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ABSTRACT

Invertebrate taphonomy can provide significant information about the *post-mortem* processes that affected the fossil record. In the East Pisco Basin of southern Peru, a *Panopea* Ménard de la Groye, 1807 shell bed was found in the upper Miocene strata of the Pisco Formation, hinting at a peculiar biostratinomic and diagenetic history. This bed contains abundant invertebrate fossil molds cemented by dolomite. The specimens of the deep infaunal bivalve, *Panopea* sp., occur together with bivalves representative of shallow infaunal species (*Trachycardium* sp. and *Dosinia ponderosa* [Gray, 1838]) and balanid barnacles, which are sessile encrusters. The *Panopea* specimens host compound molds evidencing an abundant encrusting fauna, including serpulids, ?foraminifera, bryozoans, and barnacles that colonized the inner surfaces of the valves before their final burial. We hypothesize that short-term, storm-related processes exhumed the living bivalves, resulting in a sedimentological concentration of relatively well-preserved shells. After the death of the exhumed bivalves, the inner surfaces of the articulated *Panopea* shells, representing hard-substratal, sheltered environments on an otherwise unstable sandy seafloor (i.e., "benthic islands"), were colonized by different encrusting organisms. Following the final burial, dolomite precipitated, cementing the sediment infill of the valves. Lastly, a decrease of pH occurred at the sulfate reduction-methanogenesis boundary, inducing the dissolution of the shell carbonate.

KEY WORDS
Biostratinomy,
diagenesis,
East Pisco Basin,
encrusters,
fossil geoduck,
dolomite.

RÉSUMÉ

Taphonomie d'une couche de coquilles de Panopea *Ménard de la Groye, 1807 de la Formation Pisco (Miocène, Pérou).*
La taphonomie des invertébrés peut fournir des informations importantes sur les processus *post mortem* qui ont affecté les registres fossiles. Dans la partie orientale du Bassin Pisco, dans le sud du Pérou, une couche riche en *Panopea* Ménard de la Groye, 1807 qui témoigne d'une histoire taphonomique et diagénétique particulière a été trouvée dans les strates du Miocène supérieur de la Formation de Pisco. Cette couche est riche en moules d'invertébrés cimentés par la dolomite. Les spécimens de *Panopea* sp., un bivalve endofaunique, se trouvent en plus des représentants d'espèces de bivalves endofauniques (*Trachycardium* sp. et *Dosinia ponderosa* [Gray, 1838]) et des bernacles balanidés, qui sont des organismes sessiles encroûtants. Les spécimens de *Panopea* hébergent des moules composites, témoins d'une abondante faune encroûtante, comprenant des serpulidés, des ?foraminifères, des bryozoaires et des bernacles qui avaient colonisé les surfaces internes des valves avant l'enfouissement final. Nous supposons que des processus rapides de tempête ont exhumé les bivalves vivants et ont résulté en une concentration sédimentologique de coquilles relativement bien conservées. Après la mort des bivalves exhumés, les surfaces internes des coquilles articulées de *Panopea*, représentant des substrats durs et des environnements abrités sur un fond sableux autrement instable (c'est-à-dire, des «îles benthiques»), ont été colonisées par différents organismes encroûtants. Après l'enterrement final, la dolomite a précipité, cimentant le remplissage sédimentaire des valves. Enfin, une diminution du pH s'est produite à la limite entre la zone de réduction des sulfates et la zone de méthanogenèse, induisant la dissolution du carbonate originel des coquilles.

MOTS CLÉS
Biostratinomie,
diagenèse,
partie orientale
du Bassin Pisco,
organismes encroûtants,
panope fossile,
dolomite.

INTRODUCTION

Shell concentrations result from complex sedimentologic and biologic processes and are rich sources of paleontologic and stratigraphic information as well as excellent tools for reconstructing past depositional settings (e.g. Meldahl 1993; Hendy *et al.* 2009). The biostratinomic, sedimentological, and paleoecological significance of invertebrate fossil assemblages have also proven essential for the accurate sequence stratigraphic interpretation of fossiliferous siliciclastic successions and the reconstruction of the sedimentary dynamics at key sequence stratigraphic surfaces (e.g. Abbott 1997, 1998; Kondo *et al.* 1998; Di Celma *et al.* 2002; Cantalamessa *et al.* 2005; Carnevale *et al.* 2011). However, carbonate skeletons (and especially the aragonite ones) can be altered or even entirely lost by chemical solution during post-burial diagenesis, which accounts for much of the loss of mollusk shells (e.g. Brett & Baird 1986). Although alteration and diagenetic solution may compromise paleontological reconstructions, the different modes of preservation of fossil macro-invertebrates can be used for reconstructing paleoenvironmental and diagenetic patterns and processes in the past (e.g. Feldman 1989; Kidwell &

Bosence 1991; Del Rio *et al.* 2001). In this regard, external and internal molds can be extremely useful since they provide evidence of the macro-invertebrate assemblage even when most of the shell material has been dissolved. Internal, external and compound molds resulting from authigenic preservation (Schopf 1975) may also record the organisms that encrusted the shells themselves, thus providing a more complete record of the biological diversity of the paleoenvironments in which such fossils occur (Luci & Cichowolski 2014).

This work investigates a *Panopea* Ménard de la Groye, 1807 (geoduck)-rich shell bed located within the upper Miocene portion of the Pisco Formation of southern Peru, which is globally famous as an outstanding Cenozoic vertebrate Fossil-Lagerstätte (e.g. Esperante *et al.* 2015; Gariboldi *et al.* 2015; Bianucci *et al.* 2016a, b; Gioncada *et al.* 2018a; Bosio *et al.* 2021; Collareta *et al.* 2021). In this bed, although most carbonates has been dissolved, a large number of invertebrate specimens have been preserved as molds that exhibit an exceptional degree of preservation, recording a complex community of invertebrates that grew on the inside of the *Panopea* shells. Nowadays, in soft substrates, scattered small hard-substrate settings, such as large clasts and exoskeletons of marine organisms, may become hot-spots of biodiversity (Kauffman 1978; Kidwell 1986; Sanfilippo *et al.* 2011). These "benthic islands" provide sessile benthic organisms with a relatively stable habitat in an otherwise unstable "ocean" of unconsolidated sediment (Brett 1988; Taylor & Wilson 2003). These communities and their dynamics can provide valuable information on the environmental conditions and, in particular, on the interplay between the different sclerobionts (Taylor 2016), as well as between the sedimentation rate and the stability/instability of the substrate. Furthermore, by distinguishing between *in vivo* and *post-mortem* colonization, it is also possible to gather precious information on biostratinomy (i.e., the variety of processes that occur after the death of an organism and before its definitive burial) (Luci & Lazo 2014).

In order to reconstruct the biostratinomic and diagenetic events and processes that led to the formation of the Pisco *Panopea* bed, this paper will focus on the faunal assemblage, the relationship between the different preserved taxa, the petrography of the molds, and the petrography of the embedding material. By building upon the approach provided by previous works on the encrusting fauna of both modern and fossil shells (Bottjer 1982; Bishop 1988; Lescinsky 1993; Lescinsky *et al.* 2002; Brett *et al.* 2012; Luci & Lazo 2014; Rashwan *et al.* 2019) and internal and external molds (Luci & Cichowolski 2014; Salahi *et al.* 2018), the present study aims to investigate and reconstruct the time sequence of the events that affected this faunal association.

GEOLOGICAL AND PALEONTOLOGICAL FRAMEWORK

The sedimentary succession from which the Pisco *Panopea* bed was recovered is part of the depositional fill of the East Pisco Basin (Fig. 1A), the onshore portion of an elongated extensional forearc basin that developed during the Cenozoic along the transform-convergent margin between the overriding South American Plate and the subducting Nazca/Farallon Plate (Thornburg & Kulm 1981; León *et al.* 2008). Prolonged subsidence of the basin, due to basal tectonic erosion, triggered the discontinuous deposition of Eocene to Pliocene sedimentary units, bounded by regionally extensive, conglomerate-mantled angular unconformities that reflect periods of subaerial exposure (Dunbar *et al.* 1990; DeVries 1998). During the deposition of these units, the basin was a semi-protected, shallow-marine embayment sheltered by a series of islands made of crystalline basement rocks (Fig. 1B) (Marocco & Muizon 1988; Bianucci *et al.* 2018). Nowadays, the depositional fill of the East Pisco Basin is largely exposed in the coastal Ica Desert as a consequence of rapid uplift during the late Pliocene, largely due to the subduction of the aseismic Nazca Ridge (Macharé & Pilger 1981; Hsu 1992; Ortlieb 1992; Hampel 2002).

The Miocene-Pliocene Pisco Formation is characterized by a wide range of lithofacies, including boulder beds, sandstone, diatomaceous siltstone, and diatomite, with minor dolomite beds and ash layers. Along the western side of the Ica Valley, south of the village of Ocucaje, the occurrence of three basin-wide erosional surfaces, indicating a relative sea-level drop and subaerial exposure, led to subdivide the Pisco Formation into three genetically related, unconformity-bounded stratal packages (depositional sequences or allomembers; Di Celma *et al.* 2016, 2017, 2018a), namely, P0, P1, and P2, in ascending stratigraphic order (Fig. 1C). These units are characterized by transgressive, deepening-upward facies associations, recording deposition in shoreface and offshore settings. Careful correlation between different outcrops and accurate dating by means of diatom biostratigraphy, ^{39}Ar-^{40}Ar chronology, and strontium isotope stratigraphy (Gariboldi *et al.* 2017; Bosio *et al.* 2019, 2020a, b) constrain the deposition of these three unconformity-bounded units: P0 was deposited during the Langhian-Serravallian (*c.* 14.8-12.4 Ma), P1 during the Tortonian (*c.* 9.5-8.6 Ma), and P2 during the Tortonian-Messinian (*c.* 8.4-6.7 Ma). The timing of deposition of these sequences may have been driven by eustatic sea-level variations (Di Celma *et al.* 2018a).

