

## HUESSER HORIZON: A LAKE AND A MARINE INCURSION IN NORTHWESTERN SOUTH AMERICA DURING THE EARLY MIOCENE

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### ABSTRACT

The Cenozoic stratigraphic sequence in the foothills of the Eastern Cordillera of Colombia is mostly fluvial in nature and very thick (~8000 m), but it contains very few mollusk-bearing horizons. Recent fieldwork discovered a well-preserved molluscan assemblage that occurs near the top of the Carbonera Formation (lower Miocene) in the central foothills of the Eastern Cordillera. This level, named the Huesser horizon, is laterally extensive and can be followed for tens of kilometers. The horizon is 10 m thick and was divided into eight levels, five of them highly fossiliferous. Most of the levels are dominated by the freshwater gastropod *Sheppardiconcha*, with lower abundances of the bivalves *Anodondites* and *Mytilopsis*. The top level is dominated by specimens from the bivalve family Arcidae. The taxonomic composition of the assemblage is similar to that of the Magdalena and Amazonas Basins during the early-to-middle Miocene. Paleoecologic, taphonomic, and palynological analyses indicate that the Huesser accumulated in a freshwater lake system, capped by a marine incursion. The development of a large lake and the subsequent marine event could be related to increasing subsidence coincident with eustatic sea-level rise that has been identified for the basin during the early Miocene.

### INTRODUCTION

Miocene marine faunas from the Neotropics are abundant, well preserved, and relatively well studied in the Caribbean and Central American regions (Woodring, 1959, 1973; Best and Kidwell, 2000). Well-preserved Miocene freshwater molluscan faunal assemblages from the Amazon have also been studied (Pilsbry, 1911; Ortmann, 1921; Pilsbry and Olsson, 1935; Parodiz, 1969; Nuttall, 1990; Wesselingh, 2006). During the Miocene, the South American region underwent many orogenic changes. In western South America, the uplift of the Andean range caused many geomorphologic changes and climatic variations, particularly the uplift of the Eastern Cordillera, which affected the drainages of the Amazon and Orinoco Rivers (Hoorn, 1994; Hoorn et al., 1995).

The Cenozoic sequence of the Eastern Cordillera of Colombia is dominated by continental sediments. More than 8000 m of sandstone and mudstone siliciclastic sediments, interspersed with thin layers of marginal marine sediments, were accumulated in the Barco, Cuervos, Mirador, Carbonera, León, and Guayabo formations (Cooper et al., 1995; Bayona et al., 2008). The fossil record of mollusks in these formations is very rare or exhibits poor preservation throughout the whole sequence. In 2005, during a field expedition to the Eastern Cordillera, we discovered a well-defined horizon with a rich concentration of mollusks in the upper Carbonera Formation. This horizon, which we have named Huesser after a family of local farmers, is unique and can be traced along tens of kilo-

meters along the eastern border of the Eastern Cordillera (Fig. 1). In this paper, we describe the taxonomic composition and taphonomy of this horizon in order to interpret how such a unique mollusk layer was deposited and preserved.

### METHODS

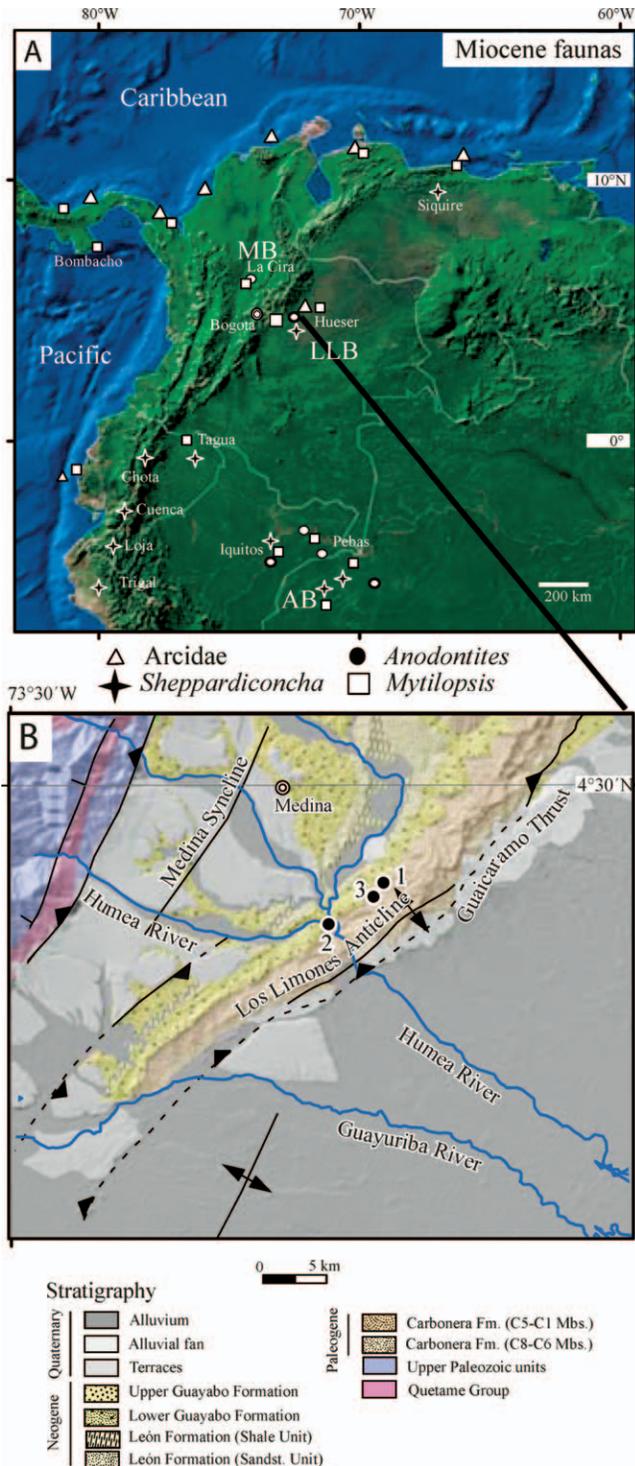
The Huesser horizon occurs at the top of the Carbonera Formation C2 unit, 12 m below the contact between Carbonera units C2 and C1 (Fig. 2). These units are informal lithostratigraphic subdivisions of the formation (Bayona et al., 2008). Three sites were sampled from the eastern side of the Eastern Cordillera of Colombia near the town of Medina, Cundinamarca: (1) Retumbadora Ravine (4° 26' 16.14" N, 73° 16' 39.78"E), (2) Gazaunta River (4° 25' 11.57" N, 73° 18' 32.9" E), and (3) Bellavista Ravine (4° 26' 0.31" N, 73° 17' 5.96" E).

The Huesser horizon is ~10 m thick and divided into eight levels according to its fossil content and lithological composition (Fig. 3). The beds containing the molluscan fauna are described in terms of lithological changes, disposition of the fossils, orientation, and packing. Fourteen horizon-level samples (about 5 kg per sample) were taken at outcrops along small creek cuts to ensure analysis of unweathered material. Sample blocks were removed for full description of the fossil assemblage. The samples were sieved using a 1 mm mesh. All material was dried, and fossils were separated, cleaned, and identified. Mollusk identifications were made following Ortmann (1921), Pilsbry and Olsson (1935), Moore (1969), Parodiz (1969), Abbott (1974), Nuttall (1990), and Wesselingh (2006). Images of the specimens were taken using a Epson 2480 scanner and a Zeiss EVO 40XVP scanning electron microscope. Eight additional lithological samples from levels 1–2 and 4–8 were prepared for palynological analysis using standard techniques (Traverse, 2007).

Three parameters were evaluated in order to determine taphonomic patterns for 680 specimens: corrosion (combined effects of abrasion, bioerosion, and pre- and postburial dissolution), fragmentation, and deformation (Brett and Baird, 1986). Taphonomic parameters and the taphonomic index were scored and plotted in a ternary diagram using a rank-quantitative scale (Kowalewski et al., 1995): 0 = good or only slightly affected; 1 = moderately affected; and 2 = poor or highly affected condition. Fragmentation was classified into three categories based on the percentage of specimens preserved: good (0) = >80%; fair (1) = 50%–80%; and poor (2) = <50%. We developed a taphonomic index (TI), which was calculated for each level. The TI summarizes the results from the taphonomic parameters (corrosion, fragmentation, and deformation) and is composed of three values (TI<sub>0</sub>, TI<sub>1</sub>, TI<sub>2</sub>), with each value defined as  $TI_i = n_i/fN$  for  $i = 0, 1, 2$ ;  $n_i$  = the total number of specimens scored as grade  $i$  when the three parameters (corrosion, fragmentation, and deformation) are summed;  $N$  = the total number of specimens in the stratigraphic level; and  $f$  = the number of parameters (3).

Packing and orientation of fossils were recorded from four 50 × 50 cm quadrants taken from horizon levels 1 and 7. A rose diagram based upon the orientation of 240 fossil gastropods was used to estimate paleo-

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**FIGURE 1**—Regional map of northwestern South America. A) Distribution of species found in the Miocene Hueser assemblage, as related to the Pebas Formation fauna (see text). MB = Magdalena Basin. LLB = Llanos Basin. AB = Amazonas Basin. B) Geologic map detail showing collecting sites in the eastern foothills of the Eastern Cordillera: 1 = Retumbadora Ravine, 2 = Gazaunta River, 3 = Belavista Ravine.

current direction (Boucot et al., 1958). The orientation was measured using a protractor. Taphofacies were defined based on taphonomic index value, packing, and disposition. Specimens are deposited in the paleontological collections of the Paleontological Museum of the Colombian Geological Survey (known as INGEOMINAS), in Bogotá.

