

## TAPHONOMIC AND PALEOECOLOGICAL FEATURES OF THE UPPER CANOA AND TABLAZO FMS SHELL BEDS

### Community Beds

Community beds (Norris, 1986) have simple internal stratigraphy, represent accumulations of indigenous benthic fauna and are ecologically and taxonomically variable, being subdivided into five associations occurring in three basic categories: infaunal-dominated communities, mixed shallow infaunal/epifaunal communities, and epifaunal-dominated communities.

**Corbula Association.** This fossil assemblage consists primarily of scattered bivalves dispersed in massive, heavily bioturbated medium- to coarse- grained sandstone. The association is paucispecific and characterized by the dominance of the infaunal suspension-feeder *Corbula porcella*, a substrate tolerant species recorded in both sandy and muddy grounds, and by the minor occurrence of very shallow burrowers small to medium size taxa (*Linga cancellaris*, *Dentalium* cf. *oerstedii*, *Polinices* sp.). Depth of burrowing and size of infaunal taxa are controlled by reduced sedimentation rates and the presence of an impenetrable subsurface (the lower Canoa Fm sediments) that impinged on benthic ecology by restricting infauna from burrowing to optimal depths.

**Pegophysema Association.** This Association is a 1.5-m-thick, matrix-supported, loose to dispersed concentration of whole and fragmented shells. It rests on an erosional surface and grade upward with diminishing shell-packing density into less fossiliferous finer sediments with the bedding completely obscured by extensive bioturbation. Fossils do not show any sign of sorting by size and/or shape and are randomly oriented throughout the bed (Fig. 6C). The association is characterized by a diagnostic, moderately diverse assemblage of sandy shoreface environment numerically dominated by the small infaunal suspension-feeder *Linga cancellaris*, a gravel- or sand-related lucinid (Piazza and Robba, 1998; Cruz, 1977, 1982). Visually, however, the molluscan assemblage is dominated by disarticulated specimens of the infaunal *Pegophysema spherica* that, locally, may also be preserved with conjoined valves in life position. Additional faunal elements include the bivalves *Nuculana elenensis*, *Corbula* sp., and the gastropods *Olivella* sp. and *Polinices hepaticus*.

**Trachycardium Association.** Although the bulk samples of this assemblage are dominated by juvenile/subadult specimens of *Chione marie*, visually it is dominated by disarticulated

individuals of *Trachycardium* cf. *procerum*, a seminafaunal bivalve. The highly diverse component fauna, which do not show any sign of sorting by size and shape, represents a shelly soft-ground community diagnostic of an inner shelf setting and also include *Nucula exigua*, *Saccella elenensis*, *Trigonocardia obovalis*, *Olivella* sp., and *Dosinia ponderosa*. Skeletal fragments of the *Trachycardium* Association are encased in thoroughly bioturbated silty fine sandstone and define a loose to dispersed biofabric either upward and downward with respect to a subtle omission surface, almost always irrevocably obscured by bioturbation. When the omission surface is preserved, a mixture of whole and broken specimens of *Trachycardium* cf. *procerum* are commonly aligned along it (Fig. 6D). Shell fragmentation ranges from low in small-bodied fauna to high in medium- to large-sized fauna, whereas bioerosion and abrasion are generally very low or absent. Given the broad range in size of shell debris, the intense bioturbation of the host sediment, and the lack of abrasion on fossils, fragmentation is inferred to reflect a biogenic rather than physical origin (Kidwell and Bosence, 1991). Although the body fossils tend to settle randomly, nested or concave-up throughout the bed, flat-lying, conjoined (but displaced from life position), large-bodied bivalves, such as *D. ponderosa*, also occur. A roughly horizontal orientation of this shallow infaunal taxon indicates that individuals have been washed out and reclined alive on the sea-floor in a more hydrodynamically stable position but were not transported far after death from their original habitats (Kondo, 1998). This implies that dynamic bypassing (i.e., short term-sedimentary processes consisting of alternating erosion and rapid deposition) occurred during the accumulation of this shell concentration.