The P1 allomember (in which the *Panopea* bed occurs) displays a maximum thickness of about 100 m in its southern outcrops, at the locality Cerros la Mama y la Hija, where it lies unconformably on P0. It thins towards the northeast to become about 40 m-thick at Cerro la Bruja, beyond which it is presumed to pinch out by progressive onlap onto the crystalline basement (Di Celma *et al.* 2017). Further northwards, in the area of Cerro Colorado (Fig. 1B), P1 lies with marked angular unconformity on the underlying Chilcatay Formation or nonconformably directly on crystalline basement and displays an approximate thickness of about 75 m (Pisco lower allomember in Di Celma *et al.* 2016). The P1 strata host an exceptionally abundant and well-preserved fossil marine vertebrate assemblage that includes cetaceans, pinnipeds, bony and cartilaginous fishes (e.g. Carcharhiniformes, Lamniformes and Myliobatiformes), seabirds,
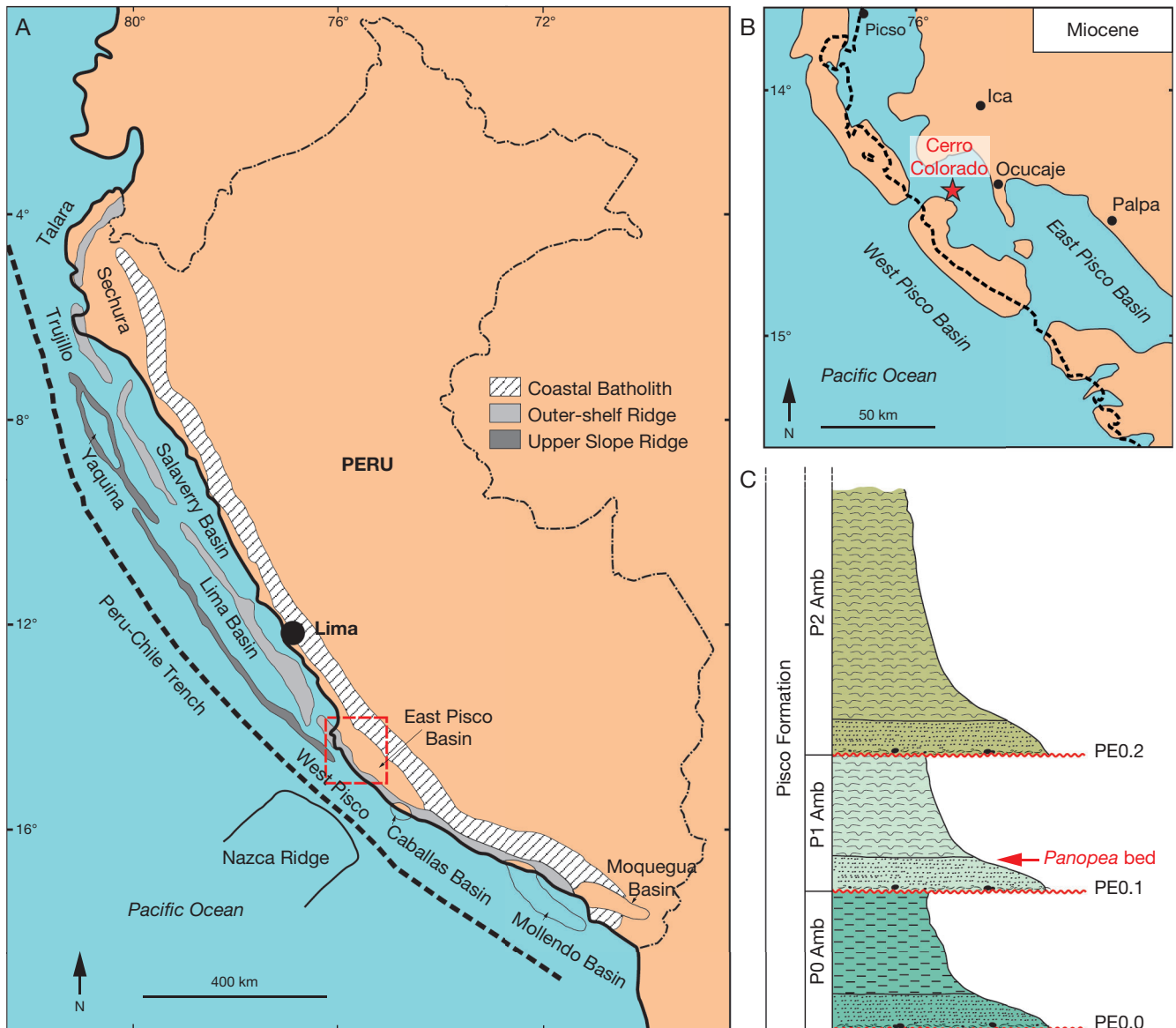
FIG. 1. — Geographic and geological setting: **A**, map of the major sedimentary basins along the Peruvian coast. The **red dotted square** indicates the East Pisco Basin and the **black dashed line** indicates the Peru-Chile Trench. Redrawn and modified from Travis *et al.* (1976) and Thornburg & Kulm (1981); **B**, possible paleogeographic configuration of the East Pisco Basin during the Miocene. The **black dashed line** indicates the present-day coastline. Redrawn and modified from Marocco & Muizon (1988); **C**, schematic stratigraphic log with the Pisco Formation allomembers (abbreviated "**Amb**") and unconformities (PE0.0, PE0.1, PE0.2, from the oldest to the youngest). The **red arrow** indicates the stratigraphic position of the *Panopea* Ménard de la Groye, 1807 bed. Redrawn and modified from Di Celma *et al.* (2018b).

sea turtles and crocodylians (Parham & Pyenson 2010; Bianucci *et al.* 2016a, b; Stucchi *et al.* 2016; Landini *et al.* 2017a, b). Cetacean remains are very common and include mysticetes (i.e., baleen-bearing whales), represented by a large-sized cetotheriid and balaenopterids (Collareta *et al.* 2015; Gioncada *et al.* 2016), and odontocetes with a diversified assemblage consisting of two physeteroids (*Livyatan melvillei* Lambert, Bianucci, Post, de Muizon, Salas-Gismondi, Urbina & Reumer 2010 and cf. *Acrophyseter* sp.), two ziphiids (*Chimuziphius coloradensis* Bianucci, Di Celma, Urbina & Lambert, 2016 and *Messapicetus gregarius* Bianucci, Lambert & Post, 2010), at least two undescribed kentriodontid-like delphinidans, and the pontoporiids *Brachydelphis mazeasi* Muizon, 1988, and *Samaydelphis chacaltanae* Lambert, Collareta, Benites-Palomino, Di Celma, de Muizon,

Urbina & Bianucci, 2020 (Muizon 1988; Bianucci *et al.* 2010, 2016c; Lambert *et al.* 2010, 2015, 2017a, b, 2020; Di Celma *et al.* 2017; Ramassamy *et al.* 2018). The P1 fossil invertebrate assemblage is relatively rich and is concentrated in mollusk-rich layers characterized by low biodiversity and high dominance (DeVries 1988; Di Celma *et al.* 2017). At various localities on the western side of the Ica River, the assemblage is dominated by the genera *Dosinia* Scopoli, 1777 (represented by the living species *Dosinia ponderosa* [Gray, 1838]), *Hybolophus* Stewart, 1930, *Miltha* Adams & Adams, 1857 (Adams & Adams 1857) and *Chionopsis* Olsson, 1932, together with gastropods of the superfamily Tonnoidea. At some localities, specimens of *Turritella infracarinata* Grzybowski, 1899 (Grzybowski 1899), *Anadara sechurana* (Olsson, 1932), *Panopea* sp. and *Trachycardium* sp.

FIG. 2. — Satellite and field photos: **A**, satellite image of the locality of the informally named Cerro Geoduck (14°24'02.8"S, 75°51'34.7"W) and position of the *Panopea* Ménard de la Groye, 1807 shell bed west of the Ica River (Ica Desert), highlighted by the **violet dotted line**. Based on a Google Earth image (© 2019 Maxar Technologies); **B**; field photo of the *Panopea* shell bed at Cerro Geoduck. The hammer is 30 cm long. Scale bar: A, 100 m.

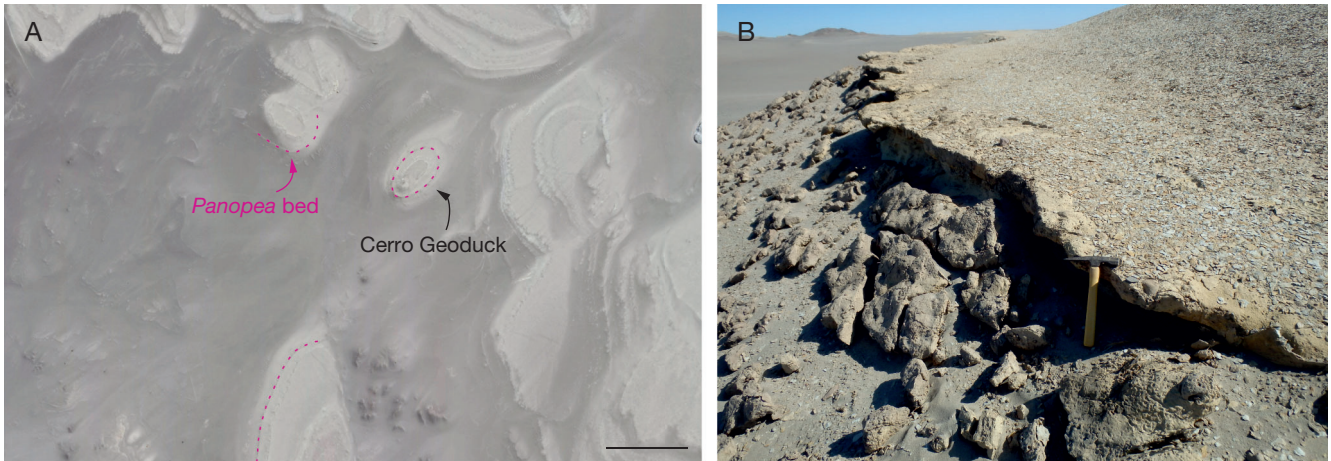have been recorded (Di Celma *et al.* 2017). All the fossil invertebrates found in the P1 allomember are commonly preserved only as dolomite/gypsum internal molds or as gypsum casts, whereas the original mineralogy of the carbonate shells is not preserved (Di Celma *et al.* 2017) as already observed for invertebrates from other Miocene localities of the East Pisco Basin (Gioncada *et al.* 2018b; Koči *et al.* 2021; Sanfilippo *et al.* 2021).

METHODS

About 6 km southeast of the locality of Cerro Colorado, a 10-15 cm-thick cemented bed enriched in mollusks can be traced around the informally named Cerro Geoduck (geographic coordinates: 14°24'02.8"S, 75°51'34.7"W) and in the surrounding area (see Fig. 2A). During fieldwork in 2016, this bed was described, walked out and mapped using a handheld GPS. A total of 61 internal molds of bivalves and three internal molds of barnacles from the *Panopea* bed were then collected for taphonomic and taxonomic investigations. All the specimens figured herein have been deposited in the invertebrate paleontology collection at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima, Peru). The East Pisco *Panopea* molds were compared with eight specimens (totaling 16 valves) of *Panopea generosa* Gould, 1850 collected by the West Coast Geoduck Research Corporation (WCGRC) of the Underwater Harvesters Association (UHA). The modern shells were collected from an area along the western coast of Vancouver Island (Pacific Canada) at 10 m of water depth.

In the laboratory, the fossil molds were cleaned with a soft brush, measured and described. For the taxonomic identification of bivalves, morphometric parameters such as length (L), height (H), and width were measured with an analogic caliper (see Table 1). For the taphonomic characterization and taxonomic identification of the encrusting fauna, only the complete *Panopea* molds (31 out of 39) were analyzed under a binocular stereomicroscope.

TABLE 1. — Mineral phases by XRD analyses of the host sediment and the internal mold of a *Panopea* specimen.

XRD	PC23-1 poorly cemented sediment	PC23-2 hard cemented sediment	P308 internal mold
quartz	>20%	5-20%	>20%
plagioclase	>20%	>20%	5-20%
ankerite	5-20%	–	>20%
ferroan dolomite	–	>20%	–
anhydrite	5-20%	5-20%	5-20%
gypsum	–	>20%	5-20%
clinochlore	traces	–	–
illite	traces	–	–

Three thin sections were prepared for petrographic and compositional analyses, one from the host sediment and two from two distinct *Panopea* internal molds. Thin sections were studied through a Leica Leitz Laborlux S transmitted light optical microscope at the Università degli Studi di Milano-Bicocca (hereinafter: UNIMIB). SEM-EDS analyses on thin sections were performed with a FEI Quanta 450 ESEM FEG provided with a QUANTAX XFlash Detector 6/10 at the Università di Pisa.

