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MASS MORTALITY OF FOSSIL DECAPODS WITHIN THE MONTE LEÓN FORMATION (EARLY MIOCENE), SOUTHERN ARGENTINA: VICTIMS OF ANDEAN VOLCANISM

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ABSTRACT

Four exposed planar surfaces within the type area of the Monte León Formation (early Miocene) of southern Patagonia, Argentina, enclose significantly different fossil assemblages positioned in close geographic and stratigraphic proximity to one another. The exposed paleosurfaces were mapped in planar view using a quadrat grid system. Precise fossil position and orientation data, stable isotope thermometry and petrographic analyses, and petrologic and taphonomic evidence suggest an inner-shelf, shallow water habitat, above storm wave base, with a well-oxygenated benthos and weak offshore bottom currents. The rate of sedimentation was generally low, interspersed with periods of non-deposition and sporadic, higher-energy pulses of sediment input. Stable isotope analyses of foraminiferans indicate bottom water temperatures consistent with a modern mid-latitude coastal setting. Two distinctly different assemblages were observed: 1) a relatively diverse, normal marine benthic fauna consisting of bivalves, gastropods, bryozoans, echinoids, and decapods; and 2) a unique assemblage consisting solely of numerous, exceptionally preserved, fully-articulated crabs. These assemblages occur in a one meter interval within the lower-most beds of the Monte León Formation. The occurrence and preservation of large numbers of decapods within the fossil record are rare, making these deposits remarkable. The crab-rich assemblage was stratigraphically positioned below the surfaces containing the normal marine assemblage. The crabs are contained within a slightly compacted, argillaceous volcanic tuff, consisting mostly of volcanic glass shards and euhedral plagioclase grains. Biogenic fragments are noticeably absent from the deposit, unlike sediments collected from the upper surfaces. Most of the crabs were preserved with their third maxillipeds in an open, gaping posture. This is consistent with postures observed in extant crabs suffering from respiratory distress. From the above evidence it is inferred that the fossil crabs were suffocated, killed, and rapidly buried. Supradjacent layers record the re-establishment of normal marine conditions. The apparent faunal disparity observed on the four paleosurfaces within the Monte León Formation is interpreted as representing the initial decimation and eventual re-establishment of the benthic marine fauna following a catastrophic volcanic event.

KEY WORDS: Argentina, Brachyura, Decapoda, mass mortality, Miocene, Portunoidea

INTRODUCTION

The purposes of this study are to document the occurrence of *in situ* invertebrate faunas exposed on paleosurfaces from a thin and presumably brief stratigraphic interval within the type area of the earliest Monte León Formation of southern Argentina and to describe their paleoecologic setting. This study is confined to the Monte León Formation within the Austral Basin, as exposed in Monte León National Park, Santa Cruz, Santa Cruz Province, Argentina (Fig. 1)

The richly-fossiliferous Cenozoic marine deposits of Patagonia, of which the Monte León is part, have been the subject of numerous investigations over the past 150 years. The invertebrate faunas of the Monte León Formation have been of particular interest because of their close stratigraphic relationship to the mammal-bearing terrestrial deposits of the overlying Santa Cruz Formation. However, until very recently, investigative efforts have concentrated almost entirely on the systematics of the enclosed faunas, with very little consideration given to precise biostratigraphic or paleoecologic analyses (del Río 2004). This was due in large part to the inaccessibility of remote exposures, poor documentation of collection localities, and conflicting stratigraphic data collected by the early expeditions to Patagonia (Zinsmeister 1981).

Nevertheless, renewed interest in these deposits, coupled with the application of modern stratigraphic and paleontologic techniques, has yielded new insight into the depositional and paleoecologic history of the Cenozoic marine deposits of Patagonia. However, very few studies within the past twenty years have involved investigation of the faunas enclosed in the type-area of the Monte León Formation. Bertels (1980) and Nañez (1991) described the foraminiferal fauna; Barreda and Palamarczuk (2000) examined the palynomorphs; Echevarría (2002) described the ostracode fauna; and Zinsmeister (1981), del Río (1995), and del Río and Camacho (1996) revised the systematic paleontology of the molluscan faunas. Del Río (2004) published the first comprehensive biostratigraphic analysis of the molluscan faunas.

Previous Work.—The Cenozoic transgressive marine deposits of Patagonia were first mentioned by d'Orbigny (1842). Darwin referred to these deposits as the Patagonian Formation, which he observed during his tenure as naturalist aboard the *H.M.S. Beagle* (Darwin 1846; Zinsmeister 1981). During the late 19th and early 20th centuries, Hatcher (1897, 1900) and Ameghino (1934) independently surveyed the stratigraphy and extensively collected the fossil faunas of the "Patagonian." Although Hatcher documented his fieldwork in several publications, the actual analysis of his field data and collections was carried out by Ortmann (1897, 1902). The material collected by Carlos Ameghino was documented by his brother, Florentino (Ameghino 1934), and by Ihering (1907). A rivalry ensued between Ortmann and Ameghino, as Ortmann contested the work of the Ameghino brothers due in large part to discrepancies between Ortmann's and Ameghino's locality data (see Zinsmeister 1981). Ameghino, however, was first to subdivide the Patagonian into three separate faunal zones: the Piso Camaronense, Piso Juliense, and Piso Leonense (Zinsmeister 1981). The last of these faunal zones, the Piso Leonense, is approximately equivalent to the present day Monte León Formation. Excellent summaries of the early Patagonian literature can be found in Bertels (1970, 1975), Camacho (1979, 1995), and Zinsmeister (1981).

Geologic Setting.—The eastern passive margin of the South American continent is characterized by elevated plateaus and basins produced by the Mesozoic rifting of the Gondwana supercontinent. During the Cenozoic (late Paleogene-early Neogene), Andean orogenic movements coupled with eustatic fluctuations (Harrington 1956; Malumián 1999) resulted in the periodic inundation of these low-lying continental areas by the Southern Atlantic Ocean, leaving thick fossiliferous marine deposits on the eastern margin of the continent. The Cenozoic marine deposits were first described by Charles Darwin in 1846. Subsequent study of these marine deposits revealed several distinct lithologies and faunas, resulting in the recognition of formations which collectively are still referred to within the literature as "Patagonian." The "Patagonian" marine deposits are composed mostly of volcanically-derived, poorly indurated rocks including pale green tuffaceous sandstones and siltstones, fine-grained tuffaceous sandstones, and light yellowish-grey massive tuff layers (Di Paola and Marchese 1973). The siltstone and sandstone lithologies are intercalated with calcareous, fossil-rich layers (Di Paola and Marchese 1973).

Paleoceanography and Climate.—During the early Miocene, the Circum-Antarctic Current began to establish the present-day steep oceanic temperature gradient between Antarctic waters and mid-latitude waters (Kennett 1982:730). Cold Antarctic water advanced northward, shifting the production of biogenic carbonate in high latitudes to silica (Kennett 1982:730). The early Neogene is also characterized by significantly increased rates of sedimentation in the high latitudes (Kennett 1982:730). Bertels (1975, 1980) characterized the water temperatures during the deposition of the "Patagonian" as temperate and warmer than present based upon foraminiferan and ostracode assemblages.

Stratigraphy.—Early investigations of the Cenozoic marine deposits of Patagonia were centered upon the description of the enclosed faunas and their temporal relationship to faunas described from North America and Europe (Ortmann 1897, 1902; Ihering 1907; Ameghino 1934). Carlos and Florentino Ameghino were the first to assign names to the marine faunal assemblages of Patagonia, such as Patagoniense and Superpatagoniense, which are currently being used in the literature (see Camacho 1979). Other names have been used interchangeably for the Patagoniense, including Formacíon Patagonica and Patagoniano. The Patagoniense fauna was further subdivided by Ameghino (1898) into the "Piso Camaronense," "Piso Juliense" and the "Piso Leonense." These designations were also used in a chronostratigraphic sense (Zinsmeister 1981). This convention has produced an often confusing and sometimes indecipherable body of literature. For example, the "Piso Leonense," contained within the "Patagoniense," has been used in reference to the "Leonense" Stage (Legarreta and Uliana 1993), the "Leonense" fauna, and the strata equivalent to the present Monte León Formation (Bertels 1970). Also, there has been considerable disagreement among authors on the stratigraphic position and duration of these faunas,

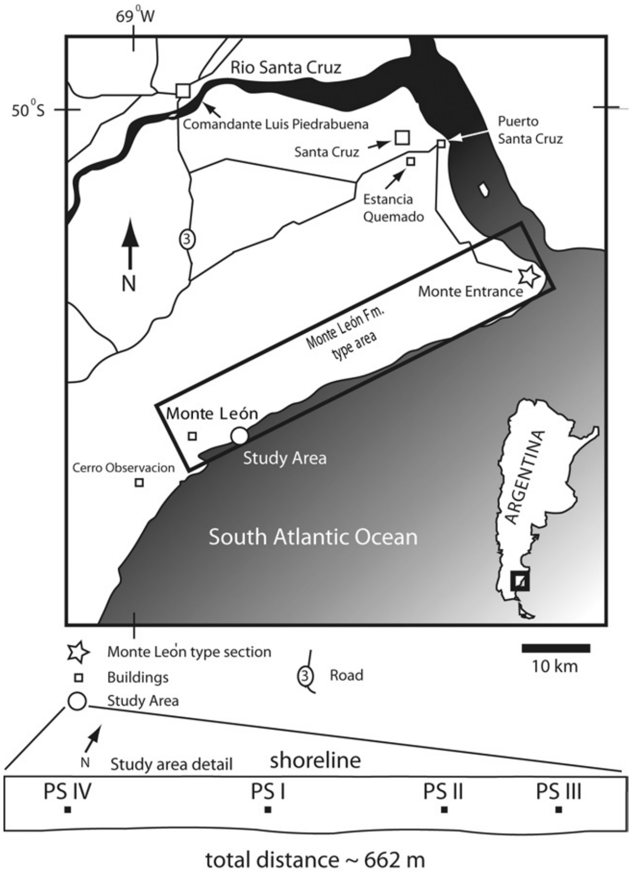

Fig. 1.—Map indicating the location of the study area (circle) within the type area of the Monte León Formation, Santa Cruz Province, Argentina, and the relative shoreline position within the study area of each examined paleosurface.

most likely due to the effects of basin geometry, correlation across separate basins, and latitudinal positions. Likewise, the stratigraphic position, thickness, and nature of lithologic contacts have also been subject to extremely varied interpretation, as summarized by Olivera et al. (1994) (Fig. 2). The *"Estratos con Monophoraster* y *Vernericor"*[sic] beds (Camacho 1974), for instance, were placed by Camacho at the upper contact of the San Julián Formation and by Bertels (1970) at the lower contact.

Bertels (1970) was the first to use the North American Code of Stratigraphic Nomenclature (NASCN 1961) as a basis by which to define the stratigraphic units included within the "Patagonian." Bertels (1970) defined the San Julián and Monte León as formations, citing distinct lithologies, and designated the type-area for the Monte León Formation as the coastal area extending from the mouth of the Santa Cruz River southward to Isla Monte León (Fig. 1). Alternatively, Di Paola and Marchese (1973) argued that the San Julián and Monte León were member facies of a larger sequence, the Patagonian Formation. Subsequent authors have used either definition, although neither Bertels (1970) nor Di Paola and Marchese (1973) provided a definition that included the characteristics of the bounding contacts.

The precise age of the "Patagonian" has also been a matter of debate. Ages for the San Julián Formation vary from early Eocene (Camacho 1974) to middle-late Oligocene (Bertels 1970), whereas the Monte León Formation has been described as late Oligocene (Parma et al. 1990) to early Miocene (Bertels 1970).

In the Austral Basin, the "Patagonian" Stage corresponds to three stratigraphic units; in ascending order, the San Julián, Monte León, and Santa Cruz formations (Bertels 1970; Camacho 1995). The contact between the San Julián and Monte León formations within the Austral Basin is considered to be disconformable (Bertels 1970; Camacho 1995; Zinsmeister 1981), and the upper contact of the Monte León Formation is transitional with the Santa Cruz Formation (Barreda and Palamarczuk 2000).

Di Paola and Marchese (1973) reported the thickness of the Monte León Formation as 95 m at Tres Puntas, just north of the type-area. In the Gran Bajo de San Julián, where a complete section is exposed, the total thickness is estimated at 180-200 m. The Monte León Formation as currently recognized is composed of silty, vitrophyric argillites and thin bioclastic layers with localized cross bedding and ripple marks in the lower portion of the section. Various facies interpretations have been postulated for the Monte León Formation, including a coastal neritic environment (Eschevarría 2002) and a hyposaline marsh and prodelta deposit (Olivera et al. 1994).

The contact between the San Julián and Monte León formations is not exposed within the study section. The lowermost portion of the Monte León Formation is exposed during low tide along the coast, with the remainder of the formation exposed in the cliffs along the coast and inland hills.

METHODS

Fieldwork.—Fieldwork was conducted by members of the Kent State University Department of Geology and members of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa along the coastline within Monte León National Park, approximately 25 km south of the mouth of the Santa Cruz River (Fig. 1). Here, the upper two-thirds of the formation are well exposed, extending from the tidal zone to the cliffs that face the coast. The substantial tidal range of the area, which can be as great as 8 m, exposes broad areas of fossiliferous bedrock during low tide. These exposures provide an ideal opportunity to observe *in situ* fossil assemblages, preserved in spatial, taphonomic, and paleoecologic context, over relatively large surfaces.

Field investigations were conducted using techniques based upon those employed by Casadío et al. (2005). Paleosurfaces were chosen that were within close stratigraphic and geographic proximity to each other, yet which

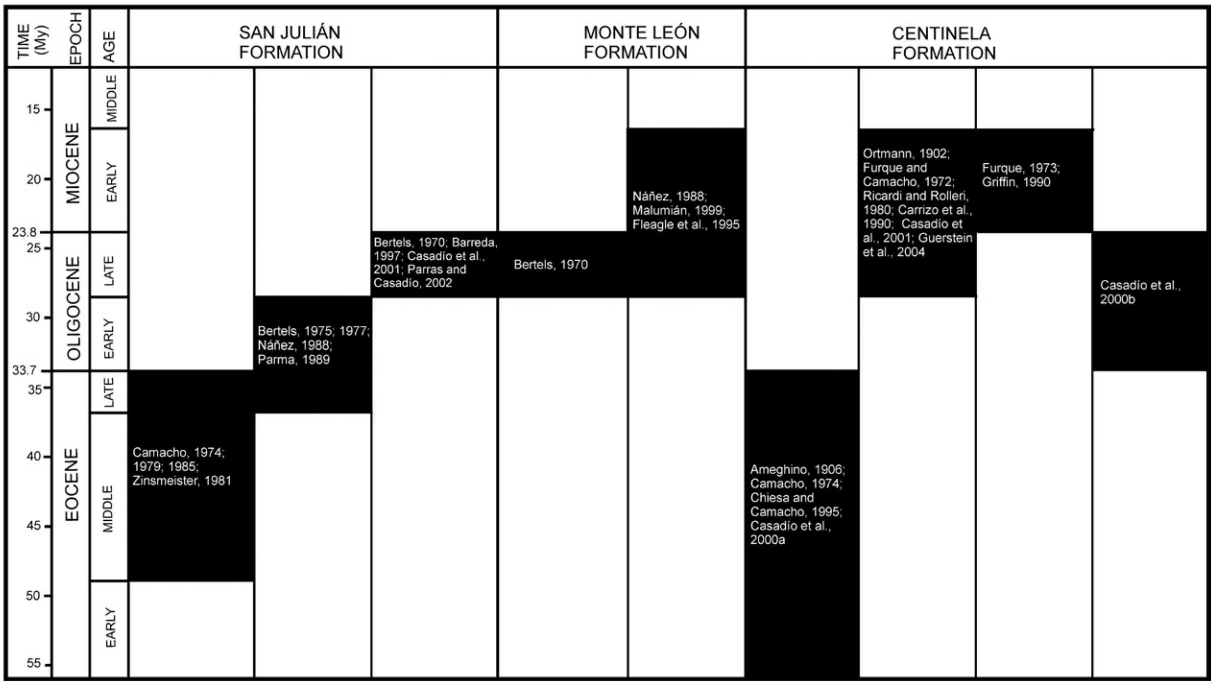

Fig. 2.—Various interpretations of the stratigraphy and formation names for the rocks of what has traditionally been called the "Patagoniano" in southern Argentina, from Parras et al. (in press).

contained distinctly different faunal assemblages. Four separate surfaces of the lower Monte León Formation were mapped using a quadrat grid system. The size of the quadrat used was determined by the size of the area to be gridded. Paleosurfaces I, II, and III were mapped using 0.5 m quadrats, whereas the largest area, Paleosurface IV, was mapped using 2.0 m quadrats. The sizes of the four surfaces mapped are as follows: Paleosurface I covered an area of 24 m^2 (2 m wide by 12 m long); Paleosurface II, 10 m^2 (2 m wide by 5 m long); Paleosurface III, 21 m^2 (2 m wide by 10.5 m long); and Paleosurface IV, 768 m^2 (16 m wide by 48 m long). In total, a combined area of 823 m^2 was mapped. The two most distant mapped surfaces lay 662 m apart. The azimuth orientation of the base line as well as the precise latitude and longitude coordinates were recorded for each paleosurface: Paleosurface I, lat. 50E19´22.5 S, long. 68E51´31.6 W; Paleosurface II, lat. 50E19´22.6 S, long. 68E51´32.2 W; Paleosurface III, lat. 50E19´26.8 S, long. 68E51´43.1 W; and Paleosurface IV, lat. 50E19´32.4 S, long. 68E51´55.1 W.