***Argopecten-Undulostrea* Associations.** The *Argopecten-Undulostrea* Association is found in mid-cycle position within a number of sequences. Within sequence C<sub>upp</sub>6 it occurs as a laterally continuous, 1-m-thick tabular shell bed and comprises whole bivalve shells in pervasively bioturbated fine-sandstone arranged in a clear shellier upward trend passing from matrix- to bioclast-supported (Fig. 6E). The fossil association consists of a very low diverse mollusk fauna forming a paucispecific concentration largely dominated by whole shells of the scallop *Argopecten circularis*, found as small clumps, and both as conjoined and as single valves (Fig. 6F). It also includes numerous specimens of the oyster *Undulostrea megodon*, the jingle shell *Anomia peruviana*, minor individuals (both reclined and vertically oriented) of the large infaunal *Dosinia ponderosa*, the seminafaunal *Trachycardium procerum*, the infaunal gastropod *Malea ringens*, the whale barnacle *Coronula*, and internal molds of other gastropods (e.g., *Turritella*

sp.). Small size mollusks are basically lacking and mainly due to rare juvenile specimens of *A. circularis* represented by single, mostly well-preserved, valves. On the whole, the association is characterized by the presence of epifaunal and very shallow-infaunal benthos requiring or tolerating shell-gravel and current swept habitats (*A. circularis*, *U. megodon*, *D. ponderosa*). In particular, the abundance of taxa indicative of firm, sandy shell-gravel bottoms (i.e., *A. circularis*) or requiring hard substrata for support (*U. megodon* and *Anomia peruviana*), represent a clear response by benthos to the alteration of substratum mass properties due to the relatively prolonged residence of shells on the seafloor (autogenic taphonomic feedback of Kidwell and Jablonski, 1983; Kidwell, 1991).

Valves are moderately bioeroded, almost invariably disarticulated (though a certain number of articulated valves of epifaunal species also occurs) and oriented randomly to sub-parallel with respect to the bedding plane. In this latter case, shells display both convex-up and –down orientation. In addition, a large number of adult barnacles (1-2 cm) encrust the scallop exteriors without any apparent preference on convex-up or –down oriented valves. The presence of barnacles on the external surface of valves implies that they grew to adulthood on the upper surface of living or dead scallops whereas their presence on convex-down valves indicates the pre- or post-mortem overturning of scallops since, as suggested by Meldahl (1993), this is a position untenable for their life.

Within sequence Tb2 the *Argopecten-Undulostrea* Association is a 20-cm-thick molluscan pavement encased in bioturbated fine sandstone below and massive siltstones above (Fig. 6N). Owing to pervasive bioturbation, density of packing varies laterally repeatedly passing, gradually, from dense to dispersed packing. Faunally, the molluscan assemblage is similar to that of BSB<sub>C7</sub> (but in this case the dominant faunal element is the oyster *U. megodon*) and displays ecologically coherent species composition largely dominated by epifauna (apart from *U. megodon*, mostly consisting of *A. circularis*, *A. peruviana* besides encrusting barnacles), but also including minor shallow burrowing infauna tolerant of shell-gravel seafloors (*Chione mariae*, *Chione* sp., *D. ponderosa*), mixed with soft-ground species reworked from immediately underlying deposits (nuculids, nuculanids, *Panopea* sp.). Shells are disarticulated but unbroken. Bioerosion, encrustation and fragmentation are low.

In sequence Tb3, this association consists of a low-density fossil assemblage where shells define a dispersed to loosely packed biofabric.

The *Argopecten-Undulostrea* Association at the base of sequence Tb5 contains a low diversity fauna similar to that described above. It consists overwhelmingly of *A. circularis* but lacks the characteristic element *D. ponderosa*. Valves are densely packed and arranged mostly randomly in the lower part and pass rapidly upward into a matrix supported, dispersed biofabric where bedding-parallel orientations dominate (Fig. 6O). They are mainly disarticulated, mostly well-preserved and in nearly pristine condition. Encrustation and bioerosion are always fairly uncommon.