X-ray diffraction (XRD) and X-ray fluorescence (XRF) analyses were also performed on both the poorly-cemented and the well-cemented bulk samples of the host sediment, as well as from one *Panopea* internal mold. Samples were first crushed in an agate mortar, then mounted on zero-background silicon plates. XRD analyses were carried out with an X'Pert PRO PANalytical diffractometer, operating at 40 kV and 40 mA, at the UNIMIB. Each sample was scanned between 5° and 80° 2θ with a step size of 0.017° 2θ and an acquisition time of 3 s per step. Qualitative analyses were carried out with the software Panalytical X'pert HighScore Plus for identifying the mineralogical phases. XRF analyses were performed with the PANalytical Epsilon 3 X-ray fluorescence spectrometer at the UNIMIB.

TABLE 2. — Chemical composition by XRF analyses of the host sediment and the internal mold of a *Panopea* specimen. All the values are reported as wt%. Abbreviation: **bdl**, below detection limit.

XRF	PC23-1 poorly cemented sediment	PC23-2 hard cemented sediment	P308 internal mold
SiO_2	45.53	14.81	20.56
TiO_2	0.88	0.27	0.29
Al_2O_3	8.94	2.89	4.18
Fe_2O_3	6.47	3.26	4.25
MnO	0.24	0.73	0.52
MgO	2.81	3.93	3.55
CaO	16.20	35.78	32.56
Na_2O	bdl	bdl	bdl
K_2O	3.82	1.00	1.58
P_2O_5	0.96	0.46	0.52
SO_3	3.23	9.11	7.71
Cl	2.39	0.19	1.02
Total	91.45	72.42	76.75
LOI	8.04	27.34	23.00
SiO_2/Al_2O_3	5.09	5.13	4.93
CaO/Al_2O_3	1.81	12.40	7.80

RESULTS

FIELD OBSERVATIONS

At Cerro Geoduck, a 10-15 cm-thick mollusk-rich shell bed was found in the basal sandstones of the P1 allomember. This horizon possibly correlates with the Nazca marker bed recognized at Cerro Colorado by Di Celma *et al.* (2016) and can be traced in the surrounding area for hundreds of meters (see Fig. 2A). The sediment that comprises the shell bed is a yellowish, well-sorted, weakly- to well-cemented, medium-grained sandstone (Fig. 2B). The fossil content is represented by internal molds and, to a lesser extent, external molds of mainly bivalves. The mollusk assemblage displays a gradient in preservation from fully disarticulated to generally well-preserved and articulated bivalves. These bivalves display a chaotic arrangement (i.e., they are neither oriented nor preserved in life position) and rarely concave-down butterflied orientation of valves. In one case, two *Panopea* specimens were found in a telescopic arrangement (one within the other). Articulated bivalves feature molds of internal anatomical features, such as the adductor muscle scars and the pallial line (Fig. 3). Barnacles are preserved as internal molds. Compound molds (i.e., deriving by the coupling of internal and external molds) of encrusting invertebrates ornament the internal surfaces of the Panopea and, to a much lesser degree, the *Trachycardium* specimens.

PETROGRAPHIC AND COMPOSITIONAL FEATURES

Under the optical microscope, the thin sections of both the host sediment and the internal mold of a *Panopea* specimen are characterized by terrigenous and, to a minor extent, bioclastic particles (Fig. 4A-D). The siliciclastic component is dominated by fine- to medium-grained sand composed of quartz and minor plagioclase angular grains. In the host sediment only, coarser millimeter-sized particles can be found. The internal sediment is enriched in foraminifera and small bioclasts, whereas, in the host sediment, larger bioclasts, such as barnacles and mollusks, are more abundant (Fig. 4A). Consequently, the porosity is higher (i.e., ranging from 10% to 35%) in the host sediment, where bioclasts are larger and porous, and coarse grains are also present. In turn, in the internal molds, grains display a higher degree of sorting and the porosity is generally lower than 5%. The bioclasts are partially or totally dissolved, thus providing a relatively high moldic porosity. In some cases, the voids left by the shells are filled with carbonatic cement. In both the host sediment and the internal molds, the cement is constituted by fine-grained, cryptocrystalline carbonate and by euhedral dolomite partially filling the voids left by the dissolution of the bioclasts (Fig. 4E, F). The voids may also be filled by anhydrite (Fig. 4E, F).

SEM images and EDS analyses confirm the observations gathered under the optical microscope. The cemented sediment of the bed and the internal molds are composed of terrigenous particles and bioclastic material, such as foraminifera and barnacles, embedded in a dolomite cement (Fig. 5A, B). The host sediment displays a higher porosity with respect to that of the internal *Panopea* mold (Fig. 5A, B), and has larger bioclasts, mostly dissolved and often filled by anhydrite or gypsum (Fig. 5C, D). In both samples, Fe oxides with the morphology of pyrite framboids (Wilkin & Barnes 1997; Butler & Rickard 2000) were also detected (see Fig. 5E, F), especially in the internal mold, where the greatest abundance of framboids was found.

XRD analyses on both the host and the filling sediment (Table 1) confirm the presence of a siliciclastic fraction, represented by quartz and plagioclase and by traces of phyllosilicates (chlorite, illite) in one sample. The carbonate cement observed under the microscope reveals to be ankerite and ferroan dolomite from XRD. On the other hand, EDS analyses on cements reveal Mg values higher than Fe values, suggesting that the carbonates are mainly composed of dolomite and ferroan dolomite. Anhydrite also has been detected in all the samples, whereas gypsum was encountered only in the hard cemented sediment both outside and inside the mold.

For the chemical composition, XRF analyses (Table 2) indicate that SiO_2 and CaO are the main components, with minor Al_2O_3, MgO, Fe_2O_3 and K_2O, in very good agreement with the mineralogical composition. The poorly cemented sediment has comparatively higher SiO_2, Al_2O_3 and K_2O contents, attributable to a comparatively more abundant siliciclastic fraction, while the well-cemented sediment samples have comparatively higher CaO and MgO, corresponding to the higher abundance of carbonates. The nearly constant SiO_2/Al_2O_3 ratio indicates that the siliciclastic fraction has similar composition in the three samples. The LOI (Loss on Ignition) is moderately high in the poorly cemented sediment (*c.* 8%), whereas in the well-cemented sediment of both inside and outside the bivalves the LOI is about 23% and 27%, respectively.

THE FAUNAL ASSEMBLAGE

Mollusks and barnacles preserved as internal and external molds
Bivalve molds in the shell bed mostly belong to three different genera. The most abundant specimens belong to the genus *Panopea*, which contains some of the largest living bivalves.
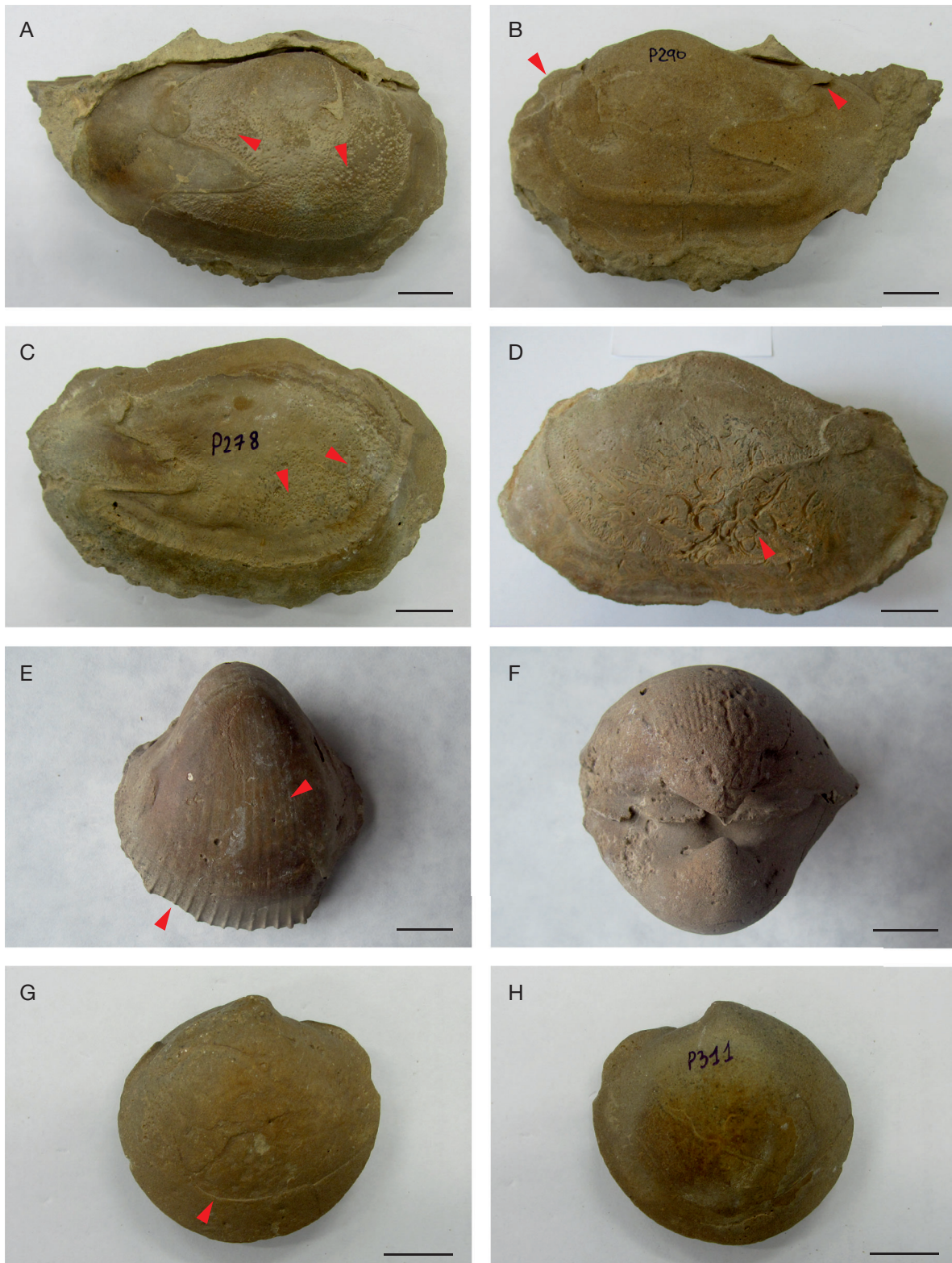
FIG. 3. — Bivalve internal molds: **A**, internal mold of a *Panopea* Ménard de la Groye, 1807 shell, right valve, showing the deeply impressed pallial sinus and the two adductor muscles (specimen P290). Note the molds of ?foraminifera once encrusting the inner part of the valve (**red arrows**); **B**, the same specimen (P290) shown in A, left valve, showing the deeply impressed pallial sinus and the two adductor muscles (**red arrows**); **C**, internal mold of a *Panopea* shell, right valve, showing the deeply impressed pallial sinus and the two adductor muscles (specimen P278). Note the molds of ?foraminifera once encrusting the anterior inner part of the valve (**red arrows**); **D**, internal mold of a *Panopea* shell, left valve, showing the deeply impressed pallial sinus and the two adductor muscles (specimen P17). Note the molds of serpulids (**red arrow**) once encrusting the inner part of the valve; **E**, internal mold of a *Trachycardium* Mörch, 1853 shell, left valve, showing one of the adductor muscles (specimen P272). Note the impression of the radial ribs (**red arrows**); **F**, internal mold of paired *Trachycardium* valves, umbonal view (specimen P7); **G**, internal mold of a *Dosinia ponderosa* (Gray, 1838) shell, right valve, showing a slightly impressed pallial line (**red arrow**) (specimen P311); **H**, internal mold of a *Dosinia ponderosa* specimen, left valve of the same specimen (P311). Scale bars: 2 cm.

