrate that taphonomic features are a very useful tool for reconstructing ancient environments.

KURZFASSUNG

Vertreter der Molluskengattungen *Protothaca, Dosinia, Chione, Tagelus, Cerithium, Cerithidea* und des Seeigels *Encope* aus verschiedenen Submilieus eines Sandwatts im nördlichen Golf von Kalifornien wurden auf Unterschiede ihrer taphonomischen Merkmale hin untersucht. Die wichtigsten Faktoren (Abrasion, Bioerosion, Inkrustierung) werden identifiziert und kurz beschrieben. Taphonomische Veränderung von Schalen äußert sich durch Verlust von Oberflächenskulptur, Farbverlust, Fragmentierung, Inkrustierung, Anbohrung, Schalenlösung und Sortierung. Diese Verände-rungen wurden für jede Zielgattung und in jedem Submilieu (Außen-, Mittel-, Innenwatt, Gezeitenrinne im Außenwatt, Mittelwatt und in der Salzmarsch) semiquantitativ erfaßt. Da sich die einzelnen Submilieus anhand ihrer taphonomischen Merkmale unterscheiden lassen, entsprechen sie verschiede-nen Taphofazies.

Übertragen auf eine subrezente Schill-Barre, einen Beachrock, sowie Schillagen in Sandsteinen jungpleistozänen Alters erweist sich der taphonomische Ansatz für die Rekonstruk-tion von Ablagerungsräumen als sehr brauchbar.

INTRODUCTION

The significance of taphonomy for interpreting geological data is twofold: In estimating the degree of taphonomic distortion fossil assemblages have been subject to, we are able to evaluate their usefulness for paleoecological analysis. In addition, taphonomic criteria themselves may be excellent tools for reconstructing ancient environments. This second aspect of taphonomy, although pursued by German paleontologists and geologists for a long time (see reviews by MULLER 1963,

1979) has been recognised by a wider audience only in the last few years. For example, facies and fossil concentrations have been classified according to taphonomic criteria (SPEYER & BRETT 1986, KIDWELL et al. 1986); and taphonomic gradients were used in interpreting skeletal concentrations (FÜRSICH & OSCHMANN 1986, NORRIS 1986). The study of taphonomic pro-cesses in present-day environments is essential for taphono-mic interpretations of ancient sediments and rocks (e. g. SCHA-FER 1962). Consequently, the present paper considers tapho-nomic aspects of a Recent depositional system. The questions which we address are: To what extent is the shelly fauna of the

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taphocoenosis distorted by taphonomic agents? What is the nature of these agents? Finally, how much can taphonomy contribute to environmental analysis?

The environmental setting is a tidal flat complex near the head of the Gulf of California. Here a rich subtropical molluscan fauna provides an ideal object for taphonomic study.

GEOGRAPHY AND ENVIRONMENTS OF BAHIA LA CHOYA

Bahia la Choya is a small, partially protected bay north of Puerto Peñasco on the northeast coast of the Gulf of California (Fig. 1). It is the smallest and southernmost bay of a larger bay system called Bahia Adair, situated about 100 km southeast of the Colorado delta. There is no freshwater influx into the bay and the part of it called estero does not refer to an estuary, but a salt marsh complex. The bay is bordered on the south by Mesozoic granites and on the east by the Sonoran desert. In places, Pleistocene sandstones and shelly conglomerates crop out in the immediate vicinity of the bay and on the tidal flat. In the northeastern part, Pleistocene deposits form a distinct terrace and are overlain by a 30 cm thick shelly beach rock.

from the intertidal flat. The salt marsh is vegetated by *Salicornia* and several other halophytes and intersected by an anastomosing channel ("estero channel") which drains the marsh and is the only major tidal channel of Bahia la Choya. Deeply incised in the marsh, it is shallow across the sandy intertidal flat. The channel contains poorly sorted shells and gravels which occur as megaripples (marsh) or form small bars (tidal flat). Where the channel cuts through the spit shell material from the spit is reworked, and is either deposited on the adjacent inner flat as a lobe (comparable to an ebb-tidal delta), or transported seaward and incorporated into the taphocoenoses of the tidal flat.

Fig. 1: Locality map.

Bahia la Choya is a macrotidal system. During spring low tide more than 10 km² of tidal flats are exposed. Net rates of sedimentation are very low so that in the northern part of the bay large areas of Pleistocene are exposed or overlain by only a few centimetres of sediment. The southern part of the bay receives more sediment, but even there, sediment thickness probably does not exceed 2–3 m. The shelly remains of the rich subtropical fauna therefore form highly time-averaged assemblages.

The tidal flat complex (Fig. 2) can be subdivided into an outer flat characterized by large sand waves and sandy substrates, a mid flat with a flat surface covered with current and mixed wave/current ripples, and an inner flat exhibiting a mesita-like topography and consisting of silty, fine sand. The consistency of the latter is fairly firm. To the east, the beach is formed by a shelly spit which is more than 3 m high and up to 100 m wide. It consists nearly exclusively of shells and shell debris which are of a mixed subtidal-high intertidal origin. The spit separates most of the salt marsh
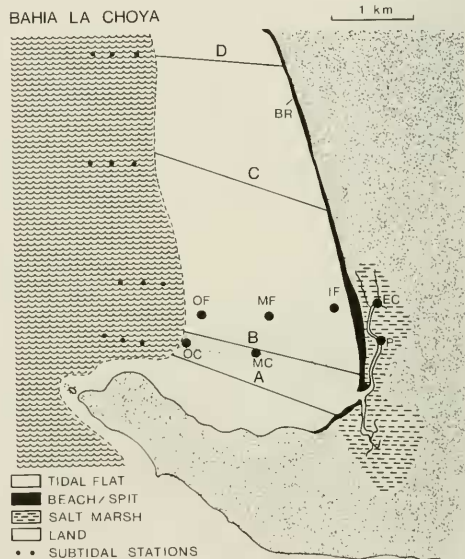

Fig. 2: Map of Bahia la Choya showing sampling stations for the target genera and location of the four transects (A–D). Dotted: desert; stippled: salt marsh; black: spit; stippled line: spring low tide mark. OF: outer flat; MF: mild flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel; P: Pleistocene locality discussed in the text; BR: beachrock.

The Pleistocene rocks are usually shell-rich. According to HERTLEIN & EMERSON (1956) they are Late Pleistocene in age.

A more detailed description of environments and fauna of Bahia la Choya is found in FÜRSICH et al. (this volume). Details on the sedimentology and paleoecology of the Pleistocene rocks are found in ABERHAN & FÜRSICH (this volume).

METHODS

Taphonomic data were collected in two ways: Most of the taphonomic analyses are based on collections of seven target genera (Table 1). These were selected from the rich macroinvertebrate fauna according to the following criteria: (1) they represent typical elements of the various subenvironments of the tidal flat, (2) they are common, and (3) they differ in life habits and mineral composition (in order to evaluate the influence of these factors on their taphonomic history). The tar-

get genera were collected from each of the following subenvironments: outer flat, mid flat, inner flat, outer channel, mid channel, and estero channel. In addition, to document changes in the degree of encrustation, boring, and general shell preservation, bulk samples were taken every 100 m along four transects from the very shallow subtidal to the salt marsh (for sampling methods see Fürsich et al., this volume). These data are based on all the individuals of mollusc species present.

Table 1. Occurrence and autecology of target species.
S: subtidal; OF: outer flat; MF: mid flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel; si: shallow infaunal; di: deep infaunal; m: mobile; e: epifaunal; s: suspension-feeder; df: detritus-feeder; h: herbivore.

Taxa	Occurrence							Life	Habit
Bivalves									
Chione californiensis (Broderip)	S?	OF	MF	–	–	–	–	si	s
Chione fluctifraga (Sowerby)	–	–	MF	IF	–	–	EC?	si	s
Chione pulicaria (Broderip)	S?	OF	MF	–	–	–	–	si	s
Dosinia ponderosa (Gray)	S	–	–	–	–	–	–	si	s
Protothaca grata (Say)	–	–	–	–	–	MC	EC?	si	s
Tagelus (Tagelus) affinis (Adams)	S	OF	MF	IF	–	–	EC?	di	s
Tagelus (Tagelus) californianus (Conrad)	–	–	MF	IF	–	–	EC?	di	s
Tagelus (Mesopleura) politus (Carpenter)	–	–	MF	IF	–	–	EC	di	s
Gastropods									
Cerithium stercusmuscarum (Valenciennes)	S	OF	F	–	OC	MC	EC?	me	h
Cerithidea mazatlanica (Carpenter)	–	–	–	IF	(+marsh)		EC	me	df
Echinoderms									
Encope grandis (Agassiz)	S	OF	–	–	–	–	–	si	df
Encope micropora (Agassiz)	S	OF	–	–	–	–	–	si	df

Each shell was examined under the binocular microscope for traces of the various taphonomic processes. The magnitude of taphonomic alteration was estimated semi-quantitatively by assigning shells to alteration classes. Where applicable, the biotic agents (e. g. the various boring organisms) were identified. Percentage or absolute figures always refer to the number of affected shells and do n o t give the number of biotic agents (such as the number of encrusting *Schizoporella*).

Diagenetic changes of hard parts were investigated using acetate peels, thin-sections and SEM samples. Resin casts were made to distinguish various types of clionid borings.

TAPHONOMIC PARAMETERS

The following taphonomic parameters were investigated: loss of ornament, loss of color, boring, encrustation, fragmentation, articulation, inorganic dissolution, and maceration.

L o s s o f o r n a m e n t regardless whether caused by bioerosion or physical wear (abrasion) was grouped into four alteration classes:

class 0: no macroscopically visible alteration; even exposed elements of shell sculpture (e. g. ribs) still possess lustre;

class I: slight to moderate alteration; loss of lustre at exposed elements of shell ornament;

class II: medium to strong alteration; exposed elements of shell ornament strongly reduced, but their shape and position still clearly visible;

class III: very strong alteration; shell ornament hardly noticeable to completely abraded.

The various alteration classes are illustrated in Pl. 1, Fig. 1.

Grazing traces made by herbivorous molluscs are a part of bioerosion, and as such are included in the four alteration classes mentioned above. To provide additional information, they have also been noted separately. Two classes, depending on presence or absence of grazing traces have been distinguished.

L o s s o f c o l o r is caused by abrasion as well as by chemical and biochemical changes in the organic matrix of the shells. Three alteration classes were distinguished:

class 0: no loss of color;

class I: fading of color or total loss of color in places;

class II: total loss of color throughout the shell.

E n c r u s t a t i o n is caused largely by serpulids, bryozoans, vermetid gastropods, cirripeds, foraminifera and crustose corallinacean algae. The following encrustation classes were recognised:

class 0: no encrustation;

class I: up to one-third of shell area encrusted;

class II: more than one-third of shell area encrusted.

B o r i n g is caused by clionid sponges, polychaetes, bivalves, bryozoans and thallophytes. The last group has not been incorporated in the semi-quantitative analysis. Four preservation classes were distinguished:

class 0: shells not attacked by macroboring organisms;

class I: up to one-third of shell area bored;

class II: between one- and two-thirds of shell area bored;

class III: more than two-thirds of shell area bored.

F r a g m e n t a t i o n is caused by water energy, predators and scavengers. The following fragmentation classes were recognised:

class 0: no fragmentation;

class I: shell margin indented or small bits of shell broken off;

class II: shell fragmented (only those shell fragments identified to the generic level are considered here).

The degree of a r t i c u l a t i o n has been expressed by percentage figures, the r i g h t - l e f t v a l v e r a t i o of shells as quotient.

To describe the intensity of i n o r g a n i c s h e l l d i s s o l u t i o n three classes were recognised:

class 0: no dissolution of shells;

class I: weak dissolution, microborings slightly enlarged;

class II: strong shell dissolution.

M a c e r a t i o n describes a state of preservation of hard parts in which the individual crystallites disintegrate through the decay of the organic matrix (LEWY 1981). Maceration was registered as present or absent.

ALTERATION INDICES

From the semi-quantitatively registered taphonomic alterations (alteration classes 0 to Y) alteration indices were calculated. Initially, this was done for each target genus in each of the subenvironments (= I_G) (1). Then, taking into account the relative abundance of the target genera, an alteration index

for each taphonomic parameter in each subenvironment (= I_s) was calculated using I_G (2).

Table 2: Alteration indices; abbreviations and minimum-maximum values

Alteration	Index	Minimum-Maximum Values
loss of ornament	I_A	$0-3$
grazing	I_{Gr}	$0-1$
boring	I_B	$0-3$
encrustation	I_E	$0-2$
loss of color	I_C	$0-2$
fragmentation	I_F	$0-2$

The alteration indices are a measure of the average effects of the taphonomic agents. The index maxima for the various taphonomic parameters are given in Table 2.

$$(1) \quad I_G = (N_G)^{-1} \times \sum_{i=0}^{y} n_i \, AD_i$$

where N_G = number of investigated shells per target genus and subenvironment

y = maximum alteration class

n_i = number of shells in the ith alteration class

AD_i = number of the ith alteration class ($= 0$ to y)

$$(2) \quad I_S = (N)^{-1} \times \sum_{i=1}^{\infty} I_{Gi} N_{Gi}$$

where N = number of all investigated shells per subenvironment

I_{Gi} = alteration index of the ith target genus

N_{Gi} = number of investigated shells of the ith target genus.

The range of shell alteration is demonstrated by the target taxa *Chione californiensis* (Pl. 1, Fig. 1), *Tagelus* sp. (Pl. 1, Fig. 2), *Cerithidea mazatlanica* (Pl. 1, Fig. 3), *Encope grandis* (Pl. 2, Fig. 1), *Cerithium stercusmuscarum* (Pl. 2, Fig. 7), and *Dosinia ponderosa* (Pl. 4, Fig. 1).

TAPHONOMIC AGENTS

BORING ORGANISMS

The usefulness of boring organisms for paleoecological and paleobathymetric analysis has been demonstrated repeatedly (e. g. BOEKSCHOTEN 1966, BROMLEY 1978, GOLUBIC et al. 1975, SWINCHATT 1969, VOGEL et al. 1987, WARME 1975). This usefulness is enhanced by the high fossilization potential and autochthony of borings. (The latter feature is not necessarily true where borings are made in shells which can undergo extensive transport.)

Here we briefly discuss the various groups of borers occurring in Bahia la Choya and the morphology of their borings.

E n d o p h y t e s (Pl. 2, Fig. 4) comprise boring algae as well as bacteria and fungi. Their tunnel systems vary between 1 and 100 μm. Endophytes colonise new substrates very rapidly; boring activity can be demonstrated after 9 days, and within 4 months the whole surface is colonised, whereby the areal size is of subordinate significance only (PERKINS & TSENTAS 1976). Hard parts which do not show any signs of endophytes despite favorable environmental conditions cannot have rested on the sea floor for more than a few days before becoming buried.

C l i o n i d s p o n g e s create a multibranched network of small chambers which are connected by more or less distinct

intercameral canals. Sponge borings (Pl. 3, Figs 1−7) are accommodated in the ichnogenus *Entobia* within which various ichnospecies can be distinguished, based on a number of morphological features such as shape and arrangement of chambers, and presence and dimensions of intercameral canals (BROMLEY & D'ALESSANDRO 1984). In Bahia la Choya, three ichnospecies of *Entobia* have been found: *E. laquaea*, *E. megastoma*, and *E. paradoxa* (Table 3, Pl. 3, Figs 1−7).

Polychaetes of the family Spionidae bore chemically as well as mechanically. Members of the genus *Polydora* create simple to meandering U-shaped borings whereby the tunnels (with a diameter of 1−2 mm) are separated by a spreite. Three ichnotaxa occur in Bahia la Choya: *Caulostrepsis* (Pl. 2, Fig. 6), *Maeandropolydora*, and *Helicotaphrichnus commensalis* (KERN, GRIMMER & LISTER).

Table 3. Boring sponges and bivalves and their zonation across tidal flat.
+: present; (+): rare; O: absent; OF: outer flat; MF: mid flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel.

Ichnotaxon	Zootaxon	Subenvironments					
		OF	MF	IF	OC	MC	EC
Porifera							
Entobia laquaea (BROMLEY & D'ALESSANDRO)	*Cliona* cf. *viridis* (GRAY)	+	+	O	+	+	(+)
E. megastoma (FISCHER)	*C.* cf. *megastoma* (FISCHER)	+	O	O	(+)	O	O
E. paradoxa (FISCHER)	*C.* cf. *paradoxa* (FISCHER)	(+)	O	O	O	O	O
Bivalvia							
Gastrochaenolithes dijugus (KELLY & BROMLEY)	*Gastrochaena truncata* (SOWERBY)	+	+	O	+	+	O
G. torpedo (KELLY & BROMLEY)	*Lithophaga* sp.	(+)	O	O	(+)	O	O
G. ornatus (KELLY & BROMLEY)	*Diplothyra curta* (SOWERBY)	(+)	O	O	O	O	O

Members of the three most important families of boring bivalves are present in Bahia la Choya: *Diplothyra curta* (SOWERBY) (Pholadidae), *Gastrochaena truncata* (SOWERBY), *G. ovata* (SOWERBY) (Gastrochaenidae), and *Lithophaga attenuata* (DESHAYES) and *L. abbotti* LOWE (Mytilidae). All these species produce a calcareous lining on the inside of their flask- to date-shaped borings. *Lithophaga* and *Gastrochaena* frequently produce siphonal tubes which extend several mm or even cm above the substrate to avoid burial by shifting sand (Pl. 4, Fig. 6). In Bahia la Choya, *Lithophaga* is largely restricted to rocky substrate, whilst *Gastrochaena* preferentially occurs in shells. When shells are colonised which are far too thin to accommodate the boring, *Gastrochaena* produces an "igloo" (Pl. 5, Fig. 5), a capsule which consists of sediment grains cemented together by aragonite (see also CARTER 1978). Three ichnospecies can be recognized: *Gastrochaenolithes dijugus*, *G. torpedo*, and *G. ornatus* (Table 3; see also KELLY & BROMLEY 1984).