## RESULTS

Levels 1, 2, 6, and 7 are highly fossiliferous (Fig. 3) and dominated by the gastropod *Sheppardiconcha* (Pachychilidae)—which constitutes as much as 87% of the collected specimens—and the articulated bivalves *Anodontites* (Mycetopodidae) and *Mytilopsis* (Dreissenidae). In contrast, level 5 contained only a few specimens of *Sheppardiconcha* (Fig. 3) and level 8 contained only specimens from the family Arcidae (Table 1). Ichnofossils were observed at the top of level 4 (Fig. 3).

Palynological samples from levels 1–7 are characterized by an abundance of freshwater algae (*Botryococcus* sp. and *Pediastrum* sp.) and amorphous organic matter (Fig. 3) and by the presence of palynomorphs from coastal tropical forests, including ferns (*Verrucatosporites usmensis*, *Magnastriatites grandiosus*), legumes (*Rhoipites guianensis*), Bombacaceae (*Retistephanopites crassianulatus*), Euphorbiaceae (*Retitrescolpites? irregularis*), Sapotaceae (*Tetracolporopollenites transversalis*), Asteraceae (*Echitricolporites maristellae*), Malpighiaceae (*Perisyncolpites pokorny*), and Polygalaceae (*Psilastephanocolporites fissilis*), among others (Table 2). The sample from level 8 displays a pollen and spore flora similar to the samples from levels 1–7 but with both a reduction in the amount of amorphous organic matter and freshwater algae and the presence of dinoflagellate cysts (*Achomosphaera* sp.), acritarchs (*Leiosphaeridia* sp.), and foraminifer linings (Fig. 3, Table 2), all considered marine indicators.

Taphonomic differences between mollusk species (Fig. 4) and four taphofacies were revealed by quantitative taphonomy and biofabric analysis (Table 1, Fig. 5). *Mytilopsis* and arcids experienced stronger corrosion than *Anodontites* and *Sheppardiconcha*, but gastropods were more affected than bivalves by deformation and fragmentation (Figs. 6, 7); for most fragmented bivalve specimens, preservation was  $\geq 50\%$  (Table 1).

Taphofacies I (levels 1 and 7) is characterized by cracked, corroded, and incompletely deformed specimens embedded in a muddy matrix, with a medium-to-low packing density, becoming denser toward the top of the level. The multimodal pattern of the azimuthal orientation measurements is shown in Figure 3. Fossils exhibit variable (mixed) patterns of deformation, corrosion, and fragmentation (Figs. 7A–K), but corrosion was more important in level 7 than level 1 (Fig. 5). *Sheppardiconcha* was more abundant than *Mytilopsis* and *Anodontites*. *Sheppardiconcha* specimens are heavy, tall- and medium-sized gastropods (~50 mm long), ornamented with axial ribs and spiral streaks (Figs. 4C–D); they are characterized by a smooth, oblique aperture and the presence of an anal channel. *Mytilopsis* specimens are compressed bivalves with acuminate beaks and fine, concentric lines over the dorsal surface (Figs. 4E–F); they are differentiated by the presence of a hinge without teeth and a septum. *Anodontites* was less conspicuous in this taphofacies.

Taphofacies II (levels 2 and 6) is characterized by a high packing density of strongly corroded, undeformed, and unfragmented specimens (ranging from 9 mm to 109 mm long), cemented with a sandy matrix, and showing a concordant disposition (*sensu* Kidwell et al., 1986). Deformation was more important in level 6 than level 2 (Fig. 5). Molds of whole specimens of *Sheppardiconcha* (Figs. 6C–F) which retain the original morphology, and molds of the thin-shelled bivalve *Anodontites* are large, subelliptical, and strong (Figs. 4A–B). *Anodontites* specimens have a rugose surface, folded borders, and eroded and poorly pronounced beaks (Figs. 4A–B). The hinge plate is robust and without teeth.

Taphofacies III (level 5) contains highly deformed, cracked, and corroded specimens of *Sheppardiconcha* forming a thin, concordant, lenticular, densely packed fossiliferous layer. Specimens range between 8.3 mm and 23.7 mm long (Fig. 3).

Taphofacies IV (level 8) is characterized by small (7–15 mm long), moderately inflated molds of arcids (Figs. 4G–H, 6J–L) embedded in a muddy matrix, preserving the original sculpture of the shells for both the left and right valves (unarticulated; see Figs. 4G–H). Undeformed and unfragmented shells are filled with sediment and are ornamented by ribs that are interrupted with fine concentric lines.

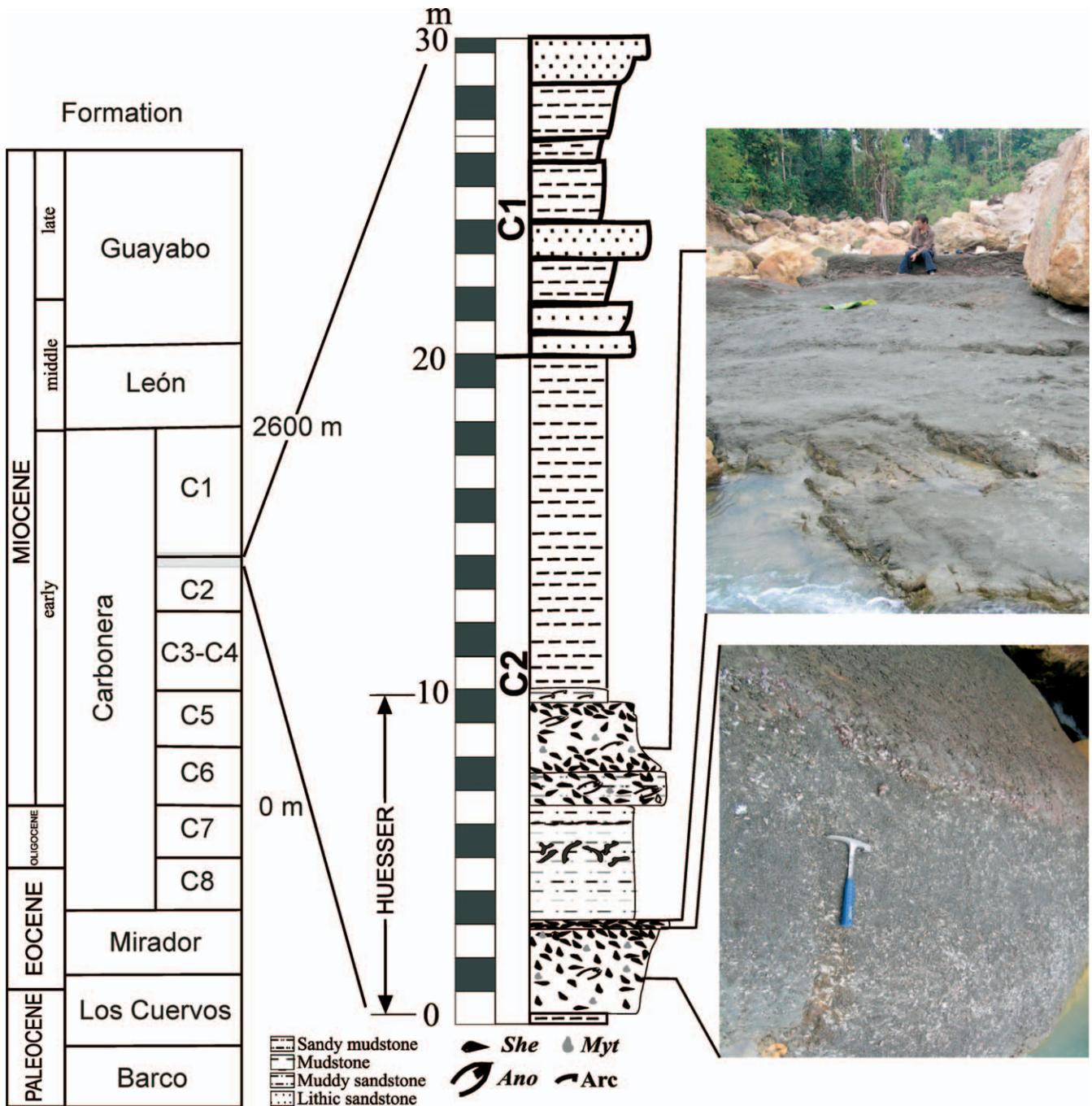


FIGURE 2—Stratigraphic position of the Huesser horizon in the Cenozoic sequence of the Eastern Cordillera and photographs of localities; She = *Sheppardiconcha*; Ano = *Anodontites*; Myt = *Mytilopsis*; ages and lithostratigraphy after Bayona et al. (2008).

