

(11). The North American ephedras now occur widely in and at the margins of the warm-temperate, subtropical deserts: their habitats show wide range in elevation, but are characterized generally by shallow, rapidly drying, highly permeable soil. To account for the presence of the Claiborne ephedras in an environment of high atmospheric humidity (1), it is possible to speculate that local conditions of edaphic aridity may have existed in highly insolated sites, on shifting sands, beach dunes, or sand-flats adjacent to the coast, without surmising that this species had environmental requirements entirely different from modern ones. However, it seems as plausible to question the assumption

that early Tertiary ephedras were physiologically as fully differentiated as the living species. Thus the tentative suggestion may be put forward that the Claiborne species did not have the limiting adaptive relations of living ephedras, although it may have been confined to drier, better-drained sites where it survived largely because of limited competition with associates.

Bearing in mind the several temperate genera now added to the Middle Eocene flora, it seems possible to postulate (i) a long southeast history for some genera whose remains have been found in this area, heretofore, only in late Tertiary sediments, and (ii) the continued survival, possibly from the Upper Cretaceous, of a temperate assemblage whose members largely lack early Tertiary megafossil records. The fossil records lend support to the thesis advanced by Cain (2) which postulates the antiquity of the vegetation of the southern Appalachians, and its essential constancy in the Southeast throughout the Tertiary. That none of the temperate genera were among the more common or widely distributed of the Claiborne plants at low elevations is supported by two facts: (i) essentially all of them have only microfossil records; (ii) the total percentage of their pollen is a small proportion (about 20 percent) of the microflora, although most of these genera are wind-pollinated, or less obligately entomophilous, and their pollen would tend to be more common if the plants had been abundant. Thus the probability of distant transport seems to explain the apparent mixture of deciduous hardwoods and broad-leaved evergreens of now unlike climatic zones, without the necessity of assuming a "greater genetic variability at the generic level" (3) or that many of these genera have changed their climatic requirements through time. One or the other of these factors may also have been operative for some genera, for example, *Ephedra*, but I do not feel that they best explain the over-all composition of the Gosport florule.

The temperate genera occurring as pollen, together with some found as megafossils, represent an assemblage which can be compared directly with the existing deciduous hardwood forest of middle latitudes, and the temperate Holarctic Eocene flora, although admittedly some of the more important members of both are still missing. This comparison strongly suggests that the temperate pollen stems from an upland community, quite modern in aspect, which clothed the inland foothills and lower slopes of the Eocene Appalachians, while a subtropical flora thrived at lower elevations and along the strand. A close parallel is found today in the

eastern Mexican forest, where communities of the tropical "tierra caliente" merge with those of the temperate "tierra templada" at elevations of about 3300 to 4000 feet at "the dividing line between elements of the great arcto-tertiary and neo-tropical floristic regions of classical phytogeography" (4, p. 313; 12).

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11. The abundant, well-preserved grains do not suggest transport from distant inland regions of more continental climate.
12. This report is contribution No. 40, Geochronology Laboratories.

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Isotopic and Zoogeographic Paleotemperatures of Californian Pleistocene Mollusca

Abstract. Pleistocene paleotemperatures inferred from zoogeographic evidence are based on temperatures at species' range limits at present. Paleotemperatures inferred from isotopic evidence are based on average former shell-growth temperatures which commonly, but not exclusively, lie between present range-limiting temperatures. With allowance for these differences, the two lines of evidence suggest similar thermal patterns.

Average temperatures of shell deposition of 43 specimens representing 22 molluscan species from 13 Californian Pleistocene fossil assemblages were estimated by the O^{18}/O^{16} method (1). For these specimens, Table 1 lists (i) isotopic paleotemperatures (based on average Recent sea water, with instrumental error $\pm 1^\circ C$), (ii) present approximate range-limiting temperatures (average February temperatures at northern and average August temperatures at southern range end-points, corrected for depth), and (iii) the most probable depth at which each specimen lived [based on the present ecology of the species and supported by paleoecologic analyses of the 13 fossil assemblages (2)].

A few forms yielded isotopic paleo-

Table 1. Identified plant fossils from the Gosport sand, Claiborne group. C, genera or families reported from other Claiborne localities.