Ctenostome bryozoans of the families Terebriporidae and Immergentiidae are easily overlooked because of their small size. As the zooids penetrate only to a depth of about 0.6 mm (SOULE & SOULE 1969), their bioerosion potential is very limited. Two species were encountered in Bahia la Choya; *Spathipora* cf. *mazatlanica* (SOULE & SOULE) (Pl. 5, Fig. 1) and *Penetrantia densa* (SILEN) (Pl. 5, Fig. 2), the latter having been found only on shells of *Cerithium stercusmuscarum*.

All groups of boring organisms require low rates of sedimentation.

BORING PREDATORS

The borings of predatory organisms are treated separately, although strictly speaking they are part of bioerosion. In Bahia la Choya borings of naticid and muricid gastropods as well as of octopus occur.

Naticid borings (Pl. 4, Figs 2, 3) have a round cross-section up to several mm in diameter and a parabolic longitudinal section. Bivalves are bored by naticids most commonly in the umbonal region, gastropods in the spiral region. In narrow turriform gastropods, such as *Cerithidea*, the shape of the boring may be oval rather than round due to the geometry of the shell.

Muricid borings are usually smaller, cylindrical to conical and occur in gastropods most often in the apical area of the shell (see also CARRIKER & YOCHELSON 1968).

Octopus borings (Pl. 4, Fig. 5) are very variable and range from oval-conical to round and cylindrical (NIXON 1979). Because of this they are often difficult to distinguish from borings produced by muricid gastropods. Octopus occasionally drill several holes in their prey and different varieties of the borings can be found on the same shell (Pl. 4, Fig. 5). In bivalves, octopus borings are most frequently encountered near the adductor muscles, in gastropods on the spire (see also ARNOLD & ARNOLD 1969, BROMLEY 1981).

Naticid borings can be accommodated in the ichnospecies *Oichnus paraboloides* (Pl. 1, Fig. 4, Pl. 4, Figs 2, 3) those of muricids and octopus in *Oichnus simplex* (BROMLEY 1981)

(Pl. 1, Fig. 4, Pl. 4, Fig. 5). In *Cerithium stercusmuscarum* the abundance of *Oichnus simplex* is positively correlated with the percentage of shells inhabited by hermit crabs. It appears that the hermit crab and not the original inhabitant, the gastropod, is the prey target of octopus.

ENCRUSTING ORGANISMS

A number of encrusting organisms are found on shells of the tidal flat. The most important groups are serpulids, bryo-zoans, vermetids, balanids, foraminifera and crustose coralli-nacean algae.

Serpulids (Pl. 6, Fig. 4) are common encrusters in Bahia la Choya. As Recent serpulids are identified by soft parts only and shell shape is not a very diagnostic feature, the serpulids have been classified according to shell morphotypes (PARSCH 1956). Where possible, these morphotypes have been attri-buted to true species using FAUVEL (1927), HARTMAN (1969), and RIOJA (1942a, b). A list of species is found in Table 4. Most common are *Pomatostegus* cf. *polytrema, Serpula* cf. *concharum, Pomatoceras* cf. *triqueter,* and *Spirorbis* cf. *varia-bilis.*

Table 4. Encrusting serpulids and their zonation across the tidal flat. Morphotype classification after PARSCH (1956).
+: present; (+): rare; O: absent; OF: outer flat; MF: mid flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel.

Morphotypes	Zootaxon	Subenvironments					
Serpulinae		OF	MF	IF	OC	MC	EC
Serpula (Pentaserpula) I	*Pomatostegus* cf. *polytrema* (PHILLIPPI)	+	+	O	+	+	+
S. (Pentaserpula) II	*Serpula* cf. *concharum* (LANGERHANS)	+	+	O	+	O	O
S. (Tetraserpula) I	?	+	O	O	(+)	O	O
S. (Tetraserpula) II	?	(+)	O	O	O	(+)	O
S. (Tetraserpula) III	?	(+)	O	O	(+)	O	O
S. (Dorsoserpula) I	*Pomatoceros* cf. *triqueter* (LINNE)	+	O	O	+	O	O
S. (Cycloserpula) I	*Vermiliopsis* cf. *multicristata* (PHILLIPPI)	(+)	O	O	O	O	O
Filograninae							
S. (Cycloserpula) II	*Josephella* cf. *marenzelleri* (CAULLERY & MESNIL)	(+)	O	O	O	O	O
Spirorbinae							
S. (Tetraserpula) IV	*Spirorbis (Spirorbella)* cf. *marioni* (CAULLERY & MESNIL)	+	O	O	(+)	(+)	O
S. (Dorsoserpula) II	*Sp. (Circeis)* cf. *pagenstecheri* (QUATREFAGES)	(+)	O	O	O	O	O
S. (Cycloserpula) III	*Sp. (Pileolaria)* cf. *variabilis* (BUSH)	+	+	O	+	+	+

Bryozoans (Pl. 5, Fig. 6, Pl. 6, Figs 1, 3) preferentially encrust the undersides of shells, a protection from being co-vered by sediment. Moreover they prefer a smooth substrate to a strongly sculpted substrate when bivalves are in a cur-rent-stable position (THOMPSEN 1977). The various growth forms of bryozoans are an expression of their morphological adaptation to different energy levels and of their differing to-lerance to suspended sediment particles. Accordingly, bryo-zoans have been classified in morphotypes (e. g. STACH 1936) whereby — among crustose taxa — membraniform, cellepori-form, and petraliiform types are distinguished. Membrani-form types are very good indicators of very low rates of net sedimentation (e. g. LAGAAIJ & GAUTIER 1965, RIDER & COWEN 1977, SCHOPF 1969), the petraliiform type, in addition, does not tolerate high energy conditions.

21 species of bryozoans have been identified using BRUSCA (1980), CANU & BASSLER (1923) and OSBURN (1950, 1952, 1953). Two very rare taxa, *Aetea* sp. and *Hippothoa flagellum* (MANZONI) could not be accommodated in the morphotypes discussed above. The latter taxon apparently prefers very low energy conditions. A list of the remaining species is found in Table 5.

The vermetid gastropods *Vermetus indentatus* (CAR-PENTER), *Tripsycha tripsycha* (PILSBRY & LOWE), and *Serpulor-bis margaritaceus* (CHENUS ex ROUSSEAU MS) occur as pro-strate growth forms largely on shells of the outer flat.

Balanids are rare on Bahia la Choya molluscs except on *Cerithium stercusmuscarum.* Apparently, they mainly colo-nise shells of live mobile organisms, this way being protected from burial by sediment.

Table 5. Morphotypes (STACH 1936) and taxa of bryozoans and their distribution across the tidal flat.
+: present; (+): rare; O: absent; OF: outer flat; MF: mid flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel.

Morphotypes and Taxa	Subenvironment					
Membraniform A	OF	MF	IF	OC	MC	EC
? *Mucronella* sp.	+	(+)	O	+	O	O
Schizoporella unicornis (JOHNSTON)	+	O	O	O	O	O
Hippoporella gorgonensis (HASTINGS)	+	O	O	O	O	O
? *Lepralia* sp.	+	O	O	O	O	O
Holoporella brunnea (HINCKS)	(+)	O	O	O	O	O
Stylopoma spongites (PALLAS)	(+)	O	O	O	O	O
? *Parasmittina* sp.	(+)	O	O	O	O	O
Hippopodinella adpressa (BUSK)	(+)	O	O	O	O	O
Fenestrulina malusi var. *umbonata* (COUCH)	(+)	O	O	+	O	O
Fasciculipora pacifica (OSBURN)	(+)	O	O	O	O	O
Tubulipora tuba (GABB & HORN)	(+)	O	O	O	O	O
? *Aimulosia* sp.	(+)	O	O	O	O	O
Membraniform B						
Conopeum commensale (KIRKPATRICK & METZELAAR)	(+)	O	O	O	O	O
Colletosia cf. *radiata* (MOLL)	(+)	O	O	(+)	O	O
Floridina antiqua (SMITT)	(+)	O	O	O	O	O
Antropora sp.	(+)	O	O	O	O	O
Thalamoporella californica (LEVINSON)	(+)	O	O	O	O	O
Petraliiform						
Lichenopora novaezelandiae (BUSK)	(+)	O	O	O	O	O
Lichenopora intricata (BUSK)	(+)	O	O	O	O	O

Encrusting foraminifera are represented by two taxa, the very abundant *Planorbulina* and the rare agglutinated *Placopsilina*. Their distribution pattern across the tidal flat is given in Table 6.

Crustose corallinacean algae occur as white to pinkish crusts on pebbles and shells.

Table 6. Species of encrusting foraminifera and their distribution across the tidal flat.
+: present; (+): rare; O: absent; OF: outer flat; MF: mid flat; IF: inner flat; OC: outer channel; MC: mid channel; EC: estero channel.

Foraminifera	Subenvironments					
Agglutinantia	OF	MF	IF	OC	MC	EC
Placopsilina bradyi (CUSHMAN & McCULLOCH)	(+)	O	O	O	O	O
Calcarea perforata						
Planorbulina cf. *vulgaris* (D'ORBIGNY)	+	(+)	O	(+)	(+)	O

LOSS OF SHELL ORNAMENT

As the influence of physical erosion (abrasion) and bioerosion cannot be separated in most cases, both aspects of erosion were considered jointly. Types and significance of abrasion have been studied for some time (e. g. DRISCOLL 1967, 1970, DRISCOLL & WELTIN 1973, EHRENBERG 1930, KLAHN 1932, PRATJE 1929, QUENSTEDT 1928, TAUBER 1942), whilst the interest in bioerosion is of more recent date (e. g. BROMLEY 1978, GYGI 1975, NEUMANN 1966, NORTH 1954, SCHNEIDER 1976). The degree of loss of shell ornament has been used to qualitatively measure the activity of abrasional and bioerosional agents.

Differences in the microarchitecture of shells result in different resistance to abrasion (e. g. CHAVE 1964) and bioerosion. For example, crossed-lamellar and composite prismatic shell structures exhibit the highest durability against abrasion (TAYLOR & LAYMAN 1972).

Bioerosion in Bahia la Choya is largely a result of the boring activity of endolithic thallophytes. Herbivorous gastropods in search of food rasp the surfaces of endolithic thallophyte-infested shells (Pl. 2, Fig. 3). During this process they rasp not only the distal ends of the thallophytes, but also part of the shell, this way destroying carbonate substrate (SCHNEIDER 1976) (Pl. 5, Fig. 4).

Loss of ornament in bivalves

In bivalves, incipient abrasion and/or bioerosion can be detected by a loss of lustre on particular parts of the shell: at the point of the highest post-umbonal convexity, on the inner shell margin, and at projecting parts of the shell ornament. Faceting, according to PRATJE (1929) and MULLER (1963:42) typical for the intertidal zone, has not been observed in Bahia la Choya bivalves. On large shells *(Dosinia, Chione)* members of calyptraeid and acmaeid gastropods (e. g. *Crucibulum spinosum)* produce circular to oval ring-like impressions up to 5 mm in width due to pressing their shells firmly against the shell substrate (Pl. 2, Fig. 8).

Reworked Pleistocene *Chione* shells sometimes exhibit a secondary ornament, the original ornament having been removed by a combination of diagenetic and abrasional processes. This secondary ornament consists of a step-like commarginal morphology which may retrace differences in the resistance of shell layers formed during winter and summer growth periods (e. g. FARROW 1972).

Examples of loss of shell ornament in bivalves are shown in Pl. 1, Figs 1, 2, Pl. 2, Fig. 3).

Loss of ornament in gastropods

In general, gastropods are easily transported and thereby quickly abraded and destroyed (compare FUTTERER 1978b). Abrasion starts at exposed places such as tubercles, varices, the apex, and near the aperture. However, due to their great thickness, varices are more resistant to abrasion than the remaining shell.

In *Cerithidea*, holes first show up on the shell surface opposite to the aperture. In part, this is due to the infestation of this area by endolithic thallophytes during the life of the gastropod. In part, the selective abrasion (faceting) could be a result of the current stable position of the shell with the aperture facing the sediment surface (TAUBER 1942). In the last stage, shortly before final destruction, *Cerithidea* is reduced to the columella from which bridge-like varices extend (Pl. 1, Fig. 3).

The mechanical breakdown of *Cerithium* differs considerably from that of *Cerithidea;* only rarely does a columella form the final stage. Faceting, on the other hand, is present (Pl. 2, Fig. 7). Shells of *Cerithium* are frequently used by hermit crabs. In carrying the shell across the sediment the hermit crab causes abrasion of a particular type: the part of shell just within the aperture is abraded by the hard carapace; moreover the part of the last whorl close to the aperture touches the substrate while the shell is being dragged across the surface and becomes abraded (see also EHRENBERG 1931, SCHAFER 1962: 211).

A particular type of mixed mechanical erosion/bioerosion is caused by endophytes which form dense mats in the upper part of the spire. When drying during subaerial exposure, these mats shrink and develop cracks. When the shell is subject to mechanical wear, they fall off and leave a pitted to polygonally structured surface.

Loss of ornament in echinoids

The disc-shaped echinoid *Encope* has a weakly concave adoral side and thus abrasion starts at the adoral shell margin. Similarly, during subsequent abrasion the adoral side is more strongly affected than the apical side. This can be only explained by the echinoid tests being dragged across the surface with their apical side facing upward. Examples of the different states of preservation are given in Pl. 2, Fig. 1.

LOSS OF COLOR

Change of original color is due either to loss of color (e. g. during maceration) or to discoloration. For example, pyrite formation results in shells turning black, whilst Fe-oxide solutions give shells a brownish tinge (e. g. FREY & HOWARD 1986).

On the tidal flat, loss of color is caused mainly by abrasion and the boring activity of endophytes. As the degree of abrasion is low, so is the loss of color. All shells with a complete loss of color are reworked from the Pleistocene.

Among the target genera, *Cerithium* shows only very little loss of color, as the color pattern is not confined to the shell surface, but extends nearly right through the shell layers.

FRAGMENTATION

The degree of fragmentation of shells is related to the energy level as well as to the abundance of predators and scavengers. Fracturing by water energy is largely caused by waves and breakers as currents are rarely strong enough to fragment mollusc shells (SCHAFER 1962: 184). Shell breakage by carnivores is caused mainly by crustaceans, fish and birds (Pl. 1, Fig. 5, Pl. 2, Fig. 5). Often, these groups produce characteristic breakage patterns (CARTER 1968, SCHAFER 1962: 459) (Pl. 1, Fig. 5). The activity of predators does not always lead to shell breakage. Sometimes only small bits of the shell margin are broken off (Pl. 1, Fig. 6) and may furnish information on the predator (CARTER 1968). The origin of shell damage often cannot be determined because roll faceting in gastropods may produce patterns similar or even identical to those caused by predators.

The breakage pattern of a mollusc shell not only depends on the kind of energy input, but on the mechanical properties of the shell (HOLLMANN 1968). Relevant parameters are shell size, convexity, thickness, microarchitecture, and organic matrix. Shell ornament and growth lines are responsible for certain breakage patterns (HOLLMANN 1968) (Fig. 16). Fracturing of hard parts is often facilitated by intensive boring activity, especially by clionid sponges (YOUNG & NELSON 1985). Clionid sponges are particularly common in large *Dosinia* shells of the outer flat. As only a limited percentage of bored *Dosinia* shells are fractured, the water energy cannot have been very high.

ARTICULATION AND RIGHT-LEFT VALVE SORTING

Articulated shells are usually regarded as indices for in situ burial or short transport of living organisms followed by rapid burial (e. g. during high energy events). Shells lying on the sediment surface quickly become disarticulated, especially in oxidizing environments. The time involved to separate valves strongly depends on the durability of the ligament. To cite an extreme example, TREWIN & WELSH (1972) found articulated Ensis which, according to their degree of encrustation, must have rested on the sediment surface for more than one year.

Sorting of disarticulated valves is a result of strong currents and/or waves (see BEHRENS & WATSON 1969, BOUCOT et al. 1958). Selective transport takes place even when valves are only slightly inequivalve, whilst differences in weight, shell ornament or durability do not play a significant role (KORNIKKER et al. 1963). In areas strongly influenced by waves even equivalve shells are sorted (BEHRENS & WATSON 1969).

If predators, borings, or fracturing select one valve over another, the hydrodynamic properties of the valves can be affected and right-left valve sorting can take place.

SHELL SOLUTION

Chemical shell solution on the sea floor is thought to account for much of the loss of mollusc shells (e. g. ALEXANDERSSON 1972, 1978, BRETT & BAIRD 1986, CHAVE 1964). In Bahia la Choya no dissolution could be observed in Recent shells, except in the estero channel. The absence of shell solution can be explained in various ways: either the chemical environment at the sediment surface and within the uppermost few centimetres of sediment is saturated with respect to calcium carbonate (PYTKOWICZ 1969), or else the carbon dioxide produced by microbial activity within the reducing zone is rapidly buffered by abundant shell material in the sediment (e. g. KREISA & BAMBACH 1982). There is also the possibility that faint traces of solution are obliterated when shells are subsequently reworked, abraded, and bored by endophytes.