DISCUSSION

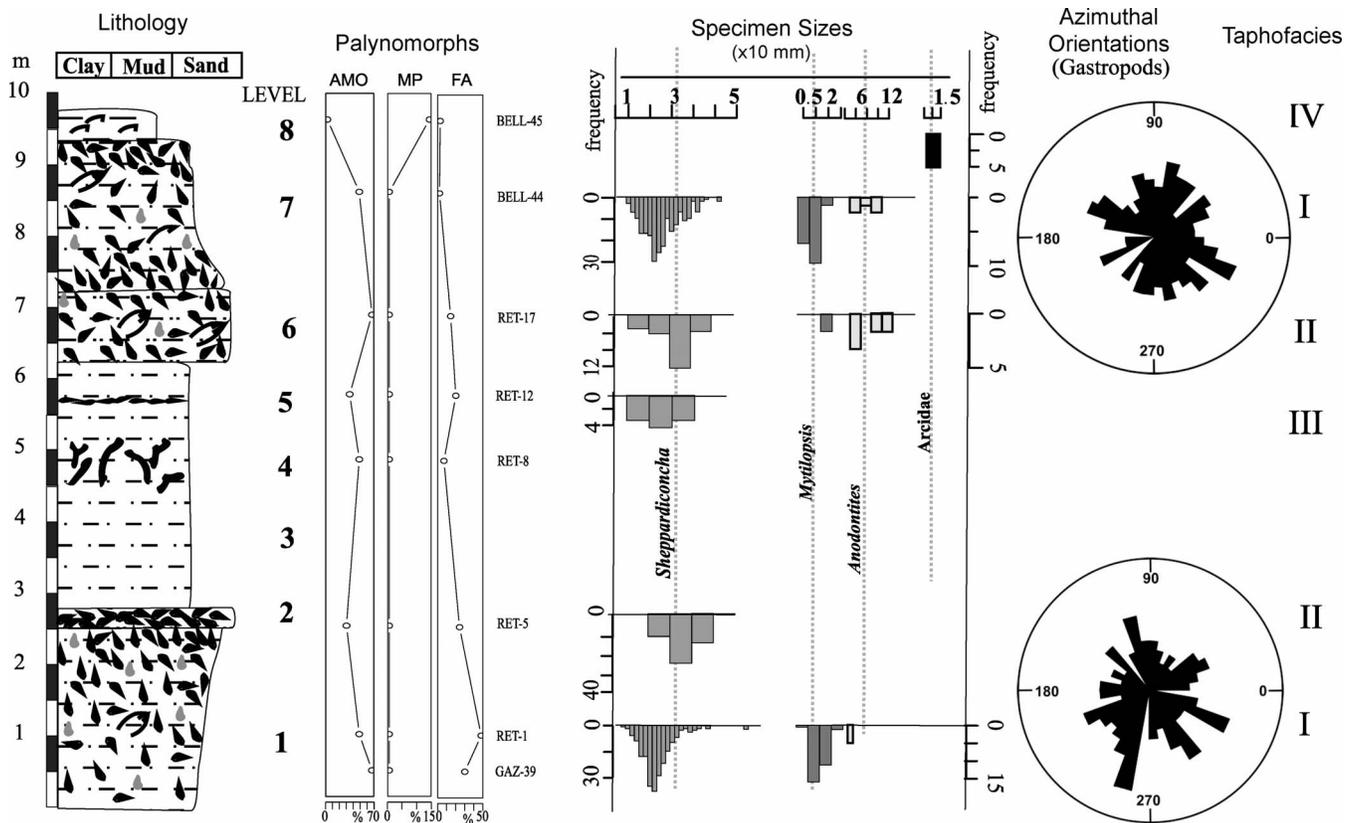
Molluscan Paleocology

Habitat preferences of the taxa in the Huesser horizon, dominance of *Sheppardiconcha*, and low diversity of the assemblage (Martens, 1997; Dillon, 2000) indicate freshwater and marginal marine environments. *Sheppardiconcha* and *Anodontites* are found abundantly in benthic communities of fluviolacustrine environments (Dillon, 2000; Wesselingh, 2006), and *Mytilopsis* in marginal or transitional environments (Gray and Marelli, 1985; Nuttall, 1990; Wesselingh, 2006) with very low salinity. Arcids are reported in marine environments (Marko and Jackson, 2001), and their occurrence at the top of the section (level 8) is probably associated with an increase in salinity that signaled the displacement of the

underlying freshwater *Sheppardiconcha*-dominated assemblage (levels 1–2, 5–7).

Freshwater and marginal marine environments are also suggested by the palynological assemblages. Levels 1–7 are characterized by abundant freshwater algae, amorphous organic matter, and a suite of plants characteristic of coastal plains (Table 2). All of these characteristics suggest a freshwater ecosystem, probably a lake (Lorente, 1986). Level 8 is clearly differentiated by the occurrence of marine palynomorphs (dinoflagellate, foraminifer linings, and acritarchs) and low levels of amorphous organic matter, which suggest a change to more marine conditions.

Differences in the distribution of the molluscan taxa are subtle (Fig. 1). *Sheppardiconcha* once had a Neotropical distribution from Central



#### Strike NE and angle of dip NW of outcrop

**FIGURE 3**—Composite column of the Huesser horizon showing distribution of fossil taxa, lithologic changes, variations in species abundances, packing, size sorting, taphofacies, and the azimuthal orientation of gastropods. Arc = Arcidae; AMO = Amorphous organic matter; MP = abundance of marine palynomorphs; FA = abundance of freshwater algae. Sample localities: RET = Retumbadora Ravine; GAZ = Gazaunta River; BELL = Bellavista Ravine (see Fig. 1); see Figure 2 for key to lithology symbols.

America (Neogene) to northwest South America (Oligocene–late Miocene), but it is now restricted to Central America (Wesselingh, 2006). *Anodontites* and *Mytilopsis* are common in northeastern and central South America from the Paleogene to the present (Pilsbry and Olsson, 1935; Parodiz, 1969; Nuttall, 1990). *Mytilopsis* has had a wide distribution in the Neotropics, today being a common genus in the Caribbean region and along the Pacific coast from Ecuador to Panamá (Wolff, 1969; Wesselingh, 2006). Arcids have been reported from the Neotropical Atlantic and Pacific coasts from the Paleogene until today (Abbott, 1974).

Taxa from the Huesser assemblage, except arcids, have been reported in the Pebas fauna of western Amazonia (Nuttall, 1990; Vermeij and Wesselingh, 2002; Wesselingh, 2006). They are closely related to the molluscan associations from Iquitos and Pebas in the Amazonas Basin (Nuttall, 1990; see Fig. 1) and La Cira, in the middle Magdalena Valley, central Colombia (Pilsbry and Olsson, 1935). This taxonomic affinity suggests a biogeographic connection between the Llanos, Amazonas, and Magdalena Valley basins (Fig. 1), an idea that was proposed by Wesselingh (2006). This connection does not exist today owing to the uplift of the Andes (Albert et al., 2006; Lovejoy et al., 2006).

#### Fidelity

Differences in preservation among taxa, suggested by taphonomic analysis (Fig. 5), would have been caused mainly by differential responses of taxa to deformation and corrosion due to differences in shape, size, width, and chemical composition of the shells (Brett and Baird, 1986). Even though the fidelity of the fossil assemblages of the Huesser horizon

could have been affected by differential preservation of taxa, the composition of the assemblages, affinity of species, and the structure of community, which is characteristic of freshwater molluscan communities, suggest that the original community is well represented by the fossil assemblage.

#### Sedimentary Processes

Diagenetic processes are an important factor in the formation of the Huesser horizon. Deformation and fragmentation would have resulted from compaction of sediments under lithostatic forces (Martello et al., 2007), and most corrosion was caused by postburial dissolution or precipitation. Differential effects of deformation, fragmentation, and corrosion, however, are due to conditions that originated during the accumulation of assemblages. Consequently, differences in taphonomy suggest that the molluscan assemblages underwent different sedimentary processes.

Deformation is common in assemblages in which fossils are incompletely filled (Hanley and Flores, 1987), as well as in fossils that are buried rapidly (Henderson and McNamara, 1985; Kidwell, 1986). Therefore, much of the deformation in level 5 (taphofacies III) would have been produced by rapid burial. In contrast, infilled specimens are common during reworking (Brett and Baird, 1986). Infilled gastropods, better cemented, are characteristic of levels 2 and 6 (taphofacies II). Therefore, levels 2 and 6 could have been the product of reworking, admixing, or exhumation (Seilacher, 1971; Krajewski, 1984; Hanley and Flores, 1987). Furthermore, most of the specimens lost some morphological features

TABLE 1—Huesser horizon fossil counts and taphonomic data. Calculation of the taphonomic index (TI) is explained in the text.

