

# LIKELIHOOD ESTIMATION OF THE TIME OF ORIGIN OF CETACEA AND THE TIME OF DIVERGENCE OF CETACEA AND ARTIODACTYLA

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## ABSTRACT

Continuity is important for tracing evolutionary lineages through geological time. Modern Odontoceti and Mysticeti can be traced backward in time to Eocene Archaeoceti, and before them to mesonychian Condylarthra. Within this shared continuum, the origin of Archaeoceti and the origin of Cetacea is marked by the first indication of a derived evolutionary transition-in-grade from terrestrial to aquatic life characteristic of later cetaceans. Archaeocetes are known from many fossil localities in Eocene marginal marine and shallow marine strata on six continents. These range in age from Priabonian (late Eocene; ca. 36 Ma) through late Ypresian (late early Eocene; ca. 49.5 Ma), a 13.5 m.y. time range, and they are widely distributed in North America (18 sites), Europe (5 sites), Asia (8 sites), Africa (8 sites), Australia (New Zealand; 2 sites), and Antarctica (1 site). Forty-two sites can be considered statistically-independent records.

With this information and a model sampling distribution of potential fossils, we can compare different hypothesized times of origin of archaeocetes by calculating relative likelihoods for each. The model sampling distribution reflects changing outcrop area of sedimentary rocks through geological time and changing numbers of archaeocetes during their diversification. The maximum-likelihood time of origin of archaeocetes is given by the age of the earliest fossil, which defines the beginning of the temporal range and requires no hypothesized extension. Likelihood ratios of 0.5 and 0.05 have associated probabilities less than or equal to 0.5 and 0.05, respectively, representing confidence limits equal to or greater than 50% and 95%. A critical likelihood  $\lambda = 0.05$  defines the maximum extension of range we can reasonably expect to find, and from this we estimate the time of origin of Archaeoceti to have been at or after about 51.6 Ma—within the early Eocene.

Fifty-six independent records of Mesonychidae and Hapalodectidae on the three northern continents range in age from Rupelian (early Oligocene; ca. 33 Ma) to Torrejonian (middle Paleocene; ca. 63 Ma). We estimate the time of origin of mesonychian condylarths to have been at or after about 66.7 Ma (virtually at the Cretaceous-Paleocene boundary). Artiodactyla, the extant sister-group of whales, has a fossil record extending to the beginning of the Eocene, with an arctocyonian ancestry extending into the latest Cretaceous. The fossil record as now known indicates evolutionary divergence of Mesonychia + Cetacea from Arctocyonia + Artiodactyla in the early Paleocene or, reasonably, at the very end of the Cretaceous.

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## INTRODUCTION

The geological time scale is based on the evolutionary succession of animal life found as fossils in superposed strata of sedimentary rocks covering large areas of the earth's surface. The *Paleo-zoic*, *Meso-zoic*, and *Ceno-zoic* eras are separated by mass extinctions and associated profound *faunal* change. Periods, epochs, ages, and biochrons are progressively finer subdivisions of the time scale distinguished by faunal differences and by extinction-origination turnovers of lesser magnitudes. The history of life through geological time is not a smooth and seamless history, but rather an episodic history. Times of turnover, whatever their scale, are critical events, often coming at a juncture of unusual extrinsic-environmental and intrinsic-biotic change, that challenges the survival of species. Those that survive may do so by moving or by changing at evolutionary rates that appear rapid in the context of geological time.

Dinosaurs and other reptiles dominated Mesozoic terrestrial and marine faunas. On land, dinosaurs were replaced by mammals that evolved to dominate succeeding terrestrial Cenozoic faunas. Condylartha or 'archaic ungulates' are common in terrestrial mammalian faunas of the Paleocene epoch, but were largely replaced by modern mammalian orders in the Eocene. In the sea, plesiosaurs, ichthyosaurs, and mosasaurs were replaced by mammals too, but marine mammals are not known from the Paleocene. The reign of dinosaurs, plesiosaurs, ichthyosaurs, and mosasaurs ended with the Mesozoic; mammals crossed the Cretaceous-Tertiary boundary and seemingly took advantage of new opportunities, diversifying broadly on land and eventually invading the sea. Most modern orders of mammals appeared at or near the Paleocene-Eocene boundary, replacing archaic orders from which they probably evolved, and the initial appearance of many orders closely spaced in time may reflect rapid evolution associated with a Paleocene-Eocene turnover event of some kind.

The geological time scale or evolutionary succession of life is calibrated in two ways that yield very different results. The conventional way in geology is to calibrate the evolutionary succession of animal life by finding interbedded crystalline rocks (principally basalts) that can be dated radiometrically ([Dalrymple 1991](#)). This assumes that the ejection or capture of energetic electrons in radioactive elements of rock-forming minerals happens randomly and independently of biotic evolution. A new and as yet unproven approach promoted by some biologists is to calibrate the evolutionary succession using molecular genetic differences between pairs of living plants or animals

as clocks of divergence time ([Zuckermandl and Pauling 1962, 1965](#)). This assumes that the genetic code changes randomly and independently of biotic evolution, which seems unlikely when development of each new generation depends so directly on the code it inherited.

Calibration of the evolutionary succession of life with molecular clocks is selective, meaning that divergences of animals like mammals that live today can be calibrated independently of faunal context, while divergences of and from animals like dinosaurs that are extinct cannot. This leads to faunal inconsistencies like wholesale overlap of otherwise Cenozoic mammalian orders with Mesozoic dinosaurs ([Hedges et al. 1996](#), [Kumar and Hedges 1998](#)). Here we consistently use the geological radiometric time scale rather than molecular clocks to calibrate evolutionary succession. The numbers we use are drawn from the [Haq et al. \(1987\)](#) time scale because sea level change is sometimes important for interpreting shallow marine habitats of whales, but taking numbers from more recent timescales (e.g., [Berggren et al. 1995](#), [Gradstein and Ogg 1996](#), or [Hardenbol et al. 1998](#)) would not change our conclusions significantly.

Our focus is on Cetacea. Looking backward from the present, whales, like other mammalian orders, undoubtedly have a pedigree extending back to the earliest mammals known from the Triassic period, and before that to the earliest vertebrates of the Cambrian or Ordovician. The continuity of the cetacean germ line, whether followed backward in time or forward in time, is not in question because individuals propagate new individuals and new species necessarily evolve from old ones. Evolution is first and foremost a history of ancestors and their sometimes-divergent descendants. What in the complex genealogy of mammals makes a whale a whale? What are the characteristics by which whales are recognized? And when did whales first appear in the evolution of mammals?