The position and orientation (relative to the grid and to horizontal) of all macrofossils exposed on the surface were carefully plotted on the field maps. Taphonomic state (degree of articulation, abrasion, breakage) for each fossil was also recorded. Sedimentologic features (grain size, bedding, presence of intraclasts, bioclastic debris) were noted in addition to the presence of any biogenic structures. Identification of macrofossils to species was made in the field when possible. Specimens that could not be readily identified in the field were collected for later identification. Laboratory identifications were then used to supplement the field data. Well-preserved crab specimens were collected to confirm field identification and for later analysis. In total, 27 crab specimens were collected from the map areas.

Rock samples were collected from Paleosurfaces I and II for laboratory analysis at regular, predetermined intervals across two of the map areas. All rock within a quadrat was removed to an arbitrary depth of 3 cm. This material was then sampled using a standardized technique of sample partitioning. Large fragments were sampled separately for thin section analysis.

Laboratory Methods.—Analysis of the sediment composition was conducted using petrographic thin sections and a transmitted light microscope. Several thin sections were prepared from material collected from each paleosurface using standard thin sectioning techniques. Because the sediment was friable, samples were vacuum impregnated with epoxy before sectioning. Constituent proportions were determined by point counting approximately 200 grains per slide.

Glass fragment morphology and surface alteration were analyzed using a scanning electron microscope (SEM). Sediment samples were also examined for microfossil content. Random samples from each paleosurface were selected and processed using standard wet-nested sieving techniques. The most commonly occurring benthic foraminiferans were collected for stable isotope testing.

The benthic foraminiferan *Cribrorotalia hornibrooki*

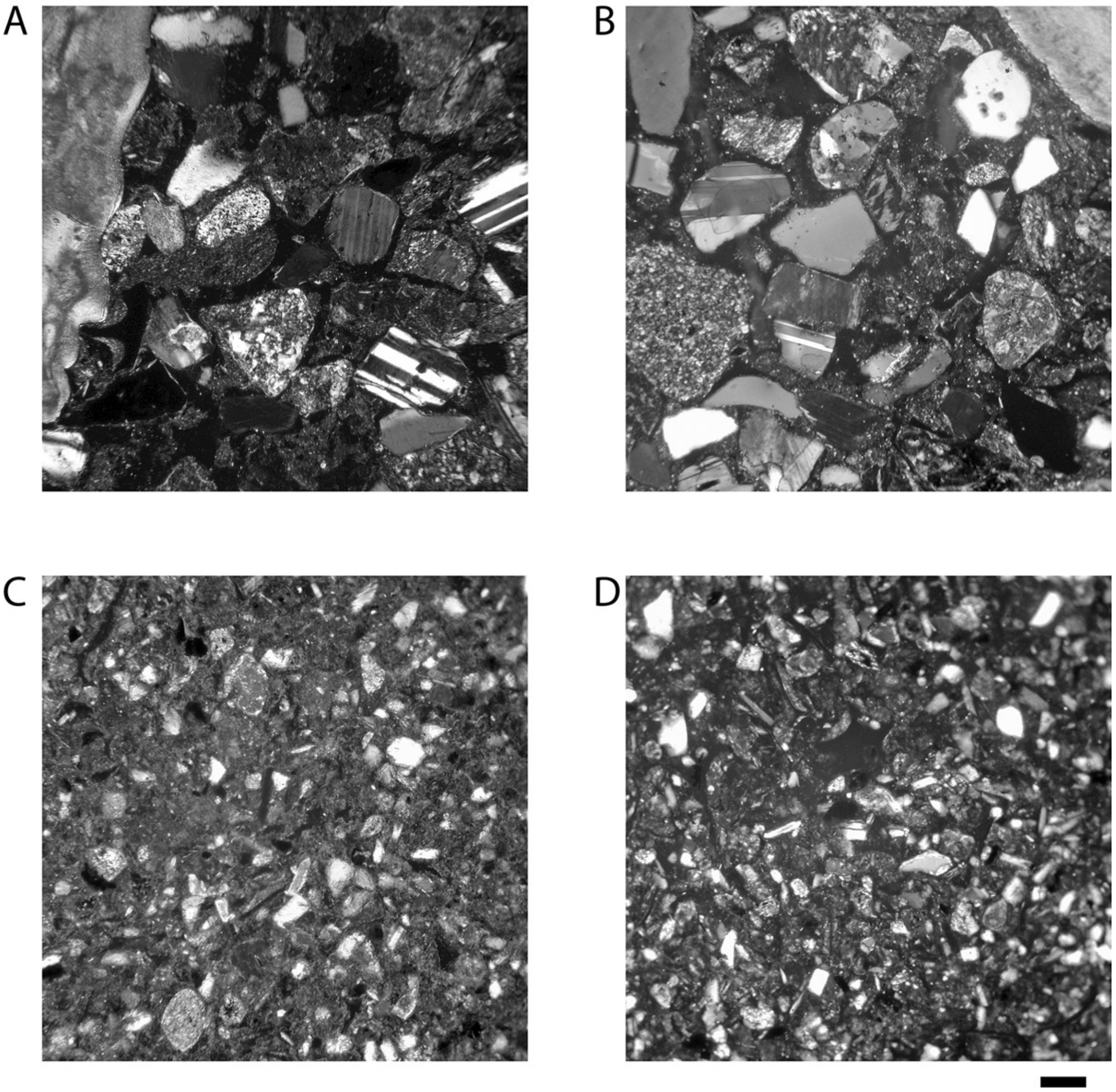

Fig. 3.—Photomicrographs of petrographic thin sections from Paleosurfaces (PS) I-IV. **A,** PS I; **B,** PS II; **C,** PS III; **D,** PS IV. Note the similarities in grain type, size, and sorting shared between PS I and II as compared to PS III and IV. Scale bar = 0.1 cm.

forma *planoconvexa* Malumián and Masiuk, 1971, was common in samples from Paleosurfaces I and II. Foraminiferan tests that lacked any observable signs of alteration were selected for ^{18}O and ^{13}C stable isotope analysis. Testing was conducted by the Isotope Geochemistry Laboratory at the University of Arizona using a mass spectrometer. Results were reported in ‰ Vienna Pee Dee Belemnite (VPDB). Paleotemperature estimates were then calculated using the equation of Epstein et al. (1953), as modified by Craig and Gordon (1965):

$$EC = 16.9 - 4.2(^{18}O) + 0.13(^{18}O)^2$$

Dextrally- and sinistrally-coiling specimens were identified and separated. A total of 60 specimens were used to form six isotope test samples consisting of ten specimens each: three samples containing dextrally-coiling tests and three containing sinistrally-coiling tests. A sample of interstitial micrite from the sediment sample was also submitted for testing. The isotope values derived from the micrite sample were used as a standard by which to gauge the extent of diagenetic alteration in the foraminiferan tests. The degree to which the metabolic processes of this particular foraminiferan influenced the isotopic ratio is unknown. Therefore, temperatures derived from the foraminiferan calcite are considered to be estimates and not absolute values.

Paleocurrent direction was calculated using the orientations of the high-spired gastropod *Turritella patagonica* Sowerby, 1846. Specimens of *T. patagonica* were common to Paleosurfaces I (n = 136) and II (n = 30). Data were plotted as rose diagrams using Stereonet version 6.3.3 software

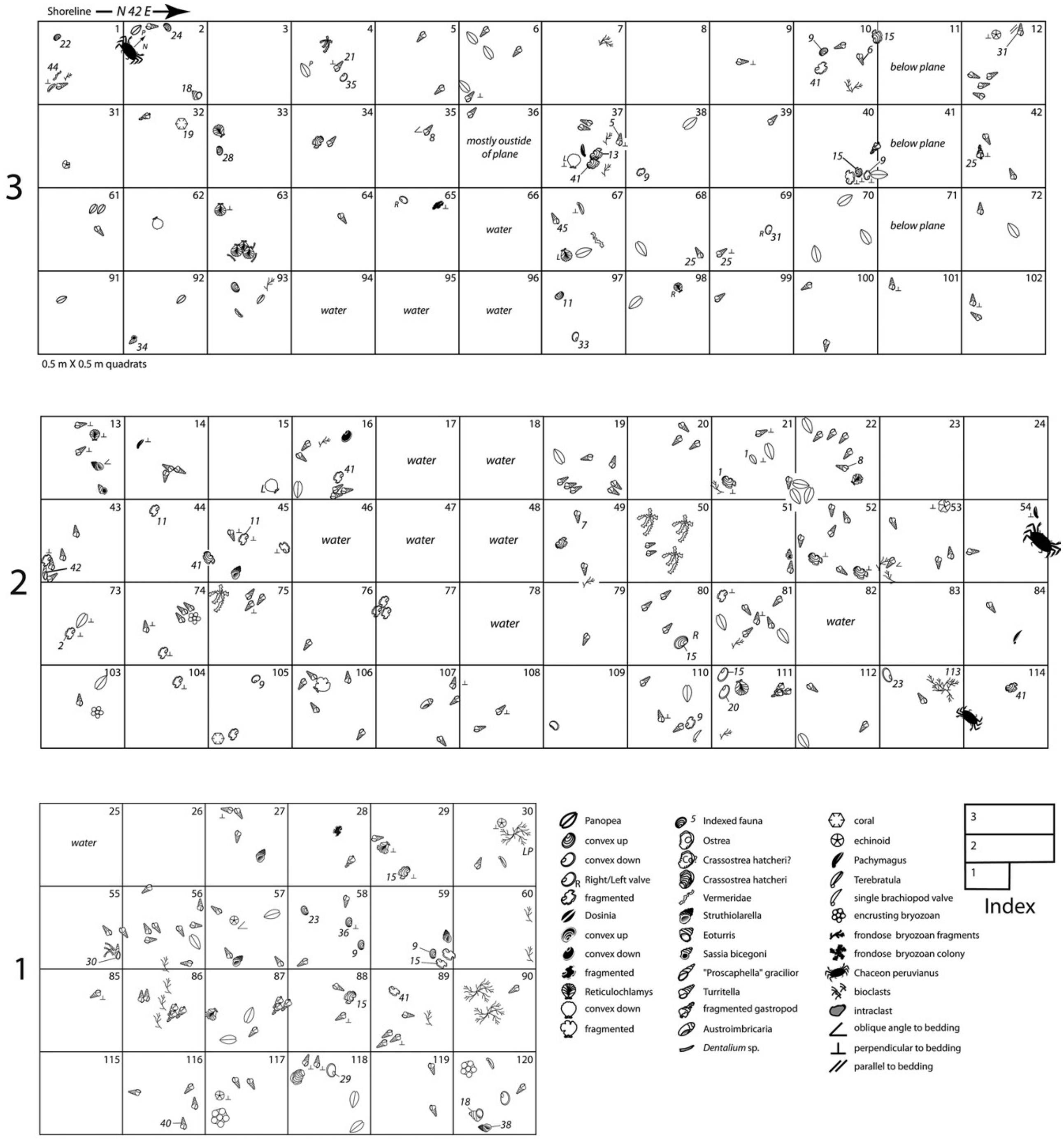

Fig. 4—Map of Paleosurface I. Unitalicized number in upper right of quadrat is quadrat number. Italicized number associated with faunal icon is index number cross-referenced in Table 1. Indexed fauna are described in Table 1.

Table 1.—Faunal and taphonomic data collected from Paleosurface I. Numbers at left are index numbers referred to in Figure 4.

	Genus	Species	w/a	cu	cuf	cd	cdf	f	v	vf	Total
1	**Ameghinomya*	sp.	1	0	0	0	0	0	0	1	2
2	*Anomiidae	sp.	0	0	0	0	0	0	0	1	1
3	**Austroimbricaria*	*quemadensis* (Ihering, 1897)	1	0	0	0	0	0	0	0	1
4	Bryozoan	indet.	2	0	0	0	0	18	0	0	20
5	*Bulbus*	sp.	1	0	0	0	0	0	0	0	1
6	*Calliostoma*	*peraratum* Cossman, 1899	1	0	0	0	0	0	0	0	1
7	*Calyptraea*	sp.	1	0	0	0	0	0	0	0	1
8	*Cancellaria*	*gracilis* (Ihering, 1897)	2	0	0	0	0	0	0	0	2
9	*Cardium*	sp.	0	2	1	2	1	0	1	0	7
10	Not noted										
11	*Cardium*	*puelchum* Sowerby, 1846	0	1	0	0	0	0	0	1	2
12	*Chaceon*	*peruvianus* (d'Orbigny, 1842)	3	0	0	0	0	0	0	0	3
13	*Chionopsis*	sp.	0	0	1	0	0	0	0	0	1
14	Not noted										
15	*Cucullaea*	*alta* (Sowerby, 1846)	0	1	1	1	1	0	0	2	6
16	*Dosinia*	*laeviuscula* Philippi, 1887	0	0	0	1	1	0	0	1	3
17	*Echinoidea*	indet.	1	0	0	0	0	0	0	4	5
18	*Eoturris*	*santacrucensis* (Ihering, 1907)	2	0	0	0	0	0	0	0	2
19	*Flabellum*	sp.	0	0	0	0	0	2	0	0	2
20	**Glycymeris*	*cuevensis* (Ihering, 1897)	0	0	0	1	0	0	0	0	1
21	*Glossaulax*	*vidali*	0	0	0	0	0	0	0	0	0
22	*Limopsis*	*insolita* (Sowerby, 1846)	0	1	0	0	0	0	0	0	1
23	*Mactra*	*patagonica* d'Orbigny, 1846	0	1	0	1	0	0	0	0	2
24	*Nucula*	sp.	0	1	0	0	0	0	0	0	1
25	*Odontocymbiola*	sp.	1	0	0	0	0	0	1	0	2
26	*Pachymagas*	sp.	5	1	0	0	0	1	1	1	9
27	*Panopea*	*quemadensis* Ihering, 1897	37	2	2	1	6	0	6	11	65
28	*Pitar*	*julianum* Ihering, 1907	0	1	0	0	0	0	0	0	1
29	**Pleuromeris*	*cruzensis* Ihering, 1907	0	1	0	0	0	0	0	0	1
30	**Proscaphella*	*gracilior* Ihering, 1986	1	0	0	0	0	0	0	0	1
31	*Pteromyrtea*	*crucialis* Ihering, 1907	1	0	0	2	0	0	0	0	3
32	*Reticulochlamys*	*proxima* (Ihering, 1897)	0	8	1	3	0	0	3	1	16
33	*Retrotapes*	*striatolamellata* (Ihering, 1897)	0	0	0	1	0	0	0	0	1
34	*Sassia*	*bicegoi* (Ihering, 1899)	2	0	0	0	0	1	0	0	3
35	**Serratina*	sp.	0	0	0	1	0	0	0	0	1
36	*Spissatella*	*longior* (Ihering, 1897)	0	0	0	0	0	0	0	1	1
37	*Struthiolarella*	*ameghinoi* (Ihering, 1897)	5	0	0	0	0	0	0	0	5
38	**Struthiolarella*	*patagoniensis* Camacho & Zinsmeister, 1989	1	0	0	0	0	0	0	0	1
39	Not noted										
40	*Sveltia*	*major* Ihering, 1899	1	0	0	0	0	0	0	0	1
41	*Tellina*	sp.	0	0	3	0	3	0	0	0	6
42	*Trophon*	*santacrucensis* Ihering, 1897	1	0	0	0	0	0	0	0	1
43	*Turritella*	*patagonica* Sowerby, 1846	129	0	0	0	0	5	28	0	162
44	Vermetidae	indet.	2	0	0	0	0	0	0	0	2
45	*Xymenella*	*dautzembergi* (Ihering, 1897)	1	0	0	0	0	0	0	0	1
46	Not noted										
47	Not noted										
48	Not noted										
49	*Crassostrea*	*hatcheri*(?) Ihering, 1897	1	0	0	0	0	0	0	0	1
50	*Arca*	*patagonica* Ihering, 1897	0	0	1	0	0	0	0	0	1
		Totals	203	20	10	14	12	27	40	24	350

w/a	whole/articulated	cuf	convex-up fragment	cdf	convex-down fragment	v	vertical
cu	convex-up	cd	convex-down	f	fragment	vf	vertical fragment