Level	Taxon	Size of specimens (mm)	Number of specimens	Deformation (%)			Corrasion (%)			Fragmentation (%)		
				0	1	2	0	1	2	0	1	2
8	<b>Arcidae</b>	<b>7.0–15</b>	<b>6</b>	<b>6 (100)</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>6 (100)</b>	<b>6 (100)</b>	<b>0</b>	<b>0</b>
7	<b>Total by level</b>	<b>3.0–82</b>	<b>255</b>	<b>62 (24.3)</b>	<b>66 (25.9)</b>	<b>127 (49.8)</b>	<b>40 (15.7)</b>	<b>84 (32.9)</b>	<b>131 (51.4)</b>	<b>85 (33.3)</b>	<b>83 (32.5)</b>	<b>87 (34.1)</b>
	<i>Sheppardiconcha</i>	4.0–47	232 (90.9)	44 (19)	62 (26.7)	126 (54.3)	39 (16.8)	82 (35.3)	111 (47.8)	67 (28.9)	79 (34.1)	86 (37.1)
	<i>Anodontites</i>	26.7–82	5 (1.9)	2 (40)	3 (60)	0	1 (20)	2 (40)	2 (40)	5 (71.4)	0	0
	<i>Mytilopsis</i>	3.0–11.6	18 (7.05)	16 (88.9)	1 (5.56)	1 (5.56)	0	0	18 (100)	13 (72.2)	4 (22.2)	1 (5.56)
6	<b>Total by level</b>	<b>9.0–109</b>	<b>38</b>	<b>5 (13.2)</b>	<b>9 (23.7)</b>	<b>15 (39.5)</b>	<b>3 (7.89)</b>	<b>4 (10.5)</b>	<b>31 (81.6)</b>	<b>14 (36.8)</b>	<b>6 (15.8)</b>	<b>9 (23.7)</b>
	<i>Sheppardiconcha</i>	9.0–35.5	29 (76.3)	5 (17.2)	9 (31)	15 (51.7)	2 (6.9)	2 (6.9)	25 (86.2)	14 (48.3)	6 (20.7)	9 (31)
	<i>Anodontites</i>	11.7–109	7 (18.4)	5 (71.4)	2 (28.6)	0	1 (14.3)	2 (28.6)	4 (57.1)	5 (71.4)	1 (14.3)	1 (14.3)
	<i>Mytilopsis</i>	11.6–14.5	2 (5.3)	2 (100)	0	0	0	0	2 (100)	2 (100)	0	0
5	<i>Sheppardiconcha</i>	<b>8.3–23.7</b>	<b>10</b>	<b>0</b>	<b>0</b>	<b>10 (100)</b>	<b>9 (90)</b>	<b>1 (10)</b>	<b>0</b>	<b>2 (20)</b>	<b>3 (30)</b>	<b>5 (50)</b>
2	<b>Total by level</b>	<b>10.7–44</b>	<b>109</b>	<b>90 (82.6)</b>	<b>14 (12.8)</b>	<b>5 (4.59)</b>	<b>1</b>	<b>3 (2.75)</b>	<b>105 (96.3)</b>	<b>68 (62.4)</b>	<b>23 (21.1)</b>	<b>18 (16.5)</b>
	<i>Sheppardiconcha</i>	10.7–44	108 (99.1)	89 (82.4)	14 (13)	5 (4.63)	0	3 (2.78)	105 (97.2)	68 (63)	23 (21.3)	17 (15.7)
	<i>Anodontite</i>	28.3	1 (0.9)	1 (100)	0	0	1 (100)	0	0	0	0	1 (100)
1	<b>Total by level</b>	<b>3.0–63</b>	<b>262</b>	<b>60 (22.9)</b>	<b>78 (29.8)</b>	<b>124 (47.3)</b>	<b>114 (43.5)</b>	<b>76 (29)</b>	<b>72 (27.5)</b>	<b>72 (27.5)</b>	<b>103 (39.3)</b>	<b>87 (33.2)</b>
	<i>Sheppardiconcha</i>	3.0–41	226 (86.3)	39 (17.3)	71 (31.4)	116 (51.3)	112 (49.6)	74 (32.7)	40 (17.7)	47 (20.8)	94 (41.6)	85 (37.6)
	<i>Anodontites</i>	7.6–63	5 (1.9)	4 (80)	0	1 (20)	2 (40)	2 (40)	1 (20)	0	3 (60)	2 (40)
	<i>Mytilopsis</i>	5.0–16	31 (11.8)	17 (54.8)	7 (22.6)	7 (22.6)	0	0	31 (100)	25 (80.6)	6 (19.4)	0
	<b>Total</b>		<b>680</b>	<b>230 (33.8)</b>	<b>169 (24.9)</b>	<b>281 (41.3)</b>	<b>167 (24.6)</b>	<b>168 (24.7)</b>	<b>345 (50.7)</b>	<b>254 (37.4)</b>	<b>219 (32.2)</b>	<b>207 (30.4)</b>
	<i>Sheppardiconcha</i>	3.0–47	605 (88.9)	177 (29.3)	156 (25.8)	272 (45)	162 (26.8)	162 (26.8)	281 (46.4)	198 (32.7)	205 (33.9)	202 (33.4)
	<i>Anodontites</i>	7.6–109	18 (2.7)	12 (66.7)	5 (27.8)	1 (5.56)	5 (27.8)	6 (33.3)	7 (38.9)	10 (55.6)	4 (22.2)	4 (22.2)
	<i>Mytilopsis</i>	3.0–16	51 (7.5)	35 (68.6)	8 (15.7)	8 (15.7)	0	0	51 (100)	40 (78.4)	10 (19.6)	1 (1.96)
	<i>Arcidae</i>	7.0–15	6 (0.9)	6 (100)	0	0	0	0	6 (100)	6 (100)	0	0

Packing

TAPHONOMIC INDEX

Level	Taphofacies	Packing			Disposition	Bivalves		Gastropods		TAPHONOMIC INDEX					
		Low	Medium	High		TI0	TI1	TI2							
8		Low	Medium	High	Random	6	100%	0	0%	4	67%	0	0%	2	33%
7		Low	Medium	High	Random	23	9%	232	91%	62.3	24%	77.7	30%	115	45%
6		Low	Medium	High	Concordant	9	24%	29	76%	7.33	19%	6.33	17%	18.3	48%
5		Low	Medium	High	Concordant	0	0%	10	100%	3.67	37%	1.33	13%	5	50%
4		Low	Medium	High											
3		Low	Medium	High											
2		Low	Medium	High	Concordant	1	1%	109	99%	53	49%	13.3	12%	42.7	39%
1		Low	Medium	High	Random	32	12%	226	88%	82	31%	85.7	33%	94.3	36%

TABLE 2—Huesser horizon palynomorph biostratigraphic range chart. RET = Retumbadora Ravine; GAZ = Gazaunta River; BELL = Bellavista Ravine.

Sample	RET-1	GAZ-39	RET-5	RET-8	RET-12	RET-17	BELL-44	BELL-45
Level	1	1	2	4	5	6	7	8
Amorphous organic matter (%)	90	70	50	70	55	90	70	20
<b>Species</b>								
<i>Achomospaera</i> sp. (dinoflagellate)	0	0	0	0	0	0	0	1
Foram lining	0	0	0	0	0	0	0	1
<i>Leiosphaeridia</i> sp. (acritarch)	0	0	0	0	0	0	0	39
<i>Botryococcus</i> sp. (freshwater alga)	16	46	28	3	5	13	0	4
<i>Pediastrum</i> sp. (freshwater alga)	1	5	6	0	0	0	0	0
<i>Cricotriporites</i> sp.	1	0	0	0	0	0	0	0
<i>Cicatricosisporites dorogensis</i> (reworked)	1	1	0	0	0	0	0	0
<i>Echiperiporites akanthos</i>	1	0	0	0	0	0	0	0
<i>Echipollenites</i> sp.	0	0	0	0	0	0	1	0
<i>Echiriletes</i> sp.	0	0	0	1	0	1	0	0
<i>Echitricolporites maristellae</i>	0	0	0	0	0	0	0	1
<i>Faveotriletes ornatus</i>	0	0	1	0	0	0	0	0
Fungi	4	3	0	1	0	0	0	0
<i>Laevigatosporites tibuensis</i>	6	5	5	4	0	4	1	19
<i>Laevigatosporites</i> sp.	0	0	0	0	0	0	2	0
<i>Laevigatosporites</i> sp.1	0	0	0	0	0	0	0	1
<i>Magnastriatites grandiosus</i>	1	0	4	3	0	3	1	0
<i>Mauritiidites franciscoi</i> var. <i>franciscoi</i>	2	0	7	4	0	3	1	46
<i>Mauritiidites franciscoi</i> var. <i>minutus</i>	0	0	0	2	0	0	1	0
<i>Monoporopollenites annulatus</i>	0	0	1	0	1	0	0	0
<i>Nijssenosporites</i> sp.	0	0	0	0	0	1	0	0
Onagraceae type	0	0	0	0	0	0	0	2
<i>Perisyncolpites pokorny</i>	0	5	1	0	0	0	0	13
<i>Psilatriletes</i> sp.	4	1	4	1	0	8	0	1
<i>Psilabrevitricolporites triangularis</i>	0	0	0	0	0	0	0	3
<i>Psilastephanocolporites fissilis</i>	0	1	0	0	0	0	0	1
<i>Psilamonocolpites</i> sp.	0	0	0	1	0	0	0	0
<i>Psilamonocolpites medius</i>	0	0	1	0	0	0	0	1
<i>Pollenites</i>	5	0	10	3	1	4	6	12
Pollen porate	0	0	1	0	0	0	0	0
<i>Polypodiisporites</i> sp. 1	6	16	34	12	12	25	13	69
<i>Psilabrevitricolporites</i> sp.	0	0	1	0	0	0	0	0
<i>Retitricolpites simplex</i>	1	0	1	0	0	4	0	18
<i>Retitrescolpites?</i> <i>irregularis</i>	0	0	0	0	0	0	0	19
<i>Reticolporites</i> aff. <i>poriconspectus</i>	0	0	1	1	0	0	0	0
<i>Retistephanoporites crassiannulatus</i>	0	0	0	0	0	0	0	4
<i>Retitricolporites</i> aff. <i>santaisabelensis</i>	0	0	0	0	0	1	0	9
<i>Retitricolpites</i> sp.	0	0	1	0	0	0	0	0
<i>Rhoipites</i> sp.	0	0	1	1	1	2	0	0
<i>Rhoipites guianensis</i>	0	2	0	0	0	0	0	0
<i>Tetracolporopollenites transversalis</i>	0	0	0	0	1	1	0	1
<i>Verrucatotriletes</i> aff. <i>etayoi</i>	0	0	1	0	0	1	0	0
<i>Verrucatosporites usmensis</i>	0	6	12	4	1	13	3	4
<i>Verrutriletes viruelensis</i>	0	0	2	0	0	0	0	0
<i>Verrutriletes</i> sp.	0	0	0	1	0	0	0	0
<i>Striatopolis</i> sp.	0	0	0	3	0	0	0	0

owing to abrasion and corrosion, as evidenced by strong corrosion. Reworking in taphofacies II is also evidenced by packing and concordant disposition of specimens.