***Pinna* Association.** Although few articulated specimens are still preserved in their upright, semi-infaunal life-habit (Fig. 6K), this 5-cm-thick, laterally discontinuous, nearly monospecific shell concentration is composed mainly of disarticulated, bedding-parallel oriented and fragmented valves of *Pinna* cf. *rugosa* eroded out of their normal life position. This species is often recorded in sandy sediments, but it may be related to different substrates from foreshore to very shallow shoreface.

### **Lag Concentrations**

Lag concentrations are up to 50-cm-thick and occur discontinuously at the base of sequence Tb3. Both the lower and upper contacts are sharp and erosive (Fig. 6L). The major components of this type of concentration are matrix- to clast-supported, mud- or silty filled internal molds of *D. ponderosa* made with sediment that differs from the surrounding coarse matrix (Fig. 6M). This is compelling evidence indicating that they are reworked from older strata cannibalized through ravinement and formed through exhumation and concentration of resistant hardparts by selective removal of sedimentary matrix. Once remobilized, the exhumed material can be admixed with newly produced hardparts, generating the time-averaged and ecologically mixed assemblages of the Wave-Winnowed Shell Assemblages.

### **Wave-Winnowed Shell Assemblages**

These laterally continuous shell beds, which range in thickness from 2 to 4 m, exhibit medium-scale trough cross-bedding (Fig. 6G, L). Their upper contacts are either sharp or rapidly gradational, whereas in contrast, their bases are invariably sharp and erosional on the underlying sediments (Fig. 6G). Wave-Winnowed Shell Assemblages are composed chiefly of well-sorted, highly abraded, coarse to finely comminuted mollusk shell debris (Fig. 6H), with subsidiary

well-ordered, disarticulated and rounded valves preserved convex-up and aligned with the bedding, and occasional well-rounded lithic pebbles and cobbles bored by lithophage mollusks. Sparse mud- or silty-filled internal molds may be present when this type of concentration is juxtaposed upon the top-truncated silty lithosome of the underlying sequence. Owing to the presence of abundant calcareous cement derived from diagenetic dissolution of shells, these assemblages are invariably strongly cemented so that fossil remains are impossible to extract and difficult to identify. Component fauna includes unbroken, encrusted and bioeroded individuals of *U. megodon*, *Turritella* sp., *Encope* sp., and *Pinna* cf. *rugosa*.

Medium-scale trough cross-stratification reflects accumulation within migrating 3-D bedforms and, therefore, this kind of shell concentration is inferred to result primarily from physical sedimentologic depositional processes. The fairly common occurrence of mud- or silty- filled internal molds and the presence of a discontinuous and variably truncated community shell bed interposed between the SB/RS and the overlying trough cross-stratified shell bed, indicate that these shell concentrations are formed by skeletons deriving, at least in part, from material exhumed during erosion of underlying beds and from the extensive reworking of coeval shoreface community beds into comminuted, coarse calcarenite under conditions of severe environmental energy.

#### REFERENCES CITED

- Cruz, M.P., 1977, Bivalvos de la plataforma continental de la region norte de Ecuador: Inocar, CM-BIO, v. 15, p. 1-55.
- Cruz, M.P., 1982, Estudio sistematico de los bivalvos recientes de la plataforma superior interna de la Provincia de Manabì [Ph.D. thesis]: Universidad de Guayaquil, Guayaquil, 162 p.
- Jones, A.P., and Omoto, K., 2000, Towards establishing criteria for identifying trigger mechanisms for soft-sediment deformation: A case study of Late Pleistocene lacustrine sands and clays, Onikobe and Nakayamadaira Basins, northeastern Japan: *Sedimentology*, v. 47, p. 1211–1226, doi: 10.1046/j.1365-3091.2000.00355.x.
- Kidwell, S.M., 1991, Taphonomic feedback (live/dead interactions) in the genesis of bioclastic beds: keys to reconstructing sedimentary dynamics, in Einsele, G., Ricken, W., and Seilacher, A., eds., *Cycles and events in stratigraphy*: Berlin, Springer-Verlag, p. 268-282.