In the estero channel and within the marsh, shell solution takes place in connection with maceration (e. g. Pl. 6, Fig. 2). Although the latter only affects the organic matrix of the shell, it produces porosity which facilitates shell solution in the acidic, carbonate-poor sediments of the marsh (e. g. WIEDEMANN 1972).

The preservation potential of calcareous hard parts is therefore considerably higher in the high energy environment than in low energy environments despite the frequent sediment reworking and high degree of abrasion there.

ONSHORE-OFFSHORE ZONATION OF TAPHONOMIC AGENTS AND PRESERVATION QUALITY OF SHELLS

LOSS OF SHELL ORNAMENT

Results

The change in the loss of shell ornament of the target genera across the tidal flat and along the tidal channel is illustrated in Fig. 3. The main results are as follows:

(a) On the tidal flat, the degree of loss of shell ornament is low to moderate (maximum alteration index = 1,37). Strongly abraded shells represent less than 10%. Relatively fresh hard parts constitute 50 to 60% in the three subenvironments (Fig. 3a).

(b) On the tidal flat, the average index of loss of shell ornament shows a pronounced decline from the outer to the inner flat as does the index of grazing (Fig. 3c).

(c) In the channel, the average degree of loss of shell ornament is low to moderate (Fig. 3a). The degree of loss of shell ornament increases from the outer to the mid channel and strongly decreases toward the estero channel (Fig. 3c).

(d) Within the channel, the various target genera differ greatly in their degree of loss of ornament (Fig. 4).

Discussion

The low average loss of ornament of bivalve shells on the tidal flat suggests relatively rapid burial and very limited transport (compare WARME 1969). This is less true of gastro-

pod shells which easily undergo transport by rolling (FUTTERER 1978b). Shells of Cerithidea (which lives in the salt marsh and inner flat) are quickly abraded and bioeroded because they are strongly infested by endophytes while still alive. They are rarely inhabited by hermit crabs and are chiefly transported along the tidal channel. The landward decrease of loss of shell ornament on the flat corresponds to the decrease of water energy and grazing activity in the same direction. Correlated is also the length of submergence, as abrasion only takes place under water cover. During low tide the breaker zone is situated at the seaward edge of the outer flat and mechanical erosion is most effective there. This is also true of bioerosion, the grazing activity being at its maximum in this subenvironment.

When the alteration indices of the individual target species are considered (Fig. 4a) no uniform trend is visible. For example, the indices of the bivalves Chione and Tagelus decrease from outer to the mid flat. The index of the gastropod Cerithium, in contrast, increases. This can be explained by differences in the hydrodynamic behavior of the two groups. In addition, the degree of loss of ornament is a function of the distance from the habitat of the taxa.

The degree of loss of shell ornament in Cerithium is strongly correlated with the percentage of shells inhabited by hermit crabs (Fig. 4b) as such shells suffer less abrasion.
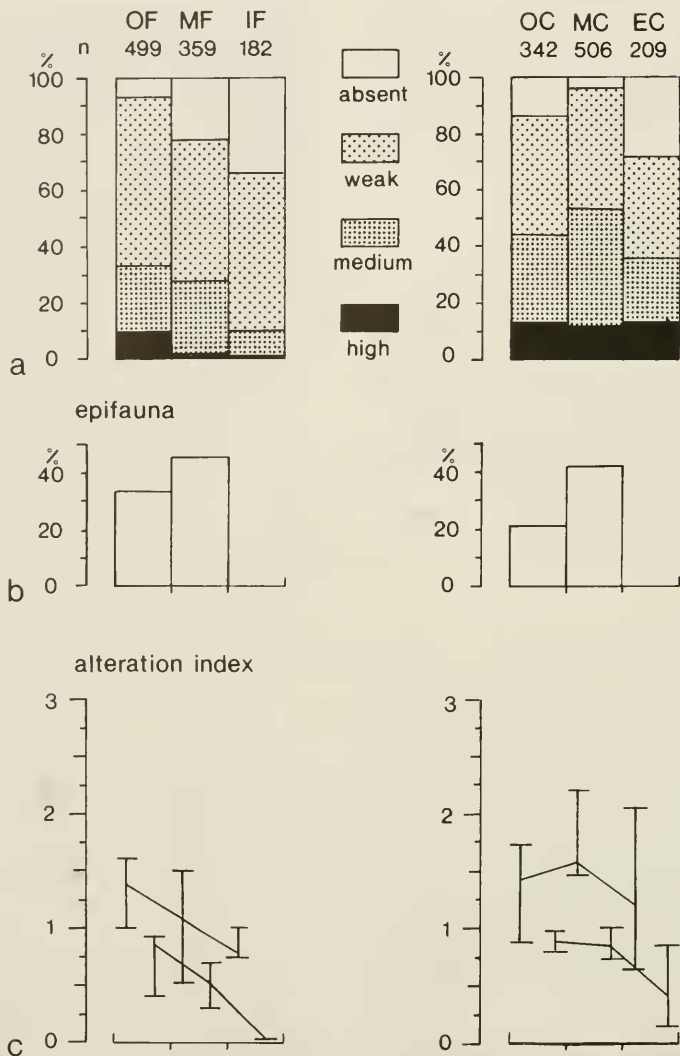
LOSS OF ORNAMENT

Fig. 3:   Loss of ornament. a: degree of loss of ornament; b: percentage of epifauna among shells of target genera; c: range and mean of alteration index. n = number of individuals studied; OF = outer flat; MF = mid flat; IF = inner flat; OC = outer channel; MC = mid channel; EC = estero channel.

The shallow burrowing *Chione* and the deep burrowing *Tagelus* differ very little in loss of ornament on the flat (Fig. 4a). This indicates that their strongly differing hydrodynamic qualities and life habits do not influence the alteration index. Shells of both taxa are therefore useful indicators of abrasion and bioerosion on the flat.

All target genera of the tidal channel show a greater loss of ornament than on the flat. This is due to a higher grazing

activity and to a longer time of submergence in a medium to high energy environment. In addition, a considerable mixing of old and new shells takes place, due to reworking of older shell layers and of the Pleistocene basement.

The differences in loss of ornament between the various target genera are also higher than on the flat, as the species found in the channel are derived from several habitats and experienced different degrees of transport.
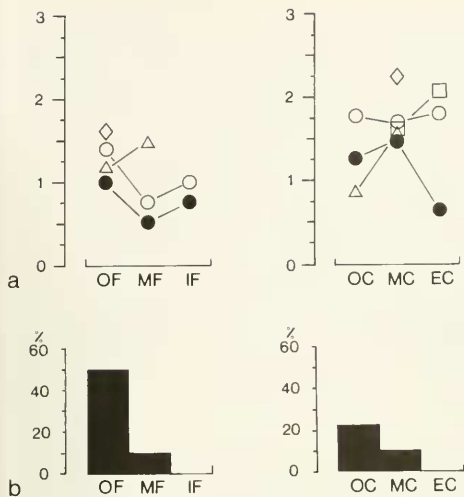
Fig. 4. a: Index of loss of ornament of various target genera in the sub-environments; b: percentage of *Cerithium* shells inhabited by hermit crabs. ○ = *Chione;* ● = *Tagelus;* ◇ = *Dosinia;* △ = *Cerithium;* □ = *Protothaca*. For additional key see Fig. 3.

Within the target genera, histograms showing the distribution of individuals in the various alteration classes invariably exhibit a distinct peak in the subenvironments of the flat and a far more uniform distribution with a shift toward higher alteration classes in the channel (Fig. 5). This difference can be explained by the great abrasive and bioerosive power of the tidal channel.
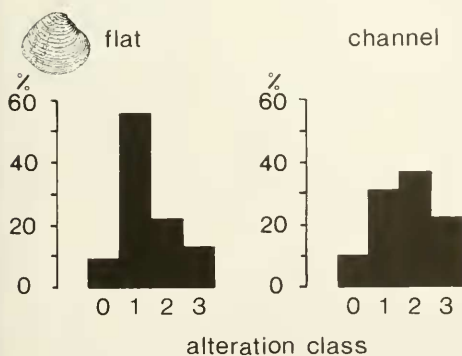
Fig. 5: Loss of shell ornament: alteration classes of *Chione* in flat versus channel subenvironments.

Conclusions

(1) The subenvironments of the tidal flat differ considerably in their degree of loss of shell ornament. This is particularly true when flat and channel subenvironments are compared.

(2) As both energy level and grazing activity decreases landward, it remains uncertain which of the two is largely responsible for the decrease of loss of ornament across the flat.

(3) In the channel, the greater loss of shell ornament is largely due to the higher energy level together with the reworking of older shell material.

(4) In gastropod shells inhabited by hermit crabs the loss of ornament is less pronounced. However, such shells exhibit a very specific abrasion pattern (compare TAUBER 1942).

(5) The low degree of abrasion on the flat indicates lack of extensive lateral transport of bivalve shells during fair weather conditions.

(6) Seaward transport (especially of gastropods) takes place in the tidal channel.

BORING

Results

The degree of boring is low in all subenvironments, I_B being less than 1 (possible maximum: 3) (Fig. 6 h). The number of bored shells and the degree of boring decrease landward both across the flat as well as along the channel (Figs 6, 7). Variation in the degree of boring between the target genera is largest in mid channel and outer flat subenvironments (Fig. 6 h). There is little difference in the degree of boring between channel and flat. Among bored shells, those bored by thallophytes are most abundant followed, in decreasing order, by clionids, polychaetes, bivalves, and bryozoans. With exception of boring polychaetes (which slightly increase in abundance from the outer to the mid flat), the absolute abundances of all boring organisms decrease landward (Fig. 7).

The trend of the boring index is independent of the percentage of epifauna among the investigated shell material (Fig. 6 h, i). The percentage of bored shells is clearly related to the thickness of Recent sediments overlying Pleistocene rocks: in Transect C in which the sediment cover is thin, a higher percentage of shells is bored than in Transect B with a largely sandy substrate (Fig. 7).

Discussion

As has been noted by several authors (e. g. BLAKE 1969, EVANS 1968, WARME 1970), there is a distinct relationship between many borers and substrate. This can be also demonstrated in Bahia la Choya. For example, the occurrence of *Gastrochaenolithes* depends on the presence of thick-shelled bivalves, especially *Dosinia*, a form that is most abundant in the outer flat. In addition, *Gastrochaena* is one of the few boring organisms which by lining its boring is able to inhabit the porous fine texture of the echinoid *Encope*. Clionid and polychaete borings very rarely occur in *Encope* or in the thin-shelled bivalve *Tagelus*. The difference in substrate preference between *Cliona* and boring polychaetes is illustrated in Fig. 8. *Cliona* prefers the thick-shelled *Chione*, whilst the polychaetes are found more often on the gastropod *Cerithium*. Obviously, the gastropod shell is a more suitable substrate for
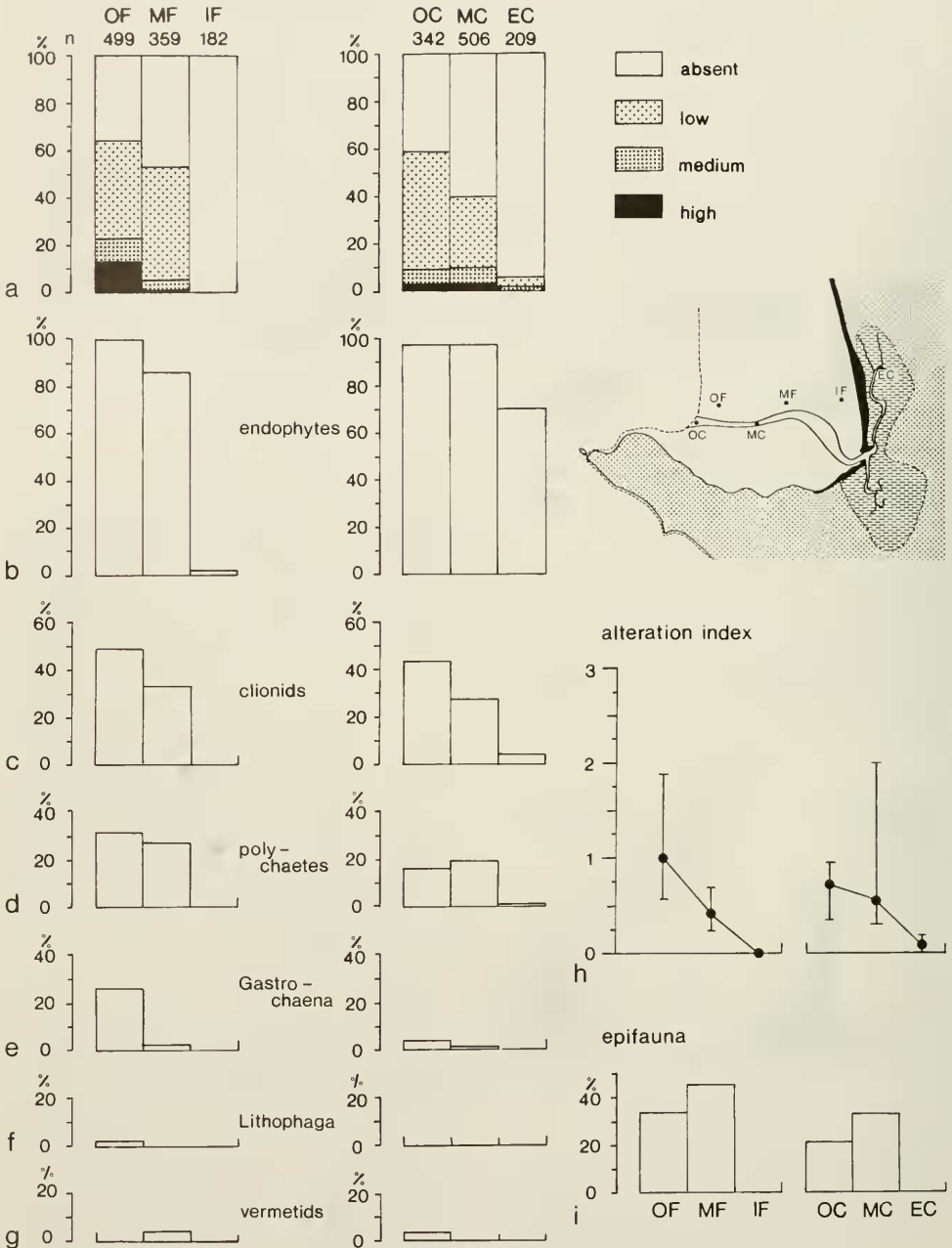
Fig. 6: Shells of target genera bored by non-predatory organisms. a: degree of boring in the various sub-environments (for key see Fig. 3). b–g: percentages of shells of target genera bored by various groups of boring organisms; h: range and mean of alteration index; i: percentage of epifauna among shells of target genera.
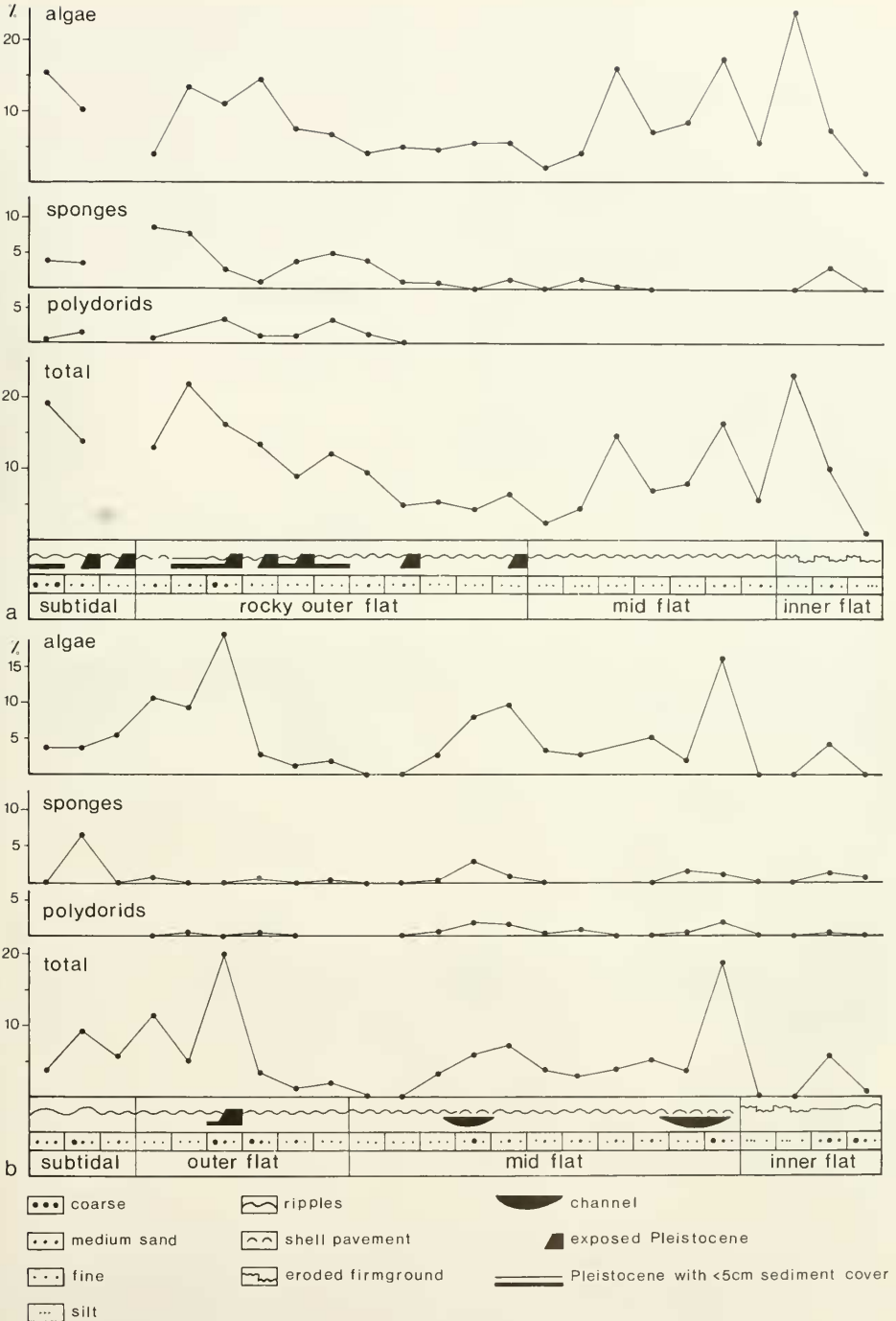
Fig. 7: Distribution of shells bored by algae, clionids, and *Polydora* across the tidal flat. a: Transect C; b: Transect B (see Fig. 2).

boring polychaetes; in addition some spionid polychaetes have a commensalistic relationship with pagurid hermit crabs (BLAKE 1969). Being relatively thin, *Cerithium* shells are an unsuitable substrate for *Cliona*. Moreover hermit crabs could transport clionid sponges onto parts of the tidal flat where they cannot thrive.