*Supplied by M. Griffin

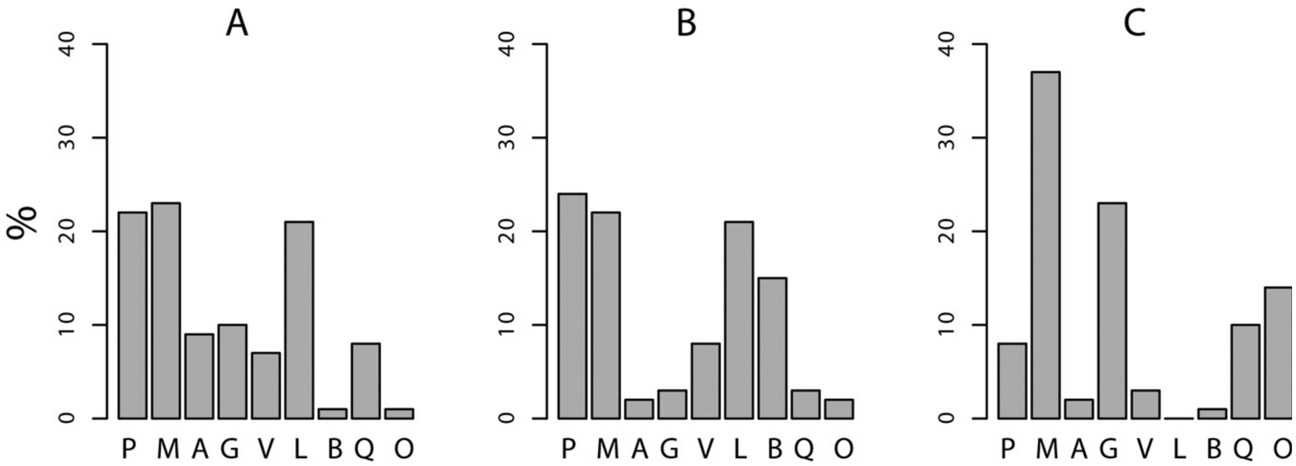

Fig. 5.—Estimated constituent proportions of paleosurface sediments. Values are presented in percentages rounded to the nearest whole number. **A,** Paleosurface I; **B,** Paleosurface II; **C,** Paleosurfaces III; and IV. P, plagioclase; M, matrix; G, volcanic glass; A, altered grains; V, volcanic rock fragments; L, lithic fragments; B, bioclasts; Q, quartz, O, other.

for Macintosh, using a 10 degree bin size. A Chi-square test for independence (using a class size of 30 degrees and significance level of 0.05) was used to determine if the shells exhibited a non-random orientation, following the method described in Reyment (1971).

Crab specimens were prepared by gently loosening the matrix with running water and a toothbrush. Slowly loosening the friable sediment preserved weakly-cemented biogenic structures which would have been unnoticed otherwise and also ensured that any epibionts which may have been attached to the specimens would be preserved. Any sediment which could be easily loosened prior to cleaning was stored and cataloged for future analysis.

Crab specimens were identified to species. Gender was determined where the abdomen could be sufficiently exposed. Size measurements of the crab specimens were also recorded, consisting of maximum carapace width, axial length, fronto-orbital width, and frontal width. Several specimens could not be measured due to erosional damage. The location and size of all epibionts found on the surface of the crab specimens were recorded and mapped.

Two specimens were sectioned (GHUNLPam 25004 and 25025) to observe the nature of the sediment filling the internal cavity and to search for bioturbation. A thin section was also prepared to observe the preservation state of the cuticle, the composition of the sediment, and the presence of fecal pellets.

SEDIMENTOLOGICAL DESCRIPTIONS

General.—Photomicrographs of petrographic thin sections representing all four paleosurfaces are provided in Figure 3. All four paleosurfaces were composed of massive, fine-grained volcaniclastic sediment, with a fresh, wet Munsell color of 5B 5/1, and a weathered color of 5Y 3/2 (Geological Society of America 1963). The color of the weathered surface was consistent throughout the study area. The stratigraphic separation of the four surfaces was estimated using a Jacob's staff. Approximately 80 cm separated the lowermost surface, Paleosurface IV, from the uppermost surface, Paleosurface I. The upper and lower bounding surfaces of the beds could not be distinguished, so the exact stratigraphic position of each surface could not be easily determined. Paleosurfaces I and II were located in close geographic proximity to one another; both contained numerous bioclasts, a diverse assemblage of body fossils, and abundant biogenic traces. Paleosurfaces III and IV were positioned at the far ends of the study area and were distinctly different from Paleosurfaces I and II. These areas lacked observable bioclasts other than the crabs or biogenic traces.

Paleosurface I (Fig. 4).—The surface was composed of poorly-sorted, silty-sand, with traces of clay. On average, the rock was poorly indurated, except for areas locally cemented by micritic cement where fine shell hash was present. *Thalassinoides* isp. traces were common and tended to contain a greater amount of clay than the surrounding sediment. Point counts revealed that the three most numerous grains types counted were matrix (22.5%), plagioclase (22.0%), and lithic fragments (20.5%) (Fig. 5).

Bioclasts of mollusk shells and bryozoans were confined to small (10's of cm^2), shallow (a few cm thick), isolated, and lenticular bodies of shell hash. Most bioclasts were angular and exhibited little-to-no abrasion (Table 1). More than half of the shells (58%) from Paleosurface I (PS I) were unbroken and fully articulated, and were oriented in either a living position or parallel to the presumed bedding (Figs. 4, 6). A large proportion of the bivalves that were articulated and in a living position belonged to the deep infaunal species *Dosinia laeviuscula* Philippi, 1887, and *Panopea quemadensis* Ihering, 1897. For reasons which will be discussed later, specimens of these two species found in living position were discounted from faunal

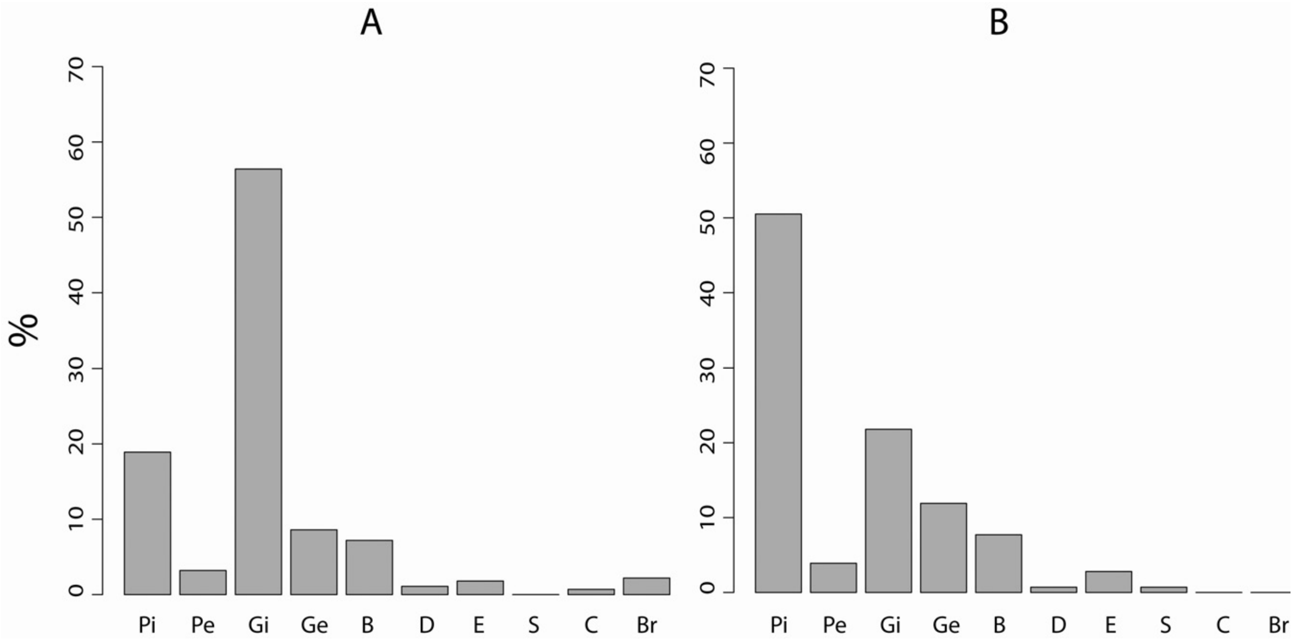

Fig. 6.—Faunal composition, in percent of fauna, of Paleosurfaces I and II, including *Dosinia laevisucula* and *Panopea quemadensis*, found in living position. **A,** Paleosurface I; **B,** Paleosurface II. Pi, infaunal bivalves; Pe, epifaunal bivalves; Gi, infaunal gastropods; Ge, epifaunal gastropods; B, bryozoans (encrusting and ramose forms); D, decapods; E, echinoids; S, scaphopods; C, corals; Br, brachiopods.

and taphonomic analyses.

Fragmented shells of bivalves and gastropods and fragments of bryozoan colonies account for 21% of the biogenic material on PS I. With respect to the complete, single valves, and fragments of valves which exhibited a convex-up (CU) or convex-down (CD) orientation, almost equal numbers of CU and CD valves were counted from PS I (Table 1). Vertically-oriented whole gastropod shells or single valves were numerous, accounting for 11% of the total body fossils. Echinoids were rare and tended to be fragmented and obliquely-to-vertically oriented with respect to the surface. The high-spired gastropod *Turritella patagonica* was the most abundant fossil found, comprising more than 37% of the total number of gastropods and a large portion of the total fauna.

Paleosurface II (Fig. 7).—The surface was composed of a poorly sorted, silty-sand with traces of clay. Bioclastic fragments constituted a much greater proportion of the sediment than on PS I. Pods and stringers of fine shell hash were present in most of the mapped quadrats. *Thalassinoides* isp. traces were present, similar to those described from PS I. Bioeroded intraclasts composed of indurated mud rock were common on Paleosurface II (PS II). These intraclasts varied in size from small pebbles 1 cm across to large cobbles several cm across. Bedding could be observed on several of these intraclasts; the variously-oriented bedding of the intraclasts distinguished them from the horizontal primary bedding. Point counts revealed that the three most numerous grains types counted were clay-silt matrix (22.2%), plagioclase (23.7%), and lithic fragments (21.1%) (Fig. 5). The lithic fragment fraction included grains composed of polycrystalline quartz, low grade metamorphic rock fragments, polycrystalline zeolite grains, and reworked fragments comprised of clayey silt. The sediment was grain supported, with a bimodal grain size distribution. Bioclasts comprised 15.5% of the sand-sized grains.

Fragmented shells of bivalves and gastropods, and fragments of bryozoan colonies account for 33% of the biogenic material found on PS II (Table 2). PS II contained a much greater number of CU valves (21%) than CD valves (5%). Vertically-oriented whole gastropod shells or single valves constituted 9% of the total bioclasts. More than half of the shells from PS II (54%) were unbroken, fully articulated, and oriented in either a living position (bivalves) or parallel to the presumed bedding (gastropods). Bivalves of the species *D. laeviuscula* and *P. quemadensis* were commonly found oriented in a living position. Specimens of *D. laeviuscula* tended to be found in tight clusters. Overall, burrowing bivalves composed the majority of the fauna from PS II (57%) (Fig. 6).

Paleosurface III (Fig. 8).—The surface was composed of moderately well sorted, silty, very fine, volcaniclastic sand, with traces of clay. Rock samples were very poorly indurated and readily crumbled when dry. Only areas proximal to the dorsal carapace of the crab fossils were well cemented. Well-cemented regions reacted vigorously when exposed to 10% HCl solution, indicating the presence of calcareous cement.

Table 2.—Faunal and taphonomic data collected from Paleosurface II. Numbers at left are index numbers referred to in Figure 7.

	Genus	Species	w/a	cu	cd	cdf	f	v	vf	Total
1	**Austrotoma*	*cuevensis*	1	0	0	0	0	0	0	1
2	*Bryozoan	indet.	1	0	0	0	10	0	0	11
3	*Calliostoma*	*peraratum*	1	0	0	0	0	0	0	1
4	*Calyptraea*	sp.	0	0	2	0	0	0	0	2
5	**Cardium*	sp.	0	1	0	0	0	0	0	1
6	**Cerithiopsis*	*juliana*	1	0	0	0	0	0	0	1
7	*Chaceon*	*peruvianus*	0	0	0	0	0	1	0	1
8	*Crassostrea?*	*hatchery*	2	0	1	0	5	1	0	9
9	*Cucullaea*	*alta*	0	1	0	0	0	0	0	1
10	*Dentalium*	sp.	1	0	0	0	0	0	0	1
11	*Dosinia*	*laeviuscula*	30	23	2	0	0	10	2	67
12	Echinoidea	indet.	1	0	0	0	0	1	2	4
13	*Mactra*	*patagonica*	0	1	0	0	0	0	0	1
14	**Natica*	sp.	2	1	0	0	0	1	0	4
15	*Neoimbricaria*	*patagonica* Ihering, 1897	2	0	0	0	0	0	0	2
16	*Odontocymbiola*	sp.	1	0	0	0	0	1	0	2
17	*Panopea*	*quemadensis*	16	3	0	0	0	1	1	21
18	*Pleuromeris*	sp.	0	4	3	0	0	0	0	7
19	*Proscaphella*	*glacilior*	1	0	0	0	0	0	0	1
20	**Retrotapes*	*striatolamellata* (Ihering, 1897)	0	1	0	0	0	0	0	1
21	*Xymenella*	*cossmani*	0	0	0	0	0	0	0	0
22	*Tellinidae	indet.	0	1	0	0	0	0	0	1
23	**Terebra*	*santacruzensis* (Ihering, 1897)	1	0	0	0	0	0	0	1
24	*Turritella*	*patagonica*	31	0	0	0	0	0	0	31
25	*Zygochlamys*	sp.	0	2	0	1	0	0	0	3
26	**Zeadmete*	*ameghinoi*	5	0	0	0	0	0	0	5
		Totals	97	38	8	1	15	16	5	180

w/a	whole/articulated	cd	convex-down	f	fragment
cu	convex-up	cdf	convex-down fragment	v	vertical
vf	vertical fragment				

*Supplied by M. Griffin

The exact proportion of constituent components could not be calculated accurately due to the fine grain size and because the grain boundaries were extremely diffuse, possibly due to the quality of the thin section. The preparation of sediment thin-sections was complicated by problems with the quality of the epoxy impregnation. Grain plucking during the polishing step was a frequently encountered problem. However, thin sections from Paleosurface III (PS III) and Paleosurface IV (PS IV) appeared to be very similar in composition, and grain counts conducted on a section from PS IV are believed to accurately portray the composition of PS III sediment. Amorphous matrix was the most common constituent component. Identifiable major components include volcanic glass fragments and bubble shards, which tended to be angular-to-very angular in shape in thin section and in SEM images (Fig. 9), and subhedral-to-euhedral phenocrysts of plagioclase.