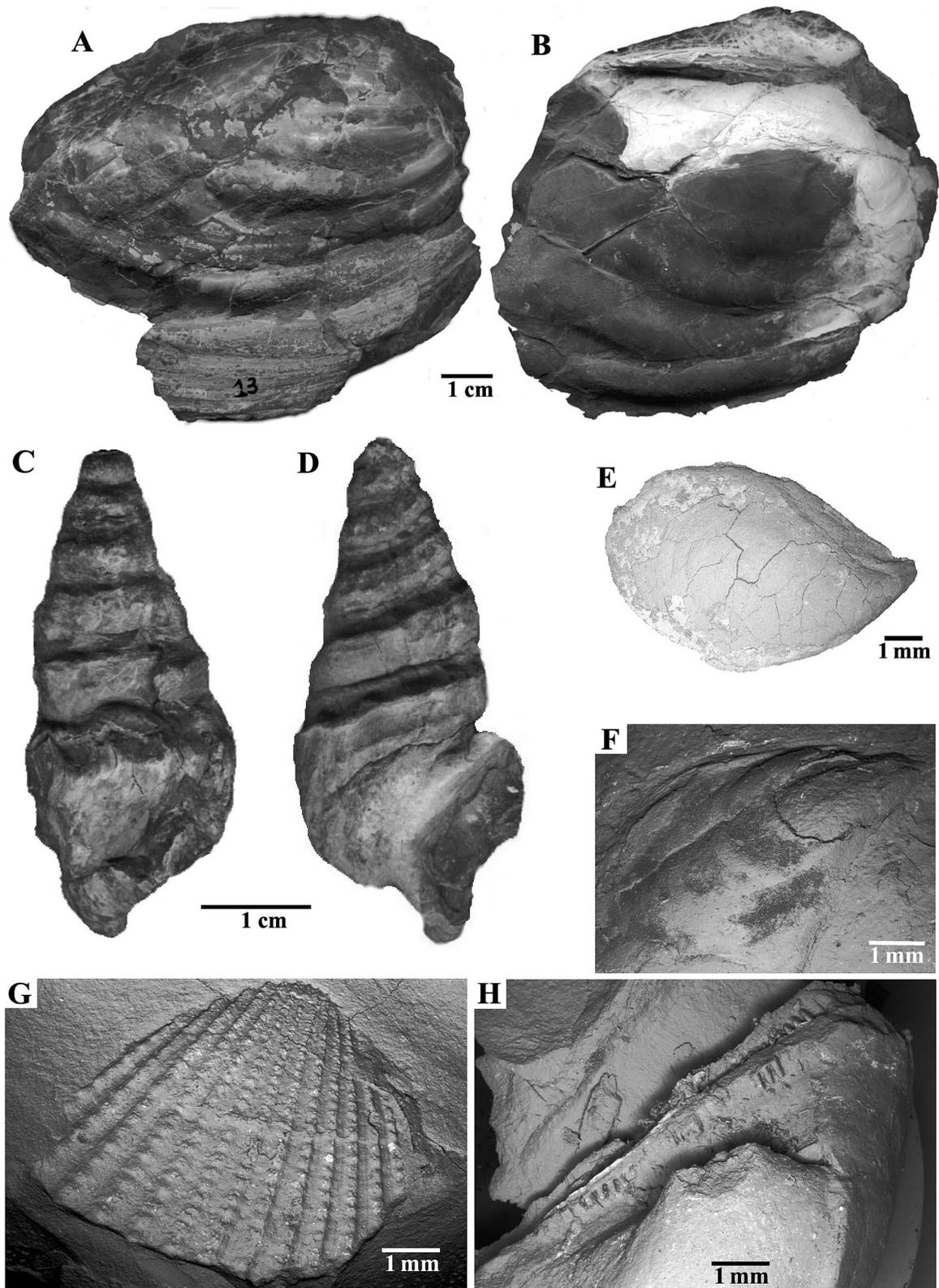
Random orientation of fossils in assemblages from level 1 and 7 (taphofacies I) indicate that specimens preserved the attitude of shells at the time of death under a low-energy regime (Menard and Boucot, 1951; Allen, 1984, 1990; Brenchley and Newall, 1970; LaBarbera, 1977; Williams and Richards, 1984; Brett and Baird, 1986).

Postburial dissolution affected all levels but is better observed in level 8 (taphofacies IV), where molds preserved the original sculpture of the shells. When sediments are rich in organic matter or have low pH, postburial dissolution of fossils is enhanced (Seilacher et al., 1985; Brett and Baird, 1986), producing corroded and thinned shells (Aller, 1982).

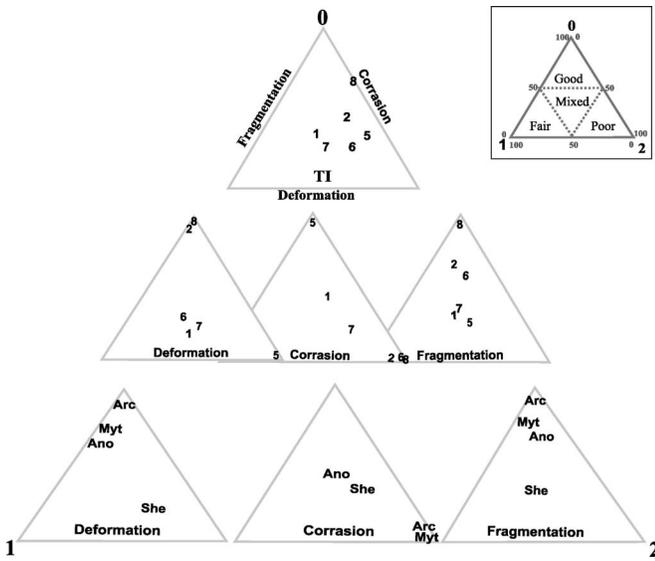
The overall taphonomy of the Huesser shows slight changes in sedimentation through time: levels 1 and 7 (taphofacies I) could have

formed during a low-energy regimen. Levels 2 and 6 (taphofacies II) would have formed by reworking and a concomitant long residence time caused by shallowing. Level 5 (taphofacies III) corresponds to an episodic event, and level 8 (taphofacies IV) to a drastic change in environment, as noted above. Sedimentary processes controlling levels 3 and 4 are difficult to establish. Level 4 is characterized by a massive, muddy sandstone—with scattered reddish mottling, a pollen flora indicative of a coastal plain (Lorente, 1986)—and ichnofossils; this level may represent episodes of subaerial exposure in a coastal plain environment. Ichnofossils present in the level could not be identified to confirm this hypothesis, however.

The Huesser horizon may have accumulated in three events, or parasequences. The first parasequence includes levels 1–5, the second, levels 6–7, and the base of a third parasequence is evident in level 8. The first parasequence includes a general trend toward more fluvial conditions,



**FIGURE 4**—Huesser horizon molluscan species. A–B) *Anodontites*. C–D) *Sheppardiconcha*. E–F) *Mytilopsis* (scanning electron micrograph). G–H) Molds of arcids (scanning electron micrograph).



**FIGURE 5**—Taphogram illustrating differences in taphonomic patterns (packing, deformation, corrosion, fragmentation) among levels 1–7 and among taxa (see Fig. 3 for stratigraphic position of the levels). Differences are reflected by discrete values (= 0, 1, 2, based on percentage of shells affected by taphonomic processes), with 0 = low; 2 = highly affected. Taphonomic index (TI), packing, and disposition define the taphofacies I, II, III, and IV (see text for further details). She = *Shepardiconcha*; Ano = *Anodontites*; Myt = *Mytilopsis*; Arc = *Arcidae*.

with the development of lakes in levels 1–2 and the subsequent development of a coastal plain in levels 3–5 (Fig. 3). The second parasequence starts with a deepening of the water depth in the deposit and development of a lake at the base of level 6. The third parasequence begins with a marine incursion at the base of level 8. The general stacking pattern of the parasequences indicates a transgressive trend from level 1 to level 8 (Fig. 3).

Changes in sedimentary processes would have been controlled by water-level fluctuations of the lake and the slope of the basin, both of which are known to play a major role in controlling deposition in lake environments (Cohen, 1989).

#### Age

The Huesser horizon can be placed within the *Verrutricolporites ro tundiporus* palynological zone of Germeraad et al. (1968), palynological zone 27 of Muller et al. (1987), or palynological zone 34 of Jaramillo and Rueda (2004), based on the co-occurrence of *Echitricolpites maristellae*, *Magnastriatites grandiosus*, *Perisyncolpites pokorny*, *Retitricolpites simplex*, *R. irregularis*, *R. santaisabelensis*, and *Psilastephanocolporites fissilis* (Table 2). These northern South American palynological zones have been calibrated, using planktonic foraminifera and nanoplankton, as early Miocene (Germeraad et al., 1968; Lorente, 1986; Muller et al., 1987).

The time span that the Huesser horizon represents is difficult to assess, owing to the occurrence of unfossiliferous and fossiliferous levels with different taphonomic patterns. The time-averaging patterns identified in shallow-marine assemblages suggest that shell beds could represent time spans of about  $10^2$ – $10^3$  years (Flessa et al., 1993; Kowalewski et al., 1998; Olszewski, 1999). According to Kowalewski et al. (1998), this estimation could be valid for many mollusk-dominated beds. There are six fossiliferous levels in the Huesser horizon (1–2, 5–8). Levels 3–4 lack fossils, and estimating their duration could be more problematic, but they could represent less time condensation than the shell beds. Here we assume that their duration was similar to that of a shell bed. Thus, taking into account the whole horizon, and assuming  $10^2$ – $10^3$  years per level,

we propose that the Huesser took from 800 years to 8000 years to accumulate.

A different approach to determining the duration of the Huesser horizon is to calculate sedimentation rates. The entire lower Miocene (7.06 myr) in the Medina region in the Llanos Basin is represented by 2600 m (Carbonera Formation C6–C1; see Fig. 2). Assuming a constant rate of accumulation ( $37 \times 10^{-5}$  m per year), the 10 m of the Huesser could represent  $\sim 27$  kyr. On the basis of these two estimates combined, the Huesser could have accumulated over 800–27,000 years. This estimate is just a first-order approximation, but it is important to make, given the possible paleoecological and evolutionary implications of a large lake.