The abundance and diversity of boring organisms in the outer flat point to low net sedimentation in this subenvironment (compare BOEKSCHOTEN 1966). Low net sedimentation and resulting higher rates of reworking are also characteristic of the northern part of Bahia la Choya (e. g. Transect C) and are reflected by the higher percentage of bored shells.

The occurrence of *Entobia* high on the tidal flat (e. g. Fig. 7) appears to contradict HARTMAN (1958) and RUTZLER (1975). They found that *Cliona* is restricted to subtidal environments. In Bahia la Choya living clionids occur only in the outer flat. The distribution of *Entobia* in the taphocoenoses of the tidal flat therefore does not correspond to the habitat of clionids. This can be explained either by lateral transport or by in-situ reworking of older shell material which accumulated in an environment more favorable for the growth of clionid sponges.

the bivalve bored into the shell. Similarly, where several ichnospecies of *Entobia* occur superimposed they most likely represent several phases of boring as clionids usually avoid each other (see DE GROOT 1977).

Conclusions

(1) A distinct landward decrease in the activity of boring organisms occurs in the southern part of Bahia la Choya. This decrease is independent of the percentage of epifaunal individuals among the investigated material.
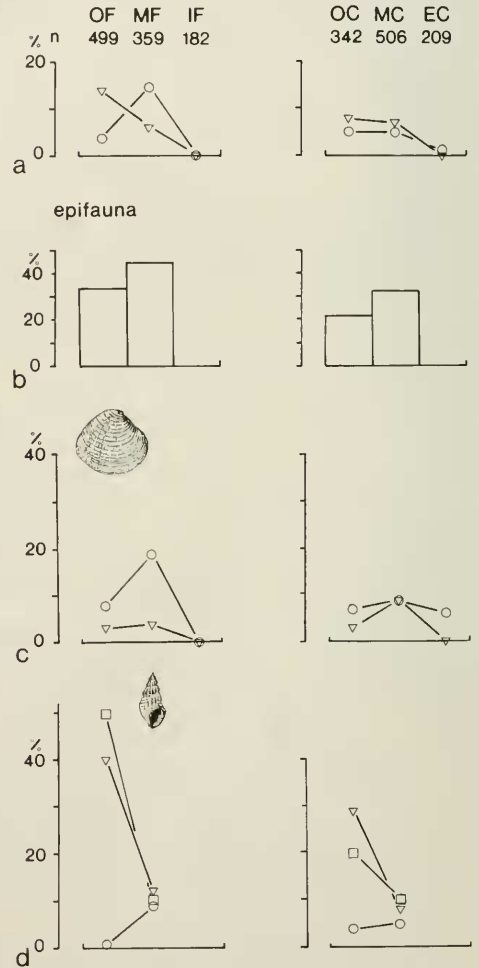
Fig. 9: Shells of target genera bored by predators. a: percentage of shells with *Oichnus simplex* (△) and *O. paraboloides* (○); b: percentage of epifauna among shells of target genera; c, d: relative abundance of *Oichnus simplex* (▽) and *O. paraboloides* (○) on shells of *Chione* and *Cerithium*. □ = percentage of *Cerithium* inhabited by hermit crabs. For key to subenvironments see Fig. 3.

Fig. 8: Relative abundance of boring *Cliona* and polychaetes on shells of *Chione* (a) and *Cerithium* (b). For key to subenvironments see Fig. 3 ○△ = *Cliona;* ○ = polychaetes; ◇ = *Cerithium* shells inhabited by hermit crabs.

As Bahia la Choya experiences a very low net rate of sedimentation (FURSICH et al., this volume, MELDAHL 1987) extensive time-averaging is likely. Several phases of colonisation by boring organisms can be observed repeatedly. For example, the occurrence of fresh *Gastrochaenolithes* which cross clionid borings indicate that *Cliona* cannot have been alive when

(2) Hermit crabs influence the taphonomy of *Cerithium* shells by attracting boring polychaetes.

(3) The high rate of boring in the outer flat subenvironment points to very low rates of sedimentation. Similarly, the higher percentage of bored shells in the northern part of the bay is related to sediment starvation and a higher frequency of reworking.

(4) Although borings in shells of the taphocoenoses show a zonation across the tidal flat, this zonation is not identical to that of living borers. The distribution of borers in the taphocoenoses indicates limited transport of shells during storms and extensive in-situ faunal mixing.

BORINGS OF PREDATORS

Results

Both the channel and the flat contain relatively few shells bored by predators (Fig. 9). On the flat *Oichnus simplex*, representing borings made by cephalopods and muricid gastropods, decreases from the outer to the inner flat, whilst *Oichnus paraboloides* (made by naticid gastropods) increases toward the mid flat and decreases again toward the inner flat. In the channel, both traces are roughly equally abundant on specimens of the target genera with *O. simplex* slightly dominating. A similar picture emerges when all shells of the taphocoenoses along Transects A, B and C are investigated (Fig. 10).
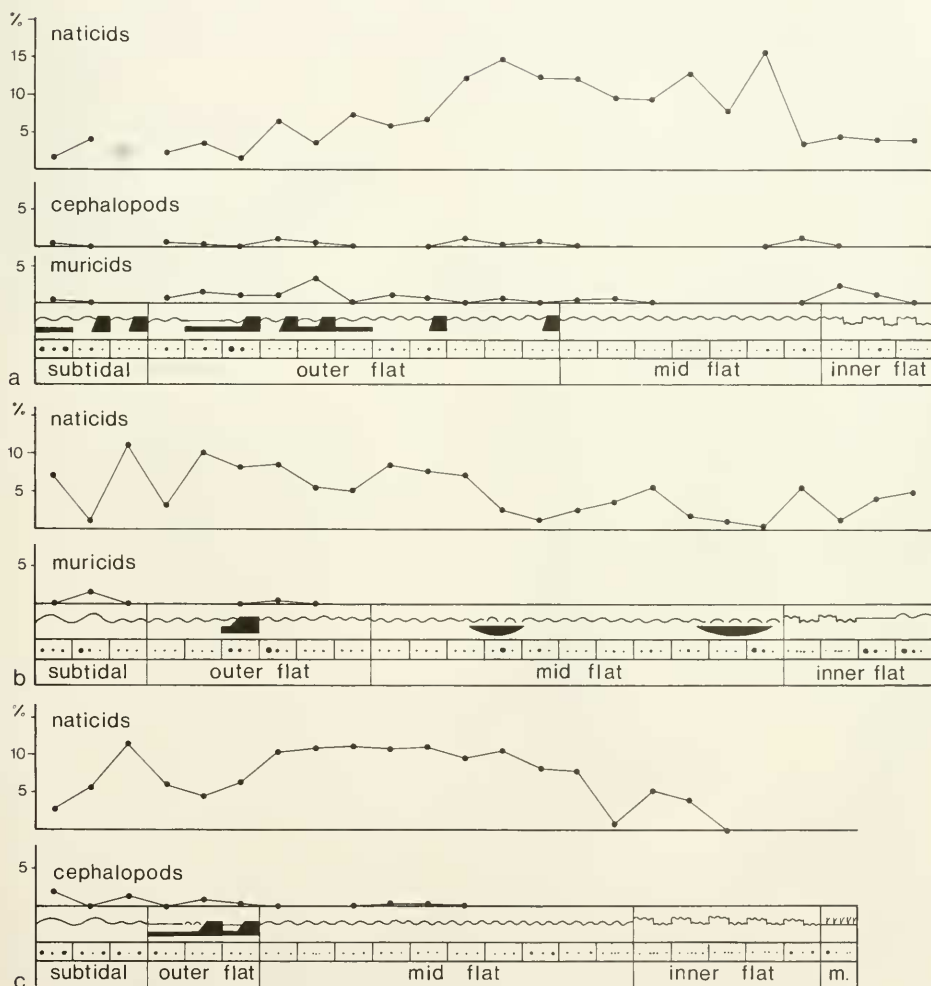
Fig. 10: Distribution of shells bored by predators (cephalopods, naticids, and muricids) across the tidal flat. a: Transect C; b: Transect B; c: Transect A; for key see Fig. 7.
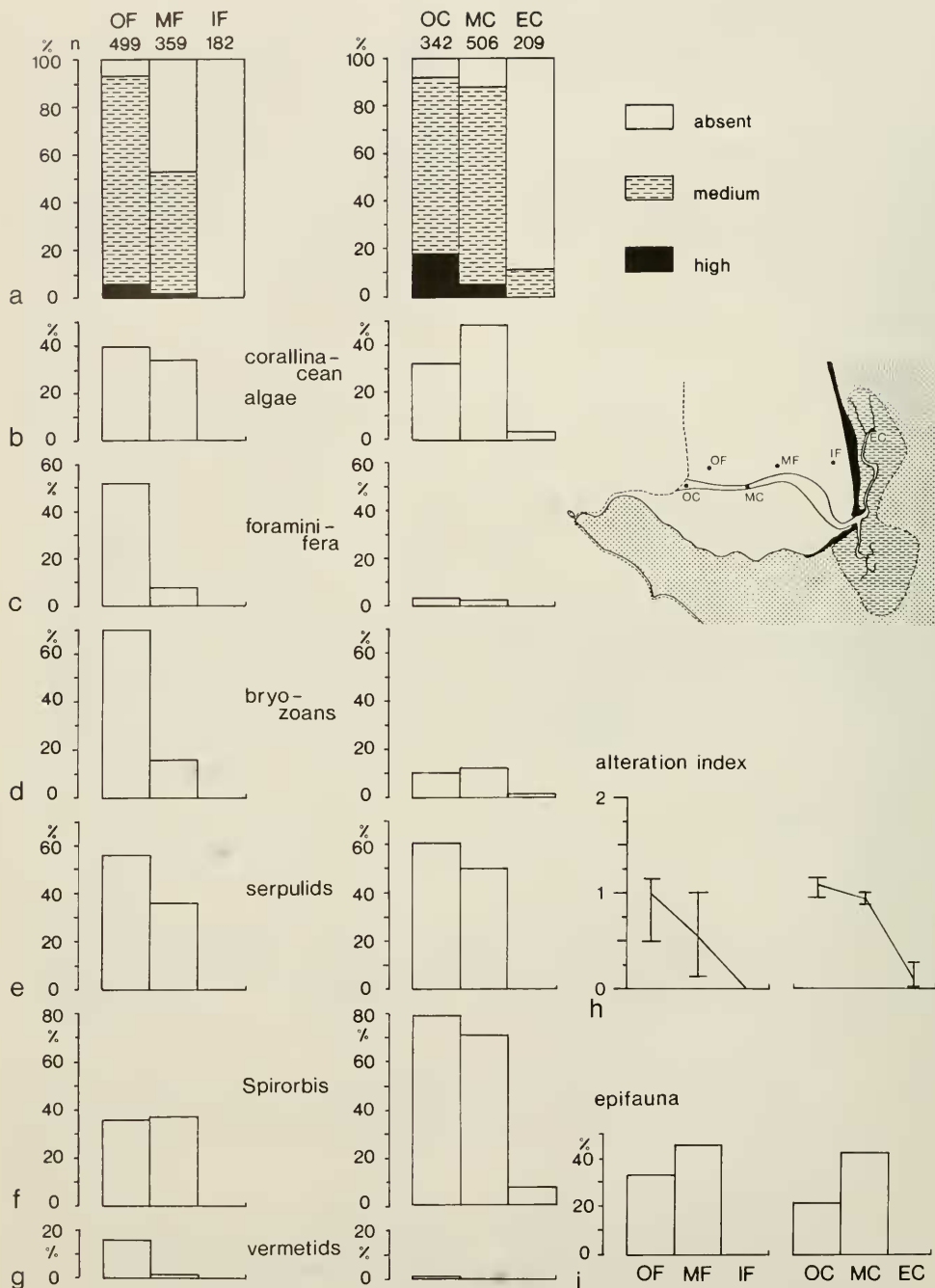
Fig. 11: Shells of target genera encrusted; a: degree of encrustation in the subenvironments; b–g: percentages of shells encrusted by various groups of encrusting organisms; h: mean and range of alteration index; i: percentage of epifauna among shells of target genera. For key see Fig. 3.
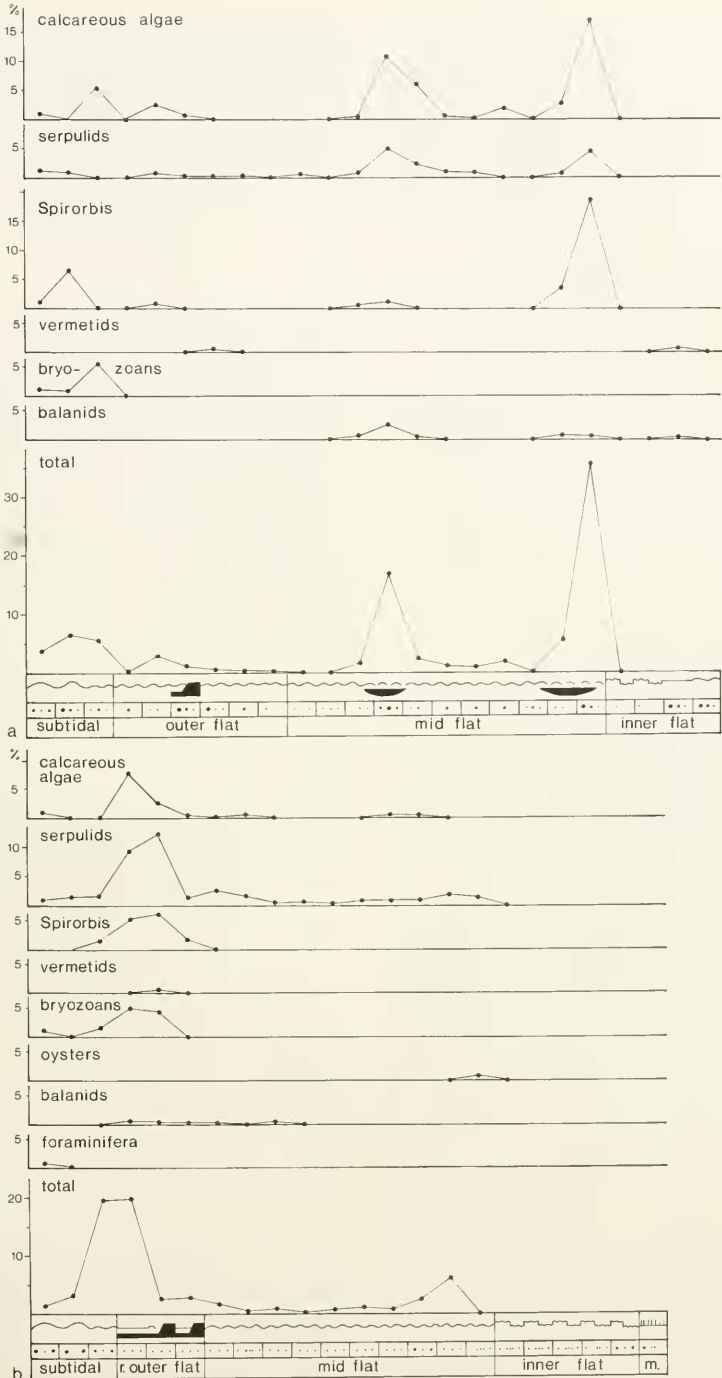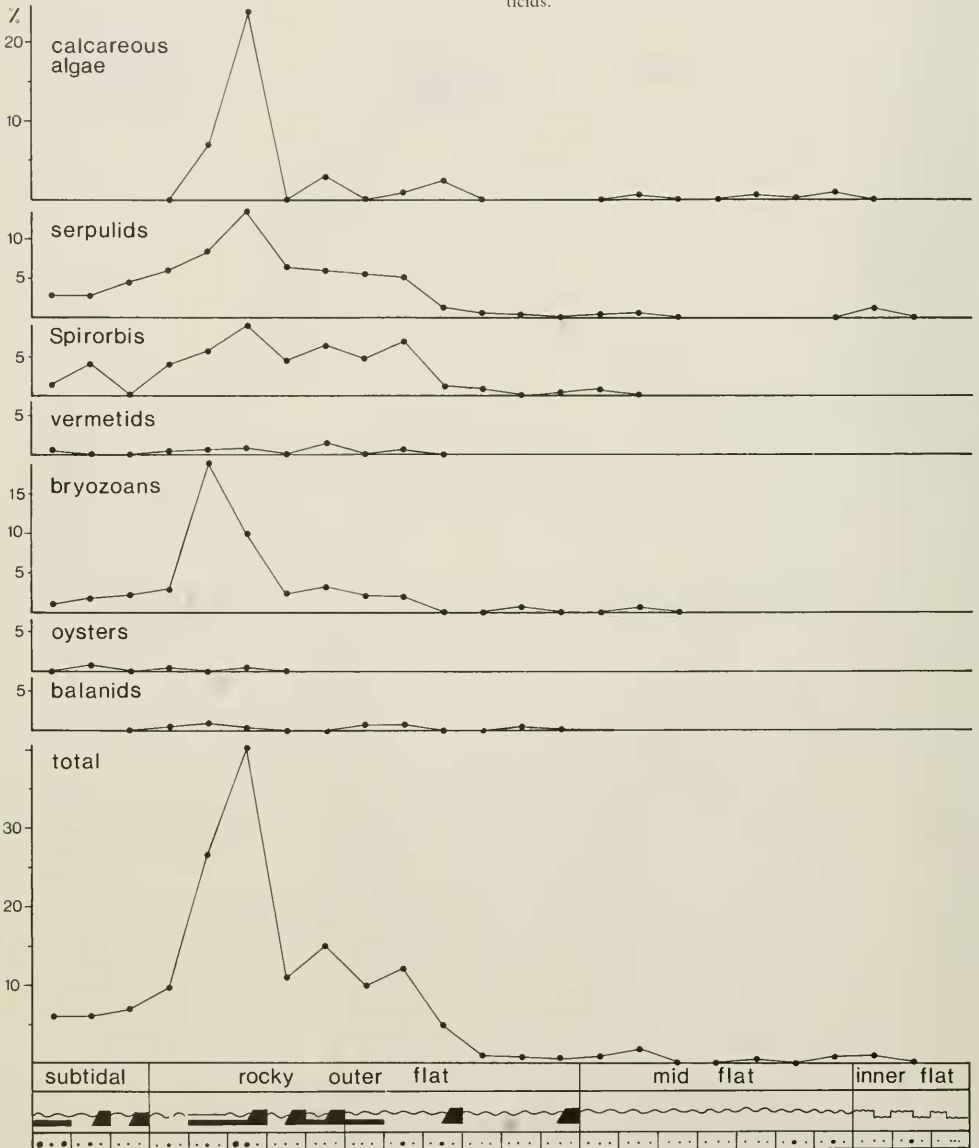
Fig. 12: Relative abundance of shells encrusted by calcareous algae, serpulids, *Spirorbis*, vermetids, bryozoans, balanids, and foraminifera across the tidal flat. a: Transect B; b: Transect A. For key see Fig. 7.