Bioclasts other than crabs were not observed in the field, in collected hand samples, or in thin section. Fully articulated crabs were the only fossils found on PS III (Fig. 8). Similarly, fully articulated crabs were the only fossils found on PS IV (Fig. 10). The occurrence of these fossils on both surfaces therefore will be discussed collectively.

Paleosurface IV (Fig. 10).—The surface was composed of moderately well sorted, silty, very fine, volcaniclastic sand, with traces of clay. Rock samples were very poorly

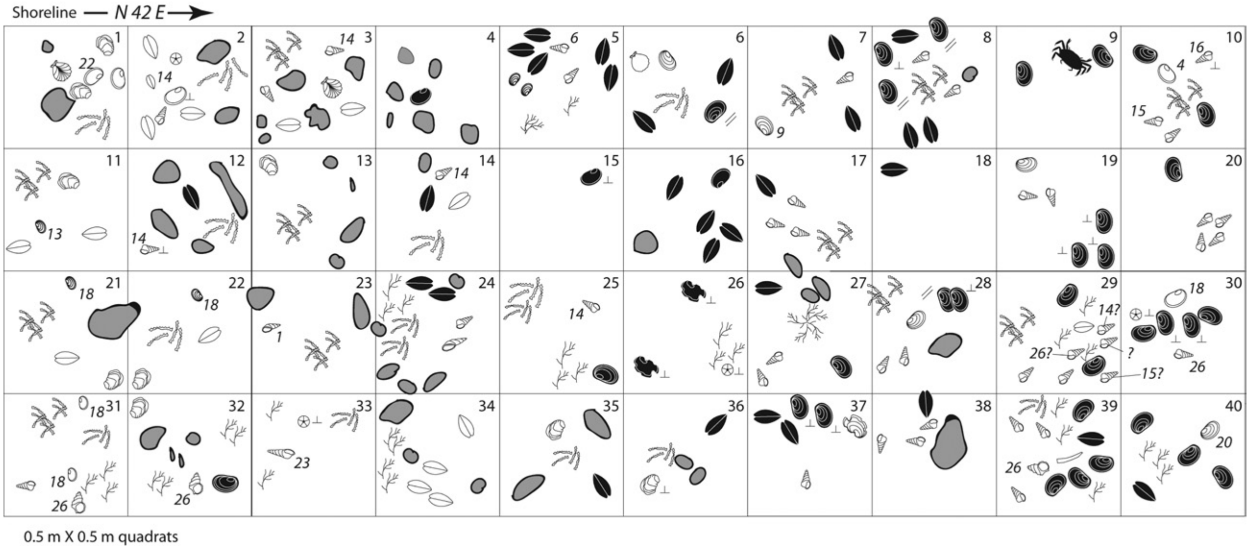

Fig. 7.—Map of Paleosurface II. Unitalicized number in upper right of quadrat is quadrat number. Italicized number associated with faunal icon is index number cross-referenced in Table 2. Indexed fauna are described in Table 2.

indurated and readily crumbled when dry. Volcanic glass fragments comprised approximately 22.6% of the sediment (Fig. 5). Matrix comprised approximately 31.5% of the sediment. The matrix was comprised of amorphous silica and very small crystals suspected to be zeolites, possibly clinoptilolite and erionite. Other minor components included quartz (9.9%), plagioclase (8.4%), and volcanic rock fragments (3.45%). Volcanic rock fragments exhibited an unusual mineralogy, containing composite grains with a very fine crystalline fabric, yellow-orange in color, and thought to be pumpellyite. SEM images of PS IV sediments show what is interpreted to be secondary alteration of the volcanic glass fragments into zeolite minerals (Fig. 9). Although calcareous bioclasts were absent from these deposits, numerous centrales diatoms were observed, with the frustules often articulated and linked together forming short strands. As with PS III, articulated crab fossils were common (Fig. 10).

Micropaleontology.—Sediment collected from PS I and II contained large numbers of the benthic foraminiferan *C. hornibrooki* forma *planoconvexa* (Fig. 11). Numerous specimens of both dextrally- and sinistrally-coiling forms were found. Centrales diatoms were also very abundant. Ostracods were rare as were planktonic foraminiferans.

The stable isotope values extracted from samples of dextrally- and sinistrally-coiling specimens of *C. hornibrooki* forma *planoconvexa* are listed in Table 3. Samples consisting of dextrally-coiling specimens produced isotopically heavier ^{18}O values than did the samples containing sinistrally-coiled specimens. The micrite sample used as a diagenetic "standard" returned values significantly different from the results for the foraminifera, suggesting that the isotopic composition of the fossil samples has not been significantly altered by diagenesis.

Temperature calculations resulted in values which suggest an approximate water temperature of 14° C . Values derived from dextrally-coiled specimens returned slightly cooler temperatures than did the sinistrally-coiled specimens, with the lowest value at 13.2° C.

Paleocurrent Calculations.—Chi-square analysis of PS I shell orientations indicated a non-random alignment of shells (χ^2 = 49.832, critical value = 19.675 with 11 degrees of freedom at .05 confidence level). PS II, however, contained too few shells to meet the criteria for the Chi-square test (average expected value < 5) with a class size of 30. Calculation of the χ^2 statistic using a class size of 60 degrees failed to reject the null hypothesis (χ^2 = 3.258, critical value = 11.07 with 5 degrees of freedom at .05 confidence level), indicating the shells were randomly oriented. The shells of *Turritella patagonica* were more or less evenly distributed across the map areas and rarely found in clusters of more than four shells. The rose diagram plot of shell orientations for PS I (Fig. 12A) indicated that approximately 20% of the shells were oriented with their apical ends between N10°W and due North. The second most significant alignment was approximately 6% with an alignment to S30°W. Minor orientations (< 5%) are scattered about the central axis.

The rose diagram plot for PS II (Fig. 12B) indicated that nearly 17% of the alignment was to N10°E, but with alignments to south (8% due S, 8% S10°E), east (8.5% N80°E), and west (8.5% S80°E).

Azimuth readings for the crabs found on PS III did not suggest a preferred orientation. Unfortunately, time constraints due to available daylight and the tidal cycle did not permit the collection of azimuthal data from PS IV.

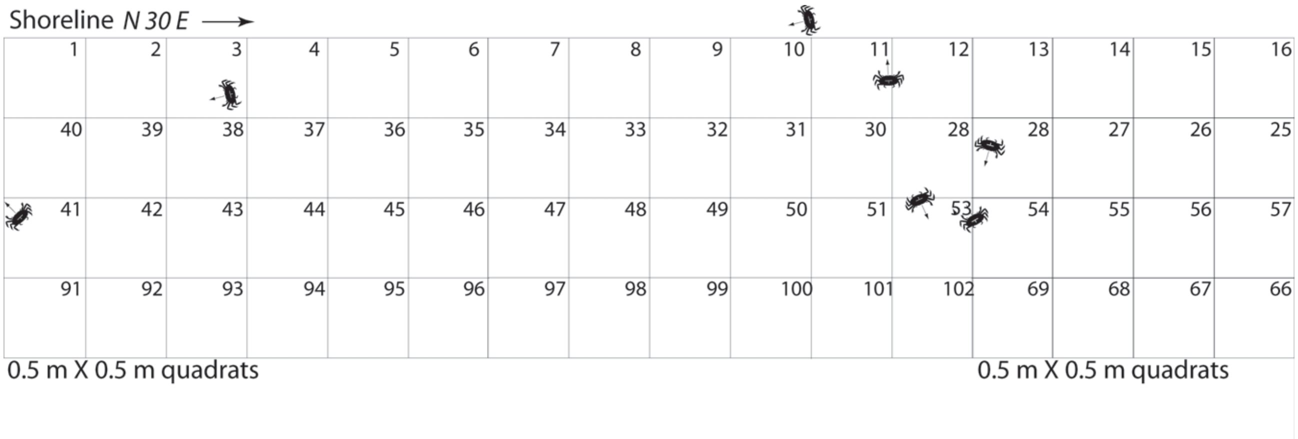

Fig.8.—Map of Paleosurface III. Crab icons indicate the relative position and orientation of each fossil as found on the paleosurface.

SYSTEMATIC PALEONTOLOGY

Institutional Abbreviations.—CM, Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **GHUNLPam**, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina.

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Macropipidae Stephenson and Campbell, 1960

Proterocarcinus Feldmann, Casadío, Chirino-Gálvez, and Aguirre Urreta, 1995

Type Species.—*Proterocarcinus lophos* Feldmann, Casadío, Chirino-Gálvez, and Aguirre Urreta, 1995, by monotypy.

Included Species.—*Proterocarcinus latus* (Glaessner, 1933), as *Archaeogeryon*; *Proterocarcinus corsolini* Casadío, De Angeli, Feldmann, Garassino, Hetler, Parras, and Schweitzer, 2004; *Proterocarcinus navidad* Feldmann, Schweitzer, and Encinas, 2005.

Proterocarcinus latus (Glaessner, 1933)
(Fig. 13)

Archaeogeryon latus Glaessner 1933:23, pl. V, figs. 4, 5.
Lebucarcinus tyro: Bahamonde and Frassinetti, 1980:276, figs. 1-7, not *Cancer tyro* Phillipi, 1887 [misidentification].
Coeloma (Coeloma) latum: Aguirre Urreta, 1987:471.
Proterocarcinus latus: Schweitzer and Feldmann, 2000:644, fig. 7.; Casadío et al., 2005:164, fig. 6, A-F.

Diagnosis.—The reader is directed to the recent diagnosis of *P. latus* by Schweitzer and Feldmann (2000:644, fig. 7).

Material Examined and Occurrence.—One specimen, GHUNLPam 25016, was collected from PS I, and four specimens were collected from PS IV, GHUNLPam 25011, 25012, 25020, and 25027.

Measurements.—Measurements are given in Table 4.

Description.—The fully-articulated specimens were partially exposed on the surface and had been damaged by the surf. The legs on both sides were truncated, with only a portion of the meri preserved. Portions of the legs and claws appear to have been fractured and partially collapsed during sediment compaction. The claws were positioned tightly against the anteroventral surface. Most of the cuticle had been removed from the dorsal carapace. Bioerosion had also removed portions of the sediment infilling the crabs. The orbits, rostrum, posterior margin, and abdomen were preserved; the shape of the abdomen indicated that the one crab for which gender was determinable was male. The sediment surrounding the specimens was well-cemented, as was the sediment in-filling the

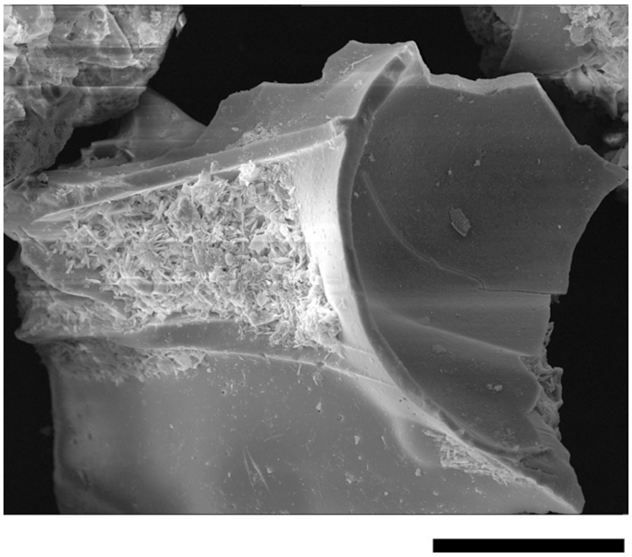

Fig. 9.—SEM image of angular volcanic glass bubble shard from Paleosurface IV. The cryptocrystalline matrix consists of aggregates of an acicular (erionite?), which is presumed to be a secondary product of the ash. Scale bar = 0.1 mm.

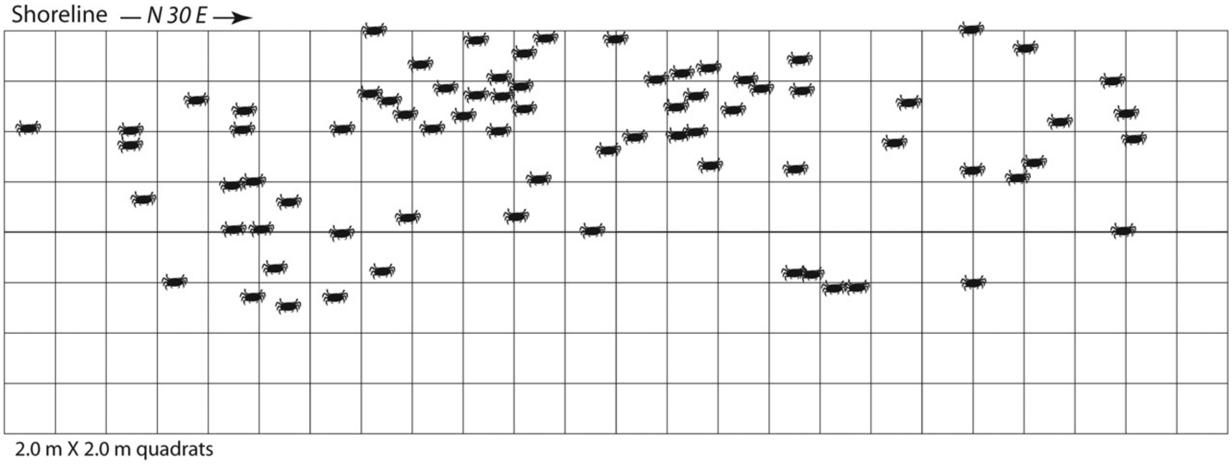

Fig. 10.—Map of Paleosurface IV. Crab icons indicate the relative position and orientation of each fossil as found on the paleosurface. Note that quadrat scale is 2.0 m X 2.0 m.

carapace and legs. The maxillipeds of specimen GHUNLPam 25011 were in an open position, whereas those of GHUNLPam 25027 appear to have been closed. Those of the other specimens were obscured by sediment

Discussion.—The specimens conform to the definition of the species. The carapace dimensions closely match those reported by Schweitzer and Feldmann (2000) (reported dimensions: L/W ratio= 0.76, fronto-orbital width to width ratio= 0.95).