TABLE 3. — Morphometrical parameters of the *Panopea* sp., *Trachycardium* sp. and *Dosinia ponderosa* (Gray, 1838) specimens. All measurements are reported in centimeters.

Species	Sample	Lenght (L)	Height (H)	Width	L/H ratio	Notes
Panopea sp.	P289	11.90	8.10	4.80	1.47	
	P290	11.80	7.85	3.80	1.50	
	P288	10.20	6.20	4.60	1.65	
	P295	9.90	7.95	3.70	1.25	
	P301	10.90	7.00	4.20	1.56	
	P279	10.30	6.90	4.10	1.49	
	P278	11.65	7.15	4.85	1.63	
	P285	10.25	6.90	3.80	1.49	
	P281	11.30	7.30	4.60	1.55	
	P286	10.20	6.70	4.05	1.52	
	P287	10.10	6.40	3.85	1.58	
	P17	13.30	7.35	4.20	1.81	
	P271	10.35	7.25	4.25	1.43	
	P300	12.60	7.00	3.60	1.80	
	P273	12.10	8.40	4.80	1.44	
	P282	12.30	7.70	7.20	1.60	
	P277	10.70	6.60	4.10	1.62	
	P297	10.40	7.60	4.45	1.37	
	P283	13.00	8.05	4.50	1.61	
	P280	11.40	6.15	3.35	1.85	
	P18	11.45	6.80	4.10	1.68	
Dosinia ponderosa (Gray, 1838)	P1	7.90	7.70	3.50	1.03	
	P311	6.60	6.20	2.80	1.06	
	P313	4.40	4.10	1.80	1.07	
	P312	7.70	4.30	2.10	1.09	
	P2	4.70	4.40	1.90	1.07	
Trachycardium sp.	P12	8.30	6.85	4.65	1.21	
	P15	6.30	5.70	–	1.11	one valve only
	P14	5.50	5.50	4.20	1.00	
	P9	7.60	7.80	–	0.97	one valve only
	P7	9.10	8.80	6.50	1.03	
	P10	8.90	8.70	–	1.02	one valve only
	P272	7.75	8.40	–	0.92	one valve only
	P16	3.30	3.10	2.30	1.06	
	P13	5.50	5.40	4.00	1.02	
	P6	10.77	9.55	–	1.13	one valve only
	P8	8.76	9.16	–	0.96	one valve only

Thirty-nine collected internal molds and rare external molds exhibit the characters typical of this genus (Fig. 3A-D), as described by Coan & Valentich-Scott (2012): an elongated, thick, ventricose, inequilateral shell with a rounded anterior end and truncate posterior end that is widely gaping; a weak hinge plate, equal in both valves; a deeply impressed pallial line and a triangular pallial sinus; and commarginal ornamentation visible in the external molds. Specimens are from 9.9 to 13.3 cm in length, from 6.1 to 8.4 cm in height, and from 3.3 to 4.8 cm in width (or thickness), except for an open one that is 7.2 cm wide (Table 3). All of the molds are more than 7.5 cm in length, suggesting that they are all adult specimens (Goodwin & Pease 1989).

The second bivalve genus present is *Trachycardium* Mörch, 1853 (Fig. 3E, F) (note that for the purposes of the present paper the genus *Trachycardium* is regarded as including also *Mexicardia* Stewart, 1930; but see also Valentich-Scott *et al.* 2020 for a different taxonomic assessment of *Mexicardia*). The 13 specimens referred to this genus exhibit a shell with similar length and height (L/H = *c.* 1), and large width (Table 3), as well as an ophistogyrate and strongly inflated umbo. In rare external molds, the *Trachycardium* specimens show evidence of high and strong radial ribs. Small specimens showing the same proportions and features probably belong to juveniles of *Trachycardium* sp. (i.e., samples P13, P14, P15 and P16 of Table 3).

The third identified bivalve is represented by nine internal molds exhibiting a subcircular and moderately compressed morphology, a well-defined, deep, short, and broad lunule, a left anterior lateral tooth, and a moderately deep pallial sinus, pointing towards the lower to middle part of the anterior adductor muscle scar (Fig. 3G, H). Rare external molds show an external sculpture of commarginal ribs with very narrow interspaces, in most specimens absent medially and ventrally. The L/H ratio ranges from 1.03 to 1.09 and the width is variable (Table 3). Based on these characters and after comparison with published data about the fauna of the Pisco Formation (DeVries & Frassinetti 2003; Di Celma *et al.* 2017) we attribute these molds to the genus *Dosinia* Scopoli, 1777, and especially the species *Dosinia ponderosa*. Four out of the nine internal molds are small specimens possibly belonging to juveniles of *D. ponderosa* (i.e., samples P2, P312 and P313 of Table 3). In addition to the three identified bivalve taxa, internal molds of gastropods and recrystallized shells of bivalves of the family Anomiidae were found within a few *Panopea* individuals.

Three acorn barnacle specimens, preserved as internal molds, have also been collected from the shell bed. They exhibit a truncated-conical body chamber bounded by a six-plated shell provided with an interdigitating, calcareous basal plate. The sheath is less than half of the total height of the shell and displays numerous transverse growth lines; below the sheath, the inner surface of each compartment is ornamented by longitudinal ribs that become thicker towards the base. In one specimen, the sutural surface of a radius shows transverse septa with secondary denticles on the upper side only. The same specimen partly preserves the impressions of the terga and scuta, lying appressed to the sheath. The large size of the preserved specimens, their overall shell structure, and especially the observation of a peculiar denticulation pattern of the sutural surfaces of the radii, allowed us to identify them as members of Austromegabalanini (Newman 1979; Buckeridge 2015), a tribe of megabalanine balanids that is known from the Miocene deposits of southern Peru, where at least three species occur (Coletti *et al.* 2018, 2019; Collareta *et al.* 2019).

The Panopea *encrusters*

The sediment that fills the *Panopea* shells is a mixed siliciclastic-carbonate, medium to fine grained sand. Its biogenic fraction is characterized by a faunal assemblage typical of shallow water depths, such as mollusks, balanid barnacles, ostracods, and benthic foraminifera (Fig. 4A-D). The foraminifera belong to *Peneroplis* Montfort, 1808 (Montfort 1808), *Cibicides* Montfort, 1808, *Quinqueloculina* d'Orbigny, 1826 (Orbigny 1826), and *Pyrgo* Defrance, 1824 (Defrance 1824) (Fig. 4B-D), which are mostly common in shallow waters (Murray 1991).

Twenty-six out of 31 inner molds of *Panopea* feature fossil evidence of a diversified invertebrate fauna encrusting the internal surfaces of one or both valves (Fig. 6). The encrusters are preserved as external molds, compound molds, recrystallized shells and shreds of the encrusters' carbonate skeletons (Table 4). No encrusters on the external molds, corresponding to the external surfaces of valves, have been recorded. Sixteen of all the encrusted geoduck molds (i.e., 61%) preserve encrusters both inside and outside the pallial line (i.e., dorsally and ventrally of the pallial line), while eight specimens (31%) preserve them exclusively inside the pallial line. In just two *Panopea* molds the encrusters are found exclusively outside the pallial line (Table 4). Almost one third of the *Panopea* specimens (eight molds, or 31%) exhibits clustering of the encrusters in close proximity to the siphonal aperture (versus only two specimens in which clustering occurs at the opposite end) (Table 4). Sixteen specimens (61% of the encrusted ones) display no particular clustering of the encrusters. Furthermore, 15 specimens out of 26 encrusted *Panopea* molds (58%) display encrusters that were originally settled inside both the left and right valves (Table 4). Finally, the orientation of the encrusters is variable, lacking any particular orientation pattern, except for one specimen where barnacles exhibit a common orientation of their carinorostral diameters towards the *Panopea* umbo.

TABLE 4. — Incidence and distribution of the encrusting fauna on the inside shells of *Panopea* Ménard de la Groye, 1807. Notes: 1, percentages calculated on a total of 26 *Panopea* specimens that display encrusters; 2, percentages calculated on a total of 23 *Panopea* specimens that preserve both valves and display encrusters.

		Number of specimens	Percentage
Entombed mollusks			
Absent (not observed)		21	68%
Present (observed)		10	32%
Encrusters			
Absent		5	16%
Present		26	84%
Taxonomic groups	serpulids[1]	17	65%
	?foraminifera[1]	16	62%
	bryozoans[1]	6	23%
	balanids[1]	4	15%
Distributional data	on one valve[2]	8	35%
	on both valves[2]	15	65%
	inside the pallial line[1]	8	31%
	outside the pallial line[1]	2	8%
	both inside and outside the pallial line[1]	16	61%
	clustering at the siphonal aperture side[1]	8	31%
	clustering at the anterior part (opposite side)[1]	2	8%
	no evident clustering[1]	16	61%

Due to the aforementioned style of preservation, the identification of the internal encrusters could only be made at taxonomic levels higher than species. Encrusters are taxonomically diverse, being referable to four major groups, namely: serpulids, ?foraminifera, bryozoans, and barnacles (Fig. 6).

Serpulids are the most common group of encrusters, having been observed on 17 specimens of *Panopea* (65% of all the encrusted specimens) (Fig. 6A, B; Table 4). Notably, the serpulids also encrust some *Trachycardium* specimens that occur together with *Panopea* in the studied horizon. They are preserved as calcareous tubes, filled by the dolomite cement, and display moderate degrees of abrasion and variable degrees of fracturing. Most serpulid tubes attain a length of a few centimeters. The tubes are attached to the adjoining valve along their entire lengths, being straight-serpentine to somewhat meandering and increasing moderately in diameter to a few millimeters. The tubes are triangular or subtriangular in cross-section and exhibit distinctly sharp longitudinal keels (Fig. 6A, B). The cellular layers are strongly developed, and the lumen is circular. The base of each tube often bears alveolar chambers (Thomas 1940; Bianchi 1981). These exoskeletal features allow us to identify the extant genus *Spirobranchus* (Pillai, 2009 regarded as a synonym of *Pomatoceros*), specifically, *Spirobranchus triqueter* (Linnaeus, 1758), described from the lower middle Miocene (Langhian) of the central Paratethyan *Lingula*-bed localities of Slovakia (personal observation by T.K.).