Discussion

The strong decrease of both types of borings toward the inner flat reflects the lack of suitable prey in this subenvironment. For example, *Tagelus*, a typical member of the inner flat community, burrows too deep and too rapidly to be preyed upon by naticid gastropods. The distribution pattern of *Oichnus* is correlated with the type of substrate: *O. simplex* is more abundant on hard substrate (shell gravels) of the outer flat and channel, whilst *O. paraboloides* dominates on sand flats (see also Fig. 10). The relative abundance of the ichnospecies of *Oichnus* is therefore related to the substrate preference of the prey species as well as that of the predator. For example, *Cerithium* and hermit crabs are more abundant on hard than on sandy substrate; they are therefore preferentially attacked by muricids and cephalopods. Shallow infaunal bivalves, in turn, are widespread on sandy substrate and are therefore nearly exclusively attacked by shallow infaunal naticids.

Fig. 13: Relative abundance of shells encrusted by calcareous algae, serpulids, *Spirorbis*, vermetids, bryozoans, balanids, and foraminifera across the tidal flat (Transect C). For key see Fig. 7.

Conclusions

The relative abundance of the two ichnospecies of *Oichnus* can be used to characterize substrate conditions in the various subenvironments and thus indirectly environmental parameters such as water energy and sedimentation rate. The dominance of *O. simplex* over *O. paraboloides*, for example, indicates low rates of sedimentation.

ENCRUSTATION

Results

The percentage of encrusted shells decreases from the outer to the inner flat. In the channel, this decrease is particularly pronounced between the mid channel and the estero channel (Fig. 11). In general the degree of encrusting is low. Even in the outer flat with its highest diversity of encrusting organisms the index of encrustation (I_E) is only medium (Fig. 11 h). There is little difference in the index of encrustation between flat and channel except between mid flat and mid channel. The range of variation of I_E is considerably larger on the flat than in the channel. A similar picture is seen in the percentage figures of encrusted shells in the taphocoenoses of Transects A to D (Figs 12–14). In addition, there is a marked difference in the percentage figures of encrusted shells between the sandy, southern part of the bay (Transects A, B) and the partially rocky northern part (Transects C, D).

Discussion

The landward decrease of encrusting organisms parallels the increase of environmental stress in the same direction, caused largely by the longer time of subaerial exposure. As only the innermost parts of the channel experience significant periods of emergence, the drop in abundance and diversity of encrusters takes place within the estero channel. The higher density and diversity of encrusters in the outer flat and outer to mid channel indicates low rates of sedimentation. Low rates of sedimentation and more frequent reworking are also suggested by the higher percentage of encrusted shells in the northern part of the bay where rocky Pleistocene crops out over large areas or is covered by a thin veneer of sediment.

The distribution of some encrusters is not only controlled by abiotic environmental parameters. This is particularly true of bryozoans encrusting *Cerithium*: the percentage of bryozoans is indirectly related to the number of living *Cerithium* and directly proportional to the number of shells inhabited by hermit crabs. The degree of encrusting of *Cerithium* shells is therefore clearly a function of the commensalism between some bryozoans and hermit crabs (see SCHÄFER 1962: 192).

Encrusting organisms provide a rough zonation of the tidal flat complex: Serpulids, in particular *Spirorbis*, and corallinacean algae dominate in the channel. The corallinacean algae increase in abundance seaward. Serpulids, *Spirorbis*, bryozoans, and corallinacean algae are most abundant on rocky outer flats, whilst bryozoans and foraminifera prevail on sandy flats.

The good preservation of most encrusters indicates lack of continuous reworking, even in the tidal channel. Episodic reworking is indicated by the co-occurrence, on shells, of several generations of encrusters in various states of preservation. Such features are common on shells occurring in troughs of the sand waves of the outer flat. Apparently these sand waves migrate only during strong storms and are stationary most of the time. This is corroborated by the presence of many membraniform bryozoans which are very sensitive to sedimentation (e. g. LAGAAIJ & GAUTIER 1965, RIDER & COWEN 1977).

Conclusions

(1) Subenvironments of Bahia la Choya differ in the relative abundance of encrusting organisms and the degree of encrustation.

(2) The relatively high density of encrusters in the outer flat and channel of the southern part of the bay and in outer to mid flat areas of the northern part, points to low rates of sedimentation. In the remaining subenvironments, the environmental stress is too high for successful colonisation of shells by encrusting organisms.

(3) Co-occurrence of several generations of encrusters in different states of preservation indicates episodic burial and reworking of shells.

FRAGMENTATION

Results

The percentage of shell fragments increases landward. This trend occurs both on the flat and in the channel (Fig. 15). The percentage of only slightly damaged shells decreases landward. The intensity of shell breakage (expressed by I_F) is low to intermediate in all subenvironments (Fig. 15 c) and only slightly higher in the channel than on the flat.

Discussion

When individual target genera are considered, it becomes clear that the index of fragmentation is pushed up by *Cerithium* (mid flat) and by the thin-shelled *Tagelus* (all other subenvironments) (Fig. 15 c). Due to the low energy level of the inner flat and estero channel, the high percent of shell breakage of *Tagelus* most likely is caused by predators. *Tagelus* is the preferred prey of the abundant blue-crab *Callinectes* (BRUSCA 1980: 150). *Chione*, with a high shell thickness/surface area ratio, is least affected by shell breakage. The relatively strong increase in the degree of fragmentation of *Chione* from the mid to the inner flat appears to be caused by predators such as shore birds.

As shell breakage increases landward, despite a decrease of the energy level in the same direction, breakage is apparently largely biogenic, being caused by predators and scavengers (see also CADÉE 1968). This is supported by the random pattern of fracturing of the shells (e. g. Fig. 16) which is not typical of the breakage pattern caused by impact during transport (see HOLLMANN 1968).

The somewhat higher fragmentation index in the channel is partly due to reworked Pleistocene *Chione* fragments and to
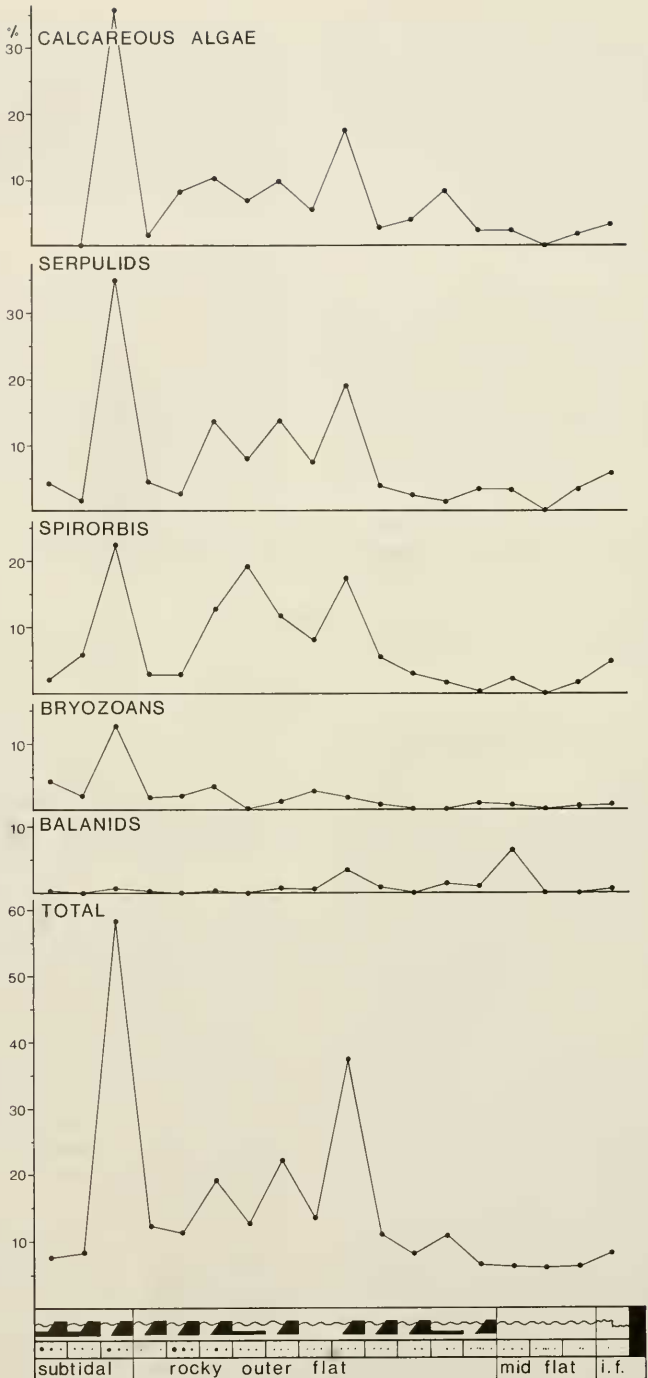
Fig. 14: Relative abundance of shells encrusted by calcareous algae, serpulids, *Spirorbis,* bryozoans, and balanids across the tidal flat (Transect D). For key see Fig. 7.
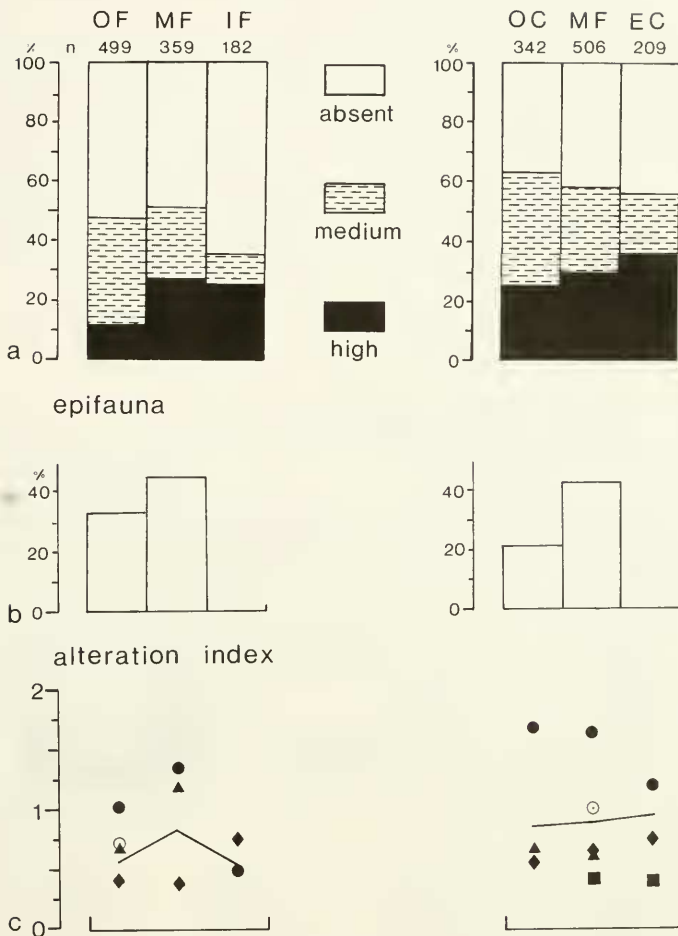
FRAGMENTATION

Fig. 15: Shells of target genera affected by fragmentation. a: degree of fragmentation in the subenvironments; b: percentage of epifauna among shells of the target genera; c: alteration index; − = average value; ◆ = *Chione*; ● = *Tagelus*; ⊙ = *Dosinia*; ■ = *Protothaca*; ▲ = *Cerithium*. For key see Fig. 3.

a lesser extent caused by the higher water energy, as the water energy there is not high enough to fracture shells (SCHAFER 1962: 184).
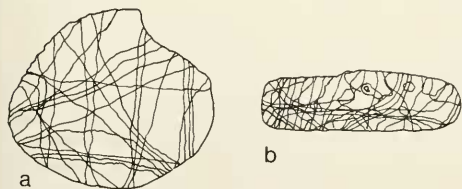
Fig. 16: Breakage pattern of *Chione californiensis* (a) and *Tagelus* sp. (b). Note the absence of preferred fracturing in *Chione* as opposed to *Tagelus*.

Conclusion

A zonation of the tidal flat using the index of fragmentation is not possible, as breakage is largely caused by predators and scavengers rather than by the hydrodynamic conditions.

ARTICULATION AND RIGHT-LEFT VALVE RATIO

Results

The percentage of articulated shells is low in all subenvironments and decreases seaward. The degree of valve sorting is low on the flat, and low to moderate in the channel (Fig. 17).

Discussion

The distribution of articulated shells roughly reflects the habitats of the various species. The low degree of sorting on the flat indicates that, under normal conditions, little shell transport takes place. Flat and channel can be distinguished by their differing degree of sorting. In the channel, shells with a high surface area/weight ratio such as *Tagelus* are preferentially transported and consequently sorted.

right-left valve ratio
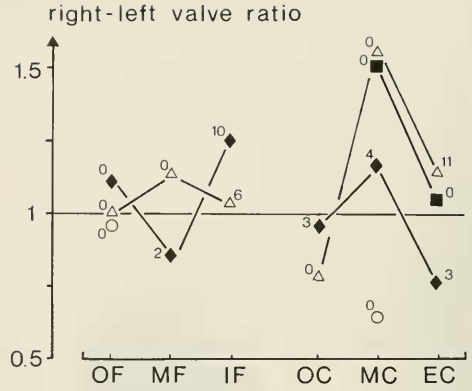
Fig. 17: Right-left valve ratio among shells of the target genera *Dosinia* (○), *Chione* (◆), *Tagelus* (△), and *Prototbaca* (■). Figures refer to percentage of articulated shells. For remaining key see Fig. 3.