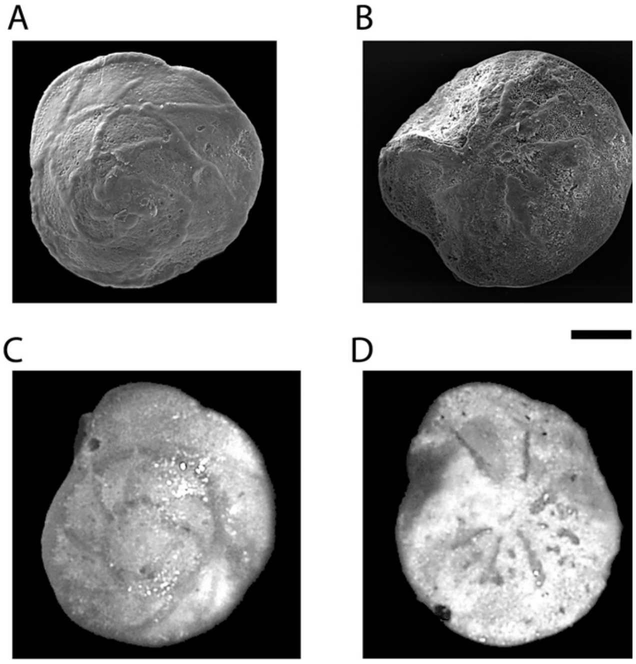

Fig. 11.—*Cribrorotalia hornibrooki* forma *planoconvexa*. **A,** SEM image, apical view; **B,** SEM image, umbilical view; **C,** reflected light, apical view; **D,** reflected light, umbilical view. Scale bars = 0.1 mm; upper bar for 11A and 11B; lower bar for 11C and 11D.

Family Geryonidae Colosi, 1923

Chaceon Manning and Holthius, 1989

Type Species.—*Geryon fenneri* Manning and Holthius, 1984, by original designation.

Included Fossil Species.—*Chaceon matsushimai* Kato and Koizumi, 2001; *Chaceon peruvianus* (d'Orbigny, 1842), as *Portunus*.

Chaceon peruvianus (d'Orbigny 1842)
(Figs. 14, 15)

Portunus peruvianus d'Orbigny, 1842:107, pl. 6, fig 17.
Podopilumnus peruviannus: McCoy, 1849:166 [incorrect subsequent spelling].
Carcinus peruvianus: A. Milne Edwards, 1860:269, pl. 8, fig. 1-c.
Cancer patagonicus Philippi, 1887:213, pl. 50, fig. 1.
Cancer patagonicus: Hatcher, 1897, p. 337.
Geryon? peruvianus: Ortmann, 1900:381; Ortmann, 1902:255, pl. 38, fig. 6; Steinmann and Wilckens, 1908:70.
Geryon peruvianus: Rovereto, 1921:25; Frenguelli, 1927:205, figs. 1 (a-b); Glaessner, 1929:182; Aguirre-Urreta, 1987:464, pl. 1, figs. A-C, pl. 2, figs. A-E, pl. 3, figs. A-B, pl. 4, fig. B.
Archaeogeryon peruvianus: Glaessner, 1933:22, pl. 5, figs. 1-2; Camacho, 1966:477, pl. 16.13, figs a-b; Glaessner, 1969:R524, figs. 332, 5a-b; De La Fuente, 1977:310; Morris, 1980, p. 1; Briggs et al., 1985:203, pl. 9.2.10 A-B.
Chaceon peruvianus: Schweitzer and Feldmann, 2000:648, figs. 9.1-3, 10.1-4; Casadío et al., 2005:165, fig. 7, A-C.

Diagnosis.—The reader is directed to the recent diagnosis of *C. peruvianus* in Schweitzer and Feldmann (2000:648, figs. 9.1-3, 10.1-4).

Material Examined and Occurrence.—Specimens of *C. peruvianus* were found on all four paleosurfaces. Two specimens were found and collected from PS I: GHUNLPam 25014-25015. One specimen which was not collected was found on PS II. Ten specimens were found on PS III, eight of which were collected: GHUNLPam

Table 3.—Measurements taken on crab specimens collected from Paleosurfaces I, III, and IV. L = axial length; W = maximum carapace width; IO = inner orbital dimension: MP = maxilliped posture; D = damaged; O = open; C = closed. Measurements in millimeters.

	GHUNLPam#	species	gender	L	W	IO	OW	OW/W	L/W	MP	#claws	claw positions
PS I	25014	*Chaceon peruvianus*	damaged								1	resting/?
	25015	"	obscured								?	
	25016	*Proterocarcinus latus*	male	33	41	6.3	40.4	0.99	0.80	?	2	both resting
PS III	25000	*C. peruvianus*	male	55	76	10	35	0.46	0.72	?	2	both resting
	25001	"	female	40	51.2	11.2	34.7	0.68	0.78	?	0	both elevated?
	25002	"	female	56	68	D	D	D	0.82	?	1	resting/?
	25003	"	female	52	74	14.4	43.4	0.59	0.70	O	1	resting/?
	25005	"	female	43	66	14.4	33.3	0.50	0.65	O	0	1 elevated?/?
	CM55378	"	female	43	64	11.2	35	0.55	0.67	O	1	resting/?
	25008	"	female	52	73.3	12	43	0.59	0.71	?	1	resting/?
	25008	"	female	36	57	D	D	D	0.63	O	0	?
	25017	"	female	56	60	10.5	40.4	0.67	0.93	C	2	1 resting/1 elevated
PS IV	25009	*C. peruvianus*	obscured	58	75	D	D	D	0.77	?	0	both elevated?
	25010	"	female	41	55	14.2	45.8	0.83	0.75	O	0	both elevated?
	25011	*P. latus*	female	47	60.7	D	D	D	0.77	O	2	1 resting/1 dislocated
	25012	"		53	61	11	40.2	0.66	0.87	?	2	both resting
	CM55377	*C. peruvianus*	female	44	63	10.5	34.6	0.55	0.70	O?	1	1 slightly extended/1 elevated?
	25019	"	male	54	60	D	D	D	0.9	?	?	?
	25020	*P. latus*	male	D	D	8	30.8	D	D	?	2	both resting
	25021	*C. peruvianus*	female	48	61	D	D	D	0.79	O	0	?
	25022	"	male	48	64	11.6	39.6	0.62	0.75	O	0	?
	25023	"	female	61	73	12	43	0.59	0.84	O	1	ventrally extended/?
	25024	"	female	42	60	11.6	31.8	0.53	0.7	O	1	ventrally extended/?
	25025	"	male?	55	72	12	44.7	0.62	0.76	?	1	resting/?
	25026	"	female	61	75	13.5	42	0.56	0.81	O	1	resting/?
	25027	*P. latus*	male	41	50	D	D	D	0.82	?	1	resting/?

25002-25005, 25007, 25008, 25017, and CM 55378. Seventy-five specimens were found on PS IV: Eleven specimens, GHUNLPam 25000-25001, 25010, 25019, 25021-25026, and CM55377 were collected.

Measurements.—Measurements of specimens are provided in Table 3.

Discussion.—Crabs present on all four paleosurfaces were exposed to the erosive force of the surf and exhibited varying degrees of erosion of the dorsal carapace, claws, or legs. On PS III, ten crabs were found in a 20 m^2 area. The crabs were not oriented in a particular compass direction. Most of the crabs were preserved in the same posture; the claws were tucked close to the carapace; the legs were in what is interpreted to be a natural resting posture, neither raised above nor extended below the dorsal carapace; and the carapace was dipping at a low angle toward the posterior. One crab, however, was found in a much different posture, with its single preserved claw extended, its legs overlapping, and its carapace steeply inclined. PS IV contained 75 crabs in an area of 144 m^2. Crabs found on PS IV were preserved in what is interpreted to be a normal resting position, similar to the majority of crabs found on PS III. A calculation of the ratio of crab fossils per square meter for both PS III and IV reveals very similar proportions, with one crab/2 m^2 on PS III, and one crab/1.92 m^2 for PS IV.

The specimens of *C. peruvianus* collected from PS III and IV tended to be small for the species, with a maximum carapace width ranging from 50 mm to 76 mm, and an average maximum carapace width of 63.5 mm (Fig. 15).

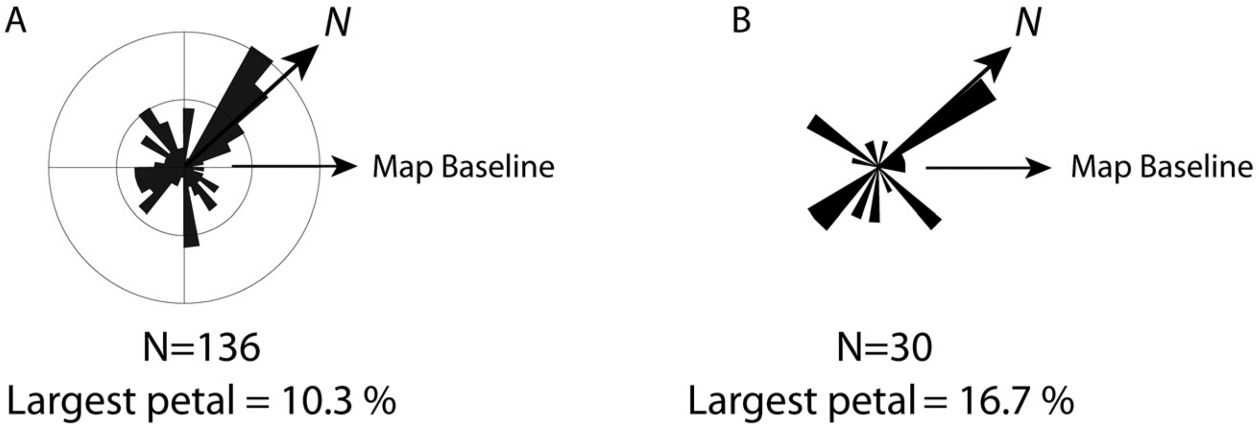

Fig. 12.—Rose diagrams generated from *Turritella patagonica* shell orientations, measured from apical end, sector size = 10 degrees. **A,** Paleosurface I; **B,** Paleosurface II.

The ratio of male to female crabs varied by locality. All the crabs collected from PS III were female; of those collected from PS IV, six were male, and eight were female. Males and females did not differ appreciably in size.

The ornamentation of the carapace, legs, and claws is well preserved on portions of the specimens that were still buried. Exposed portions of the crabs were either abraded or eroded away by surficial weathering. The third maxillipeds are well preserved on 13 of the specimens. Twelve of the crabs are preserved with the maxillipeds in an open, gaping posture. A number of the specimens exhibited signs of crushing due to post-burial compaction. Evidence for crushing includes dislocated or separated leg joints (Fig. 16B), dislocation of the pterygostomial region (Fig. 16A), and displacement of the weakly-calcified suture that separates the carapace from the sternal somites.

Thin sections of a specimen of *C. peruvianus* from PS III show that relatively little alteration of the cuticle has occurred. Visible alteration of the cuticle was limited to small sections where poorly-calcified portions of the upper endozone and lower exozone are missing. Several crushed segments of cuticle were evident, particularly along the sternum, and internally in sections of the dorsally-directed extensions of the thoracic sternites. The cuticle along the crushed segments had a splintered appearance, with fractures tending to occur between lamellae. Small, hairline fractures were also present throughout the sectioned carapace, which may have been caused by the stress of compaction or by the sectioning process.

Although the sediments of PS III and IV did not appear at first to be bioturbated, gentle cleaning of the matrix around crab specimens revealed a variety of burrows. Four patterns of bioturbation are observed; small diameter, unfilled, and vertically-oriented u-shaped tubes (type I) (Fig. 16E); small diameter, convoluted traces which give the matrix a clotted texture (type II) (Fig. 16G); filled, much larger diameter sinuous traces (type III) (Fig. 16G); and small, linear traces filled with fecal pellets (type IV) (Fig. 16F-G).

The type I burrows were 1 to 2 mm in diameter and extended 1 to 4 cm into the matrix. Sectioned burrows were often found to be stained an iron-oxide brownish-red color. The burrows only penetrated the most friable sections of the matrix, and often terminated abruptly where they encountered crab cuticle or slightly indurated sediment. A few of the burrows were observed to deflect around the crab cuticle and continue deeper. A few of the type I burrows contained fine organic threads, possibly left behind by the burrowing organism itself.

Type II burrows tended to be found on the ventral side of the specimens. The burrows were 1 to 2 mm in diameter, cylindrical in cross section, and formed clotted masses of interwoven burrows. These burrows were indurated only slightly more than the surrounding sediment. In thin section, these traces did not contain any identifiable organic traces, pyrite, or pellets. The traces were only recognizable by the faintly distinguishable alignment of sediment grains. However, application of Alizarin red-S solution to flattened sections of matrix revealed the presence of these burrows where they were otherwise undetectable. The preferential etching of the matrix indicates that type II

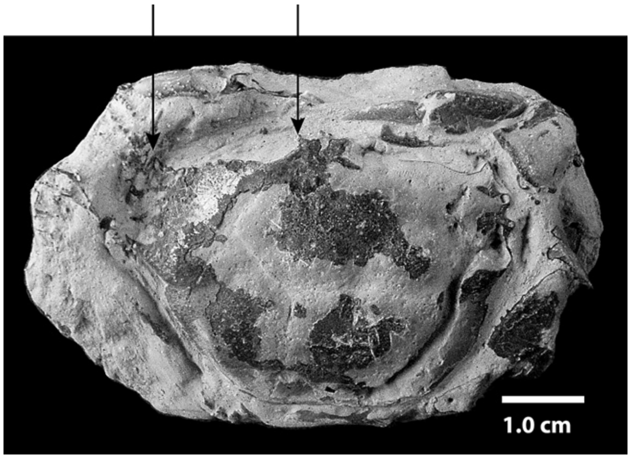

Fig. 13.—*Proterocarcinus latus*, dorsal carapace, GHUNLPam 25016. Arrows indicate wide orbit typical of the species.

Table 4.—Stable isotope data derived from *Cribrorotalia hornibrooki* forma *planoconvexa*. Samples containing sinistrally-coiled specimens denoted with and “S”; dextrally-coiled with a “D”

Sample ID	δ13C VPDB	δ18O VPDB	13C σ	18O σ	Date run	TºC
A/1/S	1.40	0.53	0.035	0.091	Sep-6-2006	14.72
A/2/S	1.46	0.62	0.013	0.073	Sep-6-2006	14.35
A/3/S	1.32	0.51	0.037	0.039	Sep-6-2006	14.78
B/1/D	1.55	0.67	0.026	0.003	Sep-6-2006	14.12
B/2/D	1.54	0.63	0.041	0.017	Sep-6-2006	14.32
B/3/D	1.45	0.91	0.033	0.038	Sep-6-2006	13.19
C/1/RC (micrite)	-1.17	1.17	0.050	0.076	Sep-6-2006	12.16

TºC using equation from Craig and Gordon (1965). $^\circ C = 16.9 - 4.2(\delta\ ^{18}O) + 0.13(\delta\ ^{18}O)$

burrows contain less calcite than the surrounding matrix. A sediment sample collected from PS IV that initially appeared to be devoid of burrows was found to be permeated with type II burrows using the above technique.

Type III burrows (Fig. 16F-G) were only found in the matrix surrounding the crab fossils. These burrows were approximately 5 mm in diameter, subcylindrical in cross section, and were crosscut by type IV burrows. The grain size of these burrows was slightly finer than the grain size of the matrix. The burrows were filled with very small (< 0.5 mm), dark amber-colored, tear drop-shaped, fecal pellets. Type IV (Fig. 16G) burrows were found only next to the carapace of the crabs. These burrows were approximately 1 mm in diameter and much more indurated than the other burrow types.

The matrix next to the ventral surface of many of the crabs was locally well cemented. These cemented areas formed pendants which extended downward from the base and the legs and around leg and claw joints (Fig. 16C).

Several of the crab specimens collected bore the skeletal remains of encrusting organisms on the dorsal carapace. Specimens of fossil *Balanus* Da Costa, 1778, were present on eight of the crabs (Fig. 16D). Barnacles ranged in size from 1 mm to 20 mm in diameter, and were often preserved with both scuta and terga in place. The barnacles did not appear to have a preferential distribution on the carapace of the crabs. Attachment locations included the protogastric regions, between the orbits on the anterior margin, the mesobranchial regions, the posterior margin, and the fifth abdominal somite.