Group	Micro-fossils	Mega-fossils (1)
Hystrichospherids	+	
Algae		
Dinoflagellates	+	
<i>Pediastrum</i> spp.	+	
Ferns		
<i>Aneimia</i> (cf. <i>Mohria</i>)	+	C
<i>Lygodium</i>		+
Polypodiaceae (cf. <i>Polypodium</i> spp.)	+	
<i>Acrostichum</i>		+
Gymnosperms		
<i>Abies</i> *?	+	
<i>Ephedra</i> (cf. <i>E. nevadensis</i>)	+	
<i>Pinus</i> * (<i>haploxylo</i> and <i>sylvestris</i> types)	+	
Taxodiaceae-Cupressaceae	+	C
Angiosperms		
<i>Alnus</i>	+	
<i>Betula</i> *?	+	
<i>Carya</i>	+	C
<i>Castanea</i>	+	
<i>Celtis</i>	+?	C
<i>Citrophyllum</i>		+
<i>Coccoloba</i>		+
Combretaceae	+	
<i>Conocarpus</i>		+
<i>Laguncularia</i>		+
<i>Terminalia</i>		+
cf. <i>Engelhardtia-Alfaroa</i>	+	
<i>Fagus</i> *	+	
Gramineae	+	
<i>Arundo</i>		+
<i>Ilex</i> *	+	
<i>Juglans</i>	+	C
<i>Liquidambar</i>	+	
<i>Liriodendron</i> *	+	
Moraceae	+	
<i>Ficus</i>		+
<i>Myrica</i>		+
Myrtaceae	+	C
<i>Nectandra</i>		+
<i>Nyssa</i>	+	C
<i>Ocotea</i> (<i>Oreodaphne</i> , <i>Mespilodaphne</i>)		+
Onagraceae	+	
<i>Ostrya-Carpinus</i>	+	
Palmae	+	C
<i>Quercus</i> *	+	
Sapindaceae cf. <i>Cardiospermum</i>	+	
<i>Sapindus</i>		+
Sapotaceae	+	C
<i>Tilia</i>	+	
<i>Ulmus</i> (cf. <i>Zelkova</i>)	+	

* Genera new to the Claiborne with Cretaceous fossil records in the middle-south Atlantic and Gulf regions (8, 9).

temperatures outside the range of average monthly temperatures at which they live today. The low shell-growth temperatures of *Acanthina lugubris* seem readily explicable, for this form lives in low-temperature patches along western Baja California where cool waters well up near the shore (3). Evidently *A. lugubris* secretes shell at low temperatures. If its northern range endpoint is thermally controlled it must be by spawning or larval survival temperatures, not by adult survival temperatures. The range-limiting temperature estimate in Table 1 does not take this into account and can therefore be too high for a shell-growth temperature. *Stramonita biserialis*, associated with *Acanthina lugubris* in the Pleistocene, also yielded low shell-growth temperatures for its present range, probably for the same reason as *A. lugubris*. Two of three shell-growth temperatures of *Dosinia ponderosa* are lower than expected. Evidently *D. ponderosa* can deposit shell at temperatures lower than

necessary for other functions at times in its life. For *Panomya beringianus*, only two depth records are available, and thus the significance of its unexpectedly high isotopic paleotemperature cannot be assessed.

Among Upper Pleistocene specimens (localities 1 to 8) the most striking temperature contrasts are between forms from exposed-shore sites (localities 2, 4, 5, 7, and 8) and forms from partially protected habitats (localities 1 and 6) or areas where warm waters may be expected to have piled up (locality 3). Northern extralimital species (*Tegula brunnea* and *T. montereyi*) are common in exposed-shore assemblages (4) and have low isotopic paleotemperatures; southern species (*Dosinia ponderosa* and *Muricanthus nigritus*) in other assemblages (4) have high isotopic paleotemperatures. Even relatively eurythermal and ecologically ubiquitous forms appear to reflect this contrast: *Olivella biplicata* has commonly given higher temperatures from protected (about

15° to 16°C) than from exposed (about 12° to 13°C) assemblages. However a single shell of *O. biplicata* from a protected assemblage (locality 1) gave a low temperature. This is not surprising, for both faunal and isotopic evidence indicates the contemporaneous presence of cool water at locality 2, only a few miles to the south. Waters cooler than today's at exposed sites and warmer than today's at protected sites are thus suggested for the Upper Pleistocene.

To judge from zoogeographic evidence, Lower Pleistocene faunas from the Lomita marl (locality 9) thermally resemble Upper Pleistocene faunas (2). Isotopic paleotemperatures seem to support this resemblance, for an exposed-shore frigophile (*Tegula*) yielded a low temperature, and a more protected shallow-water thermophile (*Eupleura*) yielded a high temperature. A deep outer sublittoral association (75 to 100 fathoms) from Lower Pleistocene silts containing a large northern element (locality 10) yielded the lowest paleotemperatures. Note that the littoral *Tegula*, doubtless washed from nearby shores, yielded a much higher temperature than the species from deeper water. Forms from locality 11 representing shallower depths (25 to 35 fathoms) yielded higher isotopic paleotemperatures. Shells from Lower Pleistocene sands, deposited in depths of 15 to 25 fathoms (locality 12) and 25 to 50 fathoms (locality 13) yielded paleotemperatures commensurate with those from the silts, depth for depth. Evidently the Timms Point silt and San Pedro sand thermal regimes were similar, and temperatures were somewhat cooler than they are in comparable habitats in the region today (5).