- Kidwell, S.M., and Bosence, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas, *in* Allison, P.A., and Briggs, D.E.G., eds., Taphonomy: releasing the data locked in the fossil record: New York, Plenum Press, p. 116-209.
- Kidwell, S.M., and Jablonski, D., 1983, Taphonomic feedback: ecological consequences of shell accumulation, *in* Tevesz, M.J., and McCall, P.L., eds., Biotic interaction in recent and fossil benthic communities: New York, Plenum Press, p. 195-248.
- Kondo, Y., 1998, Adaptive strategies of suspension-feeding, soft-bottom infaunal bivalves to physical disturbance: evidence from fossil preservation, *in* Johnston, P.A., and Haggart, J.W., eds., Bivalves: an Eon of evolution – Paleobiological studies honoring Norman D. Newell: Calgary, University of Calgary Press, p. 377-391.
- MacEachern, J.A., and Pemberton, S.G., 1992, Ichnological aspects of Cretaceous shoreface successions and shoreface variability in the Western Interior Seaway of North America, *in* Pemberton, S.G., ed., Applications of ichnology to petroleum exploration, a core workshop: SEPM (Society for Sedimentary Geology) Special Publication Core Workshop 17, p. 57–84.
- Meldahl, K.H., 1993, Geographic gradients in the formation of the shell concentrations: Pliocene Pleistocene marine deposits, gulf of California: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 101, p. 1-25.
- Norris, R.D., 1986, Taphonomic gradients in shelf fossil assemblages, Pliocene Purisima Formation, California: Palaios, v. 1, p. 256-270.
- Piazza, M., and Robba, E., 1998, Autochthonous biofacies in the Pliocene Loreto Basin, Baja California Sur, Mexico: Rivista Italiana di Paleontologia e Stratigrafia, v. 104, p. 227-262.

