Reports

Fossil Land Mammal from Antarctica

Abstract. *A fossil land mammal, apparently the first found in Antarctica, belongs to the extinct marsupial family Polydolopidae. The fossils were recovered from rocks about 40 million years old on Seymour Island, in the northern Antarctic Peninsula. The newly discovered marsupials support theories that predicted their former presence in Antarctica and strengthen proposals that Australian marsupials perhaps originated from South American species that dispersed across Antarctica when Australia still was attached to it, prior to 56 million years ago.*

We report the presence of fossil land mammals in the Antarctic continent. The fossil remains were recovered during studies of the geology, stratigraphy, palynology, and invertebrate and vertebrate paleontology of a sequence of marine and nonmarine strata of Cretaceous to probable Oligocene age (*1*) exposed on and adjacent to Seymour Island, northern Antarctic Peninsula (*2*) (Fig. 1).

The fossil mammal is referable to the extinct marsupial family Polydolopidae, known previously from strata of late Paleocene to early Oligocene age in Patagonia, southern Argentina, Bolivia (*3*), and Brazil (*4*). The Seymour Island specimens are considered to be of late Eocene age (~ 40 million years old), on the basis of associated megafossil (*5*) and microfossil invertebrates and pollen (*6*).

The presence of fossil marsupials in western Antarctica in the late Eocene has ramifications regarding (i) theories of the timing and extent of early Cenozoic land connections between South America and Antarctica, (ii) the question of the nature of the contemporaneous land vertebrate faunas of Antarctica, and (iii) the question of dispersal of marsupials to or from the Australian region during the early Cenozoic.

As presently identified, the polydolopid remains consist of a left mandible, UCR 20910, with the lower third premolar through the second molar and alveolus for the lower third molar (Fig. 2), UCR 20911, a right mandible fragment, the lower third premolar through the first molar, and isolated left, upper first (UCR 20912), and second molars (UCR 20913) (*7*). The morphology of these specimens most closely resembles that found in the genus *Polydolops* (*3, 4*) but differs from the species of that genus in the apparent absence of lower second premolar, the more elongate proportions of the molars, and in details of the coronal morphology. A relation to any other known polydolopid genera appears tenuous on present evidence (Fig. 3).

The polydolopid material was recovered from a unit of thinly bedded arkosic sandstone near the top of unit 2, 510 m above the base of the La Meseta Formation (*8*) in northwestern Seymour Island. The site appears to represent a former beach setting, in which abundant remains of megafossil invertebrates are associated with less common teeth of sharks, vertebrae and teeth of teleost fish, bones of turtles, remains of other reptiles and birds including penguins, sparse remains of large (probably marine placental) mammals, and marsupial remains. Because of the megafossil invertebrates (*9*) and fossil penguins recovered from the uppermost parts of the La Meseta Formation the beds are considered to be of late Eocene age (*10*), but palynological remains from the same part of the section suggest a possible early Oligocene age for the strata (*6*). The base of the La Meseta Formation has not been dated; the unit unconformably overlies strata of probable Paleocene age [Cross Valley Formation (*8*)], as well as sediments of late Cretaceous age (*11*).

South America and Australia appear to have been largely isolated faunally during the late Cretaceous and early Cenozoic (*12*), even though geological evidence indicates that Australia was physically connected to eastern (continental) Antarctica until about 56 million years ago (*13, 14*). The Antarctic Peninsula (to the west) thus must have acted as the main filter between Australia and South America during the late Cretaceous and early Cenozoic, but the location of the