LOSS OF COLOR
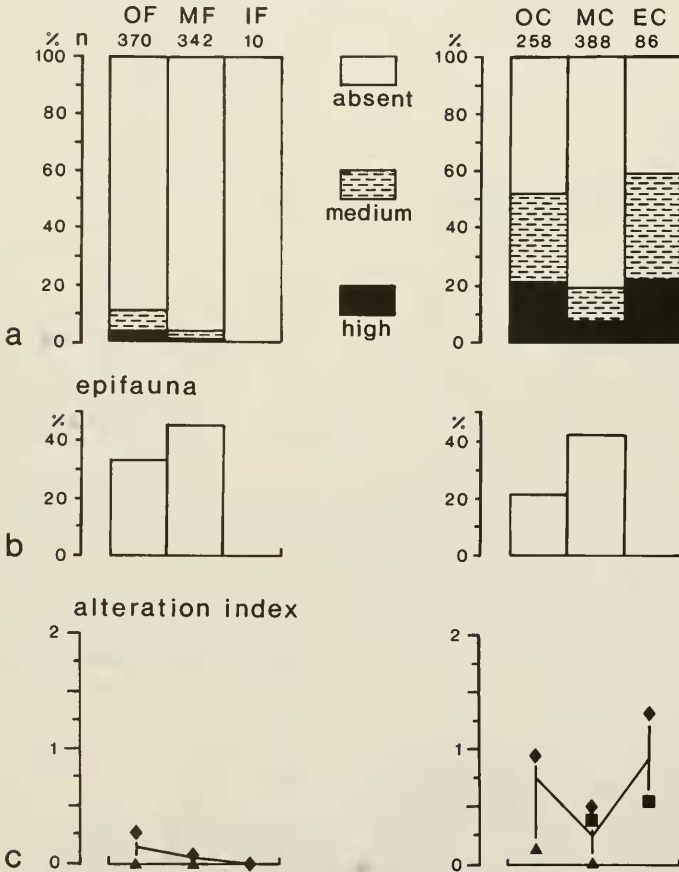
Fig. 18: Shells of target genera affected by loss of color. a: degree of loss of color in the subenvironments; b: percentage of epifauna among shells of target genera; c: alteration index; − = average value; ◆ = *Chione*; ■ = *Prototbaca*; ▲ = *Cerithium*; for key to subenvironments see Fig. 3.

LOSS OF COLOR

Results

Very little loss of color occurs on the flat and color loss decreases landward (Fig. 18). Loss of color is far more pronounced in the channel, with a minimum in the mid channel.

Discussion

Loss of color in shells from the channel is a result of several factors: the increase in water energy leads to a more pronounced shell abrasion. In addition, repeatedly reworked shells which already suffered some early diagenetic discoloration accumulate in the channel as do shells eroded from Pleistocene rocks. Mixing of shells representing different periods of time is common in the outer channel, but also occurs in the estero channel. In the latter, loss of color is particularly common in shells which suffered maceration and are derived from chalky shell layers of the salt marsh.

Conclusions

(1) Flat and channel environments can be distinguished by their strongly differing degree of loss of color in shells.
(2) The mixing of shells representing three different ages (Recent, subrecent, and Pleistocene) can be demonstrated by comparing different degrees of color loss with other taphonomic parameters.

TAPHOFACIES MODEL

We constructed a taphofacies model (Speyer & Brett 1986) for the tidal flat complex by considering the various taphonomic agents and their impact on shells in the subenvironments of Bahia la Choya (Fig. 19).

In general, the importance of all physically controlled taphonomic agents decreases landward, paralleling the energy gradient. An exception is shell breakage which increases landward − a trend that indicates extensive biogenic fragmentation caused by predatory and scavenging organisms.

Flat and channel subenvironments can be distinguished by the taphonomic features of their hard parts. The preservation of hard parts in the channel is poorer than on the flat because of the higher energy level, higher density of herbivores and extensive mixing of Recent, subrecent and Pleistocene shells.

A landward decrease is also typical for some biologically controlled taphonomic agents. Both density and diversity of boring and encrusting organisms decrease toward the shore (Fig. 20), due to the increase of subaerial exposure in the same direction. Flat and channel subenvironments can be distinguished using the relative abundance of encrusting organisms (Fig. 20). The taphonomic history of some hard parts is largely governed by biological processes such as commensalism rather than environmental factors (e. g. the influence of hermit crabs on the taphonomic history of gastropod shells). In such cases, the preservation quality of hard parts does not necessarily correspond to the general trend.

Subenvironments can also be characterized by the range and mode of preservation exhibited by individual taxa. For example, Fig. 21 shows the distribution of *Chione* shells in preservation classes covering the total range of preservation quality. The four subenvironments: outer and mid channel and outer and mid flat respectively differ clearly from each other. On the flat, reasonably well preserved shells dominate, and preservation quality is higher on the mid than on the outer flat. In the channel, a broader range of preservation classes is present without a distinct peak. The shape of the histograms can be used to separate environments with high energy, low rates of sedimentation, and frequent reworking from those with lower energy and higher rates of sedimentation. A broad curve is indicative of high energy and relatively long exposure time of shells, while a curve with a strongly positive skew characterizes either the habitat of the species and/or a short exposure time. The histogram of the outer flat occupies an intermediate position between the two extremes as both frequent reworking and a high supply of fresh shells play a major role. The histograms can be also used to recognise admixture of shells derived from other environments or representing a different slice of time.

Kidwell et al. (1986) recognised three processes responsible for the formation of skeletal concentrations: sedimentologic, biogenic, and diagenetic processes. In the tidal complex of Bahia la Choya, diagenetic processes do not play a significant role outside the salt marsh. The genesis of the molluscan taphocoenoses is governed largely by a low rate of net sedimentation in combination with episodic high energy events (responsible for reworking). This results in the mixing of Recent, subrecent and, to a lesser extent, Pleistocene hard parts, whereby the degree of mixing decreases from the outer to the inner flat. Extensive time-averaging is therefore a major feature of Bahia la Choya taphocoenoses.

APPLICATION TO THE FOSSIL RECORD

In order to test the usefulness of the taphonomic agents for interpreting the environment and genesis of ancient shell beds, target genera from three samples representing different ages have been investigated in the same way as the taphocoenoses from the Recent tidal flat. The samples represent (a) the shelly spit, (b) subrecent beachrock, and (c) a poorly lithified Pleistocene sandstone.
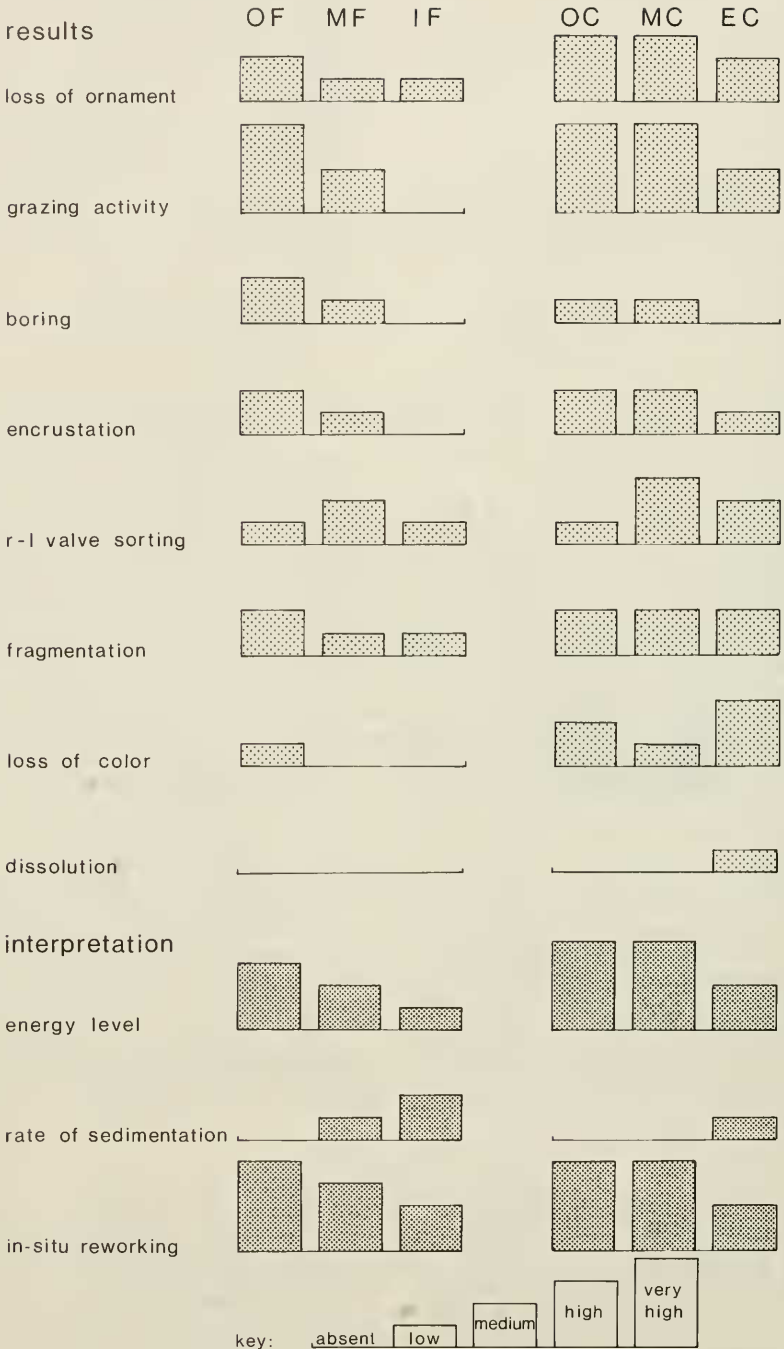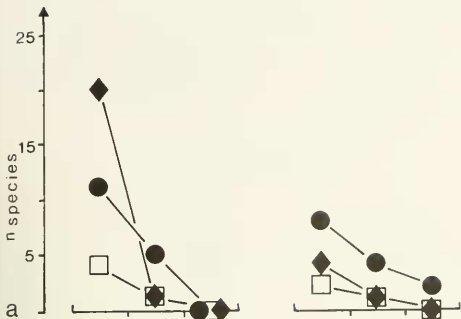
TAPHOFACIES MODEL

Fig. 19: Taphofacies model. For key to subenvironments see Fig. 3.
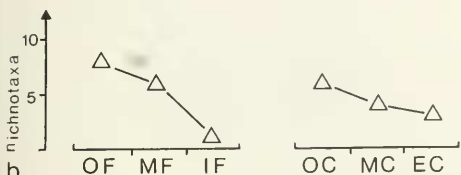
ENCRUSTERS

BORINGS

Fig. 20: Diversity of encrusting and boring organisms in the subenvironments. a: diversity of encrusting serpulids (●), bryozoans (◆), and foraminifera (□); b: diversity of ichnotaxa (△). For key to subenvironments see Fig. 3.

THE SPIT

A spit, up to 3 m high, separates the tidal flat from the salt marsh. It consists nearly exclusively of shells and shell debris. On the salt marsh side of the spit, shell beds dip toward the marsh. The top of the spit is formed by a layer of sand, up to 1,5 m in thickness, on which cholla cactus and other Sonoran desert plants grow. This indicates that the spit is not active.

Shells of the spit, formerly white, have been discolored by iron oxide and have a brownish tinge which is characteristic of deposition in an oxidizing environment.

Fig. 22 sums up some taphonomic features of the target genera. The shells are only little encrusted or bored which suggests that they either are derived from an environment such as the mid or inner flat, or were covered by sediment for most of the time. The good preservation of Chione fluctifraga in particular speaks for short residence time on the sediment surface. However, as loss of ornament is very strong in most shells, a loss of encrusters by abrasion cannot be discounted. That such a loss is likely is corroborated by the remaining encrusters which are nearly invariably found on the inside of Cerithium shells. The primary degree of encrustation, therefore, cannot be reconstructed.

The difference in preservation quality between Chione fluctifraga and C. californiensis points to differences in their taphonomic history, with C. californiensis possibly experiencing a higher number of reworking cycles before finally becoming incorporated in the spit.

Loss of ornament is the most characteristic feature of the shells and helps to explain the genesis of the spit. The degree
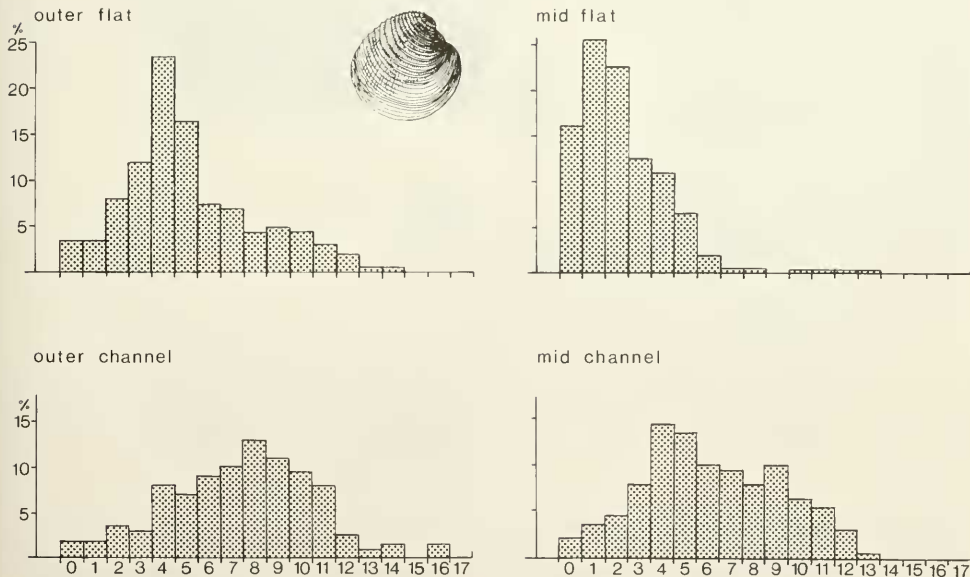

Fig. 21: Preservation quality of Chione. 0–17 = alteration classes. The higher alteration classes indicate poorer preservation.
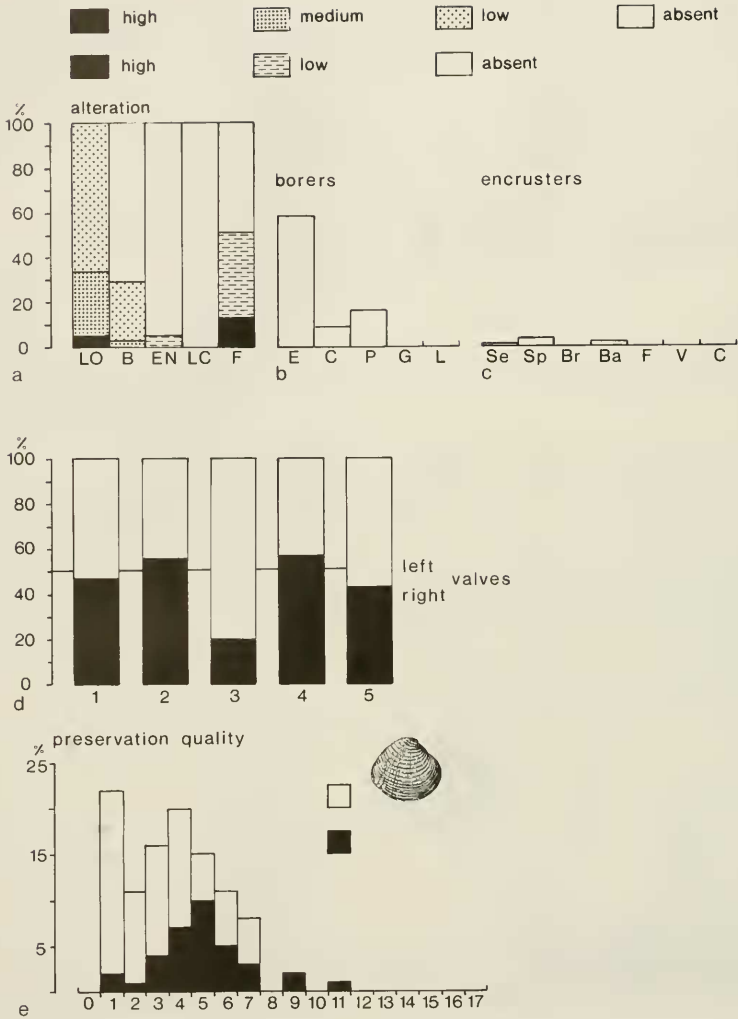
Fig. 22: Taphonomic features of shells of target genera from the spit. a: degree of alteration of shells; LO = loss of ornament; B = boring; EN = encrustation; LC = loss of color; F = fragmentation. b: percentage of shells bored by endolithic algae (EN), clionids (C), polychaetes (P), *Gastrochaena* (G), and *Lithophaga* (L). c: percentage of shells encrusted by serpulids (Se), *Spirorbis* (Sp), bryozoans (Br), balanids (Ba), foraminifera (F), vermetids (V), and corallinacean algae (C). d: right-left valve ratio; 1 = *Tagelus* sp.; 2 = *Protothaca grata*; 3 = *Dosinia ponderosa*; 4 = *Chione fluctifraga*; 5 = *Chione californiensis*. e: preservation quality of all *Chione* shells (white) and *Chione californiensis* (black). 0–17 = alteration classes, 0 = excellent, 17 = very poor.

of loss of ornament corresponds to that of the outer flat and the tidal channel, thus indicating a raised energy level. Shells and fragments exhibit well rounded edges and are strongly polished (e. g. Pl. 1, Fig. 3). According to PILKEY et al. (1967,

1979) this feature is characteristic of high wave energy and beach sedimentation. It seems therefore likely that the spit represents an ancient, now inactive, beach ridge formed during a slightly higher stand of sea level, when the present intertidal

flat was largely subtidal. Beach ridges with a similar internal structure have been described by THOMPSON (1968) from the Colorado delta. GIERLOFF-EMDEN (1959) notes that such beach ridges are also formed by spring tides at times of strongly reduced sedimentation.