## WHAT, WHEN, AND WHERE IS A WHALE?

Living Cetacea are fully aquatic and share a hydrodynamically streamlined body form with forelimbs modified into flippers and loss of external hind limbs, while locomotion is powered by a heavily-muscled tail bearing a broad terminal horizontal fluke. Communication with other whales and sensory perception in an aquatic medium are largely sound-based, for which cetaceans have characteristically-dense tympanic bullae; isolated, highly modified periotic or petrosal bones; and large mandibular canals with thin lateral acoustic fenestrae. Feeding is accomplished by straining krill and small fish in the baleen whales (Mysticeti) or by catching larger fish, squid, and other animals and swallowing these whole or in large pieces in the toothed whales (Odontoceti). These divergent specialized adaptations to life in water, and the living suborders that have them, Mysticeti and Odontoceti, can be traced backward in the fossil record from the present to the Oligocene epoch ([Fordyce and Barnes 1994](#)).

Late Eocene Archaeoceti of the family Basilosauridae (especially Dorudontinae; [Uhen](#)

[1996](#)) resemble later mysticetes and odontocetes in having a hydrodynamically streamlined body form with forelimbs modified into flippers and locomotion powered by a heavily-muscled fluked tail, while retaining reduced but functional hind limbs ([Gingerich et al. 1990](#)). Basilosaurids have dense tympanic bullae, pterygoid sinuses, partially isolated periotics, and large mandibular canals with lateral acoustic fenestrae, which would have enabled them to hear directionally in water. Feeding was different in that cheek teeth retain complex morphology and functional occlusion, and heavy wear shows that food was chewed before swallowing. Thus, late Eocene basilosaurid archaeocetes have many, but not all, characteristics of later whales. Early mysticetes and odontocetes are difficult to distinguish from basilosaurids, and all are marine and fully aquatic. Temporal, morphological, and environmental/geographical continuity between late Eocene basilosaurids and following Oligocene mysticetes and odontocetes indicates basilosaurids are closely related to modern whales, and their derived aquatic characteristics affirm inclusion in Cetacea.

Middle Eocene Archaeoceti of the family Protocetidae resemble basilosaurid archaeocetes, mysticetes, and odontocetes in having a hydrodynamically streamlined body form and locomotion powered by a heavily-muscled tail, while retaining large functional hind limbs ([Gingerich et al. 1994](#)). The form of the forelimbs is as yet poorly documented, and the presence of a fluke is only a possibility. Protocetids have dense tympanic bullae and large mandibular canals with lateral acoustic fenestrae, but isolation of the periotic was limited, making directional hearing questionable. Like basilosaurids, protocetids had cheek teeth different in detail but retaining complex morphology and functional occlusion, and here too heavy wear shows that food was chewed before swallowing. Protocetids were probably good swimmers and all are found in marine strata. Thus, middle Eocene protocetid archaeocetes have many, but not all, characteristics of basilosaurid archaeocetes and some characteristics of later whales. Here again, it is the relative continuity in time, form, and place between middle Eocene protocetids and late Eocene basilosaurids that indicates protocetid archaeocetes are closely related to basilosaurids, and their derived aquatic characteristics affirm inclusion in Cetacea.

Early Eocene Archaeoceti of the family Pakicetidae are poorly known postcranially. *Pakicetus* has a dense tympanic bulla with a characteristically cetacean sigmoid process ([Gingerich and Russell 1981](#)), but the periotic was firmly integrated in the basicranium, making directional hearing questionable ([Gingerich et al. 1983](#)). *Pakicetus* had no enlargement of the mandibular canal and the incus was intermediate in morphology between those of modern artiodactyls and cetaceans, suggesting not only that it could not hear directionally but it could not hear well in water ([Thewissen and Hussain 1993](#)). *Pakicetus* had cheek teeth retaining complex morphology and functional occlusion, with larger protocones but otherwise the same general pattern of cusps and crests as later protocetids and basilosaurids. Early Eocene pakicetid archaeocetes are found in river and estuarine deposits in association with land mammals, but these deposits are peripheral to the Tethys Sea and pakicetid-bearing deposits are overlain by protocetid-bearing marine strata. Pakicetids have some, but not all, characteristics of

later protocetid and basilosaurid archaeocetes and they have but few characteristics of later whales. Relative continuity in time, form, and place indicates early Eocene pakicetids are closely related to middle Eocene protocetids, and the derived aquatic characteristics of pakicetids affirm inclusion in Cetacea ([Gingerich et al. 1983](#), [Thewissen and Hussain 1993](#), [Thewissen 1994](#)). *Pakicetus*, the remingtonocetid *Remingtonocetus* ([Kumar and Sahni 1986](#); [Gingerich et al. 1995a](#)), and ambulocetid *Ambulocetus* ([Thewissen et al. 1994](#)), all discovered in recent years, have such important primitive and nonaquatic characteristics that all have forced us to expand our concept of Cetacea.

The Paleocene mammals most similar to pakicetids and later protocetids are Condylartha or Mesonychia of the family Mesonychidae ([Van Valen 1966, 1969, 1978](#)). Mesonychidae did fit comfortably in the archaic order Condylartha until Van Valen suggested that dental similarities to later *Protocetus* were important. This possible connection to later whales now overshadows their clear connection to earlier Paleocene condylarths but the original temporal, morphological, and geographical resemblance has not changed. Protocetid teeth and mesonychid teeth have similarly-unusual proportions, and a protocetid of uncertain generic attribution, one pakicetid (*Ichthyolestes*), and a possibly *Ambulocetus*-like genus (*Gandakasia*) were originally described as mesonychids by [Pilgrim \(1940\)](#) and by [Dehm and Oettingen-Speilberg \(1958\)](#). These were included in Mesonychidae by [Szalay and Gould \(1966\)](#), although they are now known to be primitive archaeocetes rather than mesonychids.

Some Mesonychidae like Asian late Paleocene *Sinonyx* ([Zhou et al. 1995](#)) and North American early Eocene *Pachyaena* ([Zhou et al. 1992](#); [O'Leary and Rose 1995](#)) are known from virtually complete skeletons showing them to be hoofed cursorial mammals with no aquatic specializations and no distinctively cetacean characteristics (they have ossified auditory bullae, but lack in particular the dense enlarged bullae with sigmoid processes seen in *Pakicetus*). Thus we distinguish Cetacea from non-Cetacea at a gap between Mesonychidae and Pakicetidae. This gap is not a rigid boundary, but one subject to revision in light of new discoveries (postcranial remains of pakicetids will be critical here): the connection may become weaker if similarities in form that we see now are in the future overshadowed by similarity to some other group, or the connection may become stronger if new similarities are discovered that reinforce it (similarity in any particular case, like continuity, is always relative to that in competing cases).