#### Genesis of the Huesser Horizon

The faunal and palynological assemblages and their taphonomy suggest that the Huesser horizon developed in a freshwater system. The lateral homogeneity of the layers and their large lateral extension (the horizon can be traced laterally for  $\sim 35$  km, although the aerial extent is unknown; see Mora and Parra, 2004) suggest that this body of water was a large freshwater lake, similar to those described in other deposits in South America (e.g., Räsänen et al., 1995; Vonhof et al., 1998; Wesselingh et al., 2002). This interpretation is bolstered by the laterally extensive mollusk layers, which are common in lacustrine sequences (Reineck and Singh, 1980; Owen et al., 1982; Johnson, 1984; Olsen, 1985; Cohen, 1989; Talbot and Allen, 1996).

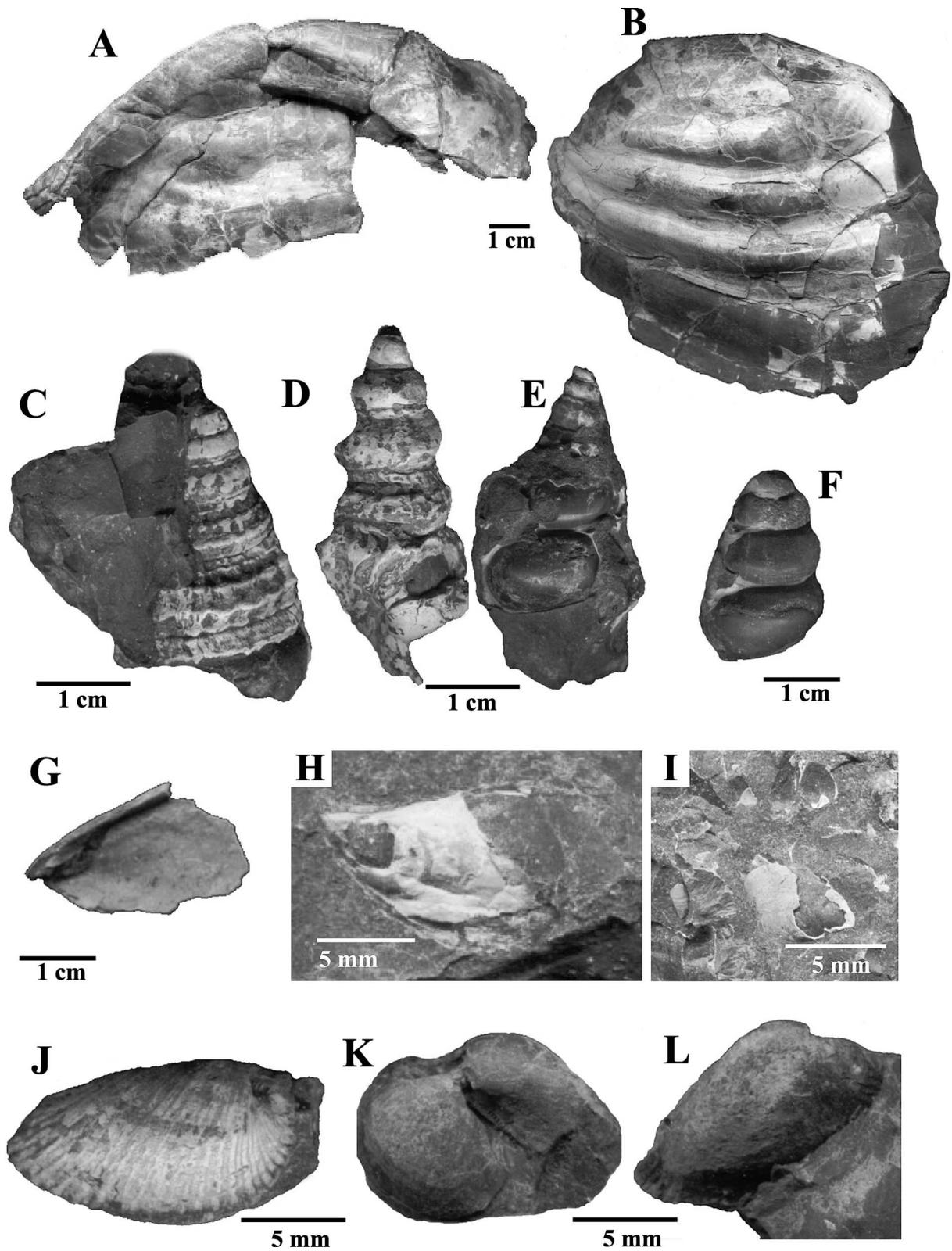
The Pebas fauna, related to the Huesser horizon assemblages, has been interpreted as having accumulated in an extensive lake, thousands of kilometers wide, called the Pebas Megalake, although these middle Miocene deposits are younger than the Huesser (Vonhof et al., 1998; Wesselingh et al., 2002; Wesselingh, 2006). A possible correlative of the Pebas Megalake could be the middle Miocene Léon Formation, which is stratigraphically 1000 m above the Huesser horizon (Fig. 2). The Pebas fauna has been interpreted as originating in northern South America and later expanding to Amazonia via the Llanos Basin (Wesselingh, 2006).

The presence of arcids at the top of the Huesser sequence represents a brief marine incursion into the Llanos Basin during the early Miocene. This southward marine incursion would have occurred from the Caribbean, as has been suggested by Guzman and Fischer (2006), via Lake Maracaibo (Fig. 8). If the Andes of Mérida were already uplifted at that time (De Toni and Kellogg, 1993; Villamil, 1999), communication between the Llanos and Maracaibo basins would have been closed. The timing of the uplift is highly controversial, however, and could have occurred during the middle Miocene (Hoorn et al., 1995).

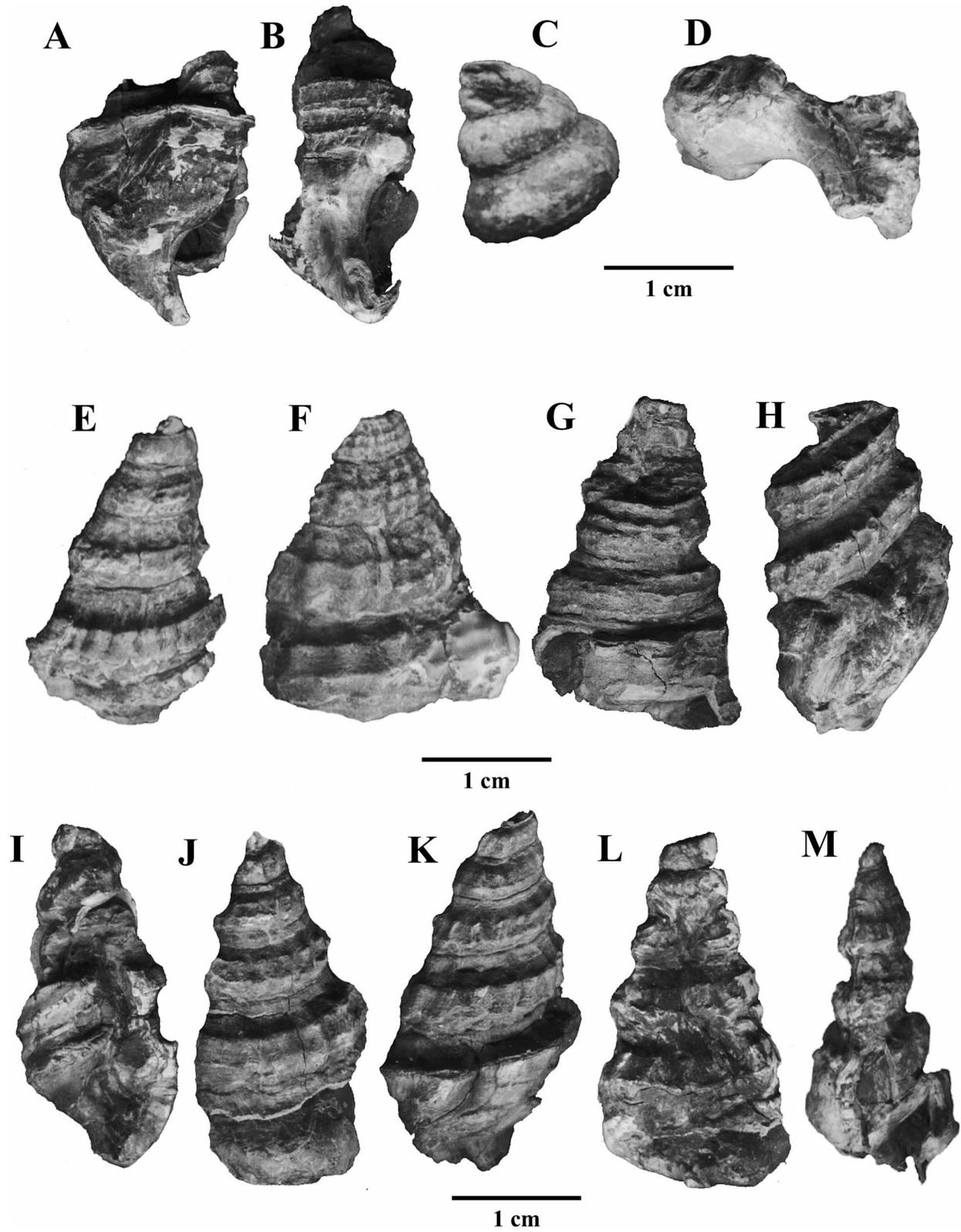
The presence of marine elements in the Huesser might be evidence that the connection between Lake Maracaibo and the Llanos Basin was active during the early Miocene and thus that the Mérida Andes were not yet uplifted during that time (Hoorn et al., 1995). A second alternative is a marine flooding through the Venezuelan Llanos (Barinas-Apure Basin), where the Guardulio Member (Guafita Formation, Oligocene–Miocene), which was deposited in fluviodeltaic environments, shows evidence of more marine conditions toward the top of the sequence (Ortega et al., 1987; *Léxico Estratigráfico de Venezuela*, 1996; Pindell et al., 1998). This formation is overlain by the fluvially dominated Parangula Formation (*Léxico Estratigráfico de Venezuela*, 1996). A more precise dating of the marine flooding at the top of the Guardulio Member is needed to prove a connection with the Huesser horizon.