BEACHROCK

The Pleistocene terrace in the northern part of the bay, situated now high in the intertidal zone, is overlain by a beachrock about 30 cm in thickness. It consists of a modera-
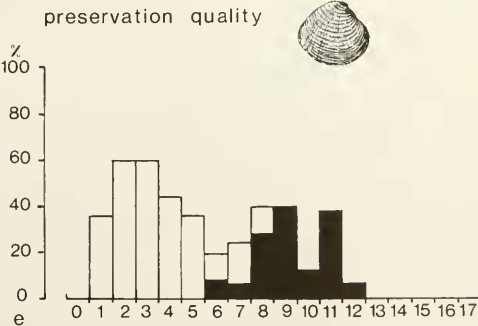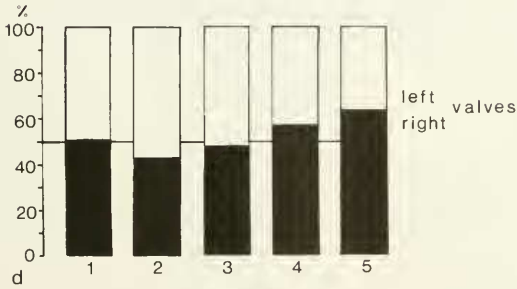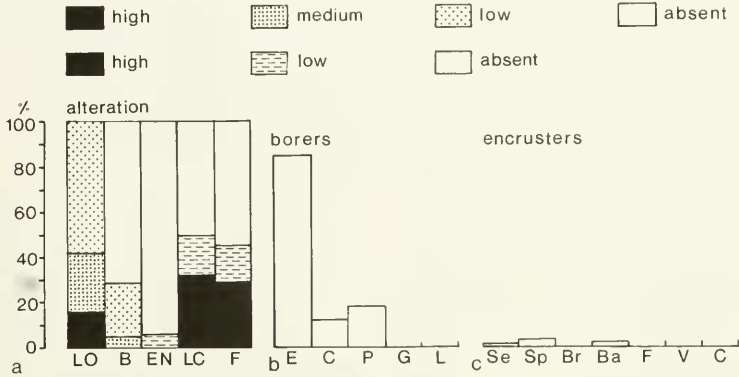

Fig. 23: Taphonomic features of shells of target genera from the beachrock. For key see Fig. 22. a: degree of alteration of shells; b: percentage of shells bored; c: percentage of shells encrusted; d: right-left valve ratio; 1 = *Dosinia ponderosa;* 2 = *Protothaca grata;* 3 = *Chione fluctifraga;* 4 = *Chione californiensis* (Recent); 5 = *Chione californiensis* (Pleistocene). e: preservation quality of *Chione.* White: all *Chione;* black: Pleistocene *Chione.*

tely well cemented conglomerate of shells, shell fragments, and reworked Pleistocene. The matrix between the shells is sandy to gravelly and frequently does not fill the available pore space.

The shells exhibit a medium degree of loss of ornament and a low degree of boring and encrustation (Fig. 23). The range of loss of color and fragmentation shows that hard parts from the Recent tidal flat and the Pleistocene have become incorporated in the beach rock. Pleistocene hard parts represent 28 % of the shells and consist solely of *Dosinia* and *Chione*. In *Dosinia* shells only the inner, homogeneous layer is preserved which is colored dark-brown (Pl. 4, Fig. 4). This is a result of the enrichment of the organic matrix during paramorphic transformation of the outer shell layers (BATHURST 1971: 497). The preservational differences between Recent and Pleistocene shells can be demonstrated by the preservation quality of *Chione* (Fig. 23 e). As all other taphonomic features of the Recent shells suggest little alteration, their residence time on the sea floor apparently was short before they became incorporated in the beachrock.

Preservational features of some *Chione* shells and of *Cerithium* indicates that the taphocoenosis of the beachrock contains also shells from the spit. This can be demonstrated by abrasion and discoloration patterns identical to those found in the spit.

Shells from three different sources have become mixed in the taphocoenosis of the beachrock. This can be shown by comparing the preservation quality of the shells. Most shells are derived from the Recent tidal flat, many are reworked from the Pleistocene, and some have come from the adjacent spit.

PLEISTOCENE

Most Pleistocene rocks in the vicinity of Bahia la Choya are well cemented, an exception being a poorly cemented, shelly, medium- to coarse-grained sandstone on the southern bank of the estero channel. The layer is about 60 cm thick, most shells are disarticulated and oriented convex-up (see also ABERHAN & FÜRSICH, this volume) (Fig. 24 g).

Apart from recrystallized *Encope*, all shells are moderately to strongly macerated, but their ornament is largely preserv-ed. The sandy matrix is cemented by a micritic high Mg-calcite cement, the source of which are most likely the shells themselves as small bivalves are partly preserved as internal molds and many large shells exhibit signs of solution. Incipient neomorphic transformation of shells can be observed whereby cavities are filled with dog tooth cement.

Apart from diagenetic breakage of *Chione pulicaria*, *Tagelus*, and *Dosinia* (e. g. Fig. 24 f) the degree of fragmentation is low, as is the degree of right-left valve sorting (Fig. 24 d).

There are two groups of shells which differ distinctly in their preservation quality (except for loss of ornament). The first group consists of strongly macerated shells (*Chione californiensis*, *C. pulicaria*, *C. fluctifraga*, *Tagelus* sp., *Cerithidea* sp.) which are little bored (mainly by polychaetes) and rarely encrusted by serpulids. The taphonomic features of this group point to an inner or mid flat origin of the shells when compared to present-day data. Alternatively, they could have been covered with sediment very quickly.

Shells of the second group (*Chione californiensis*, *Encope* sp.) are less strongly macerated and more frequently bored and encrusted by *Cliona*, *Gastrochaena*, *polydora*, and bryozoans and balanids respectively. Apparently, these shells had a longer residence time on the sea floor. Their taphonomic features are similar to those of Recent outer flat taphocoenoses. However, preservation quality of shells of the second group is only little lower than that of the first group (Fig. 24 e). It appears that both groups were not exposed to high energy conditions for any considerable length of time. Based just on taphonomic criteria, the origin of the shell bed cannot be reconstructed with certainty. Preservational features and orientation patterns point to relatively rapid deposition which could have been caused by a storm. Alternatively, the shell layer may represent the basal shell lag of a meandering tidal channel. The second possibility could explain the mixing of two differently preserved faunas representing different subenvironments. Older shells, representing an outer flat to very shallow subtidal environment, could have become exhumed through bank erosion and then mixed with shells derived from the surface of the flat. The relatively good preservation of the shells requires a high rate of lateral migration of the channel, quite in contrast to the present tidal channel (see also ABERHAN & FÜRSICH, this volume).

FOSSILIZATION POTENTIAL OF TAPHONOMIC PARAMETERS

The three examples from the spit, beach rock, and Pleistocene show that a taphonomic analysis of shells often contributes substantially to the interpretation of a particular environment or of the genesis of a shell bed. However as the example of the Pleistocene shell bed illustrates, a taphonomic analysis should be accompanied by a sedimentological and palaeoecological analysis. One reason for this is that the fossilization potential of the various taphonomic features differs considerably and impairs the taphonomic analysis.

The fossilization potential of the shell ornament depends on the degree of shell solution and on the timing of cementation of the matrix. If cementation preceeds shell solution, an external mold can preserve evidence of pre-diagenetic loss of ornament depending on the the grain size of the matrix (e. g. Pl. 4, Fig. 7). Diagenetic artefacts such as selective dissolution along growth lines (e. g. KAMIYA 1980) may overemphasize the primary ornament or even lead to formation of a secondary shell ornament (see also FLESSA & BROWN 1983).

Grazing traces have a very low fossilization potential. Rarely preserved in the fossil record (e. g. VOIGT 1977, AKPAN et al. 1982), their absence does not imply that grazing herbivores were not present.
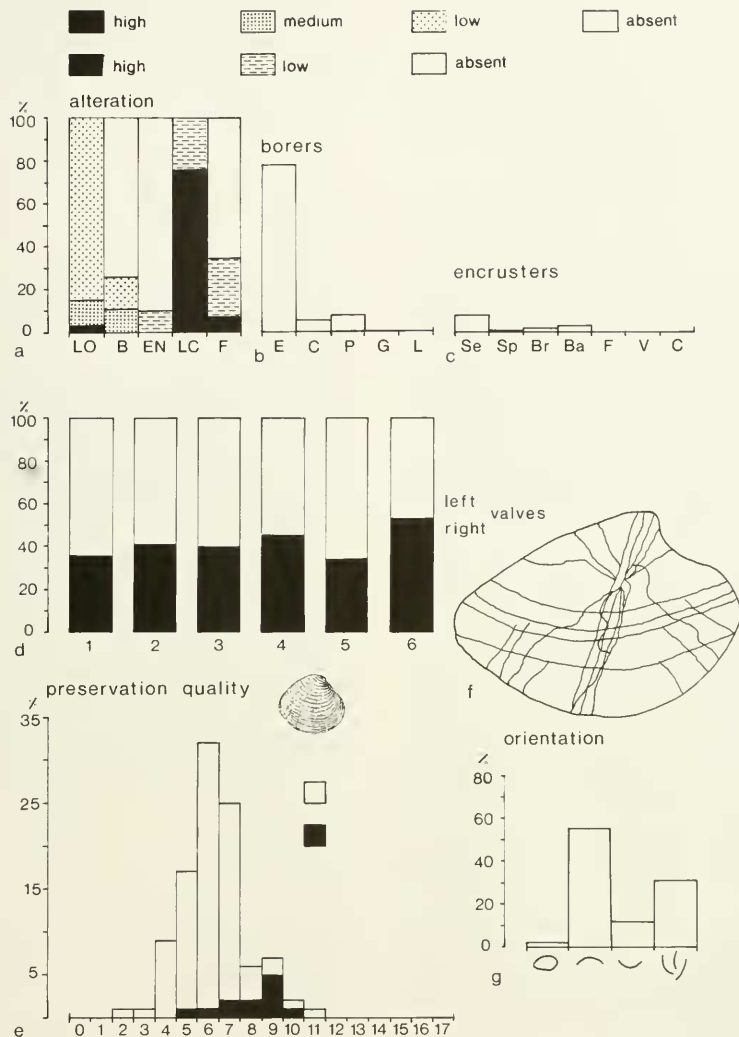
PLEISTOCENE

n = 250

Fig. 24: Taphonomic features of shells of target genera from a Pleistocene shell bed. For key see Fig. 22. a: degree of alteration of shells; b: percentage of shells bored; c: percentage of shells encrusted; d: right-left valve ratio; 1 = *Dosinia ponderosa*; 2 = *Tagelus* sp.; 3 = *Chione pulicaria*; 4 = *Chione fluctifraga*; 5 = *Chione californiensis* type a; 6 = *Chione californiensis* type b; e: preservation quality of *Chione*. White: all *Chione*; black: *Chione californiensis* type b. f: breakage pattern of *Chione pulicaria*. g: cross-sectional orientation of shells.

Because the fill of borings is frequently cemented early on during diagenesis, traces of boring organisms are commonly preserved. Multiphased borings recording repeated burial and reworking can be recognised in the fossil record by different sediment fills or crossing over of borings which cannot have formed at the same time.

The fossilisation potential of encrusting organisms heavily depends on their skeletal mineralogy. For example, at higher average water temperatures serpulids change their skeletal mineralogy in favor of less stable carbonate phases which are more prone to dissolution than that of other encrusters (e. g. CHAVE 1964, BORNHOLD & MILLIMAN 1973). The predomin-

antly calcitic bryozoans, in contrast, have a very high fossilisation potential, if they are not lost by abrasion. Aragonitic vermetids in turn are big enough to produce internal molds from which their presence can be reconstructed.

Degree of articulation and right-left valve sorting of shells can be established even when shells are very poorly preserved and thus have a very high fossilisation potential. Shell color, in contrast, may become bleached at any time and very rarely survives later stages of diagenesis.

In conclusion, it appears that several taphonomic features of molluscan shells are modified by or lost during diagenesis which itself is an important taphonomic parameter. Last not least, in strongly cemented rocks, much of the desired taphonomic information may be lost due to the difficulty of extracting the shells, molds or casts which record this information.

CONCLUSIONS

(1) The taphonomy of Recent mollusc shells from Bahia la Choya differs among the outer, mid, inner flat, and outer, mid, and estero channel subenvironments of the tidal flat complex. The tidal flat complex can be subdivided into taphofacies based on the degree of alteration of shells by biotic and abiotic taphonomic agents as well as on the diversity and density of biotic taphonomic agents.

(2) Loss of ornament, right-left valve sorting, boring, and encrustation are largely related to physical environmental gradients, in particular to rate of net sedimentation, water energy, time of subaerial exposure, and amount of sediment kept in suspension.

(3) In Bahia la Choya fragmentation is mainly caused by the activity of predatory and scavenging organisms, and is independant of physical parameters.

(4) The taphonomic history of the epifaunal gastropod *Cerithium* is greatly influenced by hermit crabs and their commensals and is therefore only partially related to physical parameters of the environment (see also FREY 1987).

(5) As some taphonomic parameters (e. g. fragmentation, loss of ornament) are produced by several agents, it is

dangerous to base environmental interpretations on a single parameter only. Best results are achieved when sedimentologic, paleoecologic, and taphonomic criteria are combined.

(6) The taphonomic parameters of the tidal flat fauna suggest very low rates of net sedimentation and extensive time-averaging. This is in agreement with MELDAHL (1987) who reports radiocarbon dates of 3230 +/- 75 yrs b. p. for a large *Dosinia* shell collected from the sediment surface.

(7) In the fossil record, the usefulness of taphonomic parameters depends on their fossilization potential and on whether they can be extracted from the rock. Several important parameters are little affected by diagenesis and can be used to reconstruct the taphonomic history of shells and shell concentrations.

(8) The detailed investigation of the taphonomy of skeletal elements is a useful tool, when used in combination with other criteria, to reconstruct environments and origin of skeletal concentrations. An increasing knowledge of the autecology of biogenic taphonomic agents will enhance their usefulness for the interpretation of taphonomic data even further.

ACKNOWLEDGEMENTS

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TAFELN

Plate 1

Fig. 1: Range of preservation quality of *Chione californiensis* illustrated by preservation classes II, 0, I, I (upper row from left to right) and II, II, III (lower row from left to right). Middle row: reworked Pleistocene shells. ×0.6. (BSP 1990 XI 27−34).

Fig. 2: Range of preservation of *Tagelus* sp.; tidal flat. ×0.5 (BSP 1990 XI 35−39).

Fig. 3: Range of preservation quality of *Cerithidea mazatlanica*. a, d: live specimens; e: strongly abraded specimen from the shelly spit; f−i: typical preservation quality of specimens from the channel. ×1 (BSP 1990 XI 40−48).

Fig. 4: Shell of *Cerithium stercusmuscarum* with *Oichnus simplex* (near apex), *Oichnus paraboloides* (midway on the spire), and predation mark of crab (at aperture); outer flat. ×2 (BSP 1990 XI 49).

Fig. 5: Shells of *Cerithium stercusmuscarum*. Breakage caused by crab predation; tidal flat. ×2 (BSP 1990 XI 50−52).

Fig. 6: Chipped shells of *Chione californiensis*. Breakage caused by predators; tidal flat. ×0.7 (BSP 1990 XI 53−55).
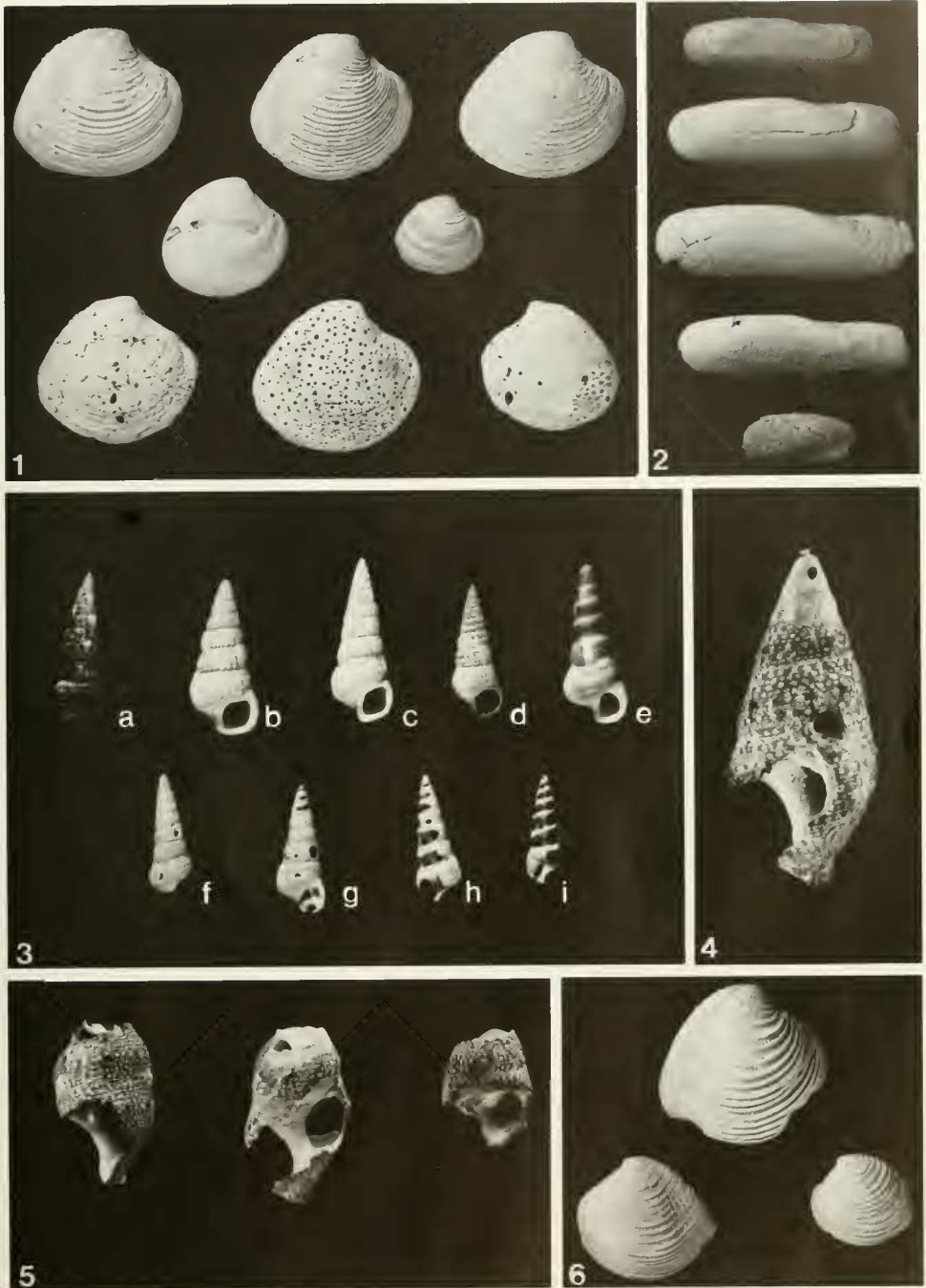
Plate 2

Fig. 1: Range of preservation quality of *Encope grandis*, outer flat; scale in cm.