TABLE DR1. SUMMARY OF THE PRINCIPAL FACIES AND FACIES ASSOCIATIONS OF THE UPPER CANOA AND TABLAZO FORMATIONS

Facies associations	Facies code	Description	<sup>†</sup> Depositional environment	Depositional sequence
Carbonate shell bed associations	CG1	Discontinuous shell-gravel layers composed of mud- or silty-filled internal molds suspended within a massive mixture of shell-debris and coarse terrigenous sand.	Owing to the difference in nature and grain size between the sediment composing the internal molds and the surrounding coarse matrix, internal molds are regarded as non-coeval. This type of shell bed formed through exhumation after burial and concentration of hardparts by selective removal of sedimentary matrix (exposed upper shoreface).	Tb4
	CS1	Intensely burrowed, massive, medium- to coarse-grained sandstone with loosely-packed, matrix-supported fossil remains. Infauna dominated.	Shell concentration formed during periods of substantial bypass of terrigenous flux in a sheltered, upper shoreface setting.	Cupp5, Cupp6, Tb1
	CS2	Intensely burrowed, massive, medium- to coarse-grained sandstone with dispersed, matrix-supported fossil remains. Infauna dominated.	Ditto, but with higher sediment supply.	C <sub>upp</sub> 5, C <sub>upp</sub> 6
	CS3	Massive, densely-packed, (bio)clast-supported, epifauna-dominated shell conglomerate in Almost starved inner shelf.		Cupp 6, Tb5
	CS4	Massive, loosely-packed, matrix-supported shells in fine-grained sandy matrix.	Ditto, but with higher sediment supply.	Cupp6, Tb5
	CS5	Well-sorted, trough cross-bedded comminuted skeletal debris including reworked internal moulds and pebble size clasts.	The abundant trough cross-beds represent subaqueous migration of dunes in a high-energy, exposed upper shoreface. Wave-reworking leads to mixing of autochthonous forms and older, exhumed skeletal material.	Tb1, Tb2, Tb3, Tb4, Tb5, Tb6
	CS6	Laterally discontinuous, one-clast-thick shell conglomerate composed of infaunal taxa.	Erosion and reworking at the LFS of nearly contemporaneous shells; palimpsest innermost-shelf (Abbott, 1997).	Tb2
	CZS1	Intensely burrowed, massive, silty fine blue sandstone with dispersed, matrix-supported fossil remains. Dominated by mixed infaunal/epifaunal taxa.	Inner-shelf with relatively high rate of sediment supply. Episodic winnowing of fines with exhumation of shallow infauna (e.g., <i>D. ponderosa</i> ) suggests sporadic bottom stirring by weak storm-induced flows.	Cupp5, Tb3
	CZS2	Intensely burrowed, massive, silty fine blue sandstone with loosely-packed, matrix-supported fossil remains. Dominated by mixed infaunal/epifaunal taxa.	Ditto, but with lower rates of sediment supply.	Cupp5, Tb3
	CZS3	Massive, densely-packed, (bio)clast-supported shell conglomerate in silty fine blue sandstone. Dominated by mixed infaunal/epifaunal taxa.	Ditto, but completely starved.	Cupp5
Siliciclastic sandstone associations	S1	Massive, intensely bioturbated, medium-grained yellow sandstone with rare fossil remains. Infaunal dominated	The high bioturbation index, reflecting biogenic activity during more prolonged periods of fair weather suggests a quiet, lower shoreface environment.	Cupp5, Cupp6, Tb2, Tb3, Tb4, Tb5, Tb6
	S2	Ditto, but with vertical or steeply inclined shafts of <i>Ophiomorpha nodosa</i> . Infaunal dominated.	Vertically oriented <i>O. nodosa</i> burrows develop mainly in high-energy conditions associated with shifting sediments (MacEachern and Pemberton, 1992) and are consistent with deposition within an exposed, lower shoreface setting.	Tb3, Tb5, Tb6
	S3	Intensely bioturbated, <i>Thalassinoides</i> burrowed fine sandstone with scattered, mainly in situ, mollusk remains.	Lower shoreface/inner-shelf transition	Tb2, Tb5
	S4	Well sorted, planar-bedded medium sandstone with soft-sediment deformation features (convolute bedding).	Soft-sediment deformation can be triggered by a number of mechanisms, such as earthquakes, overloading, the passage of storm-waves, and the impact of breaking waves (Jones and Omoto, 2000). However, owing to the systematic occurrence of this facies in the same stratigraphic position within sequences, we infer that it is the product of sea ground deformation due to mechanical effect of storms within an exposed, upper shoreface setting, close to the transition with the lower shoreface (MacEachern and Pemberton, 1992).	Tb1, Tb3, Tb4, Tb5
	ZS1	Barren to poorly fossiliferous, massive, intensely bioturbated silty fine sandstone.	Inner shelf.	Cupp5, Cupp6, Tb2, Tb3
Siliciclastic mudstone association	MS <sub>1</sub>	Dark, massive mudstone interbedded with minor, lenticular and poorly sorted medium-grained sandstone	Estuarine (bay-head) delta	Tb2
	M1	Massive black to bluish mudstone rich in vegetal remains and rare sandstone lenses	Central mud basin	Tb2
	M2	Massive silty mudstone with large concentrations of continental vertebrate remains and molluscan shells	Estuary-lagoon	Tb6

Note : <sup>†</sup>Intertidal/shoreface (0-10 m); inner shelf (10-50 m); mid-shelf (50-100 m); outer shelf (100-200 m).