What makes a primitive archaeocete like *Pakicetus* ([Gingerich and Russell 1981](#)) or *Ambulocetus* ([Thewissen et al. 1994](#)) a whale, when mesonychids like *Sinonyx* and *Pachyaena* are not whales? [Berta \(1994\)](#) asked: "What is a whale?". [Gish \(1994\)](#) asked: "When is a whale a whale?" And a third question might be: "Where is a whale a whale?" It is not possible to answer one question without the others, and the answer to all three is that a primitive early fossil whale is a whale when continuity in temporal, morphological, and geographical range connects it to living whales—ideally through a closely-connected series of temporal, morphological, and geographical intermediates—and its form shows one or more of the specializations of whales. The former reflects the "shared" and the latter the "derived" components of synapomorphy diagnosing Cetacea.

In our view as paleontologists, whales became whales when they first showed evidence of the evolutionary transition in grade from terrestrial to aquatic life characteristic of living cetaceans.

## ORIGIN OF WHALES

If everyone agreed that whales became whales when they first showed evidence of the evolutionary transition in grade from terrestrial to aquatic life, then it would still be possible to view the *origin* of whales in different ways, depending on whether one assumed a predominantly *comparative* or predominantly *historical* perspective. We do not view such a dichotomy as necessary so much as matter-of-factly descriptive of perspectives colleagues have.

To comparative biologists concerned solely with living organisms, a whale is a whale after the time of separation of Cetacea from its closest living noncetacean relative. [Flower \(1883\)](#) interpreted an elongated larynx, complex stomach, simple liver, reproductive organs, and fetal membranes as linking Cetacea to Artiodactyla anatomically, but later authors did not find this convincing ([Kellogg 1936](#); [Simpson 1945](#)). We owe our present understanding that extant Artiodactyla are the sister-group of extant Cetacea to comparative immunology ([Boyden and Gemeroy 1950](#)), to the fossil record ([Van Valen 1966, 1969](#)), and more recently to molecular gene sequencing ([Arnason et al. 1991](#); [Irwin et al. 1991](#); [Milinkovitch 1992](#); [Krettek et al. 1995](#); [D'Erchia et al. 1996](#)). Claims that (1) sperm whales are mysticetes ([Milinkovitch et al. 1993, 1994](#); [Douzery 1993](#); [Milinkovitch 1995](#); [Milinkovitch et al. 1995](#); but see [Ohland et al. 1995](#) and [Messenger and McGuire 1998](#)); (2) Cetacea originated within Artiodactyla as the sister-group of extant camels ([Goodman et al. 1985](#)), hippopotami ([Sarich 1993](#); [Irwin and Arnason 1994](#); [Arnason and Gullberg 1996](#)), ruminants ([Graur 1993](#); [Graur and Higgins 1994](#)), or suids ([Kumar and Hedges 1998](#)); and (3) whales are the sister group of perissodactyls ([McKenna 1987](#)) cast doubt on the efficacy of molecular systematics, but we accept that Artiodactyla is probably the closest living sister-group to Cetacea. If true, then to a comparative biologist the time of origin of Cetacea is the time Cetacea diverged from Artiodactyla.

To paleontologists like us concerned with both living and extinct organisms, a whale is not a whale until it has both (1) separated from its closest living sister taxon (Artiodactyla), becoming a distinct clade, and (2) acquired one or more characteristics of Cetacea, achieving a distinctive grade. Cetacea and Artiodactyla can be traced back in geological time to different stem groups within Condylarthra (Mesonychia and Arctocyonia, respectively; [Van Valen 1966, 1971, 1978](#); [Rose 1996](#)). Consequently, there is a possibly-significant interval of time between events (1) and (2) that we consider here. In the following analyses we first estimate the time of origin of whales as conceived by paleontologists, based on the fossil record, where Cetacea is not only a distinct clade but also a distinct grade. We then estimate the time of divergence of Cetacea from Artiodactyla by estimating the time of origin of Mesonychia and comparing

that to the ranges of Arctocyonia and Artiodactyla in the fossil record.

One way to evaluate the time of origin of whales is to consider it to be close to the time of first preservation of whales in the fossil record. This is reasonable because whales are relatively large animals with well-ossified skeletons, most whales have distinctive dental and osteological characteristics related to aquatic or partially aquatic adaptations enabling them to be identified, and life in water enhances preservation potential in the fossil record. We can then consider the distribution of ages of known fossils and estimate an acceptable confidence limit for this distribution.

In the following calculations we use the fossil record of Archaeoceti to estimate the time of origin of Cetacea as a whole. We do this because Archaeoceti represents the Eocene initial diversification of whales and is thus the subgroup having the greatest bearing on the time of origin of the order. We concentrate on Archaeoceti too because this is the group for which we can best determine the number of independently-sampled site records. Occurrences of non-cetaceans, even when thought to be broadly ancestral (like mesonychians for example), contribute little in constraining the time of origin of cetaceans, just as the stratigraphic distribution of Archaeoceti contributes little to knowledge of the time of origin of later Odontoceti or Mysticeti.

Calculations similar to those presented here can be carried out for Cetacea as a whole (and for Artiodactyla and other orders of mammals) when counts of independently-sampled site records are known, but these are not yet available. If we can generalize based on what we demonstrate here about the statistical power of even modest numbers of independent sites, the temporal ranges of all of the better known orders of mammals are already closely constrained by the known fossil record.

## CLASSICAL CONFIDENCE INTERVALS FOR TEMPORAL RANGES

[Strauss and Sadler \(1989\)](#) derived a one-tailed confidence interval for a taxon's stratigraphic or temporal range that we shall use here:

$$p_1 = 1 - (1 + \alpha)^{-(n-1)} \quad (1)$$

where  $p_1$  is the confidence level (e.g., 0.95), their  $\alpha$  is the range extension expressed as a proportion of the known stratigraphic or temporal range (not to be confused with conventional use of  $\alpha$  to represent level of significance, see below), and  $n$  is the number of independently-sampled fossiliferous horizons. Solving for  $\alpha$  by rearranging terms yields the required range extension as a function of the confidence level and number of samples ([Marshall 1990](#)). Derivation of equation 1 by Strauss and Sadler and discussion of this by Marshall both make it seem unduly complicated (due in part to the complexity of their notation), but the derivation is actually both simple and intuitive, as we discovered by deriving this independently ([Gingerich and Uhen 1994](#)).

Start by assuming that fossils are uniformly distributed throughout the unknown

estimated temporal range or *expected temporal density* [ETD] of a taxon of interest (Fig. 1). This assumption of uniformity is too simplistic, and we will relax it later (when the density associated with an area or volume need no longer correspond to the temporal range). Assume that sampling is random. A uniform ETD means that fossils from different times have an equal probability of being sampled. Construct a sample of some size  $n$  by drawing  $n$  independent samples at random from ETD. We can now sort these from oldest to youngest and they define the observed temporal range or *observed temporal density* [OTD]. We are interested in the time of origin of Archaeoceti and do not care about their time of extinction (or conversion into Odontoceti and Mysticeti), meaning that we are interested in a one-tailed range extinction. This is, in any case, more conservative (yielding a broader interval) in allocating all of the tail probability to one tail. One sample is required to define the youngest end of the OTD ( $t_3$ , the time we are not interested in here), so  $n - 1$  samples remain for estimation of ETD and  $t_1$  from OTD and  $t_2$ .