Fig. 2: Preservation of shell ornament of a Pleistocene gastropod as cast made by encrusting bryozoans. The gastropod shell has been nearly completely dissolved. Borings of *Entobia* and *Caulostrepsis* in the shell, however, have been preserved as moulds. ×2.5.

Fig. 3: Shell of *Dosinia ponderosa*, strongly abraded by endophytes and rasping herbivores; tidal flat. ×0.5 (BSP 1990 XI 56).

Fig. 4: Borings of endophytes; cross-section through *Tagelus* sp.; tidal flat. SEM photograph; scale: 100 µm.

Fig. 5: Fragmentation of *Chione californiensis* caused by predators. Note the sharp edges and the otherwise excellent preservation of the shells; tidal flat. ×1.3 (BSP 1990 XI 57–58).

Fig. 6: *Caulostrepsis* sp., the boring of a polydorid polychaete, in the posterior end of *Chione californiensis*. The position of the boring indicates that infestation by the polydorid took place while the bivalve was in growth position; tidal flat. ×3.5.

Fig. 7: Range of preservation in *Cerithium stercusmuscarum*; tidal flat and channel. ×1 (BSP 1990 XI 59–65).

Fig. 8: Circular groove on shell of *Dosinia ponderosa* caused by *Crucibulum spinosum*; outer flat. ×1 (BSP 1990 XI 66).

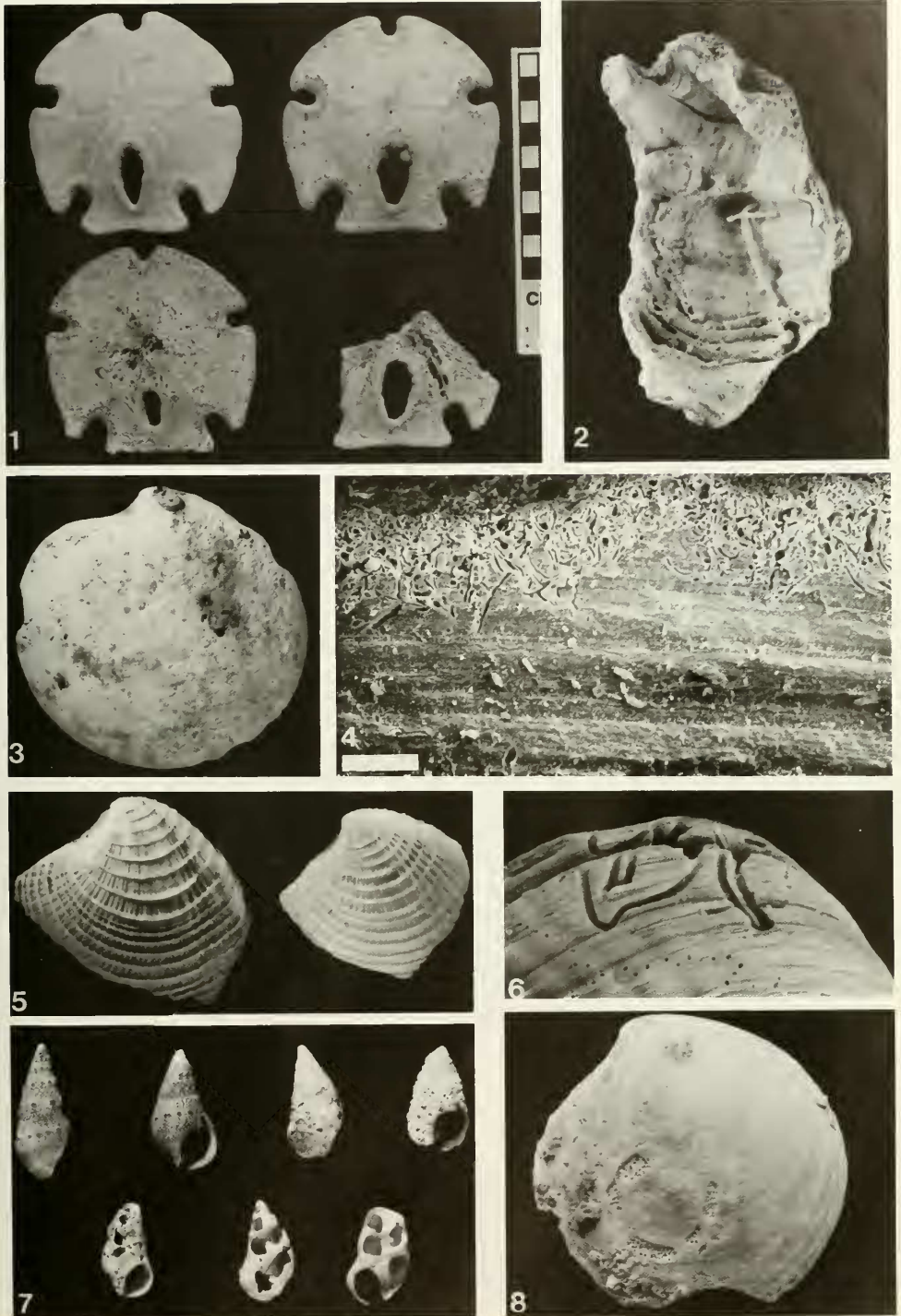FEIGE, A. and FÜRSICH, F. T.: Taphonomy of the Recent molluscs.

Plate 2

Plate 3

Borings of clionid sponges from the Recent tidal flat.

Figs. 1, 2:   *Entobia megastoma.* Fig. 1: resin cast, ×4 (BSP 1990 XI 67); Fig. 2:   pattern of apertures on *Dosinia ponderosa*; ×0.5 (BSP 1990 XI 68).

Figs. 3, 4:   *Entobia laquaea;* Fig. 3:   resin cast, ×3.7 (BSP 1990 XI 69); Fig. 4:   pattern of boring on *Dosinia ponderosa;* ×1.3 (BSP 1990 XI 70).

Figs. 5, 6:   *Entobia paradoxa* on *Dosinia ponderosa;* Fig. 5: pattern of boring; ×1.5; Fig. 6:   resin cast; ×4.5 (BSP 1990 XI 71).

Fig. 7:   Wall structure of *Entobia* and spiculae. SEM photograph, ×300.

Feige, A. and Fürsich, F. T.: Taphonomy of the Recent molluscs.
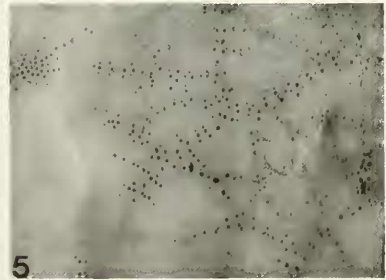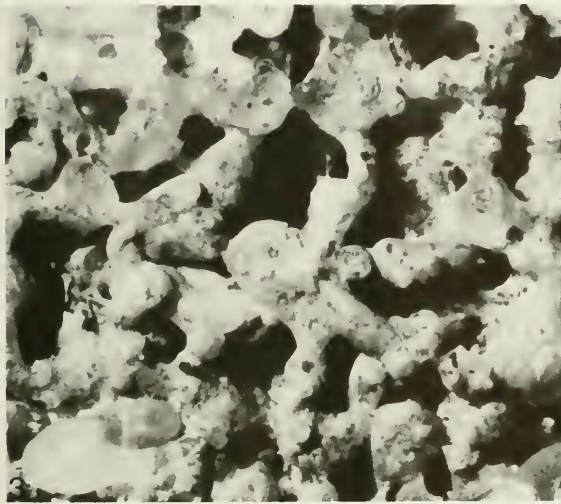
Plate 3

Plate 4

Fig. 1:   Range of preservation quality of Recent *Dosinia ponderosa* (BSP 1990 XI 72–75).
Figs. 2, 3:   *Oichnus paraboloides* in shell of *Felaniella sericata* (Fig. 2) and juvenile *Chione californiensis*
(Fig. 3); tidal flat. ×2.
Fig. 4:   Range of preservation quality of *Dosinia ponderosa* from the beachrock (b–d) (BSP 1990 XI 76)
as opposed to specimen from the Recent outer flat (a) (BSP 1990 XI 72).
Fig. 5:   *Oichnus simplex* produced by *Octopus* in shell of *Cardita affinis*; rocky outer flat. ×4 (BSP 1990
XI 77).
Fig. 6:   Calcareous siphonal tubes of *Gastrochaena*; outer flat. ×1 (BSP 1990 XI 78).
Fig. 7:   External mould of *Chione californiensis* from the Pleistocene. Both shell ornament and the sponge
boring *Entobia* have been preserved by early lithification of the surrounding sediment. ×2 (BSP
1990 XI 79).
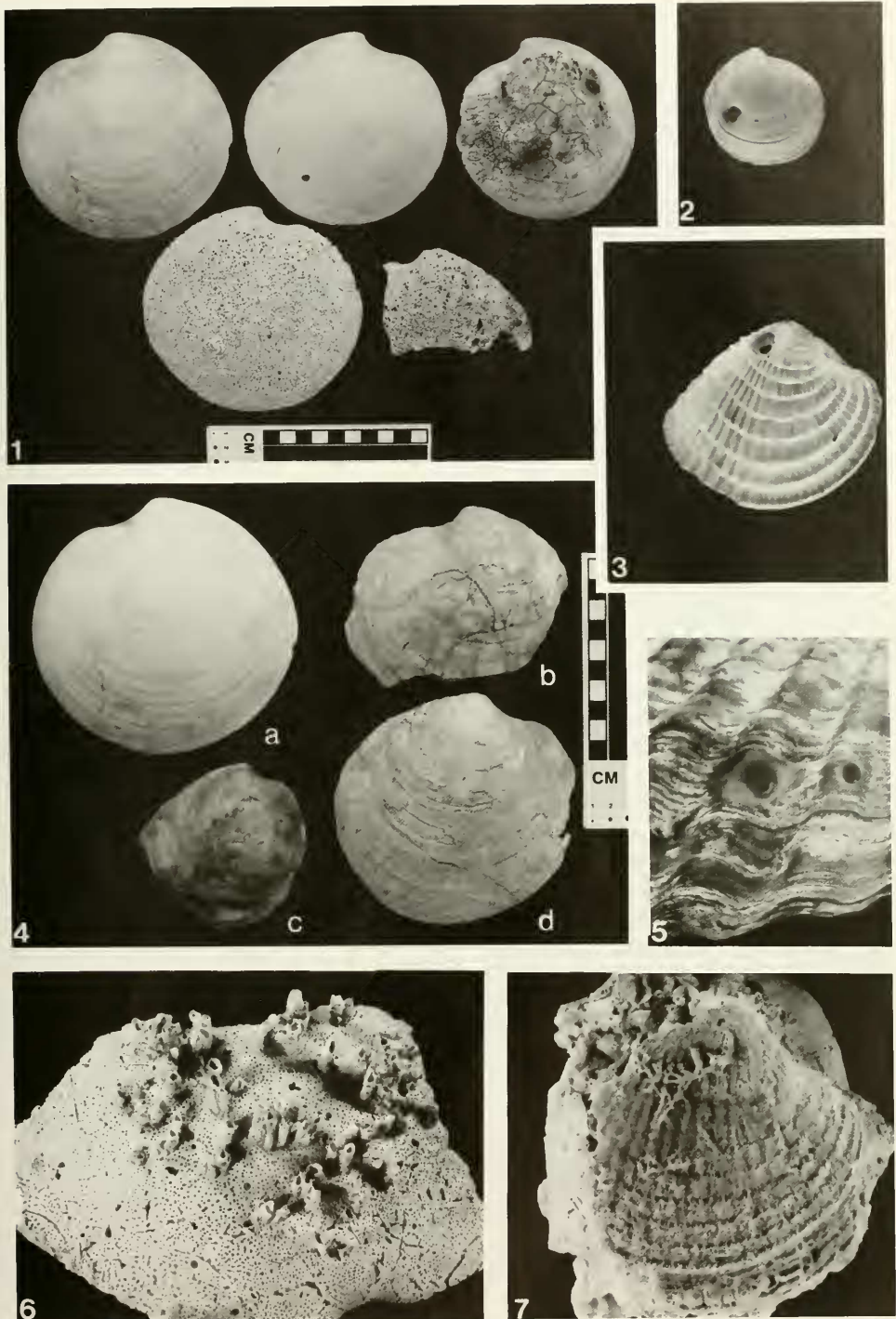
Plate 4

Plate 5

Bioerosion and borings in shells from the tidal flat.

Fig. 1: Boring bryozoan *Spathipora mazatlanica;* ×12.
Fig. 2: Boring bryozoan *Penetrantia densa;* ×12.
Fig. 3: Phoronid boring *(Talpina* sp.); ×
Fig. 4: Bioeroded surface of *Dosinia ponderosa* caused by herbivores grazing on epilithic and endolithic thallophytes. ×40.
Fig. 5: "Igloos" produced by the boring bivalve *Gastrochaena.* ×2 (BSP 1990 XI 75).
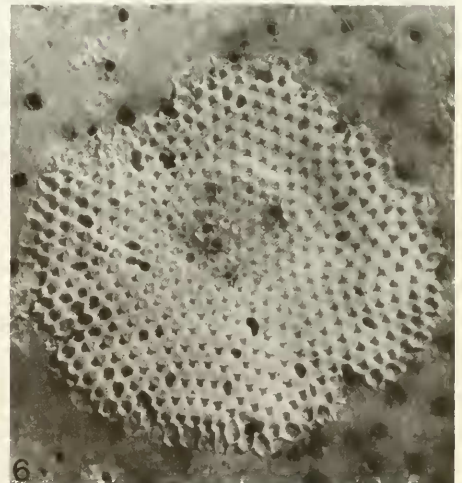Fig. 6: *Floridina antiqua* (Bryozoa); ×2.
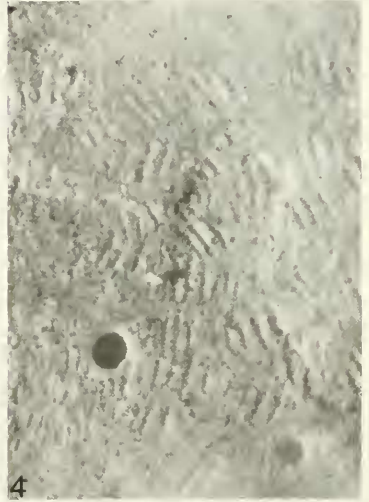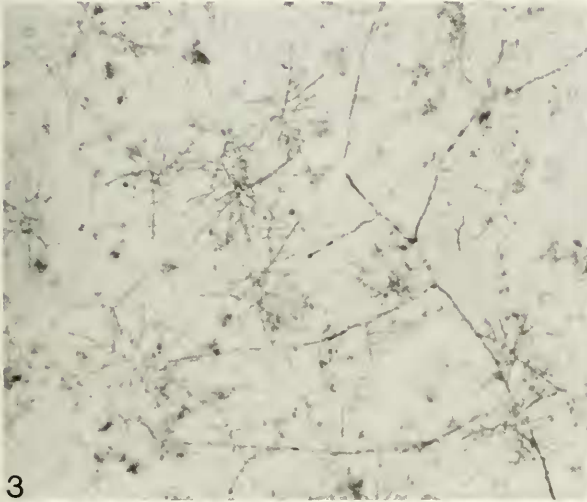
Plate 6

Fig. 1: *Schizoporella unicornis* (Bryozoa); tidal flat. ×10.
Fig. 2: Maceration of the crossed lamellar layer of *Chione californiensis* from a layer of chalky molluscs of the salt marsh. SEM Photograph, ×12.
Fig. 3: *Lichenopora intricata* (Bryozoa); ×7 (BSP 1990 XI 80).
Fig. 4: Inside of *Chione* shell densely encrusted by serpulids *(Pomatoceras* cf. *polytrema* and *Spirorbis (Pileolaria)* cf. *variabilis);* tidal channel; ×7.5 (BSP 1990 XI 81).