TABLE DR2. CHARACTERISTIC FEATURES OF SHELL CONCENTRATIONS FROM THE UPPER CANOA AND TABLAZO FORMATIONS

Formation	Sequence Number	Shell Bed Type	Associated stratal attenuation	Shell Bed Name	Cause of Condensation	Thickness (m)	Biofabric			Taphonomy	Fossil Assemblage	Macrobenthic community (ecology)	a) Lower Contact b) Upper Contact
							Orientation	Close-Packing	Vertical Trend (Facies Succession)				
Canoa	5	Community	Onlap	OSB <sub>C5</sub>	Sediment bypassing	0.50	Chaotic	Loose to dispersed	Dispersing-upward (CS1/CS2)	Mainly fresh shells. Articulated bivalves common	<i>Corbula</i>	Relatively low-diversity, infauna-dominated community	a) Sharp, erosion-soled b) Gradational
	5	Community	Backlap	BSB <sub>C5</sub>	Sediment starvation	0.40	Concave-up to chaotic, nesting of shells occurs locally	Dispersed to dense	Shellier-upward (CZS1/CZS2/CZS3)	Mainly fresh shells. High degree of fragmentation in medium- and large-bodied fauna. Rare articulated bivalves	<i>Trachycardium</i>	High-diversity, mixed shallow infaunal/epifaunal community	a) Gradational b) Omission-capped
	5	Community	Downlap	DSB <sub>C5</sub>	Sediment starvation, but rapid sedimentation beginning	1.40	Concave-up to chaotic, nesting of shells occurs locally	Dense to dispersed	Dispersing-upward (CZS3/CZS2/CZS1)	Mainly fresh shells. Rapidly buried, articulated bivalves common	<i>Trachycardium</i>	High-diversity, mixed shallow infaunal/epifaunal community	a) Omission-soled b) Gradational
	6	Community	Onlap	OSB <sub>C6</sub>	Sediment bypassing	1.50	Concave-down and -up to chaotic	Loose to dispersed	Dispersing-upward (CS1/CS2)	Mainly fresh shells. Articulated bivalves common	<i>Pegophysema</i>	Relatively low-diversity, infauna-dominated community	a) Sharp, erosion-soled b) Gradational
	6	Community	Backlap	BSB <sub>C6</sub>	Sediment starvation	1.00	Concave-down and -up to chaotic	Dispersed to dense	Shellier-upward (CS4/CS3)	Mainly fresh shells, encrustation articulated bivalves common	<i>Argopecten-Undulostrea</i>	Low-diversity, epifauna-dominated community	a) Gradational b) Omission-capped
				Compound									
Tablazo	1	Community	Onlap	OSB <sub>T1</sub>	Sediment bypassing	0.05	Bedding-parallel, either concave-down or -up	Dispersed	None (CS1)	Mainly broken shells, articulated bivalves uncommon	<i>Pinna</i>	Monospecific, semi-infaunal dominated community	a) Sharp, erosion-soled b) Gradational to sharp
	2	Community	Backlap	BSB <sub>T2</sub>	Sediment starvation	0.20	Concave-down and -up to chaotic	Loose or dispersed	None (CS/CS4 or CS6/CS3)	Mainly fresh shells, articulated bivalves, some preserved in situ, common	<i>Argopecten-Undulostrea</i>	Low-diversity, epifauna-dominated community	a) Sharp, erosion-soled b) Omission-capped
	3	Community	Backlap	BSB <sub>T3</sub>	Sediment starvation	0.30	Concave-up to chaotic, nesting of shells occurs locally	Loose to dispersed	Shellier-upward (ZS2/CZS1)	Mainly fresh shells, articulated bivalves uncommon	<i>Argopecten-Undulostrea</i>	Ditto	a) Gradational b) Omission-capped
	5	Community	Backlap	BSB <sub>T5</sub>	Sediment bypassing	0.50	Chaotic	Dense to dispersed	Dispersing-upward (CS3/CS4/CS5)	Mainly fresh shells, articulated bivalves rare	<i>Argopecten-Undulostrea</i>	Ditto	a) Sharp, erosion-soled b) Gradational
	1,2,3,4,5,6	Wave-winnowed	Onlap	OSB <sub>T1,2,3,4,5,6</sub>	Sediment bypassing	Up to 4.00	Chaotic to aligned with the bedding	Dense	None (CS5 or CG1/CS5 or CS1/CS5)	Mainly broken and abraded shells and fragments. Well-sorted, coarse to finely comminuted shell debris with reworked internal moulds sparse or concentrated along the base	Unnamed		a) Sharp, erosion-soled b) Sharp to gradational