We require one additional number  $\alpha$ , the level of significance or error rate we are willing to accept. This determines the confidence interval  $1 - \alpha$  that we seek. By convention,  $\alpha = 0.05$  is the usual error rate, which corresponds to a 95% confidence interval for observed temporal density OTD.

The probability that any sample drawn from unknown ETD falls in OTD is the ratio of lengths (or areas or volumes) OTD/ETD, which cannot be greater than 1 (because ETD is greater than or equal to OTD). If the probability that one sample drawn from ETD falls in OTD is OTD/ETD, then the probability that two samples drawn independently from ETD both fall in OTD is the product of OTD/ETD times OTD/ETD or (OTD/ETD)<sup>2</sup>. The probability that  $n - 1$  samples drawn from ETD all fall in OTD is (OTD/ETD) <sup>$n-1$</sup> . Setting this quantity equal to the error rate  $\alpha$ :

$$\alpha = (\text{OTD}/\text{ETD})^{n-1} \quad (2)$$

which is, in simpler form, exactly the same as equation 1 [where  $p_1 = 1 - \alpha$  and  $(1 + \alpha)^{-(n-1)} = (\text{OTD}/\text{OTD} + (\text{ETD}-\text{OTD})/\text{OTD})^{-(n-1)} = (\text{OTD}/\text{ETD})^{n-1}$ ]. Solving for ETD yields:

$$\text{ETD} = \text{OTD} / \alpha^{1/(n-1)} = \text{OTD} / {}^{(n-1)}\sqrt{\alpha} \quad (3)$$

With  $\alpha = 0.05$  and an observed range OTD based on two independent samples, meaning  $n - 1 = 1$ , the 95% confidence limit for ETD is  $20 \times \text{OTD}$ . When OTD is based on three independent samples, meaning  $n - 1 = 2$ , the 95% confidence limit for ETD is  $4.47 \times \text{OTD}$ . ETD/OTD is the inverse of the  $(n - 1)$ th root of  $\alpha$ . This quantity converges rapidly to 1 as  $n$  increases, meaning ETD approximates OTD even for relatively small  $n$ . Further, this result is not very sensitive to  $\alpha$ .

If we assume that the distribution of fossils representing the temporal duration of a group of organisms is uniform through time, and if we know (1) the beginning and end of the group's stratigraphic or observed temporal range ( $t_2$  and  $t_3$ , respectively, in Fig. 1), and (2) the number of independent samples this range is based on ( $n$ ), then we can

estimate the time of origin of the group ( $t_1$  in Fig. 1). The beginning and end of the observed range encompass the observed temporal density OTD. OTD is necessarily represented by  $n$  is greater than or equal to 2 samples. Estimated temporal range ETD can be calculated using equation 3, and the difference between ETD and OTD is added to the beginning of the observed temporal density. This yields a classical  $1 - \alpha$  confidence limit for the time of origin of the group.

## LIKELIHOOD ESTIMATION

Probability is a way of comparing observed data or results for a given hypothesis. Likelihood on the other hand is a way of comparing hypotheses for a given set of data or results. The two are related, differing only by an arbitrary constant, with the likelihood of a hypothesis given the data or results being proportional to the probability of the data given the hypothesis ([Edwards 1972](#)). When hypotheses are compared, this is conveniently done in the form of likelihood ratios or relative likelihoods,  $L$ , ratios of any individual likelihood to the maximum, scaled from 0 to 1. With the maximum likelihood scaled to 1, as it is in the following calculations, the likelihood ratios are just the individual likelihoods, which are in turn upper limits of the individual probabilities of the data for each hypothesis.

Likelihood estimation involves comparison of the relative likelihoods of different hypotheses concerning  $t_1$  and ETD (Fig. 1), where the likelihood of a particular hypothesis is proportional to the probability of the observed results,  $n$  samples in OTD, for that hypothesis:  $k \cdot P(\text{OTD}, n | \text{ETD})$ , with  $k$  being an arbitrary constant. Given the geometric model shown here and the observed results,  $n$  samples falling in OTD, the hypothesis about  $t_1$  and ETD that has maximum likelihood is the hypothesis that  $t_1 = t_2$  and  $\text{ETD} = \text{OTD}$ . No matter what the size of  $n$ ,  $\text{ETD} = \text{OTD}$  has maximum likelihood because the exponentiated quotient  $(\text{OTD}/\text{ETD})^n = (\text{OTD}/\text{OTD})^n = 1^n = 1$ , and by definition no probability of observed data can be greater than 1. Maximum likelihood, by convention, has an associated likelihood ratio  $L$  of  $k \cdot P$  divided by itself:  $L = (k \cdot P)/(k \cdot P) = 1$ , and competing likelihood ratios are necessarily smaller, lying in the range 0 to 1. Note that while  $P$  is greater than or equal to 1, there is always a likelihood ratio  $L = 1$  and  $L$  is consequently an upper bound for  $P$ .

It is useful to distinguish sets of hypotheses that satisfy some minimal likelihood criterion, and we are here interested in all hypotheses for which likelihoods exceed the critical likelihood  $\lambda = 0.5$  and all hypotheses for which likelihoods exceed  $\lambda = 0.05$ , that is, hypotheses with at least 1 in 2 chances of occurrence (for which the betting odds are an even "50-50") or at least 1 in 20 chances of occurrence (for which the odds are "5-95"). These lambdas are upper limits for ordinary levels of significance  $\alpha = 0.5$  and  $\alpha = 0.05$  and hence define conservatively narrow 50% and 95% confidence limits for  $t_2$  and OTD in terms of an hypothesized origination time  $t_1$  and ETD. In the uniform case, as before,

$$\lambda = (\text{OTD}/\text{ETD})^{n-1} \quad (4)$$

and

$$\text{ETD} = \text{OTD} / \sqrt[n-1]{\lambda} \quad (5)$$

We are interested to know how large we can make ETD and still expect all samples from ETD to fall in OTD in 1 out of 2 or in 1 out of 20 trials—in other words, how large can ETD be and still yield OTD some small, but still reasonable, proportion of the time?

The hypotheses being compared are constructed to differ by some number of arbitrarily small increments  $i$  added to OTD, and there is in theory no limit on the fineness of the increment nor on the number of incremented hypotheses that can be compared. Increments of  $i$  are added to OTD until the sum ETD satisfies equations 4 and 5. OTD,  $n$ , and  $\lambda$  are, of course, known or specified in advance. Relationship of ETD to OTD is not sensitive to  $n$  nor to  $\lambda$  if  $n$  is in the range considered here ([Fig. 2](#) and [Fig. 3](#)). Increments of  $i$  added to OTD correspond to addition of some amount of time to  $t_2$ . The time involved is proportional to  $i$  in the uniform case, but not in the nonuniform models considered here.