Very small encrusting organisms left their impressions on 16 *Panopea* molds (61% of encrusted individuals) as clustered,
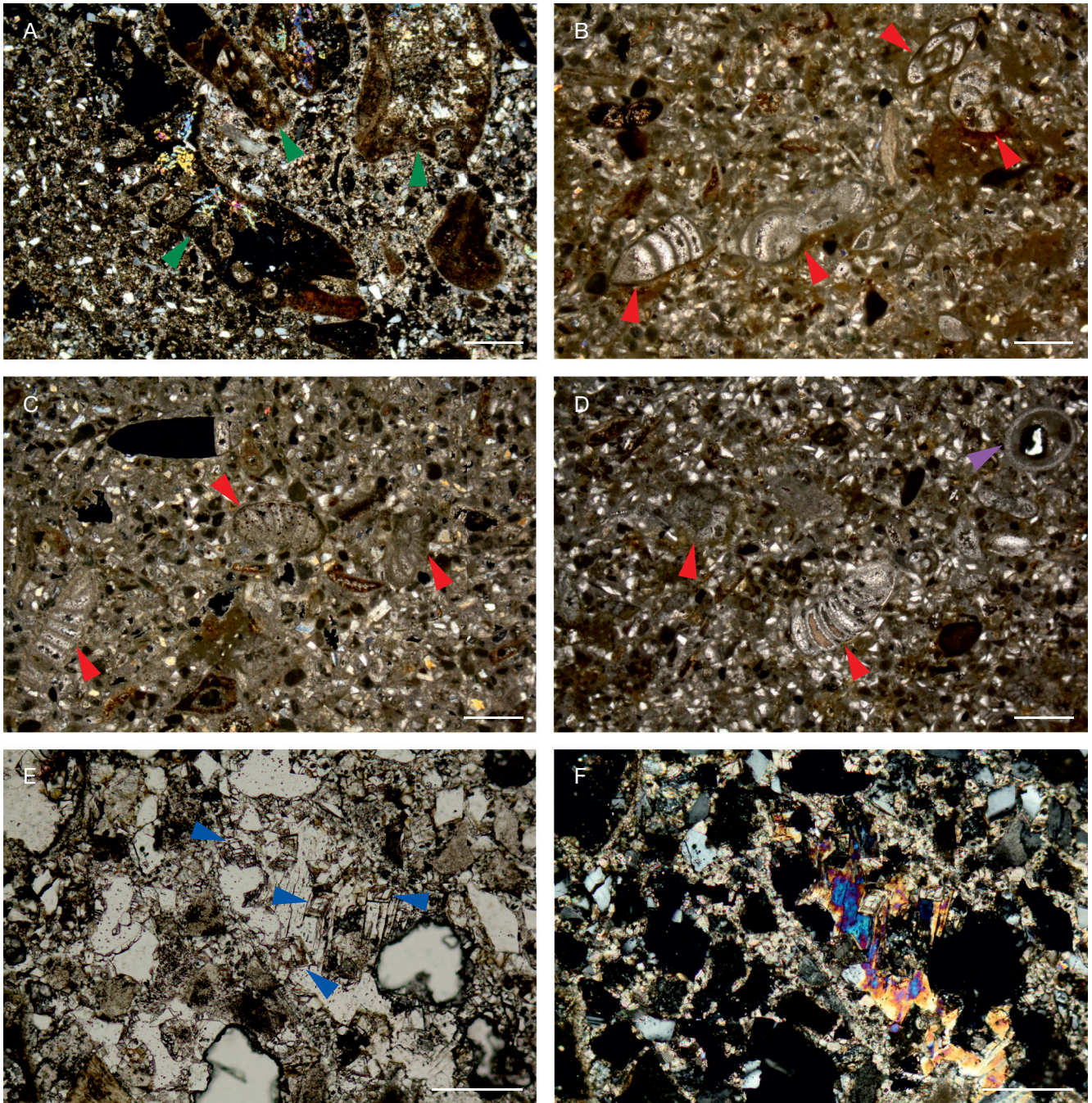
Fig. 4. — Photomicrographs of the internal molds of bivalves and the host cemented sediment: **A**, host sediment showing siliciclastic grains and large bioclasts such as barnacle shells (**green arrows**) in cross-polarized light; **B**, internal mold of *Panopea* Ménard de la Groye, 1807 (specimen P299) showings siliciclastic grains and bioclasts, such as the foraminifera (miliolids and *Cibicides* Montfort, 1808) highlighted by **red arrows** in cross-polarized light; **C**, internal mold of *Panopea* (specimen P299) showing siliciclastic grains and bioclasts such as foraminifera (miliolids) (**red arrows**) in cross-polarized light; **D**, internal mold of *Panopea* (specimen P299) showing siliciclastic grains and bioclasts such as foraminifera (*Peneroplis* Montfort, 1808) (**red arrows**) and serpulids (**violet arrow**) in plane-polarized light; **E**, terrigenous grains cemented by dolomite, which exhibit euhedral rhomboidal crystals (**blue arrows**), and secondary anhydrite in plane polarized light; **F**, the same as in E, in cross-polarized light. Scale bars: A-D, 500 µm; E, F, 200 µm.

pitted, sometimes irregular depressions not exceeding 1 mm in equatorial diameter (Fig. 6C, D; Table 4). Although generally shallow and poorly defined, the outline of these depressions hints at disc-like, multi-chambered tests in which new, larger chambers are added spirally. The observed depressions are reminiscent of encrusting shallow-water benthic foraminifera, such as *Cibicides* or *Planorbulina*.

About one fourth of the encrusted specimens (23%; six specimens) features large patches (1-3 cm) of cheilostomate bryozoans (Fig. 6E, F; Table 4). The colonies present unilaminar encrusting growth form (*sensu* Smith 1995), with the shape of the zooids generally very well preserved. They were distributed on the internal surface of the valves, both inside and outside the pallial line, and in one case they overgrow on to serpulids.
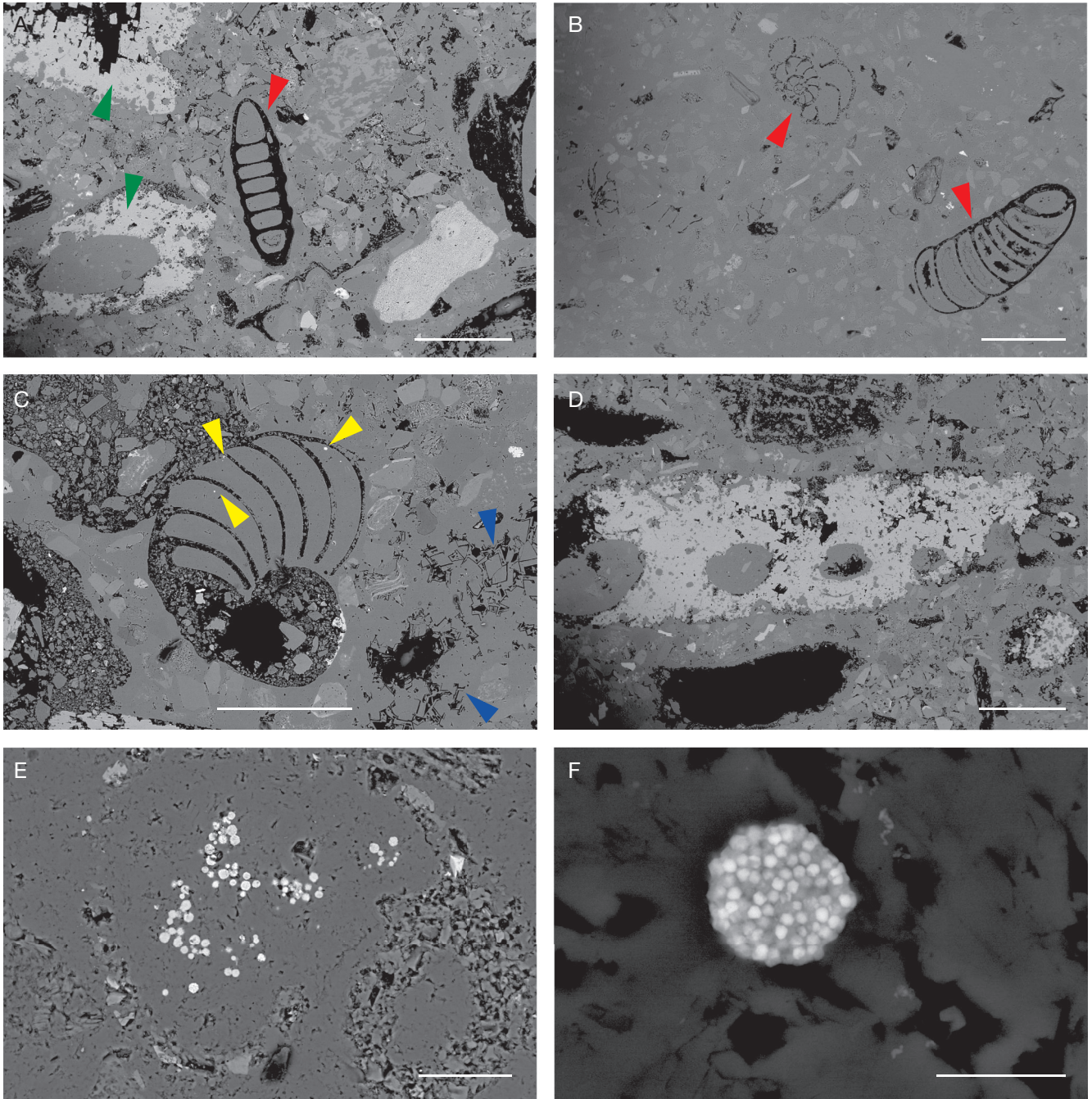
Fig. 5. — SEM images of the internal molds of bivalves and the host cemented sediment: **A**, host sediment exhibiting siliciclastic clasts, dissolved barnacle shells replaced by anhydrite/gypsum (**green arrows**), and dissolved shells of foraminifera (**red arrow**). Note the high porosity; **B**, internal mold of *Panopea* Ménard de la Groye, 1807 (specimen P299) exhibiting siliciclastic clasts and dissolved shells of foraminifera (*Peneroplis* Montfort, 1808) (**red arrows**). Note the low porosity compared to A; **C**, dissolved shell of the foraminiferan species *Peneroplis* filled and embedded by dolomite cement in the sediment of the studied bed. Note the small framboids of Fe oxides (**yellow arrows**) in the foraminiferan chambers and the rhomboidal crystals of dolomite (**blue arrows**) on the right side of the image; **D**, dissolved barnacle shell replaced by anhydrite/gypsum in the sediment of the studied bed; **E**, framboids of Fe oxides, relics of framboidal pyrite, in the internal mold of *Panopea*; **F**, detail of a Fe oxide framboid exhibiting the ex-pyrite microcrystals. Scale bars: A, B, D, 500 µm; C, 400 µm; E, 50 µm; F, 5 µm.