The origin of a large lake in the Huesser horizon might be explained by a rapid increase in the tectonic subsidence rates in the foreland Llanos Basin, which started at the same time that the upper Carbonera Formation accumulated (early Miocene–earliest middle Miocene,  $\sim 18$ – $14$  Ma) in the Llanos Basin (Sarmiento, 2002; Bayona et al., 2008). This initial rapid change in subsidence could have produced an extensive lake, as has been shown in other foreland basins (Rogers, 1994; Uba et al., 2005). This tectonically driven subsidence seems also to coincide with a first-order event of sea-level rise (Haq et al., 1987), generating conditions that may

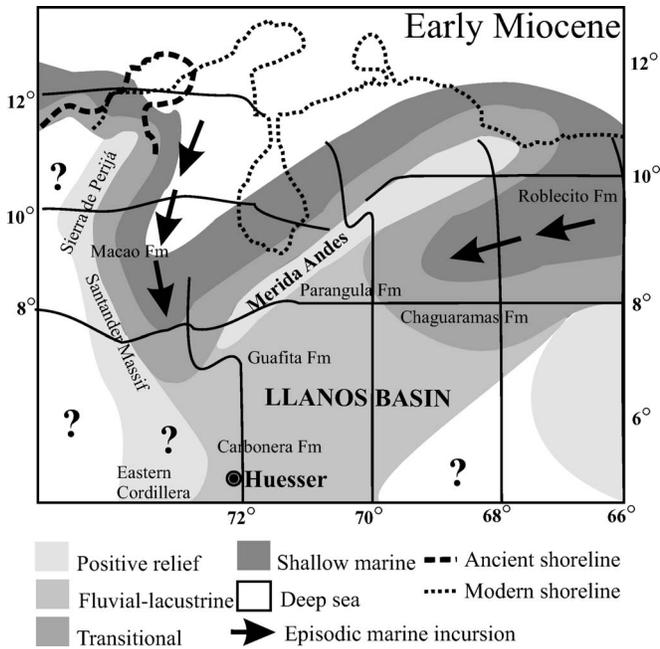




**FIGURE 6**—Fossils illustrating corrosion. A–F) Specimens of taphofacies II. Strong corrosion in all specimens and deformation in *Anodontites* can be observed. Scale bar below for both A and B. G–I) Cracked and corroded specimens of *Mytilopsis* in taphofacies I. J–L) Specimens of taphofacies IV. Molds of arcids with the original sculpture exhibiting strong dissolution. Scale bar below for both J and K.



**FIGURE 7**—Fragmentation and deformation in gastropods. A–D) Poor (2) = <50% of specimen is preserved. E–H) Fair (1) = 50%–80% preserved. I–M) Good (0) = >80% preserved. A–K) Specimens of taphofacies I. L–M) Strong deformation in taphofacies III.



**FIGURE 8**—Paleogeographic map during the early Miocene in northern South America. Changes in configuration and two possible marine incursions are proposed based on the paleogeographic reconstructions of Pindell et al. (1998) and Guzman and Fischer (2006).

have favored extensive lacustrine-estuarine deposition in the Llanos Basin during the early and middle Miocene (Bayona et al., 2008).

#### ACKNOWLEDGMENTS

This project was supported by the Smithsonian Paleobiology Endowment Fund. Thanks to M. Zuschin and J. Hartman for detailed reviews of the manuscript. F. Wesselingh helped with mollusk taxonomy, and S. Morón, T. Gaona, and L. Quiroz helped with fieldwork. N. Atkins improved the readability of the manuscript. Special thanks go to M. I. Barreto for her continuous support and ideas.

#### REFERENCES

- ABBOTT, R.T., 1974, *American Seashells*: D. van Nostrand Reinhold Co., New York, 663 p.
- ALBERT, J.S., LOVEJOY, N.R., and CRAMPTON, G.R., 2006, Miocene tectonism and the separation of cis- and trans-Andean river Basins: Evidence from neotropical fishes: *Journal of South American Earth Sciences*, v. 21, p. 14–27.
- ALLEN, J.R.L., 1984, Experiments on the settling, overturning and entrainment of bivalve shells and related models: *Sedimentology*, v. 31, p. 227–250.
- ALLEN, J.R.L., 1990, Transport-hydrodynamics, in Briggs, D. E. G., and Crowther, P. R., eds., *Palaeobiology: A Synthesis*: Blackwell Scientific Publications, Oxford, UK, p. 227–230.
- ALLER, R.C., 1982, Carbonate dissolution in nearshore terrigenous muds: The role of physical and biological reworking: *Journal of Geology*, v. 90, p. 79–95.
- BAYONA, G., JARAMILLO, C., RUEDA, M., and REYES-HARKER, A., 2008, An integrated analysis of an orogen-sedimentary basin pair: Latest Cretaceous–Cenozoic evolution of the linked Eastern Cordillera orogen and the Llanos foreland basin of Colombia: *Geological Society of America Bulletin*, v. 120, p. 1171–1197.
- BEST, M.M.R., and KIDWELL, S.M., 2000, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings: pt. 1, Environmental variation in shell condition: *Paleobiology*, v. 26, p. 80–102.
- BOUCOT, A.J., BRACE, W., and DEMAR, R., 1958, Distribution of brachiopod and pelecypod shells by currents: *Journal of Sedimentary Petrology*, v. 28, p. 321–332.
- BRENCHLEY, P.J., and NEWALL, G., 1970, Flume experiments on the orientation and transport of models and shells: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 7, p. 185–220.
- BRETT, C., and BAIRD, G., 1986, Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation: *PALAIOS*, v. 1, p. 207–277.
- COHEN, A., 1989, The taphonomy of gastropod shell accumulations in large lakes: An example from Lake Tanganyika, Africa: *Paleobiology*, v. 15, p. 26–45.
- COOPER, M.A., ADDISON, F.T., ALVAREZ, R., CORAL, M., GRAHAM, R.H., HAYWARD, A.B., HOWE, S., MARTINEZ, J., NAAR, J., PEÑAS, R., PULHAM, A.J., and TABORDA, A., 1995, Basin development and tectonic history of the Llanos Basin, Eastern Cordillera, and Middle Magdalena Valley, Colombia: *AAPG (American Association of Petroleum Geologists) Bulletin*, v. 79, p. 1421–1443.
- DE TONI, B., and KELLOGG, J., 1993, Seismic evidence for blind thrusting of the northwestern flank of the Venezuelan Andes: *Tectonics*, v. 12, p. 1393–1409.
- DILLON, R.T., 2000, *The Ecology of Freshwater Mollusks*: Cambridge University Press, Cambridge, UK, 509 p.
- FLESSA, K.W., CUTLER, A.H., and MELDAHL, K.H., 1993, Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat: *Paleobiology*, v. 19, p. 266–286.
- GERMERAAD, J.H., HOPPING, C.A., and MÜLLER, J., 1968, Palynology of Tertiary sediments from tropical areas: Review of Palaeobotany and Palynology, v. 6, p. 189–348.
- GRAY, S., and MARELLI, D.C., 1985, Comments on the status of recent members of the genus *Mytilopsis* (Bivalvia: Dreissenidae): *Malacological Review*, v. 18, p. 117–121.
- GUZMAN, J.I., and FISHER, W.L., 2006, Lower and middle Miocene depositional history of the Maracaibo Basin, Western Venezuela: *AAPG (American Association of Petroleum Geologists) Bulletin*, v. 90, p. 625–655.
- HANLEY, J.H., and FLORES, R.M., 1987, Taphonomy and paleoecology of non-marine Mollusca: Indicators of alluvial plain lacustrine sedimentation, upper part of the Tongue River Member, Fort Union Formation (Paleocene), northern Powder River Basin, Wyoming and Montana: *PALAIOS*, v. 2, p. 479–496.
- HAQ, B.U., HARDENBOL, J., and VAIL, P., 1987, Chronology of fluctuating sea levels since the Triassic: *Science*, v. 235, p. 1156–1166.
- HENDERSON, R.A., and MCNAMARA, K.J., 1985, Taphonomy and ichnology of cephalopod shells in a Maastrichtian chalk from Western Australia: *Lethaia*, v. 18, p. 305–322.
- HOORN, M.C., 1994, Fluvial palaeoenvironments in the intracratonic Amazonas Basin (early Miocene–early Middle Miocene, Colombia): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 109, p. 1–54.
- HOORN, M.C., GUERRERO, J., SARMIENTO, G.A., and LORENTE, M.A., 1995, Andean tectonics as a cause for changing drainage patterns in Miocene northern South America: *Geology*, v. 23, p. 237–240.
- JARAMILLO, C., and RUEDA, M., 2004, Impact of biostratigraphy on oil exploration, in ACGGP (Asociación Colombiana de Geólogos y Geofísicos del Petróleo), ed., III Convención Técnica ACGGP, La Inversión en el Conocimiento Geológico: v. P4 [CD-ROM], Bogotá, p. 1–6.
- JOHNSON, T.C., 1984, Sedimentation in large lakes: *Annual Review of Earth and Planetary Sciences*, v. 12, p. 179–204.
- KIDWELL, S.M., 1986, Models for fossil concentrations: Paleobiologic implications: *Paleobiology*, v. 12, p. 6–24.
- KIDWELL, S., FÜRSCHE, F.T., and AIGNER, T., 1986, Conceptual framework for the analysis and classification of fossil concentrations: *PALAIOS*, v. 1, p. 228–238.
- KOWALEWSKI, M., FLESSA, K., and HALLMAN, D.P., 1995, Ternary taphograms: Triangular diagrams applied to taphonomic analysis: *PALAIOS*, v. 10, p. 478–483.
- KOWALEWSKI, M., GOODFRIEND, G.A., and FLESSA, K.W., 1998, High-resolution estimation of temporal mixing within shell beds: The evils and virtues of time-averaging: *Paleobiology*, v. 24, p. 287–304.
- KRAJEWSKI, K.P., 1984, Early diagenetic phosphate cements in the Albian condensed glauconitic limestone of the Tatra Mountains, Western Carpathians: *Sedimentology*, v. 31, p. 443–470.
- LABARBERA, M., 1977, Brachiopod orientation to water movement: pt. 1, Theory, laboratory behavior, and field orientations: *Paleobiology*, v. 3, p. 270–287.
- LÉXICO ESTRATIGRÁFICO DE VENEZUELA, 1996, 2nd ed., *Boletín de Geología, Publicación Especial 4*, Ministerio de Energía y Minas, Caracas, Venezuela, 756 p.
- LORENTE, M.A., 1986, *Palynology and Palynofacies of the Upper Tertiary of Venezuela: Dissertatione Botanicae*, J. Cramer, Berlin, 222 p.
- LOVEJOY, N.R., ALBERT, J.S., and CRAMPTON, W.G.R., 2006, Miocene marine incursions and marine/freshwater transitions: Evidence from neotropical fishes: *Journal of South American Earth Sciences*, v. 20, p. 14–27.
- MARCO, P.B., and JACKSON, J.B.C., 2001, Patterns of morphological diversity among and within arcid bivalve species pairs separated by the Isthmus of Panama: *Journal of Paleontology*, v. 75, p. 509–606.
- MARTELLO, A.R., KOTZIAN, C.B., and SIMÕES, M.G., 2007, Quantitative fidelity of recent freshwater mollusk assemblages from the Touro Passo River, Rio Grande do Sul, Brazil: *Iheringia, Serie Zoologia*, v. 96, p. 453–465.
- MARTENS, K., 1997, Speciation in ancient lakes: *Trends in Ecology and Evolution*, v. 12, p. 177–182.
- MENARD, H.W., and BOUCOT, A.J., 1951, Experiments on the movement of shells by water: *American Journal of Science*, v. 249, p. 131–151.