## MODEL DISTRIBUTION OF POTENTIAL FOSSILS

A uniform distribution of fossils is a good initial assumption, but there are several reasons not to expect the distribution of fossils representing the temporal duration of a group of organisms to be uniform through geological time: (1) the number of organisms in the group and their geographic distribution may have changed through time, changing the probability of preservation as fossils; (2) the outcrop area accessible for sampling today is different for rocks of different ages; and (3) the proportions of marine and non-marine environments on the surface of the earth have changed through time. All of these may affect distributions of fossils and make them nonuniform. Here we consider diversity to have increased at a constant rate during the interval between the time of origin of archaeocetes and their first appearance in the fossil record. We consider that the outcrop area of fossil-bearing sedimentary strata decreases exponentially for rocks of increasing age through the course of Phanerozoic time, as shown in [Figure 4](#) (based on data in [Blatt and Jones 1975](#)). We use an exponential model fit to data for the Phanerozoic because we lack detailed knowledge of changing exposure of sedimentary strata during epochs of Cenozoic time—when detailed information about Cenozoic strata is available it can be substituted to permit a more refined calculation.

Our nonuniform model distribution of potential fossils is shown graphically in Figure 4. It has a geological age or time dimension, a diversity dimension, and a fossiliferous strata dimension. The fossiliferous strata and time dimensions define an area of potential fossils under the exponential curve (stippled), and this area plus the diversity dimension define a volume of potential fossils. Regions of interest within the whole volume of potential fossils have been lettered A, B, C, D, and E: A is the partially shaded volume at the left representing the distribution of sedimentary rocks lacking the taxon of interest

because it had not yet originated and diversified; B is the narrow, hatched, wedge-shaped volume representing diversification after origination but before any appearance in the known fossil record; C is the cross-hatched volume of observed temporal density OTD representing the known fossil record of archaeocetes; D is not used here (because the temporal extension is left-tailed); and E is the partially shaded volume at the right representing the distribution of sedimentary rocks lacking the taxon of interest because it had by now given rise to something else or become extinct. Volumes B and C together correspond to the expected temporal density ETD. Total volumes and normalized proportions of A, B, C, D, and E are given in Figure 4 for the 95% confidence limit calculation shown graphically.

It is important to emphasize that a model distribution of potential fossils is a *model* assuming 'all else' not represented here to be equal. Fossils may or may not be evenly distributed through time, and we have explicitly built some of the ways that they are not evenly distributed into our model. When there is knowledge of additional structure shaping the fossil record such factors can and should be built into a better model. All inference about stratigraphic ranges depends on random sampling in the context of some model, explicit or not, and explicit models are always better than vaguely-conceived implicit models. The actual ages of most fossil samples and the temporal differences between most samples are often poorly known or not known at all, but only two ages are important in our calculations: the age of the oldest known sample ( $t_2$ ), the age of the youngest known sample ( $t_3$ ). We require, in addition, some estimate of the number of independently-sampled fossiliferous horizons ( $n$ ). Finally, the purpose of this exercise is less calculation of precise cut-off ages than comparison of the relative likelihoods of different possibilities.

## TIME OF ORIGIN OF ARCHAEOCETES

There are approximately 42 independently sampled sites yielding archaeocete whales distributed on six continents ([Table 1](#)). These range in age from late Priabonian ( $t_3$ , ca. 36 Ma) to late Ypresian ( $t_2$ , ca. 49.5 Ma), for an observed temporal range  $t_2 - t_3 = 13.5$  m.y. Calculation of ETD from equation 3 yields an expected temporal range of 14.78 m.y., and adding the difference between expected and observed ranges to the oldest stratigraphic record at 49.5 yields a classical 95% confidence limit for the time of origin of archaeocetes and hence all whales at 50.78 Ma, an extension of about 1.3 m.y. beyond the earliest stratigraphic record known to date.

Likelihood calculation of the time of origin of whales is outlined in the work sheet of [Table 2](#) and shown graphically in Figure 4. Here the origination volume OTD is successively incremented by 0.001 units until critical likelihoods  $\lambda = 0.5$  and  $\lambda = 0.05$  are reached and exceeded. Hypothesized times of origin are interpolated at 49.99 and 51.64 Ma, respectively, with the latter, an extension of about 2.1 m.y. beyond the earliest stratigraphic record, being the likelihood equivalent of a 95% confidence limit. This limit at 51.64 Ma is almost 1 m.y. earlier in time than the classical confidence

interval of [Strauss and Sadler \(1989\)](#) based on a uniform distribution of potential fossils. The difference is due to assumptions built into our geometric model of increasing density and diversity of whales during their initial diversification and to the exponentially increasing availability of fossil-bearing sedimentary rocks in more recent geological times.

The likelihood function calculated for the time of origin of Archaeoceti is shown in [Figure 5](#). Both of the confidence limits calculated here, a 50% limit at 49.99 Ma and a 95% limit at 51.64 Ma, fall comfortably within the early Eocene on the [Haq et al. \(1987\)](#) time scale used here. Thus we can be confident, given present evidence, that whales originated in the early Eocene. Any discovery older than the known temporal range of archaeocetes would of course extend both the range and the ages associated with all critical likelihoods.

## TIME OF ORIGIN OF MESONYCHIA

There are approximately 56 independently sampled sites yielding mesonychian condylarths distributed on the three northern continents ([Table 3](#)). These range in age from Rupelian early Oligocene ( $t_2$ , ca. 33 Ma) to Torrejonian middle Paleocene ( $t_3$ , ca. 63 Ma), for an observed temporal range  $t_2 - t_3 = 30$  m.y. Likelihood calculation of the time of origin of mesonychians is outlined in the work sheet of [Table 4](#) and shown graphically in [Figure 6](#). Critical likelihoods  $\lambda = 0.5$  and  $\lambda = 0.05$  correspond to hypothesized times of origin at 63.83 and 66.68 Ma, respectively, with the latter, an extension of about 3.7 m.y. beyond the earliest stratigraphic record, being the likelihood equivalent of a 95% confidence limit.

The likelihood function calculated for the time of origin of Mesonychia is shown in [Figure 7](#). The 50% confidence limit at 63.83 Ma falls within the early Paleocene, and the 95% confidence limit at 66.68 Ma falls within the very latest Cretaceous close to the Cretaceous-Tertiary boundary at 66.5 on the [Haq et al. \(1987\)](#) time scale used here. Considering what we know of their fossil record, mesonychians evidently originated at or near the Cretaceous-Tertiary boundary. Any discovery older than the known temporal range of mesonychians would of course extend both the range and the ages associated with all critical likelihoods.