Barnacles constitute the least abundant group of encrusters, being present on only four geoduck specimens (15%) (Table 4). They appear on the surface of the *Panopea* specimens as thin, ring-like cavities, ranging in diameter from a few millimeters to about one centimeter (Fig. 6G, H). The geometry of these ring-like cavities ranges from circular to slightly elliptical, reflecting different degrees (null to

moderate) of carinorostral stretching of the barnacle shells. The areas of dolomite bounded by these ring-like cavities are very slightly depressed with respect to the surrounding regions, thus hinting at the presence of a thin, calcareous basal plate. These cavities continue as truncated-conical cavities (i.e., compound molds) that extend inwards, some of which host radiating, tubular rods of dolomite that rep-
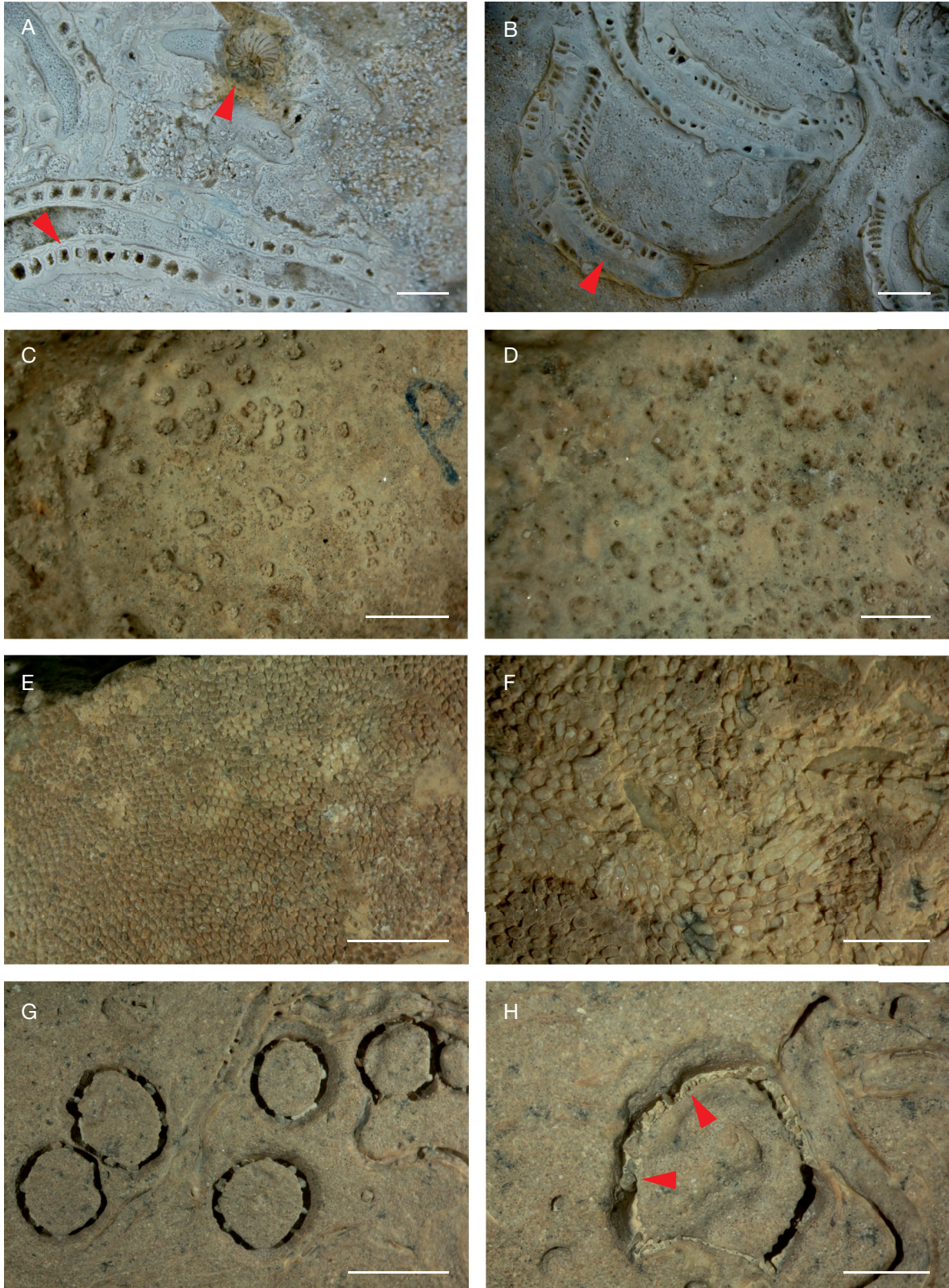
Fig. 6. — The encrusting fauna: **A**, **B**, encrusting serpulids, identified as *Spirobranchus* Blainville, 1818 (Blainville 1818), preserved as calcareous tubes filled by dolomite cement on a *Panopea* Ménard de la Groye, 1807 (specimen P297). In **A**, the **red arrow** on the top indicates a foraminiferan specimen of the genus *Peneroplis* Montfort, 1808, whereas the **red arrow** in the bottom left indicates the alveolar chambers of the serpulid. In **B**, the **red arrow** indicates the longitudinal keel of the serpulid; **C**, **D**, small disc-like, seemingly multi-chambered molds of encrusting ?foraminifera on a *Panopea* (spécimen P276); **E**, **F**, molds of cheilostomate bryozoans showing a unilaminar encrusting growth form on two different *Panopea* specimens (P277 and P297, respectively); **G**, compound molds of encrusting barnacles on a *Panopea* (specimen P18); **H**, compound molds of encrusting barnacles on a *Panopea* (specimen P18). Note the tubular rods of dolomite that represent the partial infilling of a single row of longitudinal parietal tubes (highlighted by the **red arrows**). Scale bars: A, 1 mm; B, D, F, 2 mm; C, E, H, 4 mm; G, 10 mm.

Fig. 7. — Modern *Panopea* Ménard de la Groye, 1807 shells. Modern specimen of *Panopea generosa* Gould, 1850 from the Vancouver Island (Canada) showing encrusting organisms on the inner surface of the valves. **Red arrows** indicate encrusting barnacles and barnacle traces. Scale bar: 2 cm.

resent the partial infilling of a single row of longitudinal parietal tubes (see Fig. 6H). In rare cases, the space between adjacent compartments is preserved as thin, radiating plates of dolomite, suggest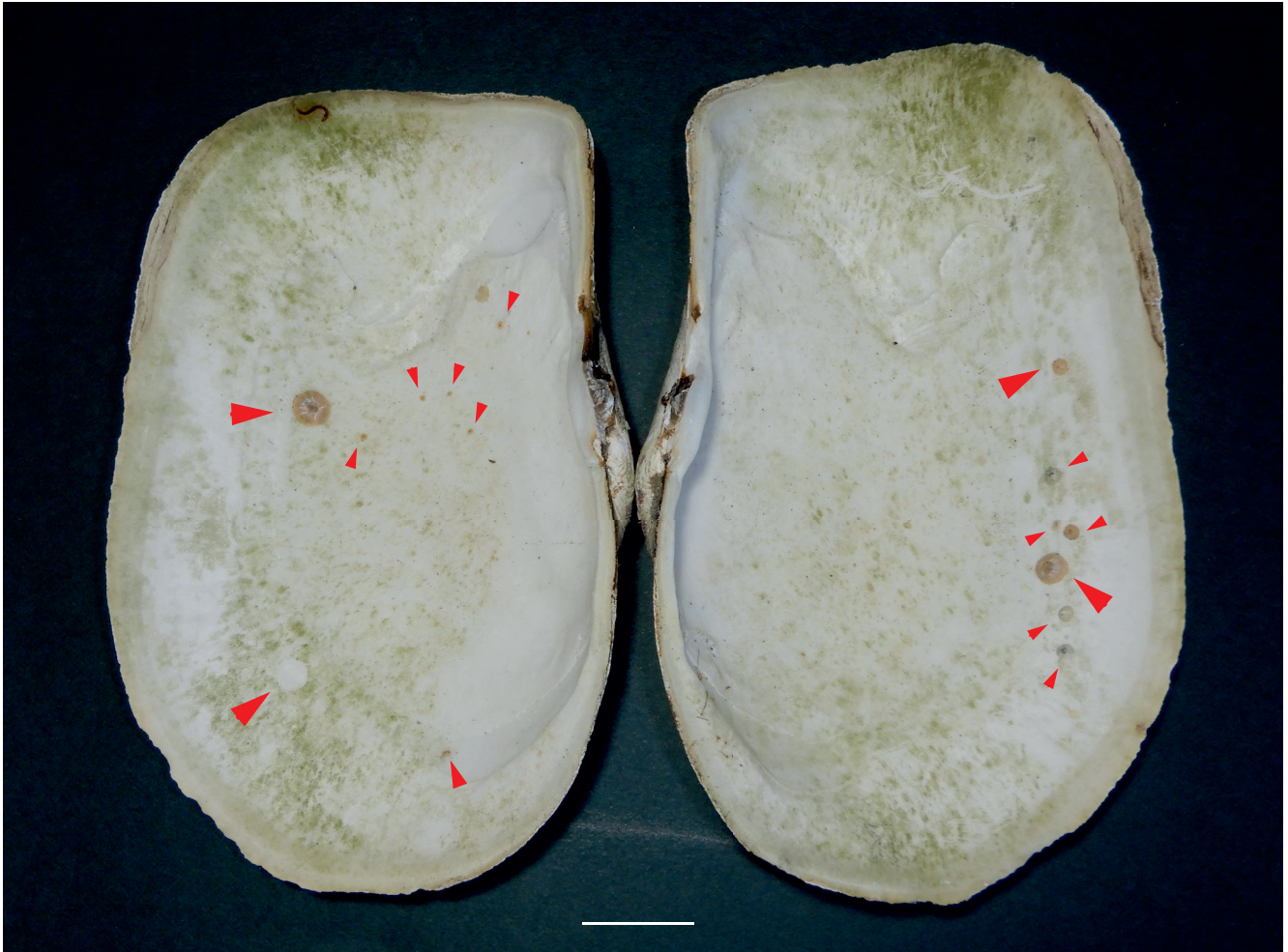ing that the capitulum was formed by six wall-plates. Given these considerations, the encrusting barnacles are recognized as belonging to the family Balanidae. However, due to their much smaller size, they are possibly not conspecific with the barnacles preserved as internal molds together with the *Panopea* specimens.

The modern Panopea shells

The eight specimens of the extant species *Panopea generosa* collected from the Pacific coast of Canada (Vancouver Island) were found articulated at the seafloor. Later, they disarticulated very quickly once they had dried out (personal communication by G. Hay). The organic matter had completely decayed at the moment of collection, but the periostracum was almost completely preserved. The inner surface of the shells appears to be colonized by bryozoans, balanid barnacles, and red algae (see Fig. 7). The encrusters do not show a particular distribution on the inner surface of the valve, but they are not present on the outer surface of the shells.

DISCUSSION

DISTRIBUTION AND PALEOENVIRONMENTAL SIGNIFICANCE OF THE FAUNAL ASSOCIATION

When attempting a reconstruction of the paleoecological and paleoenvironmental significance of the Pisco *Panopea* shell bed, the oryctocoenosis (*sensu* Lawrence 1979; i.e., fossil remains found together in an outcrop) may be split into two different assemblages. The first assemblage includes all the macro-invertebrates – namely, bivalves (*Panopea*, *Trachycardium*, and *Dosinia ponderosa*) and barnacles (Austromegabalanini indet.) – that are preserved as internal molds. The second assemblage includes all the sclerobionts – serpulid polychaetes, cheilostomate bryozoans, probable foraminifera, and balanid barnacles – that are found as encrusters of the *Panopea* and, to a much lesser degree, the *Trachycardium* specimens. Such encrusters were often recorded inside the pallial line of *Panopea*, therefore the second assemblage obviously followed the decay of the soft parts of the geoducks and, as such, corresponds to a later stage in the taphonomic history and might reflect different paleoenvironmental conditions. Therefore, the primary and secondary assemblages are here analyzed separately.