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Table 1. Isotopic and zoogeographic paleotemperature estimates of Pleistocene Mollusca (P, pelecypods; G, gastropods) by locality, with estimated living depth.

Locality	Species	Depth (fathoms)	Isotopic temp. (°C)	Present range-limiting temp. (°C)
1. N. San Pedro, Calif., UCLA 1053	<i>Dosinia ponderosa</i> (Gray) P	0-5	18.2	18-29
	<i>Olivella biplicata</i> (Sowerby) G	0-5	15.2, 12.3	8-23
2. S. San Pedro, Calif., UCLA 4101	<i>Tegula montereyi</i> (Kiener) G	shore	11.3, 12.3	10-14
	<i>Olivella biplicata</i> (Sowerby) G	0-15	12.3, 12.6	8-23
3. Newport Beach, Calif., UCLA 3195	<i>Dosinia ponderosa</i> (Gray) P	0-10	17.1	18-29
	<i>Muricanthus radix</i> (Philippi) G	0-10	20.8	21-29
4. Point Loma, Calif., UCLA 3605	<i>Tegula montereyi</i> (Kiener) G	shore	12.4, 12.6	10-14
	<i>Littorina scutulata</i> (Gould) G	shore	13.8	6-29
	<i>Stramonita biserialis</i> (Blain) G	shore	13.1	17-29
	<i>Acanthina lugubris</i> (Sowerby) G	shore	14.0, 15.2	14-23
	<i>Olivella biplicata</i> (Sowerby) G	0-5	11.6	8-23
5. Tahiti Beach, Baja Calif., UCLA 3160	<i>Littorina scutulata</i> (Gould) G	shore	13.4	6-29
	<i>Acanthina lugubris</i> (Sowerby) G	shore	12.8	14-23
	<i>Olivella biplicata</i> (Sowerby) G	0-5	13.3	8-23
6. San Quintin, Baja Calif., UCLA 2411	<i>Dosinia ponderosa</i> (Gray) P	0-10	15.6	18-29
	<i>Macoma yoldiformis</i> (Carpenter) P	0-10	13.0	7-17
	<i>Olivella biplicata</i> (Sowerby) G	0-10	16.9	8-23
7. N. of Punta Baja, Baja Calif., UCLA 2723	<i>Olivella biplicata</i> (Sowerby) G	0-5	11.7	8-23
8. Punta Baja, Baja Calif., UCLA 2714	<i>Macoma irus</i> (Hanley) P	0-2	11.0	2-16
	<i>Tegula brunnea</i> (Forbes) G	shore	11.2	9-14
	<i>Tegula montereyi</i> (Kiener) G	shore	11.8	10-14
	<i>Littorina scutulata</i> (Gould) G	shore	13.8	6-29
	<i>Acanthina lugubris</i> (Sowerby) G	shore	11.3, 11.9	14-23
9. Lomita marl, Hilltop quarry, San Pedro, Calif., UCLA 335	<i>Chlamys hastatus</i> (Sowerby) P	0-15	15.7	5-16
	<i>Tegula montereyi</i> (Kiener) G	shore	13.2	10-14
	<i>Eupleura muriciformis</i> (Broderip) G	0-15	19.0	17-29
10. Timms Point silt, Timms Point, San Pedro, Calif., UCLA 2383	<i>Cyclocardia occidentalis</i> (Stear) P	50-100	7.6	5-11
	<i>Macoma calcarea</i> (Gmelin) P	50-100	5.7	1-11
	<i>Tegula funebris</i> (A. Adams) G	shore	13.8	8-20
	<i>Fusitriton oregonensis</i> (Redf.) G	50-100	5.7	2-8
11. Silt, Cheviot Hills, Calif., UCLA 3395	<i>Panomya beringianus</i> (Dall) P	25-35	12.5	2-8
	<i>Mya truncata</i> (Linnaeus) P	25-35	10.0	1-11
12. San Pedro sand, San Pedro, Calif., UCLA 1824	<i>Macoma irus</i> (Hanley) P	15-25	10.4	2-16
	<i>Boreotrophon multicostatus</i> (Esch.) G	15-25	10.7	2-14
13. San Pedro sand, Torrance, Calif., UCLA 3773	<i>Cyclocardia californica</i> (Dall) P	Extinct	8.1	
	<i>Spisula cf. S. falcata</i> (Gould) P	25-50	6.4	7-17
	<i>Pachypoma gibberosum</i> (Dillwyn) G	15-50	9.4	9-15

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