## DISCUSSION

The time of origin of archaeocetes calculated here takes nonuniform aspects of the distribution of potential fossils into account. The resulting estimate at ca. 51.64 Ma, is a little more than 2 m.y. before the first fossil archaeocetes appeared in the fossil record at ca. 49.50 Ma. This is a substantial 16% increase in the estimated temporal range of archaeocetes compared to their observed temporal range ( $15.64/13.50 = 1.16$ ), but it is a rather small 4% increase in the estimated temporal range of cetaceans as a whole ( $51.64/49.50 = 1.04$ ). The fossil record of early cetaceans is not yet adequate to answer

all questions we ask of it, but it is adequate to constrain the time of origin of Cetacea. Further, the early Eocene time of origin we calculate here is consistent with the very primitive transitionally-aquatic remains of early Eocene fossil cetaceans found in recent years.

The temporal range of mesonychians, from at least 63 to 33 Ma (middle Paleocene through early Oligocene) and possibly from 66.7 Ma to about 33 Ma (latest Cretaceous through early Oligocene), precedes and overlaps the origin of archaeocetes in the early Eocene. The temporal range of arctocyonians plus artiodactyls, from at least 67 to 0 Ma (latest Cretaceous to the present), coincides with or overlaps the origin of mesonychians in the latest Cretaceous or early Paleocene. These temporal relationships, with times of origin of Archaeoceti and Mesonychia constrained to a range of reasonable likelihoods, are shown in [Figure 8](#). Phylogenetic relationships shown in [Figure 8](#) are the same as those outlined in a cladistic analysis by [Geisler and O'Leary \(1997\)](#). Mesonychia are monophyletic in the sense that all are thought to be descendants of a single common ancestor, but paraphyletic in the sense that some descendants (principally those in Cetacea) are not included.

Claims that whales originated or whale ancestors separated from artiodactyls 80-90 million years ago, based on cladistic analyses ([Novacek 1992](#); [Archibald 1996](#)) and/or molecular clocks ([Hedges et al. 1996](#), [Kumar and Hedges 1998](#)), conflict with our results. It may be possible to shape the cladograms in question to conform more closely to the fossil record (since cladistic analyses are rarely constrained by geological time or the age of fossils in any case), but there appears to be no way to reconcile our results with early divergence times hypothesized from molecular studies. The many conflicting hypotheses of cetacean relationship to and within Artiodactyla in the current literature suggest that times of divergence based on present molecular 'clocks' cannot be taken seriously either. From the point of view of the fossil record and geological time scale, the idea that whales might be found in the mid-Cretaceous involves vanishingly small likelihoods (on the order of 1 to 10 in a billion). This does not prove that a mid-Cretaceous origin of whales is impossible, but shows the conjecture to be beyond reasonable expectation given what we know about the fossil record of whales (in the same way that 28 heads and no tails is beyond reasonable expectation when a coin is tossed 28 times).

A distinction is sometimes drawn between the beginning of an estimated stratigraphic or temporal range and the 'true' time of origin of a taxon, and it is possible that there is a slight difference. However the geological time scale that is almost universally used as a context for discussion of animal history is itself based on the fossil record, and it necessarily takes account of whatever this slight difference might be, meaning, possibly, that the whole Phanerozoic time scale should be inflated by some small percentage. However, this would affect all times calibrated from geological evidence uniformly, it would affect all inferences concerning evolutionary time and rates uniformly, and the difference, consequently, is negligible.

It will undoubtedly be possible to discover and quantify additional factors influencing

estimation of the time of origin of Cetacea, but these are not likely to add more than possibly another 0.5 to 1.0 m.y. to the estimate given here. There is a high probability that additional fossil whales will be found intermediate in time between known records, and there is a reasonable probability that the fossil record can be extended earlier than any record known at present. There is of course some chance that a fossil whale could be found at any time in the geological past, but this chance diminishes with predictable rapidity farther back in time. In Figure 5 we provide quantitative estimates of how likely we are to find fossil whales older than any known at present. The importance of earlier discoveries would be inversely proportional to such vanishing likelihoods (that is, of *great* importance), and we hope skeptics will channel their energy and attention into a search for earlier fossil whales.

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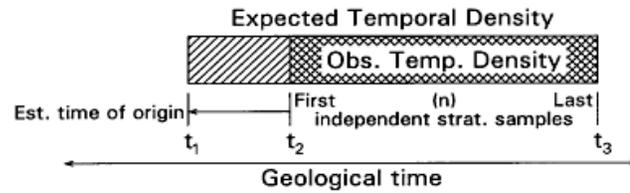
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**Figure 1.** Geometric relationship of the observed temporal range or density, OTD, for a taxon of interest, and the estimated temporal range or density, ETD, which is the sample space from which OTD is inferred to have been drawn. OTD is cross-hatched here and in following illustrations. ETD involves a one-tailed extension of OTD backward in geological time from  $t_2$  to an inferred time of origin at  $t_1$ . The sample space here is uniform, meaning that it has a constant width and there is a constant probability of drawing a sample from any part of the linear range of ETD—making  $OTD \propto (t_3 - t_2)$  and  $ETD \propto (t_3 - t_1)$ —this simplification is relaxed in the applications considered here. For purposes of inference, sample size  $n$  is restricted to the number of stratigraphic samples in OTD drawn independently from ETD (total sample size in OTD could of course be much larger than  $n$  if recovery of one sample led, directly or indirectly, to recovery of others). The probability that a sample drawn from ETD falls in OTD is the ratio of areas (or volumes)  $OTD/ETD$ , the probability two samples drawn independently from ETD both fall in OTD is the product of their independent probabilities, and the probability  $n - 1$  independent samples from ETD fall in OTD is consequently  $(OTD/ETD)^{n-1}$  (we consider observed  $t_2$  and inferred  $t_1$  to be a function of  $n - 1$  samples rather than all  $n$  because one sample is committed to fix the end of both OTD and ETD at  $t_3$ ).

Likelihood estimation involves comparison of the relative likelihoods of different hypotheses concerning  $t_1$  and ETD, where the likelihood of a particular hypothesis is proportional to the probability of the observed results,  $n$  samples in OTD, for that hypothesis:  $k \cdot \underline{P}(OTD, n|ETD)$ , with  $k$  being an arbitrary constant. Given the geometric model shown here and the observed results,  $n$  samples falling in OTD, the hypothesis about  $t_1$  and ETD that has maximum likelihood is the hypothesis that  $t_1 = t_2$  and  $ETD = OTD$ . Maximum likelihood, by convention, has an associated likelihood ratio  $L$  of  $k \cdot P$  divided by itself:  $L = (k \cdot P)/(k \cdot P) = 1$ , and competing likelihood ratios are necessarily smaller, lying in the range 0 to 1. Note that while  $P$  less than or equal to 1, there is always a likelihood ratio  $L = 1$  and  $L$  is consequently an upper bound for  $P$ .