PALEOECOLOGY OF PALEOSURFACES I AND II

Overview.—Field mapping of the four paleosurfaces exposed at Monte León revealed two distinctly different faunal assemblages: one comprised of a relatively diverse benthic fauna and one comprised solely of numerous, fully-articulated crabs. The preservation of a large number of fully-articulated crabs, all confined to a single horizon, is an unusual occurrence within the geologic record (Feldmann 2003). This crab-rich layer contrasts dramatically with stratigraphically-adjacent layers, which contain an abundant and diverse, normal marine fauna. The close stratigraphic proximity of these disparate faunas provides a unique framework by which the paleoecology of the crab-rich surfaces can be compared and assessed.

Paleoecologic Setting, PS I and II.— PS I and II exhibit a fauna rich in organisms that are commonly considered to be indicative of shallow, fully marine conditions with normal salinity, such as echinoids, corals, and mollusks. The abundance of *C. hornibrooki* forma *planoconvexa* indicates conditions of normal marine salinity and a moderately turbulent, shallow (0-70 m), inner-shelf depth, based upon the habitat preference of extant species of the genus (Hayward and Brook 1994). The abundance of *Thalassinoides* isp. traces suggest that the benthos was well oxygenated during deposition (Bottjer et al. 1986; Bromley 1990). Water temperature estimates based upon the isotopes extracted from the benthic foraminifera provide a temperature range of 13-15° C, suggesting an average annual bottom water temperature of approximately 14° C. Previously reported temperature estimates calculated for the upper Oligocene-lower Miocene Centinela Formation revealed a seasonal temperature variation from 15-21° C (Casadío et al. 2000a). Although slightly colder, the temperatures reported for the Monte León Formation are consistent. These reported temperatures are comparable to those reported from shallow shelf waters off the Atlantic coast of Virginia today (NOAA_ERSST_V2 data). Based upon these data, it is reasonable to infer that the near shore marine climate in Southern Argentina during the earliest Miocene was temperate.

Paleocurrent analysis of shell orientations of *Turritella patagonica* indicate that the bottom current was predominantly unidirectional, flowing due south, and seaward. The bottom current was not strong enough to preferentially align larger, more dense, or less elongate shells. The unidirectional, offshore flow is interpreted as being a tidal current.

PS I and II both contained a relatively high diversity

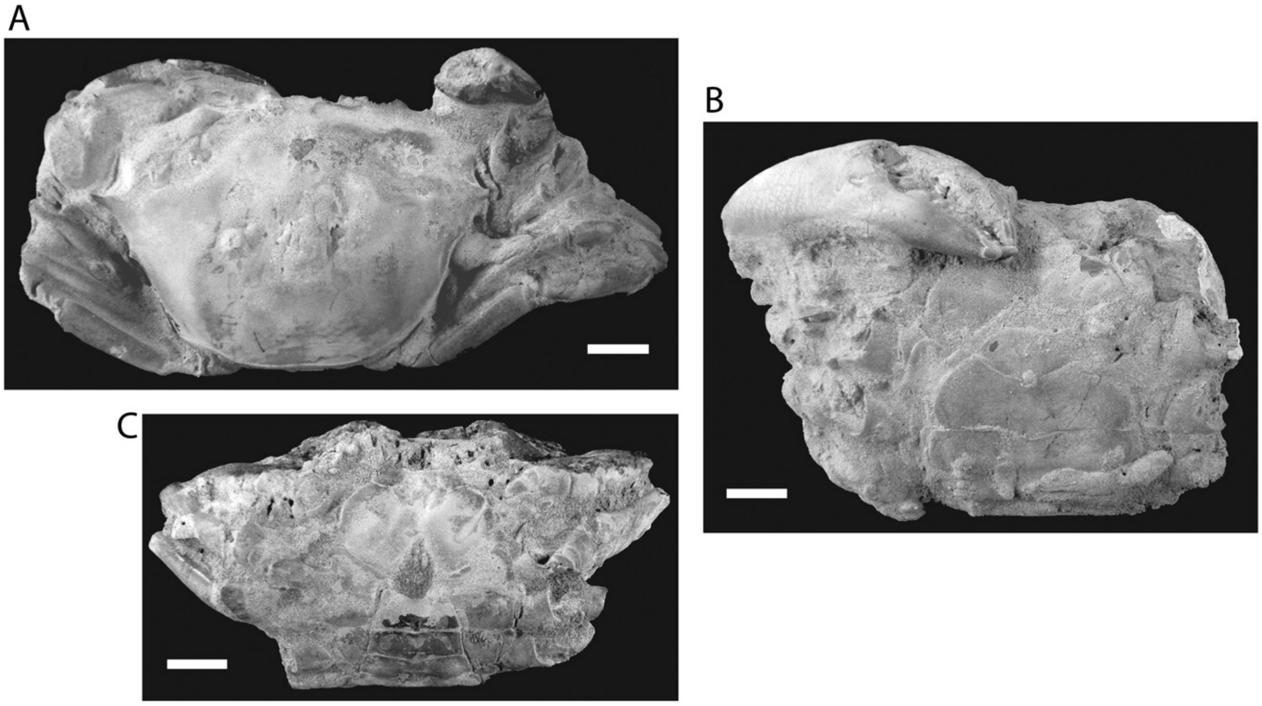

Fig. 14.—*Chaceon peruvianus*. **A-B,** GHUNLPam 25017, female: **A,** dorsal view; **B,** ventral view; **C,** GHUNLPam 25008, male, ventral view. Scale bars = 1 cm.

fauna comprised mostly of epifaunal and shallow infaunal gastropods and bivalves, comparable to the RSP (*Reticulochlamys zinsmeisteri-Struthiolarella patagoniensis-Pleuromeris cruzensi*) Assemblage of del Río (2004). Most trophic levels are represented, including epifaunal and shallow infaunal suspension feeders, deposit feeders, and carnivores. A greater number of taxa was found on PS I, possibly resulting from a sample size bias, because the map of PS I incorporates an area three times that of PS II.

Taphonomy: Deep Infaunal Bivalves.—In addition to the epifaunal and shallow infaunal organisms, clusters of the deep burrowing bivalves *D. laeviuscula* and *P. quemadensis* were found articulated and oriented in living position. In contrast, the majority of the fauna found on both PS I and PS II have been either disarticulated or fragmented. This difference in preservation suggests that these deep burrowing bivalves did not follow the same taphonomic path as the other skeletal remains found on the two paleosurfaces. Extant species of the genus *Panopea* Ménard, 1807, such as *Panopea zelandica* (Quoy and Gaimard 1835), have been reported to burrow to depths up to 70 cm within the substrate (Kondo 1997, citing Beu and Maxwell 1990). Therefore, these deep infaunal bivalves are most likely representatives of a later fauna that burrowed downward through the sediment to the level of the paleosurfaces. Given this consideration, a taphonomy-based interpretation of the prevailing sedimentologic conditions that existed during the time the paleosurfaces were exposed should exclude the deep burrowing bivalves preserved in living position.

Nevertheless, the preservation of these bivalves in living position is in itself noteworthy. Bivalves are not typically preserved in living position (Schäfer 1972). According to Schäfer (1972), the most frequent cause of death in burrowing bivalves results from their inability to cope with extremes in the rate of sediment erosion or deposition. In events where significant erosion takes place (storms), downward burrowing is often halted by compacted sediment and/or shell horizons, commonly resulting in the exhumation of the animal (Schäfer 1972). Conversely, rapid deposition of a large volume of sediment may confine the animal within its burrow, preventing it from reaching its optimal depth (Schäfer 1972; Brett and Allison 1998). *Panopea* is often preserved in living position because it dwells below the depth to which sediments are commonly reworked by currents (Kondo 1997). Based upon the previous statements, the numerous specimens of *D. laeviuscula* and *P. quemadensis* found preserved in a living position are inferred to have been entombed within their burrows by rapidly deposited sediment.

Taphonomy: PS I.—The majority of the taphonomic features observed on PS I are consistent with those associated with a low rate of background sedimentation and weak bottom currents (Brett and Baird 1986; Brett and Allison

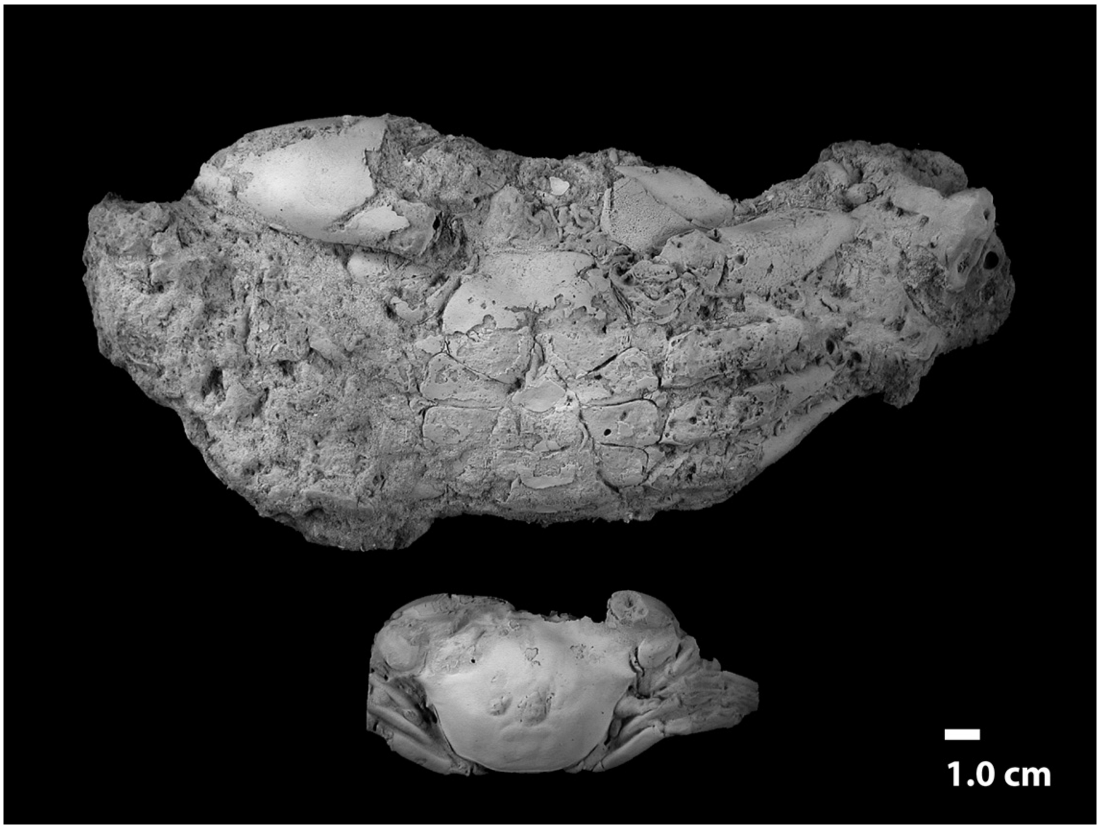

Fig. 15.—Two specimens showing size difference between typical adult *Chaceon peruvianus* (GHUNLPam 25013) from the Monte León Formation (collected at a locality inland and upsection from the 4 paleosurfaces) and a typical specimen from Paleosurfaces III and IV (GHUNLPam 25017).

1998). The skeletal remains found on PS I consisted primarily of dispersed, matrix-supported fossils of bivalves, gastropods, and bryozoan fragments. Most of the shallow infaunal and epifaunal bivalves were represented by single whole valves exhibiting a high concavo-convex ratio. Roughly one-third of the bivalves were missing minor fragments. The sediment contained very little shell debris, and many of the gastropod and bivalve shells retained their ornamentation. Several intact frondose bryozoan colonies were also observed.

A long residence time on the sea floor would account for the high percentage of disarticulated bivalve shells (Brett and Baird 1986; Brett and Allison 1998; Parsons-Hubbard et al. 1999). Low rates of sediment accumulation would also allow time for the development of the complex *Thalassinoides* burrow structures (Bromley 1990).

However, low rates of sedimentation and time-averaged shell accumulations have been commonly associated with higher rates of encrustation, bioerosion, and shell corrosion (Kidwell and Jablonski 1983; Brett and Baird 1986; Brett and Allison 1998; Goldring 1995; Smith and Nelson 2003). An exception to this generalization was reported by Best and Kidwell (2000), who observed that the frequency of encrusting organisms on shells is related to the firmness of the substrate. Very low percentages of encrusted shells have been observed on soft substrates (Best and Kidwell 2000). The presence of the *Thalassinoides* burrows indicates that the substrate was probably firm, although the surface sediments were most likely poorly consolidated. Background sedimentation will also inhibit encrustation (Parsons-Hubbard et al. 1999) if persistent bottom currents are not present to remove the sediment.

The paucity of shell fragments could be attributed to dissolution within the sediment. This explanation is regarded as highly implausible. First, the sediment contains numerous, well-preserved calcareous benthic foraminifera. Second, thin gastropod, bivalve, and brachiopod shells of varying mineralogy are equally well-preserved. Dissolution would be expected to differentially attack these shells.

A high concavo-convex ratio may not necessarily be an indicator of weak bottom currents. Emery (1968) attributed the frequency of convex-down shell orientation in inner-shelf environments (up to 91% found in a convex-down orientation) to predation and scavenging. It is highly likely that some degree of scavenging or predation may have influenced the orientation of the shelly remains, but without direct evidence, this hypothesis is merely speculative.

Brett and Allison (1998) ascribed high concavo-convex ratios to the effect of bioturbation. Significant percentages of bivalve and gastropod shells on PS I were found in a vertical or near-vertical position. Bromley (1990) calculated that as much as 90% of the substrate has been reworked where *Thalassinoides* isp. traces are abundant. Bioturbation has been reported to mix sediments to a depth of as much as 1 m in shallow marine environments (Smith and Nelson 2003). The poor-sorting of the sediment may also have resulted from activity of bioturbating organisms. Interbedded fine- and coarse-grained sediments may become mixed through bioturbation, resulting in a homogenized, poorly-sorted layer (Fürsich and Pandey 2003).

The community structure also suggests that the background sedimentation rate was low. More than half of the taxa found on PS I represent either very shallow infaunal (*Turritella patagonica)* or epifaunal forms, indicating that the substrate was stable for extended periods.

Based upon the provided evidence and the above considerations, the following interpretation has been made. The number of disarticulated bivalves, the number of epifaunal taxa, and the presence of complete bryozoan colonies and sparse shell fragments indicates a low background rate of sedimentation and weak bottom currents. During periods of quiescence, clayey silt was deposited. These conditions were interspersed with short periods of higher rates of sediment deposition, stronger currents, and coarser, sandy sediment. During these higher energy intervals the sediment was locally reworked; dead bivalves on the surface or shallowly buried were separated and dispersed, while bryozoan fronds were broken off colonies and scattered by the current. Several small scours on PS I that contain current oriented shells were probably formed during these higher energy pulses. As the pulse waned, settling fine sediment would blanket the scattered shells and inhibit encrustation. Infaunal taxa then became more abundant. These alternating conditions would have formed coarse and fine grained couplets. The high proportion of terriginous sand grains, coupled with the prevailing seaward current, suggests a shallow, near shore environment, with fluctuating rates of sedimentation and energy related to seasonal precipitation, or the redirection of tidal channels. Bioturbating organisms slowly mixed the fine and coarse layers, while also reorienting shells. Shells from several colonization episodes became mixed over time, resulting in an artificially high diversity (Fagerström 1964).

Three fully-articulated and upright crabs and several bryozoan colonies were buried intact, indicating that the last pulse of sediment that covered the surface must have been deposited rapidly and been thick enough to prevent the crabs from escaping. Burial experiments have demonstrated that a deposit approximately 30 cm thick is sufficient to trap most benthic organisms (Nichols et al. 1978). Because the overlying sediment has been eroded away, and bioturbation has obscured the bedding, the nature of the "entombing" deposit cannot be determined with confidence. It is speculated that the surface was most likely buried by a density-driven flow, possibly storm-induced. The final burial would likely have preserved many of the organisms in an articulated, living position. The paucity of articulated bivalves, presence of few intact bryozoan colonies, and the preservation of articulated crabs suggest that the actual density of the benthic community was very low, and support the interpretation that current winnowing and bioturbation produced a time-averaged parautochthonous assemblage.