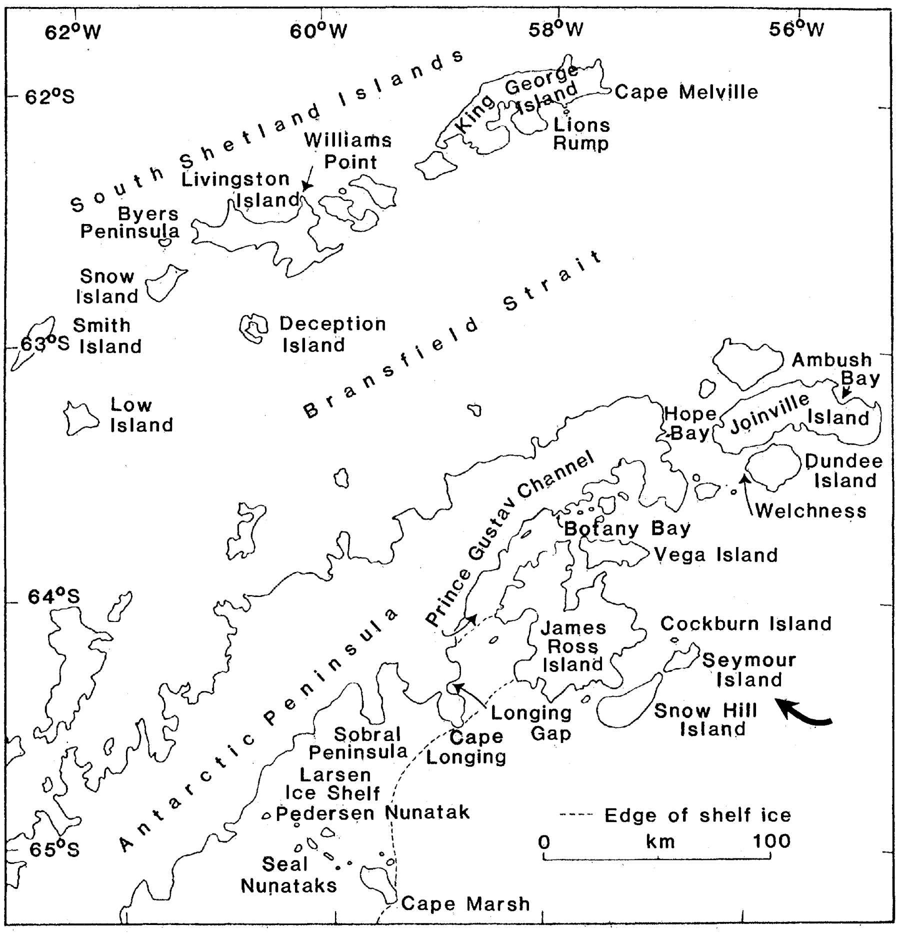

Fig. 1. Map location of Seymour Island (arrow) and adjacent areas, Antarctic Peninsula.

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Fig. 2 (left). Lateral view of UCR 20910, left lower jaw of the polydolopid from the La Meseta Formation (upper Eocene), Seymour Island, Antarctic Peninsula. The teeth shown are the last premolar, which is plagiaulacoid (compressed laterally, and bladelike for cutting), and the first two molars (grinding teeth). Alveoli (holes) for the roots of the last molar are visible behind the second. MOW 8212 is the field number given at the time the fossil was collected on 5 March 1982. Scale shows that the specimen is about 15 mm long. [Photograph by R. A. Hicks, University of California, Riverside] Fig. 3 (right). Artist's reconstruction of the possible form of the new Antarctic polydolopid. On the basis of the size of the recovered jaw fragment, the animal may have been about 20 cm in length, minus the tail. It is unknown whether the tail should have been essentially naked as in living North American opossums, or hairy as in some South American forms and many Australian taxa.

main (if a single) barrier presently is moot. Geological evidence suggests that at least a disjunct dispersal route, with shallow water barriers, existed from the northern Antarctic Peninsula to eastern (continental) Antarctica during the times in question (*13*), and the generally similar late Cretaceous and early Cenozoic geological history of the Antarctic Peninsula and southern South America also has been taken as evidence of their potential connection then (*13*).