How small a likelihood ratio  $L$  is acceptable depends on our choice of a critical likelihood or critical likelihood ratio  $\lambda$ . In the following applications we consider two values of  $\lambda$ ,  $\lambda = 0.5$  and  $\lambda = 0.05$ ; these are upper limits for ordinary levels of significance  $\alpha = 0.5$  and  $\alpha = 0.05$  and hence define conservatively narrow 50% and 95% confidence limits for  $t_2$  and OTD in terms of an hypothesized origination time  $t_1$  and ETD.

In general,  $ETD = OTD / {}^{(n-1)}\sqrt{\lambda}$  and we are interested to know how large we can make ETD and still expect all samples from ETD to fall in OTD in 1 out of  $1/\lambda$  trials—in other words, how large can ETD be and still yield OTD some small but still reasonable proportion of the time?



Critical likelihood  $\lambda = 0.5$  or  $0.05$  is effectively an upper limit for level of significance  $\alpha$  in defining a conservatively narrow  $1 - \lambda = 50\%$  or  $95\%$  ( $\leq 1 - \alpha$ ) confidence limit for OTD

How large can we make ETD and still get all samples from ETD to fall in OTD some small but still reasonable proportion of the time (say once in  $1/\lambda$  trials)?

$$(OTD/ETD)^{n-1} = \lambda$$

$$OTD / ETD = {}^{(n-1)}\sqrt{\lambda}$$

$$ETD = OTD / {}^{(n-1)}\sqrt{\lambda}$$

**Figure 2.** Relationship of estimated temporal range or density [ETD] of a taxon to its observed temporal range or density [OTD], expressed as a function of the number of independent samples  $n$  found in OTD, for critical likelihood  $\lambda = 0.05$ . Note that ETD is  $20 \times$  OTD for  $n = 2$  (exceeding OTD by 1900%), but this proportion falls rapidly to less than  $2 \times$  OTD when  $n = 6$  (exceeding OTD by 82.1%) and less than  $1.1 \times$  OTD when  $n = 33$  (exceeding OTD by only 9.8%). For values of sample size  $n$  considered in applications here,  $n = 42$  and  $n = 56$ , differences in ETD are insensitive to small changes in  $n$  (addition or subtraction of a sample changes the difference between ETD and OTD by 0.002 to 0.001 or 0.2 to 0.1%).

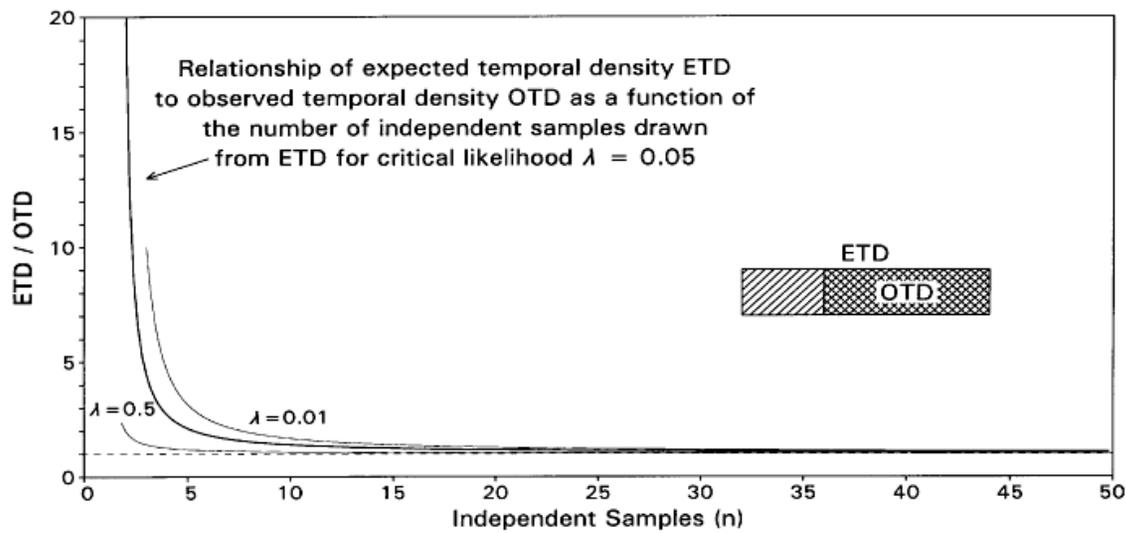
Expected temporal density	n	ETD > OTD (%)
20.000	n = 2	1900.0
4.472	n = 3	347.2
2.714	n = 4	171.4
2.115	n = 5	111.5
1.821	n = 6	82.1
1.648	n = 7	64.8
1.534	n = 8	53.4
1.454	n = 9	45.4
1.395	n = 10	39.5
1.349	n = 11	34.9
1.313	n = 12	31.3
1.284	n = 13	28.4
1.259	n = 14	25.9
1.239	n = 15	23.9
1.221	n = 16	22.1
1.206	n = 17	20.6
1.193	n = 18	19.3
1.181	n = 19	18.1
1.171	n = 20	17.1
1.162	n = 21	16.2
1.153	n = 22	15.3
1.146	n = 23	14.6
1.139	n = 24	13.9
1.133	n = 25	13.3
1.127	n = 26	12.7
1.122	n = 27	12.2
1.117	n = 28	11.7
1.113	n = 29	11.3
1.109	n = 30	10.9
1.105	n = 31	10.5
1.101	n = 32	10.1
1.098	n = 33	9.8
1.095	n = 34	9.5
1.092	n = 35	9.2
1.089	n = 36	8.9
1.087	n = 37	8.7
1.084	n = 38	8.4
1.082	n = 39	8.2
1.080	n = 40	8.0
1.078	n = 41	7.8
1.076	n = 42	7.6
1.074	n = 43	7.4
1.072	n = 44	7.2
1.070	n = 45	7.0
1.069	n = 46	6.9
1.067	n = 47	6.7
1.066	n = 48	6.6
1.064	n = 49	6.4
1.063	n = 50	6.3
1.062	n = 51	6.2
1.060	n = 52	6.0
1.059	n = 53	5.9
1.058	n = 54	5.8
1.057	n = 55	5.7
1.056	n = 56	5.6

$\lambda = 0.05$

OTD



**Figure 3.** Relationship of estimated temporal range or density [ETD] of a taxon to its observed temporal range or density [OTD], expressed as a function of the number of independent samples  $n$  found in OTD for critical likelihood  $\lambda = 0.05$  (heavier line) and also for  $\lambda = 0.5$  and  $\lambda = 0.01$  (lighter lines). For values of sample size  $n$  considered in applications here,  $n = 42$  and  $n = 56$ , differences in ETD are not very sensitive to small changes in  $\lambda$ .