Taphonomy: PS II.—The taphonomic features observed on PS II indicate that bottom currents were stronger than during the deposition of PS I; fewer bivalves were articulated, a higher proportion of single valves were oriented convex-up, and shell fragments were common (Brett and Baird 1986; Brett and Allison 1998). Disarticulated valves included those of exhumed deep infaunal bivalves, suggesting seafloor erosion (Fürsich and Pandey 2003). Body fossils were more concentrated on PS II, with an average of 35% more fossils per quadrat than on PS I.

The fauna of PS II is composed of a greater percentage of epifaunal taxa (54% on PS I; 63% PS II), which may also indicate extended periods of low or non-deposition (Fürsich 1978). The large oyster *Crassostrea (?) hatcheri* (Ortmann, 1897), was not present on PS I, while several disarticulated and articulated specimens were found on PS II. The presence of the oysters is also interpreted as an indication of a low sedimentation rate and persistent bottom currents.

The presence of numerous, partially overturned, bioeroded, intraclastic cobbles signifies erosive bottom currents and periods of non-deposition. The bioeroded cobbles present on PS II were most likely produced by the exhumation and prolonged exposure of an early diagenetic concretion horizon. The brown color of the cobbles differs from the surrounding sediment, and indicates the presence of oxidized iron (limonite) resulting from prolonged exposure on the sea floor (Hesselbo and Palmer 1992). Exhumed horizons such as these have been previously described (Hesselbo and Palmer 1992) as "coinstone horizons." Concretion horizons have been interpreted as representing basin-wide hiatal conditions (Hesselbo and Palmer 1992) when present over a large outcrop area. However, early diagenetic cementation within the upper layers of sediment can also be very localized (Wilson and Palmer 1992). Previous studies of the Monte León Formation have not identified similar horizons, nor was the horizon observed elsewhere. Therefore, it is suspected that the cobbles were limited to a small area of the sea floor.

The cobbles appeared to have been partially buried by the sediment that contained the shell hashes, indicating that the cobbles were bioeroded prior to the deposition of the shell hash. The lenticular geometry of the shell concentrations indicates that the shell fragments lie within scours. The scours provide evidence that strong, erosive bottom currents had briefly returned.

The areas between the shell hash lenses contained

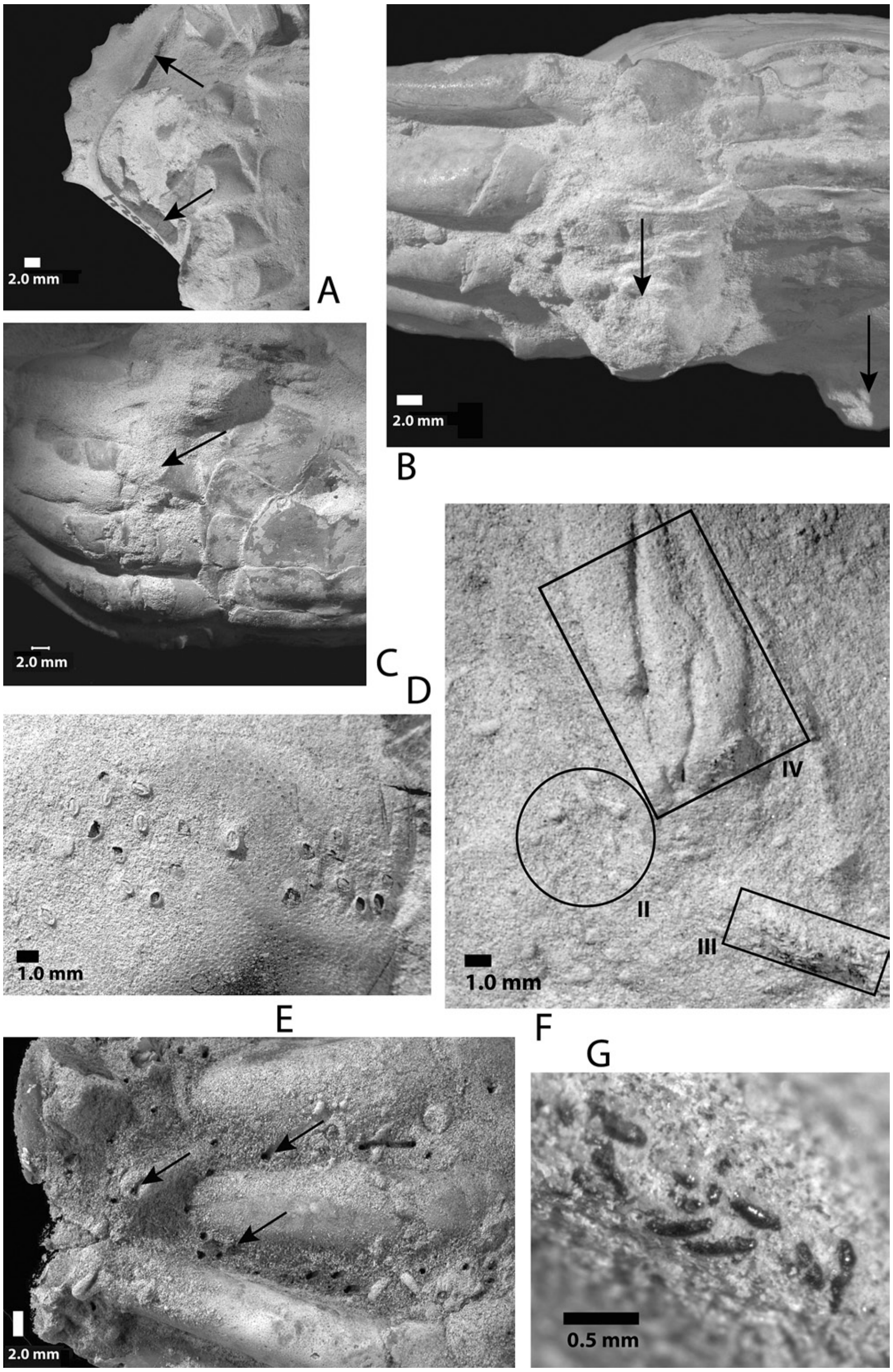

Fig. 16.—Trace fossils and diagenesis associated with specimens of *Chaceon peruvianus*. **A,** GHUNLPam 25024, ventral view, arrows denote region of crushing along suture between dorsal carapace and pterygostomial region; **B,** GHUNLPam 25017 "pendants," areas of sediments cementation, indicated by arrows, restricted to the ventral side of the crab and occurring proximal to joints of the pereiopods; **C,** GHUNLPam 25017, arrow indicates region of separation between basis and coax of second pereiopod; **D,** GHUNLPam 25026, cluster of small barnacles on mesobranchial region, many with terga and scuta preserved in place (barnacles are not Recent); **E,** type I burrows, indicated by arrows, GHUNLPam 25003; **F,** types II, III, and IV burrows, GHUNLPam 25026; b, magnification of type-III burrow from (F), showing fecal pellets within trace, GHUNLPam 25026.

biogenic traces similar to PS I, as well as sediment that was comparable in composition, size, and degree of sorting. The orientation of *Turritella patagonica* shells, although not statistically significant, appears to result from an offshore current similar to PS I, and may also indicate the influence of oscillating, wave-generated currents (Fig. 12). As with PS I, a fully-articulated and upright crab was present, indicating the rapid final burial of the surface.

Based upon the previous evidence, PS II is interpreted as representing a higher-energy environment than PS I. The cobbles and disarticulated, deep, infaunal bivalves represent a period of erosion and non-deposition. It is speculated that this erosive period was followed by a quiescent period when epifaunal organisms colonized the firm sediment and cobbles. Furthermore, a return to a low rate of background sedimentation would have provided the necessary substrate for shallow infaunal bivalves and gastropods, and partially buried the cobbles. Episodic interludes of increased current strength winnowed the sediment, forming scours and concentrating shell fragments. Bioturbating organisms may have mixed the inter-areas between the scours, destroying the sedimentary structures and creating a mixed, poorly sorted sediment layer. As with PS I, the final burial event was probably rapid and thick enough to ensure that crabs could not escape. Although the relative species diversity was lower on PS II, the number of articulated specimens suggests that most of the skeletal remains are current-winnowed and time-averaged and represent a parautochthonous assemblage.

In summary, PS I and II lay within close geographic and stratigraphic proximity to each other and to the crab-dominated assemblages found on PS III and IV. Therefore, it can be reasonably inferred that all four paleosurfaces formed within a brief span of time, at similar positions on the seafloor, and therefore were formed under similar hydrodynamic conditions. The nearshore marine climate was temperate, consistent with present day mid-latitude conditions. The seafloor occupied a shallow subtidal position, lying above storm wave base, and below normal wave base. The prevailing bottom current was flowing in a southerly, offshore direction, and probably was generated by tidal flow.

It is not known if PS I and II occurred within the same stratigraphic horizon. The two surfaces most likely represent two successive surfaces separated by a short interval of time, given the observed taphonomic differences. The faunas found on these surfaces indicate that they were deposited under normal marine conditions, and that the bottom was not oxygen restricted. Similar proportions of molluscs with similar life habits were present on both surfaces (Figs. 5, 7). The faunal diversity differed, although that may be explained by time averaging (Fägerstrom 1964), exotic input due to storm wave transport (Staff and Powell 1990), or within-habitat variation (Davies et al. 1989). The low prevalence of articulated specimens preserved by the final burial events supports this interpretation. The presence of abundant suspension and filter feeders suggests that turbidity was low. Vagrant and sessile epifaunal organisms were present on both surfaces, indicating that the substrate must have been stable for some period of time.

In summary, the data presented here are consistent with a near-shore, sublittoral environment. The habitat was below normal wave base, but not removed from the influence of storms. This interpretation is similar to previously published interpretations for the Monte León Formation (Bertels 1980; Barreda and Palamarczuk 2000).

PALEOECOLOGY OF PALEOSURFACES III AND IV

Crab-Rich Assemblages in the Fossil Record.—In general, decapods are scarce within the fossil record (Feldmann and McPherson 1980; Bishop 1986), due in large part to the post mortem disarticulation of their multi-element exoskeletons (Schäfer 1951, 1972; Bishop 1986; Plotnick et al. 1988). Intact crabs are typically found as isolated specimens (Feldmann 2003), often being preserved within concretions (Bishop 1986). Bishop (1986) reported that 42% of all crab taxa are known from single specimens. Because of their high susceptibility to taphonomic degradation, few documented occurrences exist of *in situ* fossil assemblages containing numerous, articulated, and well-preserved crabs. The preservation of intact fossils with multi-element skeletons necessitates the rapid deposition of sediment (Brett and Baird 1986). In cases where strata have yielded numerous specimens, the individuals are typically dispersed throughout the section and not confined to single bedding planes (Feldmann 2003). A thorough review of the decapod literature has revealed only a few examples where numerous crabs were found confined to a single horizon (Bishop 1981; Hidenao et al. 1997; Feldmann et al. 1999; Feldmann 2003).

Bishop (1981) documented the occurrence of numerous layers rich in *Dakoticancer overana* Rathbun, 1917, (referred to as the *Dakoticancer* assemblage) from the Late Cretaceous Pierre Shale of the Western Interior of North America. Large numbers of disarticulated crab carapaces were found that were confined to specific horizons. Bishop (1986) hypothesized that the crab population had dramatically increased in response to a burgeoning soft-bodied benthic fauna that had colonized the substrate following some type of event that enriched the sediment in organics. In this instance, the preservation of the crabs was attributed to an increased preservation potential resulting from an unusually dense population (Bishop 1981, 1986).

Feldmann et al. (1999) described the occurrence of a decapod-rich fauna from the Cretaceous of Colombia, including several bedding planes containing numerous articulated carcineretid crabs. These bedding planes were interpreted as mass mortality events stemming from either dysoxic waters or the advection of toxic trace elements from the sediment, followed by rapid burial (Feldmann et al. 1999).

Feldmann (2003) described the preservation of numerous articulated cancrid crabs from the Puente Formation (late middle to early late Miocene) of California. He identified the assemblage as a mass mortality event, speculating that a toxic algal bloom may have been responsible for the die-off (Feldmann 2003).

Hidenao et al. (1997) reported the occurrence of more than 100 specimens of *Romaleon gibbosulus* (Rathbun, 1898), within a marginal marine facies from the Pleistocene Higashiyatsu Formation of Japan. All of the crabs were found fully-articulated, oriented in living position, and preserved within a single bedding plane. Many of the crabs were identified as being ovigerous, possibly indicating that the crabs were entombed while living.

Monospecific Occurrences and Migration of Decapods in Modern Oceans.—Monospecific assemblages or assemblages with small numbers of species of decapods, including brachyurans, are not uncommon in modern environments. Jesse and Stotz (2003) noted clear segregation of species of brachyurans, presumably by habitat and niche-partitioning, within a shallow-water area in Chile. Images of swarming galatheid decapods at hydrothermal vents are known from the published literature (Chevaldonné and Olu 1996: fig. 1; Baba and Williams 1998: fig. 3).

It has been well documented that modern species of *Chaceon* segregate by depth and gender, with females generally inhabiting shallower waters (Lockhart et al. 1990; Lindberg and Lockhart 1993 and references therein). All of the specimens collected from PS III were females; those from PS IV were about equal in number between males and females. Interestingly, Lindberg and Lockhart (1993) noted that in their transects of deep water habitats (500+ m), they encountered no juveniles of species of *Chaceon*. Thus, the juveniles must have been aggregating elsewhere, perhaps in shallower water. It is possible that the specimens collected from PS III and IV were juveniles, inhabiting a shallow water area away from adults of the species. This is supported by the observation that all of the individuals collected from PS III and PS IV are smaller than the general size for *C. peruvianus* from other localities. It is important to note that specimens of *C. peruvianus* collected from Miocene rocks of Peninsula Valdés, Argentina, a shallow water deposit, (Casadío et al. 2005) were quite large. However, it is nevertheless true that the specimens from Monte León were entirely small, suggested some type of behavioral, gender-specific, or ecological segregation.

Other reports have found similar behavioral differences and gender segregation as well as high densities of individuals of a single species. PS IV exhibits a density of about two crabs per m^2. Lovrich et al. (1995) reported densities of the spider-crab *Chionoecetes opilio* (Fabricius, 1780) at an average of 860 crabs per 1000 m^2. They also reported that females were more gregarious and less active than males. In near-shore and estuarine communities, individuals of *Polybius henslowi* Leach, 1820, a member of the Carcinidae MacLeay, 1838, within the same superfamily as *Chaceon* and *Proterocarcinus*, were found in densities of 1.6 per m^2 during the summer (Gonzalez-Gurriaran 1986). Woll (2003) reported a density of 20 crabs in a 30 m^2 area in a study of ovigerous *Cancer pagurus* Linnaeus, 1758, including males and females. She also noted that females do indeed nest in shallow areas, suggesting that the crabs observed in the Monte León Formation could have been juveniles hatched in a shallower area. Individuals of a single species of brachyuran can achieve a relatively high density.

Migration behavior is well known for decapods. The migration of red crabs at Christmas Island is commonly used footage on nature documentaries. The freshwater crab *Gecarcinus ruricola* (Linnaeus, 1758), migrates at least 50 m on land as a megalops before molting to the first juvenile crab stage (Hartnoll and Clark 2006). Many decapods migrate even further. Onshore-offshore migration for reproduction is known in palinurid lobsters (Hunter 1999), the American lobster (Moriyasu et al. 1999), and galatheid squat-lobsters (Vinuesa 2007). Hill (1994) reported that the brachyuran *Scylla serrata* (Forskål, 1775), a member of the Portunidae Rafinesque, 1815, within the same superfamily as *Chaceon* and *Proterocarcinus*, migrates far offshore to reproduce, on average about 18 km. *Callinectes danae* Smith, 1869, another portunid crab, was discovered to exhibit a higher number of juveniles than adults in near-shore areas, whereas females were more abundant in offshore areas which was suggested to represent a possible migration route (Branco and Masunari 1992). The occurrence of swarms or simply living individuals of decapods as well as extensive migrations of large numbers of individuals are well-recorded in the literature. Thus, the occurrence of a large number of fossils belonging to one or a small number of species on one bedding plane is congruent with reports of decapod occurrences and behavior from the neontological literature.