The primary assemblage is dominated by shells of the geoduck *Panopea* sp. Nowadays, *Panopea* clams represent the largest burrowing bivalves in the world, reaching 25 cm in length and a maximum of 168 years in age, and they are currently found in intertidal and subtidal marine and estuarine waters, down to depths of about 110 m (Bureau *et al.* 2002). Today, in the eastern Pacific, only two *Panopea* species are found, living along the North American coasts: *P. generosa* Gould, 1850, occurring from Alaska to Baja California, and *P. globosa* Dall, 1898, which is endemic to the Gulf of California (Vadopalas *et al.* 2010; Leyva-Valencia *et al.* 2012, 2015; González-Peláez *et al.* 2013; Tapia-Morales *et al.* 2015). Along the Peruvian coast, *Panopea* occurs in the fossil record of several sedimentary basins. In the Talara Basin, in northern Peru, *P. similaris* Dall & Ochsner, 1928 and *P. coquimbensis* d'Orbigny, 1842 (Orbigny 1842) are found in the late Pliocene Taime Formation (DeVries 1986). *Panopea coquimbensis* is reported also by Olsson (1932), and later by Alleman (1978), as *P.* cf. *coquimbensis*, in Miocene strata of northern Peru. DeVries & Frassinetti (2003) also report this species from the East Pisco Basin, in the Miocene Pisco Formation. Some fossil specimens of *Panopea* sp. were also found in the Miocene Pisco and Chilcatay formations and in the Eocene Paracas Formation in the Ica River Valley, in upper Miocene strata from the Nazca area, and in middle Miocene strata from the Paracas area (DeVries personal communication). The only *Panopea* species that resemble the studied fossil specimens are *P. coquimbensis* and *P. oblonga* Philippi, 1887, but additional taxonomic investigations are required for species-level identification.

Together with *Panopea*, the genus *Trachycardium* is dominant in the primary assemblage. This genus today is typical of subtropical to tropical shallow-water environments (Vidal 1999). Nowadays, the Peruvian coasts in front of Ica are inhabited by *Trachycardium procerum* (Sowerby, 1833), which is typical of the intertidal zone to 70 m depth (Valentich-Scott *et al.* 2020). In the Miocene strata of northern Peru, the genus *Trachycardium* is represented by *T. zorritensis* Spieker, 1922 and *T. peruvianum* Spieker, 1922 (Olsson 1932). In the Pisco Formation, the only form of *Trachycardium* that has been reported to date is *T. procerum domeykoanum* Philippi, 1887 (DeVries & Frassinetti 2003). Additional comparative information would be necessary for species identification of the *Trachycardium* material of the assemblage documented herein. A shallow-water environment is also suggested by the occurrence of *Dosinia ponderosa*, an extant species that is typical of the intertidal and shallow subtidal zones, down to depths of *c.* 60 m (Coan & Valentich-Scott 2012). The modern distribution of *D. ponderosa* ranges from 31.4°N, into the Gulf of California, to 27.8°N, along the Pacific coast of southern Baja California, reaching southern Mexico, the Galapagos Island, Ecuador and northern Peru. *Dosinia ponderosa* is also reported from the Pleistocene of southern California, Baja California, southern Mexico, and Ecuador, from the Pliocene of Ecuador, and from the Miocene of Trinidad, Panama, Peru, and Chile (Pilsbry & Olsson 1941; Piazza & Robba 1998; Di Celma *et al.* 2002, 2005; Ragaini *et al.* 2008; Coan & Valentich-Scott 2012). The primary assemblage includes barnacles belonging

to the tribe Austromegabalanini, although they are probably allochthonous organisms. This tribe includes extant and extinct forms characterized by intertidal or shallow subtidal environmental preferences (e.g. López *et al.* 2008), as well as extinct mid-shelf dwellers (e.g. Buckeridge 2015). The two formally named Miocene members of Austromegabalanini of the East Pisco Basin, to which the reported specimens are closely related, are interpreted as intertidal and shallow subtidal organisms (Coletti *et al.* 2019; Collareta *et al.* 2019).

The secondary assemblage associated with the *Panopea* and, to a much lesser degree, *Trachycardium* molds is dominated by serpulids and ?foraminifera. Serpulids are assigned to the extant genus *Spirobranchus* and the inner structure of their tubes is similar to that of the living species *S. triqueter*, which encrusts stones, rocks and shells, and some species of decapods (Holme & Wilson 1985; Campbell & Kelly 2002; Ben-Eliahu & Ten Hove 2011; Tillin *et al.* 2016). *Spirobranchus triqueter* is a mainly infralittoral species that lives down to 70 m depth (Riley & Ballerstedt 2005). The small depressions interpreted as impressions of small benthic foraminifera are consistent with the tests of shallow-marine encrusting forms such as *Cibicides* spp.

Third in abundance among the members of the secondary assemblage are the cheilostomate bryozoan colonies, which display an unilaminar encrusting growth form and, as such, suggest colonization of the geoduck shells in an intertidal to inner shelf environment, not deeper than 50 m (Smith 1995), and presumably shallower than 30 m (Nelson *et al.* 1988). The presence of balanid barnacles also fits well with a shallow-water setting (Coletti *et al.* 2018).

The keel worms belonging to the genus *Spirobranchus* are filter feeders (ten Hove & Nishi 1996; Riley & Ballerstedt 2005), the same is true for the bryozoans and balanid barnacles (Schäfer 1972), and most benthic foraminifera also rely on particulate organic matter (Murray 1991). These observations suggest a relatively high concentration of particulate organic matter in the seawater passing through the encrusted *Panopea* shells. This high concentration might also explain why about one third of the *Panopea* molds exhibits clustering of encrusters in close proximity to the siphonal aperture: indeed, this likely reflects a larger flow of water laden with particulate organic matter close to the siphonal aperture at the time when the articulated valves of dead *Panopea* were on the seafloor. The secondary assemblage can be regarded as typical of shallow-water (likely less than 30 m in depth), hard-substrate, relatively high-energy settings and with available particulate organic matter.

A COMPLEX TAPHONOMIC HISTORY

The peculiar *Panopea* bed documented in this study is the result of a complex taphonomic history. All the bivalve internal molds were found together, forming an accumulation level, no longer in their original life position, but mostly preserving an intact articulation. The articulation, mainly observed in the *Panopea* specimens, suggests that the fossils had not undergone significant lateral transport. The association is characterized by the presence of deep infaunal (*Panopea* sp.)

and very shallow-infaunal (*Trachycardium* sp. and *Dosinia ponderosa*) taxa occurring together with barnacles and other epifaunal encrusters. This fossiliferous bed can be interpreted as resulting from a sedimentologic concentration (Kidwell *et al.* 1986). We hypothesize that a storm event above a soft-bottom shoreface setting washed out and laid down on the seafloor live specimens of *Panopea* and other infaunal species, in some cases without entirely exhuming them (Fig. 8). This hypothesis is supported by the finding of a few bivalves with butterflied valves and the telescopic arrangement of two *Panopea* specimens which is evidence of high-energy events (Cantalamessa *et al.* 2005). A negligible lateral transport is further supported by the finding of specimens of different dimensions, including juvenile specimens of *Trachycardium* sp. and *Dosinia ponderosa*. As such, the bivalves form a parautochthonous assemblage comprising reworked but virtually untransported shells. The Austromegabalanini barnacles are interpreted to represent allochthonous shelly material introduced into the mollusk assemblage from an adjacent intertidal or shallow subtidal rocky environment during the storm. To support this hypothesis, we can refer to the occurrence of modern *Panopea*. Nowadays, living geoducks grow very long siphons and gradually dig deeper into the substrate as the siphon gets longer, which allows for great burrowing depths (Goodwin & Pease 1989). Extant *Panopea* spp. live buried in muddy to sandy soft sediments at depths ranging from 60 cm to 100 cm below the seafloor, so that only the end of the siphon is exposed at the sediment surface, allowing the mollusks to breathe, forage, and release secretion/excretion products, as well as gametes (Goodwin & Pease 1987; Miller & Harley 2005; Tapia-Morales *et al.* 2015). Once dislodged from the sediment and exposed, for example after severe storms, juvenile geoducks may survive and slowly rebury themselves, whereas adult individuals with siphons too big to retract and a relatively small muscular foot appendage are unable either to gain an upright position or dig into the substrate and will die if discarded on the seafloor (Goodwin & Pease 1989; Lochead *et al.* 2012; Łaska *et al.* 2019). In the Pisco bed, this can explain the presence of only adult *Panopea* specimens, which were unable to rebury themselves, and the absence of *Panopea* juveniles. A rough assessment of the amount of substrate erosion produced by the storm episode can be made from the size of the adult *Panopea* specimens. Kondo (1987) estimated the burrowing depth of adult *Panopea* to a depth about four times the length of the shell. Based on this, it can be deduced that to exhume the studied *Panopea* specimens, which are about 10-13 cm in length, at least 50 cm of sediment must have been winnowed and removed by the high-energy event.

Since most of the *Panopea* molds exhibit encrusting fauna on the internal surface of the valves, the geoduck shells must have been exposed at the seafloor, without being disarticulated, and colonized by encrusters before being filled by sediment (Fig. 8). Furthermore, no encrusters have been recorded on the external molds (i.e., onto the external surface of the valves), likely because the interior of the *Panopea* shells represented not only a hard substrate, but also a place protected from wave exposure and, possibly, predation. Literature data also highlight how the internal surfaces of bivalve shells are usually preferred by encrusters both in the past (Bottjer 1982; Bishop 1988) and in the present (Lescinsky *et al.* 2002). Among bivalves of the Pisco locality, the *Panopea* specimens mostly feature compound molds of encrusting organisms. This is possibly due to the peculiar shell morphology of geoducks. The other articulated bivalve species represent relatively closed environments, without connections with the exterior, whereas the *Panopea* shells are naturally gaping, with a large opening at the siphonal side – a site where a high abundance of encrusters often occurs in our fossil samples (Table 4). Our biostratinomic observations on the fossil specimens agree with those of modern individuals of *Panopea generosa* from Vancouver Island. As in the fossil molds, the encrusters of the modern Canadian geoducks were observed only on valve interior, whereas the external surfaces were barren of encrusters.