- MOORE, R.C., 1969, *Treatise on Invertebrate Paleontology: Part N, Mollusca: Bivalvia*: University of Kansas and the Geological Society of America, Inc., New York, 489 p.
- MORA, A., and PARRA, M., 2004, Secciones Estratigráficas de las Formaciones Guadalupe, Barco y Carbonera, Anticlinal del Guavio: Informe Final: Instituto Colombiano del Petróleo, Bucaramanga, Colombia, 28 p.
- MULLER, J., DI GIACOMO, E., and VAN ERVE, A., 1987, A palynologic zonation for the Cretaceous, Tertiary and Quaternary of northern South America: American Association of Stratigraphic Palynologists Contribution Series, v. 19, p. 7–76.
- NUTTALL, C.P., 1990, A review of the Tertiary non-marine molluscan faunas of the Pebas and other inland Basins of north-western South America: Bulletin of the British Museum (Natural History), Geology, v. 45, p. 165–371.
- OLSEN, P.E., 1985, Significance of great lateral extent of thin units in the Newark Supergroup (lower Mesozoic, eastern North America): AAPG (American Association of Petroleum Geologists) Bulletin, v. 69, p. 1444.
- OLSZEWSKI, T., 1999, Taking advantage of time-averaging, Paleobiology, v. 25, p. 226–238.
- ORTEGA, J.F., VAN ERVE, A., and MONROY, L., 1987, Formación Guafita: Nueva unidad litoestratigráfica del Terciario en el subsuelo de la cuenca Barinas-Apure, Venezuela suroccidental: Boletín de la Sociedad Venezolana de Geólogos, v. 31, p. 9–35.
- ORTMANN, A.E., 1921, South America naiades; a contribution to the knowledge of the freshwater mussels of South America: Memoirs of the Carnegie Museum, v. 8, p. 451–684.
- OWEN, R.B., BARTHELME, J.W., RENAULT, R.W., and VINCENS, A., 1982, Palaeolimnology and archaeology of Holocene deposits north-east of Lake Turkana, Kenya: Nature, v. 298, p. 523–529.
- PARODIZ, J.J., 1969, The Tertiary non-marine Mollusca of South America: Annals of the Carnegie Museum, v. 40, p. 1–242.
- PILSBRY, H.A., 1911, The non-marine Mollusca of Patagonia: Reports of the Princeton University Expedition to Patagonia (Zoology), v. 3, p. 513–633.
- PILSBRY, H.A., and OLSSON, A.A., 1935, Tertiary fresh-water mollusks of the Magdalena embayment, Colombia: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 7, p. 7–39.
- PINDELL, J.L., HIGGS, R., and DEWEY, J.F., 1998, Cenozoic palinspastic reconstruction, paleogeographic evolution and hydrocarbon setting of the northern margin of South America, in Pindell, J.L., and Drake, C.L., eds., Paleogeographic Evolution and Non-glacial Eustasy, Northern South America: SEPM (Society for Sedimentary Geology) Special Publications, v. 58, p. 45–85.
- RÄSÄNEN, M.E., LINNA, A.M., SANTOS, C.R., and NEGRI, FR., 1995, Late Miocene tidal deposits in the Amazonian foreland basin: Science, v. 269, p. 386–390.
- REINECK, H.E., and SINGH, I.B., 1980, Depositional Sedimentary Environments: Springer-Verlag, Berlin, p. 241–242.
- ROGERS, R.R., 1994, Nature and origin of through-going discontinuities in nonmarine foreland basin strata, Upper Cretaceous, Montana: Implications for sequence analysis: Geology, v. 22, p. 1119–1122.
- SARMIENTO, L.F., 2002, Mesozoic rifting and Cenozoic basin inversion history of the Eastern Cordillera, Colombian Andes: Inferences from tectonic models: Unpublished Ph.D. dissertation, Vrije Universiteit, Amsterdam, 295 p.
- SEILACHER, A., 1971, Preservation history of ceratite shells: Palaeontology, v. 14, p. 16–21.
- SEILACHER, A., REIF, W.E., and WESTPHAL, F., 1985, Sedimentological, ecological and temporal patterns of fossil Lagerstätten: Philosophical Transactions of the Royal Society of London, ser. B, v. 311, p. 5–23.
- TALBOT, M.R., and ALLEN, P.A., 1996, Lakes, in Reading, H. G., ed., Sedimentary Environments: Processes, Facies, and Stratigraphy: Blackwell Science, Cambridge, UK, p. 104–106.
- TRAVERSE, A., 2007, Paleopalynology: 2nd ed., Springer-Verlag, Dordrecht, Netherlands, 813 p.
- UBA, C., HEUBECK, C., and HULKA, C., 2005, Facies analysis and basin architecture of the Neogene Subandean synorogenic wedge, southern Bolivia: Sedimentary Geology, v. 180, p. 91–123.
- VERMEIJ, G.J., and WESSELINGH, F.P., 2002, Neogastropod mollusks from the Miocene of Western Amazonia, with comments on marine to freshwater transitions in mollusks: Journal of Paleontology, v. 76, p. 265–270.
- VILLAMIL, T., 1999, Campanian–Miocene tectonostratigraphy, depocenter evolution and basin development of Colombia and Western Venezuela: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 153, p. 239–275.
- VONHOF, H.B., WESSELINGH, F.P., and GANSSSEN, G.M., 1998, Reconstruction of the Miocene Western Amazonian aquatic system using molluscan isotopic signatures: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 141, p. 85–93.
- WESSELINGH, F.P., 2006, Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia: Scripta Geologica, v. 133, p. 19–290.
- WESSELINGH, F.P., RÄSÄNEN, M.E., IRION, G., VONHOF, H.B., KAANDORP, R., RENEMA, W., ROMERO PITTMAN, L., and GRINGAS, M., 2002, Lake Pebas: A palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia: Caineozoic Research, v. 1, p. 35–81.
- WILLIAMS, S.H., and RICKARDS, R.B., 1984, Palaeoecology of graptolitic black shales, in Brunton, D. L., ed., Aspects of the Ordovician System: Palaeontology Contributions of the University of Oslo, Universitetsforlaget, Oslo, no. 295, p. 159–166.
- WOLFF, W.J., 1969, The Mollusca of the estuarine region of the rivers Rhine, Meuse, and Scheldt in relation to the hydrography of the area: pt. 2, The Dreissenidae: Basteria, v. 33, p. 93–103.
- WOODRING, W.P., 1959, Geology and paleontology of the Canal Zone and adjacent parts of Panama: Description of Tertiary mollusks (gastropods: Vermetidae to Thaididae): U.S. Geological Survey Professional Paper, v. 306B, p. 147–239.
- WOODRING, W.P., 1973, Geology and paleontology of the Canal Zone and adjacent parts of Panama: Description of Tertiary mollusks (additions to gastropods, scaphopods, pelecypods; Nuculidae to Malleidae): U.S. Geological Survey Professional Paper, v. 306E, p. 453–539.

ACCEPTED SEPTEMBER 16, 2008