Paleoecology of Crab-Rich Deposits: PS III and IV.—Numerous occurrences of well-preserved decapods have been documented from Cenozoic deposits in Argentina (summarized in Casadío et al. 2005). The extent of aerial exposure, the large number of fully-articulated fossil crabs, and the tuffaceous character of the sediment found on PS III and IV make this occurrence extraordinary within the geologic record. This is especially true considering that the deposit does not contain the more commonly encountered remains of other benthic organisms, such as bivalves and gastropods. The assemblage is comprised almost entirely of a single species of crab, *C. peruvianus*. The specimens are composed entirely of complete carapaces, interpreted as corpses. There is no evidence that the specimens were molts (i.e., Salter's position). All of the specimens retained portions of the dorsal and ventral carapace as well as appendages, typical only of corpses. The size of the crabs indicates that they were juveniles, and there appear to have been slightly more females than males. Size segregation in *C. peruvianus* has been noted by Schweitzer and Feldmann (2000) and has also been identified in populations of extant *Chaceon* species (Steimel et al. 2001). Based upon the close stratigraphic proximity of the two surfaces, and because the enclosed faunas, character of the sediment, and nature of bioturbation are so similar between PS III and IV, it is inferred that the two exposures represent the same depositional event and are simply two separate exposures of the same surface.

The apparent absence of other body fossils, skeletal fragments, and large burrow structures on both surfaces is unusual, especially when compared to the composition of the stratigraphically-adjacent paleosurfaces. One possible explanation is that the horizon represents a period when adverse water chemistry, such as abnormal salinity or low dissolved oxygen, inhibited colonization of the substrate. However, it is important to note that time constraints and the encroaching high tide made it difficult to observe small fossils on the crab-rich surface. It is possible that there were small fragments or bioturbation that went undetected. It is clear, however, that there were no large fossils other than the specimens of *Chaceon* and *Proterocarcinus*.

Abnormal salinity conditions, whether hypersaline, hyposaline, or fluctuating salinity, would have limited the kinds of organisms that could have occupied the substrate. However, no faunal elements or sedimentary structures indicate that there was other than normal marine salinity. An environment of reduced dissolved oxygen may also have been responsible for the absence of other benthic organisms. Small diameter burrows were prevalent on both paleosurfaces, which may indicate dysoxic conditions (Bottjer et al. 1986; Bromley 1990), but this does not necessarily indicate that dissolved oxygen levels were low at the time of deposition (Bromley 1990; Ekdale 1992). Additional evidence such as undisturbed sediment laminations or organic-rich layers of sediment would be needed to corroborate this interpretation (Ekdale 1992). The absence of calcareous skeletal fragments on these two surfaces could be attributed to post-burial dissolution. This seems highly implausible, given that no remnants of dissolved shells were observed in thin-section, and that the crabs and the calcareous barnacles they bore did not exhibit any signs of dissolution. In addition, extant species of *Chaceon* inhabit normal marine conditions (Manning and Holthuis 1984, 1989).

The composition and character of the sediment collected from PS III and PS IV provides evidence that volcanism was partially if not wholly responsible for preservation of the crabs in this deposit. The sediment from PS III and IV do not contain the well-rounded terrigenous rock fragments, bioclasts, or reworked clay intraclasts found in sediments from PS I and II (Fig. 3). Volcanic glass shards and bubble fragments comprise a significant proportion of the sediment collected from both Paleosurfaces III and IV. The majority of the cryptocrystalline and clay-sized matrix observed in thin section appears to have been produced by diagenetic alteration of volcanic ash (Wilson et al. 2003). The plagioclase, quartz, pyroxene, amphibole, and volcanic rock fragment grains may have been components of an ash. The angularity of the grains indicates that the sediment had not been subaqueously transported very far or extensively reworked, yet was well-sorted (Fig. 3). The composition, angularity, and sorting are consistent with those features observed in wind transported, distal ash fall deposits (Hart and Miller 2006).

Tuffaceous beds are found throughout the Monte León Formation, and suspected ash fall deposits have been previously identified within it (Di Paola and Marchese 1973). The prevailing wind direction is currently from west-to-east and would have been the same during the early Miocene based upon the continental position. Although the Andes lay over 500 km away from the Patagonian coast, an ash plume could easily have traveled that distance. In the early 1990's, the eruption of Hudson Volcano in Chile deposited a centimeters thick layer of ash 535 km away on the Argentinian coast near the town of San Julián, approximately 100 km north of Monte León. Volcanic ash deposits are known to exhibit progressively finer size-sorting with distance from the source (Kennett 1981). The silt-size of the volcanic sediment found on PS III and IV is consistent with the expected size of ash fall particles given the distance from the Andes Mountains (Sigurdsson et al. 1980; Kennett 1981). Thus, the nature of the ash enclosing the crab fossils, being angular, unreworked, and not subaqueously transported, as well as the large numbers of crabs on the paleosurfaces suggests strongly that a catastrophic ashfall was responsible for the death and entombment of the crabs on PS III and IV.

The posture in which the crabs were preserved lends additional support to this hypothesis. All but one of the 70+ crabs found on PS III and IV were preserved in what is interpreted to be a normal resting posture on the ocean floor. Schäfer (1951) observed that crabs, once buried, will attempt escape by extending claws and elevating legs in an attempt to push their carapace upward through the sediment. Only one crab from the study was found in a position which might be interpreted as an escape posture, with one of its claws outstretched and its carapace oriented in a steeply inclined position. This suggests that the crabs were killed rapidly, giving them little time to assume an escape or other defensive posture.

In addition to the resting posture exhibited by all but one crab, many of the crabs were preserved with their third maxillipeds in an extended, open posture (Fig. 17A). A review of the literature and examination of the Kent State University Department of Geology fossil decapod collection (1000+ specimens) revealed that the ventral surface and maxillipeds are usually not exposed in preparation of the specimens or not preserved in fossil crabs. Most fossil crab specimens are known from their dorsal

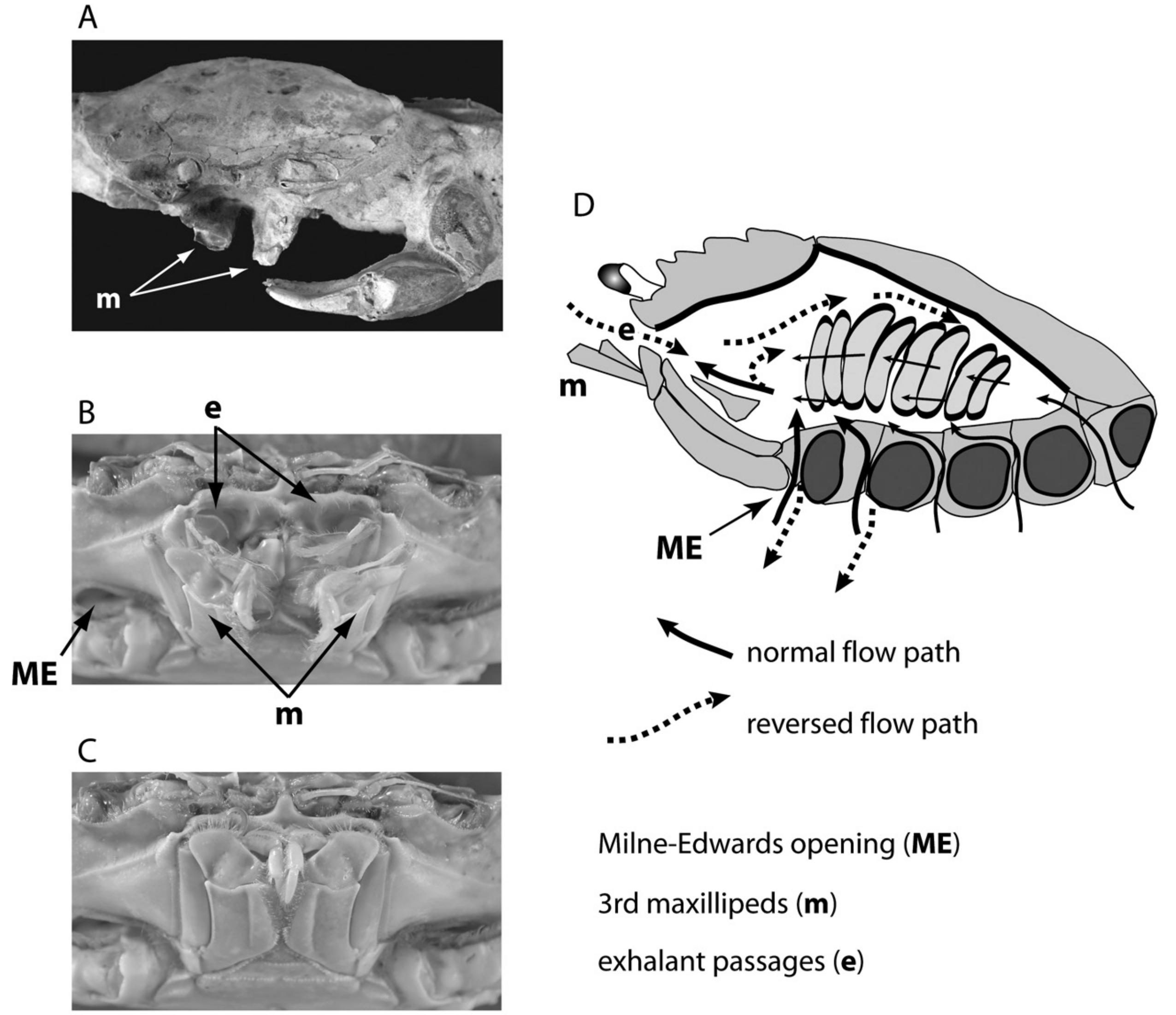

Fig. 17.—Respiration in a typical brachyuran crab. **A,** *Chaceon peruvianus*, CMNH 55377, arrows indicate open third maxillipeds, specimen collected from PS IV; **B,** recent specimen of *Callinectes sapidus* Rathbun, 1896, housed in the spirit collection at KSU, arrows indicate respiratory passages; **C,** same specimen as in (2), note typical resting, closed position of third maxillipeds; **D,** cartoon cross-section of brachyuran crab showing normal and reversed respiratory flow, modified from Arudpragasm and Naylor (1964).

carapace. In the specimens where the maxillipeds could be observed, they were always positioned lying against the carapace. Photographs taken from living crabs (i.e., Woll 2003: fig. 3), show the maxillipeds held against the carapace. A thorough search of the literature has revealed scant references to the maxilliped posture of extant or fossil crabs. What can be inferred though, is that crabs typically hold their maxillipeds close to their carapace (Fig. 17C). Only when the crab is grooming, eating, or, most importantly, under respiratory stress (Warner 1977), are they extended.

A volcanic ashfall would have resulted in a significant amount of suspended, fine particulate matter on the sea floor, which may have adversely affected the ability of the crabs to respire. Crabs typically ventilate their branchial gills by drawing water into the carapace through the Milne-Edwards openings, located at the basal joint of the chelipeds, and through openings located at the basal joint of each leg (Batterton and Cameron 1978) (Fig. 17B, D). The flow of water into the branchial chambers is maintained by the rhythmic motion of the scaphognathites, which sweep over the gills (Batterton and Cameron 1978). The exhalent current flows out of the carapace anteriorly through two openings located in a depression below the ocular cavities (Batterton and Cameron 1978) (see Fig. 17B, D). The depression is typically covered by the third maxillipeds, allowing the exhalent current to flow out while protecting the respiratory openings. Crabs and other decapods are known to be able to reverse the flow of water through the carapace, bringing water in through the anterior openings, and out through the Milne-Edwards and leg openings (Batterton and Cameron 1978). To best facilitate this flow, the third maxillipeds need to be lowered, exposing the respiratory passages. The purpose of these flow "reversal" periods is poorly understood. Experiments conducted on the crab *Carcinus maenus* (Linnaeus, 1758), concluded that the flow reversal was not an attempt to flush sediment or other foreign matter from the gills (Arudpragasm and Naylor 1964). Batterton and Cameron (1978) observed that flow reversals in decapods occurred most often when the crabs were either under respiratory stress (hypoxia), or when the gills were irritated by changes in salinity, an elevated level of carbon dioxide, or air bubbles within the branchial chambers. Batterton and Cameron (1978) postulated that reversals were probably a mechanism for increasing flow rate and gill ventilation. The gaping posture of the third maxillipeds preserved in the crabs collected from PS III and IV strongly suggests that the crabs were experiencing respiratory distress when they died. It is likely that the fine-grained volcanic glass raining down upon the seafloor fouled the crab gills, resulting in their deaths.

Surprisingly, very few studies have been conducted on the effect of volcanic ash on marine organisms (Eldredge and Kropp 1985). Studies concerning the affect of ash falls on corals (Heikoop et al. 1996) and benthic foraminiferans (Hess et al. 2001) have been conducted, but none has been published that examines the effect that volcanic fallout has on decapods. It can be reasonably inferred that silt-sized, sharp, glass fragments would be detrimental to the soft tissues of bottom dwelling marine organisms. The glass in ash falls is very abrasive, known to damage shells and other skeletal structures shortly after being deposited (Eldredge and Kropp 1985). Crabs can efficiently flush sediment from their gills, but the glass fragments would not have been easily removed, lodging in the soft tissues of the gills.

Studies of ash falls from recent eruptions suggest that even if the initial eruption event were quite large, only a few centimeters of ash would have been deposited at Monte León (Kennett 1981). Terrestrial deposits could be expected to have been reworked and concentrated by winds for a period of years after the eruption. However, there is no evidence of the ash in the sediment enclosing the crabs having been reworked. In addition, the posture of the crabs as well as their being corpses suggests that they were killed instantaneously. Had they been subjected to long-term accumulation of sediment, especially abrasive ash, it is highly probable that they would have left the area. Species of *Chaceon* today inhabit a broad range of depths, including relatively deep water, so it may have been possible for them to escape to deep water habitats (Lindberg and Lockhart 1993). In addition, as noted above, it is well-documented that crabs and lobsters can migrate very long distances, making it plausible that they could escape a long-term accumulation of ash. Thus, a large volume of ash must have rapidly blanketed the ocean floor.

Summary of Events Leading to PS III and IV.—In summary, the following sequence of events is proposed to explain the occurrence and preservation of the numerous crabs on PS III and IV. An eruption in the southern Andes blanketed the eastern coast and continental shelf with ash. Primary ash fall deposits blanketed the sea floor. The distal ash fall contained a high proportion of silt-sized glass fragments. The background sedimentation rate was low, and the ash fall was not diluted by other sediments. The crabs spread their maxillipeds wide and reversed their respiratory flow. The sedimentation of ash however, potentially smothered, and certainly buried, the crabs. The single crab that was found in a steeply-inclined position may have been attempting to remain unburied, but was too weak to effectively dig out.

Soon after the crabs were buried, scavengers burrowed into the sediment to feed on the carcasses. The deposit was thick enough to partially crush some of the crabs before they decayed. Small scavengers, tolerant of the low dissolved oxygen conditions deep within the sediment (> 0.5 m) (Ekdale 1992), harvested the rotting crabs while also destroying the primary sedimentary fabric. As the crabs decomposed within the sediment, organic fluids seeped out of their carapaces. The bacterially-mitigated decay of these fluids promoted the formation of early-diagenetic cements, forming the stalactitic, cemented regions around the joints and sutures of the crab carapaces.

Above PS III and IV, large burrowing structures eventually were formed, perhaps marking the decreasing influence of ash deposition and a return to a more normal depositional environment. The fauna found on PS I and II are interpreted as representing the return of the normal marine community.

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