The encrusting assemblage found on the modern Canadian specimens is very similar to that of the fossil Peruvian ones, being comprised of bryozoans, balanid barnacles, and red algae. The abundant and diverse encrusting fossil fauna observed on the *Panopea* fossil molds indicates that these shells facilitate the colonization by encrusters, not otherwise present in the soft-bottom depositional setting, and acted as an attractive hard substrate for sessile organisms. The association of apparently indigenous but ecologically disparate organisms (e.g. soft-bottom mollusks co-occurring with hard-substrate taxa) represents a clear response by benthos to the relatively prolonged residence of shells on the seafloor (taphonomic feedback of Kidwell & Jablonski 1983; Kidwell 1991). This resulted in an ecologically mixed, time-averaged fossil assemblage generated from the mixture of multiple generation of organisms into a single stratigraphic horizon. The spatial distribution of the encrusters, which moderately concentrate inside the pallial line, demonstrates that most of the geoducks had been completely defleshed before they were encrusted (*post-mortem* colonizers of Luci & Lazo 2014). As already mentioned, the concentration of the encrusters at the siphonal aperture of some specimens can be explained by evoking a high concentration of particulated organic matter close to this gaping extremity, although the persistence of some shells as partly buried in the sediment in life position may also account for this observation. Following Fernández-López (1997), the moderate to high degree of encrustation intensity observed on the Pisco geoducks seemingly suggests a moderate to prolonged duration of the exposure of the shells on the seafloor. Sclerobionts may establish intense competition for space related to the access to resources (Buss 1979; Rosso & Sanfilippo 2005; Taylor 2016). In a few fossil specimens from the studied bed, serpulids were overgrown over bryozoans – an observation indicating that the exposure lasted enough for two different successive generations of encrusters to settle. The presence of adult barnacles on the internal surface of valves implies that they grew to adulthood inside the dead mollusk, further supporting a relatively long exposure at the seafloor.

After a prolonged exposure on the seafloor, *Panopea* shells with the encrusting organisms were buried in loco and completely filled by sediment, together with the shells of

Trachycardium, *D. ponderosa*, and Austromegabalanini indet. (Fig. 8). Petrographic, mineralogical and chemical analyses reveal that the shells filled by terrigenous sediment particles were later cemented by dolomite and ferroan dolomite. No pristine calcite is preserved, neither in the shell molds nor in the bioclastic portion of the sediment infill. To explain these facts, we suggest an early dolomite precipitation – before the dissolution of the pristine shells – cementing the sediment infill of the valves and the host sediment (Fig. 8). The carbonate cement formation probably occurred because of the increased alkalinity of porewater during early diagenetic processes, as suggested by Allison (1988), Shapiro & Spangler (2009) and Gariboldi *et al.* (2015). The presence of Fe oxide framboids resulting from the oxidation of framboidal pyrite, identified especially in the internal molds, suggests a sulfide production during dolomite precipitation (Gariboldi *et al.* 2015), probably related to bacterial activity during the decay of organic matter within the sediment (Wilkin & Barnes 1997). To explain the dissolution of the calcite shells, which leaves only the internal, external and compound molds of these organisms (Fig. 8) and voids within the sediment, a decrease of pH is required. pH variations may occur during early diagenesis at the boundary between the sulphate-reduction and methanogenesis zones (Meister *et al.* 2007, 2011; Xu *et al.* 2019). The formation of the mineral phases of gypsum and anhydrite follows the dissolution of the carbonates, probably due to pre-Miocene seawater-derived brines circulating within the East Pisco Basin sedimentary successions (Gioncada *et al.* 2018b).

To summarize, the following taphonomic history is proposed (see Fig. 8): phases I, II, a storm event brought live specimens of *Panopea*, *Trachycardium* sp., and *Dosinia ponderosa* to the surface, mixing them with shells of Austromegabalanini indet. from an adjacent rocky shoreline (Fig. 8A, B); phase III, the inner part of the shells, representing a hard substrate and a place protected from wave exposure, was colonized by a rich encrusting fauna, as is the case for modern specimens of *Panopea generosa* resting on the sediment surface (Fig. 8C); phase IV, the articulated bivalve shells with their encrusters and barnacles were buried and completely filled by sediment (Fig. 8D); phase V, as a consequence of an increase of alkalinity during early diagenesis, dolomite precipitated, cementing the bed and forming the molds (Fig. 8E); phase VI, and finally, pH variations at the sulphate reduction-methanogenesis zone boundary caused the dissolution of the pristine shells, and the circulation of pre-Miocene seawater-derived brines brought about the precipitation of anhydrite and gypsum phases (Fig. 8F). It is important to note that the above taphonomic history cannot be extended to all the shell beds that are observed in the Pisco Formation. For example, in the P1 strata exposed at Cerro Colorado, monospecific accumulations of *Dosinia* sp. are ubiquitous (Di Celma *et al.* 2017); these accumulations are comprised of dolomite inner molds that lack any evidence of encrusters and are entombed within an uncemented sediment. However, some of the taphonomic stages identified for the *Panopea* bed analyzed herein could also explain the origin of other shell beds of the Pisco Formation.

CONCLUSIONS

Southeast of the locality of Cerro Colorado, at the informally named site of Cerro Geoduck, the basal sandstones of the P1 allomember feature a highly idiosyncratic, invertebrate-rich bed. An abundant invertebrate assemblage with a peculiar biostratinomic and diagenetic history characterizes this 10-15 cm-thick shell bed. All the fossils are preserved as internal and external molds composed of sediment particles embedded in a dolomite cement. The faunal assemblage is composed of invertebrates that live at different depth in the sediment, such as the deep infaunal *Panopea* sp., the shallow infaunal *Trachycardium* sp. and *Dosinia ponderosa*, and the encruster austromegabalanine barnacles. Biostratinomic features suggest a quick exposure of live mollusks, which have not undergone significant transportation, and mixture with a minor amount of allochthonous megabalanine barnacles, resulting into a sedimentologic, mixed autochthonous-allochthonous assemblage. The identification of compound molds of encrusting organisms on the *Panopea* and few *Trachycardium* molds suggests a colonization of the internal surfaces of the *Panopea* valves employed as "benthic islands" by different taxa and generations of sclerobionts, forming a second autochthonous assemblage dominated by serpulids, bryozoans and barnacles. The resulting benthic fossil assemblage is a time-averaged sedimentologic accumulation largely dominated by indigenous skeletal material. After the burial of the encrusted shells, dolomite precipitated due to an increase of alkalinity during the early diagenesis creating the internal molds and cementing the bed. The absence of preserved shells is due to the pH decrease in correspondence to the sulphate reduction-methanogenesis zone boundary, which allows a dissolution of all the aragonitic and calcitic shells. Late fluid circulation from a supersaturated brine let the precipitation of gypsum and anhydrite in the voids.

This fossil scenario shows the possibility of inferring fundamental information on the paleoenvironmental conditions of the faunal assemblage together with biostratinomic and diagenetic processes that affected fossil macroinvertebrates when they do not preserve the pristine carbonate shells.
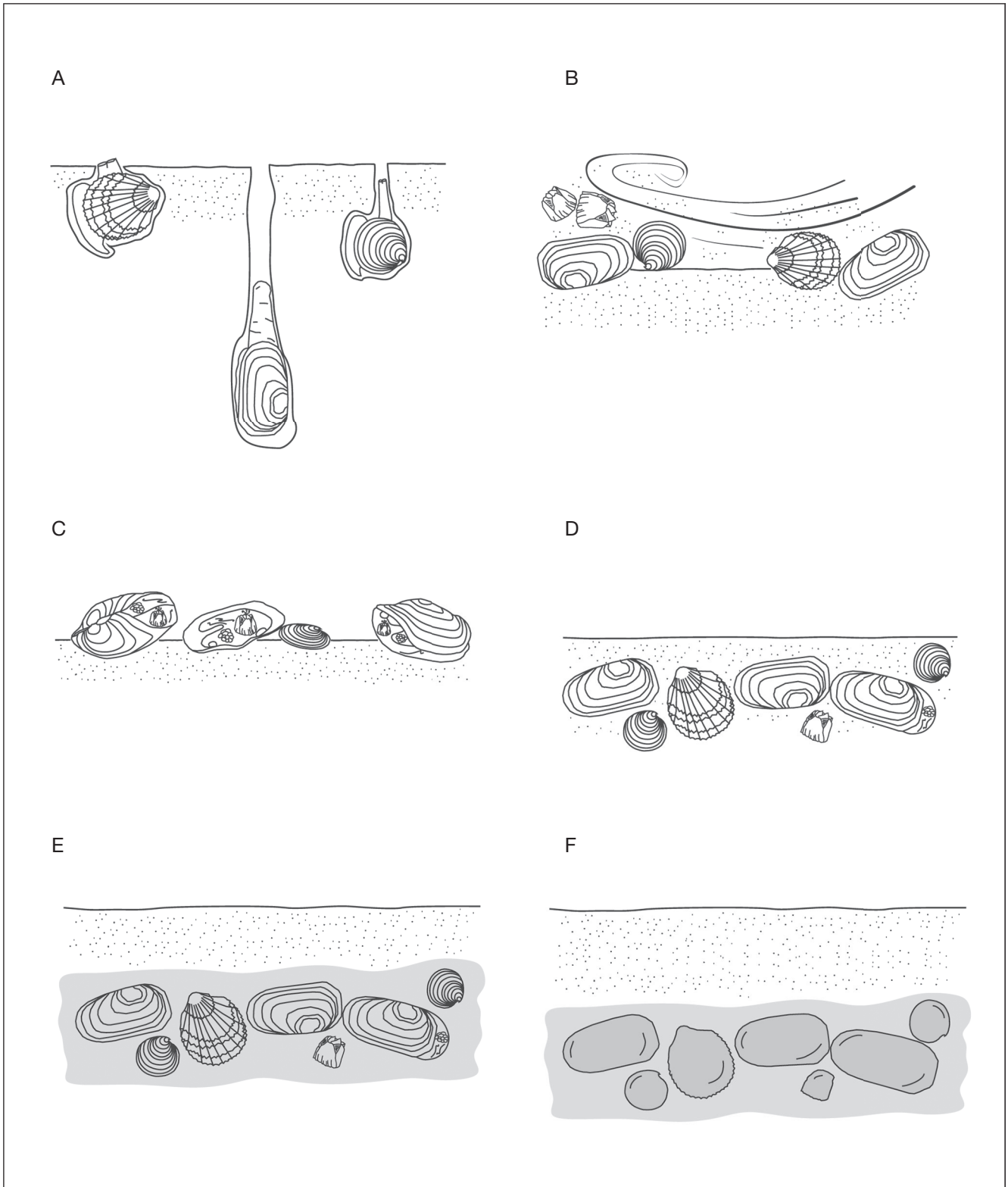
Fɪɢ. 8. — Schematic reconstruction of the taphonomic history of the *Panopea* Ménard de la Groye, 1807 bed faunal assemblage: time sequence from the living individuals (phase I) to the precipitation of dolomite (phase VI). **A** (phase I), living infaunal invertebrates; **B** (phase II), infaunal invertebrates were exhumed by a storm event that also mixed them with epifaunal invertebrates; **C** (phase III), on the seafloor, the still articulated *Panopea* specimens were colonized by a rich encrusting fauna for which they represented open but shielded environments; **D** (phase IV), after hundreds and thousands of years, the shells and the encrusting fauna of the *Panopea* specimens were buried together; **E (**phase V), during the early diagenesis, dolomite precipitated, cementing the inner part of the bivalves, resulting in dolomite molds, and the host sediment of the *Panopea* bed; **F** (phase VI), finally, diagenetic processes dissolved the pristine skeletal carbonate, leaving only the internal and external molds of the shells.

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