Until now, the Polydolopidae were considered to have been endemic to South America. The Antarctic specimens are direct evidence of land mammal dispersal from South America to another southern continent in the early Cenozoic. It is not possible to assert yet that the Antarctic specimens represent anything other than waif dispersal; a minimum of two or three individuals is represented by the new fossils, which appear to belong to a single species. Nevertheless, it is most plausible that dispersal was from South America to Antarctica, and took place at or some time before the late Eocene (when they are now known from Antarctica), but not earlier than late Paleocene [when polydolopids first are known from South America (*3*, *4*)], or between about 55 and 40 million years ago (*1*). This is consistent with the geological evidence.

The Antarctic polydolopids have no direct bearing as yet on the question of land mammal dispersals to or from Australia. Strong separation of Australia from Antarctica began about 56 million years ago (*13*), but even then the continental shelves of the two continents are thought to have been continuous, so that chance dispersal of land mammals between these regions may have been possible up to the late Eocene when polydolopids are now known to have inhabited the northern tip of the Antarctic Peninsula. In this context, the Seymour Island materials raise again the question of the site (or sites) of the major barrier (or barriers) to dispersal to or from South America and Australia and the role, if any, played by South American polydolopid or related marsupials—known or inferred to have been present in the late Cretaceous or early Tertiary—in the deployment and development of the early marsupial fauna of Australia.

Paleogeographic details to account for the faunal discontinuities between South America and Australia in the late Cretaceous and early Cenozoic are obscure; better geological and paleontological data will help in evaluating this question. The presence of the Polydolopidae on the Antarctic Peninsula in the late Eocene, at about the time when Australia had only just separated from the Antarctic lithospheric plate (*14*), independently corroborates suggestions that early Cenozoic climates were tolerant of land life in Antarctica (as well as life on whatever type of land avenue connected Antarctica to South America), renews speculation about the adaptive breadth of marsupial and possibly placental land mammals on the Antarctic continent before fully regional glacial conditions were established in the early Miocene (*15*), and raises the question as to which, if any, other family groups from South America colonized Antarctica, or vice versa. The Seymour Island polydolopids invite discussion of the nature of the biogeographic filter between the Antarctic peninsula and the east Antarctic continent during the early Cenozoic and perhaps make more perplexing the absence of any evidence that placental land mammals (known contemporaneously in South America) were present on either the Antarctic or Australian continents during that time.

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2. Latitude, 64°13′S; longitude, 56°40′W.
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7. Enumeration according to (*4*).
8. The Tertiary sequence on Seymour Island was described in detail by D. H. Elliot *et al.* [*Antarct. J. U.S.* **10**, 183 (1975)] and divided into five lithologic units, informally numbered 1 through 5; the sequence was revised by D. H. Elliot and T. A. Trautman [*Antarctic Geosciences*, C. Craddock Ed. (Univ. of Wisconsin Press, Madison, 1982), pp. 287–297]: unit 1 was elevated to formational rank, the Cross Valley Formation, and the name, La Meseta Formation, was proposed for units 2 through 5, with units 3 and 4 being combined. Fieldwork conducted in 1982 showed that the La Meseta Formation unit 1 is approximately 300 m thicker than previously thought, so the interval with marsupial remains is about 510 m above the base of the La Meseta Formation, in the upper part of unit 2, as revised.
9. Marine molluscs associated with the polydolopid are *Antarctodarwinella nordenskjoldi* (Wilckens), *Sthruthioptera camachoi* Zinsmeis-

ter, *Lahillia larseni* (Sharman and Newton), *Eutrephoceras argentinae* del Valle and Fourcade, *Aturia* sp., *Eurhomalia antarctica* (Wilckens), *Nielo* n. sp., and a number of undescribed gastropods.

10. Bartonian (European marine stage) and Runangan (New Zealand marine stage). Closest regional biogeographic affinities are with the invertebrate faunas of the early Paleogene of New Zealand. The La Meseta molluscs show surprisingly weak affinities with contemporaneous faunas of southern South America (*13*).
11. The Sobral and Lopez de Bertodano formations (Campanian, ?Danian in age) were proposed and characterized by C. A. Rinaldi, A. Massabie, J. Morelli, L. Roseman, and R. Del Valle, [*Inst. Antarct. Argent. Contrib.* **217**, 1 (1978)].
12. Marsupials are known to have populated North America, western Europe, South America, and Antarctica, and are inferred to have inhabited Australia during the late Cretaceous and early Cenozoic [R. H. Tedford, *Soc. Econ. Paleontol. Mineral. Spec. Publ.* **21**, 109, (1974)]. Placental mammals radiated vigorously in North America during the late Cretaceous and early Cenozoic, [G. G. Simpson, "Evolution and geography," Condon lectures, Oregon State System of Higher Education, Eugene (1953), pp. 1–64] and a large group of nearly endemic, herbivorous, placental mammals were contemporaneous in South America [G. G. Simpson, *Proc. Am. Phil. Soc.* **122**, 318 (1978); B. Patterson and R. Pascual, *Q. Rev. Biol.* **43**, 409 (1968)]. These are generally bulky, medium-sized herbivorous animals, considered to have been selectively disadvantaged with respect to dispersal across shallow or deep water barriers, and none of these is known to have populated Australia, which had, by about 30 million years ago, and probably earlier as well, a strong diversity of endemic and largely herbivorous marsupials [W. D. L. Ride, *J. R. Soc. West Aust.* **47**, 97, 1964; J. A. Kirsch, *Nature (London)* **217**, 415 (1968); M. Archer, *J. Linn. Soc. Lond. Zool.* **59**, 217 (1976); M. Archer and A. Bartholomai, *Alcheringa (Adelaide)* **2**, 1 (1978)].
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16. Critical logistical support, without which the work could not have been accomplished, was provided by personnel of the U.S. Coast Guard Cutter *Glacier*, J. W. Coste, commanding officer, with invaluable assistance by Aviation Detachment 88, Lieutenant Commander J. Williams, leader. Scientific personnel included W. J. Zinsmeister, P. Webb, T. de Vries, C. Macellari, and B. Huber (Institute of Polar Studies, Ohio State University; invertebrate paleontology); M. O. Woodburne and W. R. Daily (Department of Earth Sciences, University of California, Riverside; fossil mammals and birds); S. Chatterjee (The Museum, Texas Tech University, Lubbock; fossil reptiles and fish); R. Askin and F. Fleming (Department of Geology, Colorado School of Mines, Golden, and Department of Geology, University of Colorado, Boulder; palynology). Supported by NSF grant DP8020096 to D.H.E. and W.J.Z.

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Nonimmunological Production of Leukotrienes Induced by Platelet-Activating Factor

Abstract. *Platelet-activating factor caused rapid pulmonary vasoconstriction and edema in isolated lungs perfused with albumin-free salt solution devoid of formed blood elements. These effects may be due in part to the action of leukotrienes D_4 and C_4, which were identified by bioassay and high-pressure liquid chromatography in the lung effluent after stimulation by platelet-activating factor. These findings help illuminate some of the deleterious effects that platelet-activating factor elicits in anaphylactic reactions and possibly in other forms of lung injury.*

Platelet-activating factor (PAF; 1-0-alkyl-2-acetyl-*sn*-glyceryl-3-phosphorylcholine) (*1*) was first derived from rabbit basophils that had been sensitized with a specific immunoglobulin E–antibody (*2*) and has since been identified from neutrophils, alveolar macrophages, and monocytes (*3–5*) of various species including man. The factor is known to promote calcium-dependent platelet aggregation, serotonin secretion, and thromboxane A_2 production (*6–7*). In the guinea pig, aspirin-resistant bronchoconstriction has been reported after intravenous PAF administration (*8*). In addition, intravenous injection of PAF in the rabbit induced bronchoconstriction and increased right ventricular pressure that appeared to be platelet independent (*9*). We have now conducted experiments showing that PAF causes pulmonary vasoconstriction in isolated lungs perfused with albumin-free salt solution (*10*).

Lungs were isolated from male Sprague-Dawley rats weighing 250 to 300 g and perfused as previously described with a warm (37°C), oxygenated Greenberg-Bohr buffer solution (*11*), which was osmotically stabilized with Ficoll (Sigma; 4 percent by volume). The lungs were pump-perfused at a constant rate of 0.03 ml per gram of body weight per minute and ventilated with a Harvard animal respirator with a gas mixture containing 21 percent O_2, 5 percent CO_2, and 74 percent N_2 (tidal volume 2 cm^3, rate 60 per minute). Thirty minutes of nonrecirculating perfusion allowed stable baseline conditions (the perfusion pressure was 7 ± 1 mmHg) and a practically cell-free lung effluent (platelets 500, leukocytes 0.01, erythrocytes 0.01 per milliliter) perfusate. Semisynthetic PAF was obtained from Avanti (Birmingham, Alabama) or Bachem (Bubendorf, Switzerland). The latter compound produced a single molecular species (MH^+, mass to charge ratio, 524) when analyzed by fast atom bombardment mass spectrometry. The PAF was injected rapidly as a bolus into the pulmonary artery cannula (1 to 5 μg in 0.1 ml of normal saline). The pulmonary artery pressure change after injection was measured with a Statham P23AA transducer and the lung weight change with a force displacement transducer (Statham G1-15-300). Both variables were recorded on a Gilson polygraph recorder.

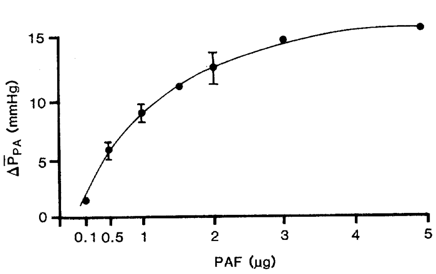

Fig. 1. Dose-response characteristic of bolus injection of PAF into the pulmonary artery. The PAF was stored in chloroform and freshly made up in 0.25 percent bovine serum albumin and Tyrode solution. Dots represent single experiments; closed circles and bars represent the mean (± standard error) of four experiments. The increase in mean pulmonary artery pressure ($\Delta \bar{P}_{PA}$) was determined three minutes after PAF injection.

The injection of PAF caused rapid dose-dependent vasoconstriction (Fig. 1) and edema (as measured by lung weight gain) within 1 minute. The lung weight gain was arbitrarily measured at 3 minutes after PAF injection and was 0.8 to 1.6 g in three lungs that received 1 μg and 2.4 to 7 g in three lungs that received 2 μg. Two lungs receiving 5 μg of the lysoanalog of PAF developed neither vasoconstriction nor edema. In three lungs, two doses of 1 μg of PAF were administered 15 minutes apart. The second injection caused less vasoconstriction, suggesting development of tachyphylaxis.

Prior treatment of the rats with indomethacin (Sigma; 5 mg/kg) and the addition of indomethacin (0.5 μg/ml) to the perfusate blocked the lung cyclooxygenase pathway. The concentration of 6-keto-prostaglandin $F_{1\alpha}$ in the lung effluent was less than 25 pg/ml, compared to greater than 1000 pg/ml in the lung effluent from untreated rats (*12*). In addition, indomethacin blunted the vasoconstriction response and delayed edema formation after PAF administration (Fig. 2). In the indomethacin-treated lungs the maximum rise in mean pulmonary artery pressure after the administration of 2 μg of PAF was 10 to 11.5 mmHg ($N = 3$) and the weight gain in the third minute after PAF administration was 2.0 to 6 g ($N = 3$). Thus cyclooxygenase products were probably not the major cause of this PAF effect on the lungs.

In three lungs perfused with physiological salt solution containing diethylcarbamazine (Sigma; 1 mg/ml), an inhibitor of leukotriene biosynthesis (*13–14*), vasoconstriction and edema did not occur after PAF administration. Since the

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