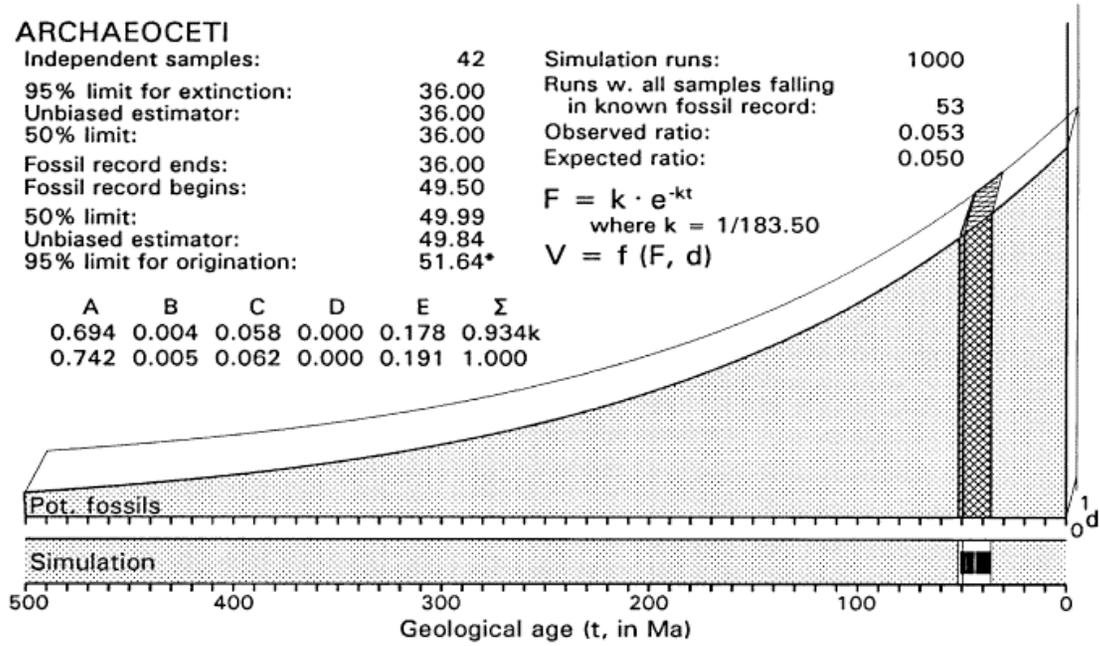


**Figure 4.** Graphical model for analysis of the time of origin of Archaeoceti, assuming that all uncertainty is in the left or origination tail of the confidence interval (compare work sheet in [Table 2](#)). Sample space is three-dimensional and composed of five volumes: A is the partially-stippled volume preceding inferred origination and diversification of the taxon of interest; B is the thin wedge-shaped origination volume (hatched) reflecting the density of potential fossils during diversification; C is the volume representing the density of the known fossil record (cross-hatched); D is negligible because we are not concerned with extinction here; and E is the partially-stippled volume succeeding inferred extinction or conversion to another taxon. For comparison with other figures, tables, and text, volume C is the observed temporal density OTD, and volumes B + C together are the expected temporal density ETD. The sample space shown here reflects the exponentially declining availability of older fossil-bearing sedimentary rocks at the earth's surface ( $F$ ), and diversification of Archaeoceti at a constant rate in the  $d$  dimension from the time they are first inferred to have existed until they are first found as fossils. Simulation built into the analysis tests analytical assumptions by repeatedly drawing samples of size  $n = 42$  from B + C (or ETD) and counting the number of times all fall in C (or OTD) in 1000 trials (one sample is shown in simulation bar at bottom of figure). All samples drawn from B + C fell in C in 53 of 1000 simulation trials, which is close to the 50/1000 times expected with a critical likelihood  $\lambda = 0.05$ .

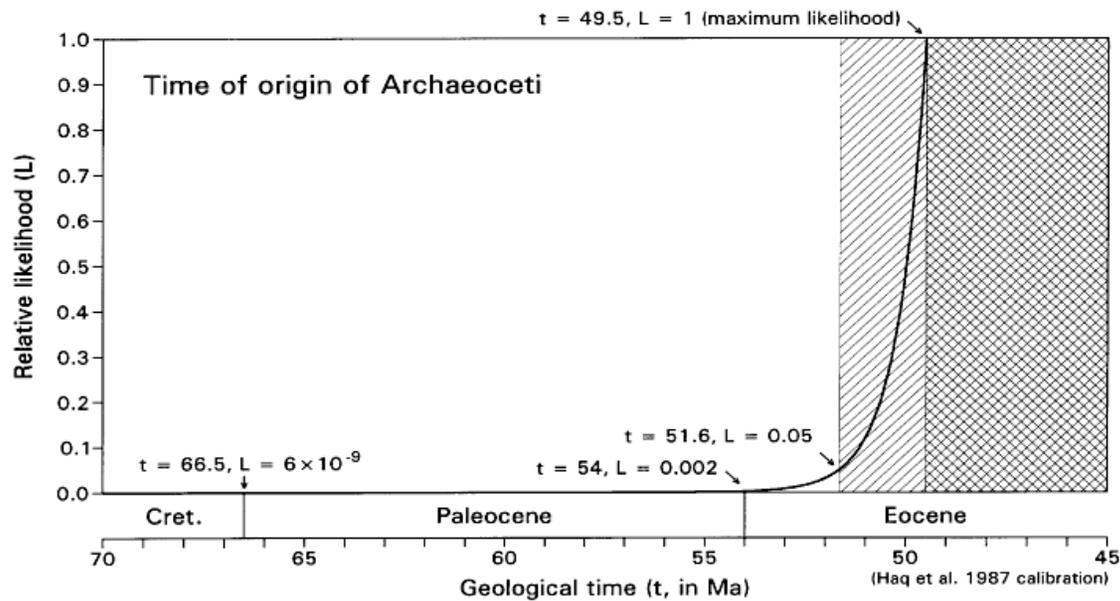
**ARCHAEOCETI**

Independent samples:	42	Simulation runs:	1000
95% limit for extinction:	36.00	Runs w. all samples falling	53
Unbiased estimator:	36.00	in known fossil record:	
50% limit:	36.00	Observed ratio:	0.053
Fossil record ends:	36.00	Expected ratio:	0.050
Fossil record begins:	49.50		
50% limit:	49.99	$F = k \cdot e^{-kt}$	
Unbiased estimator:	49.84	where $k = 1/183.50$	
95% limit for origination:	51.64*	$V = f(F, d)$	

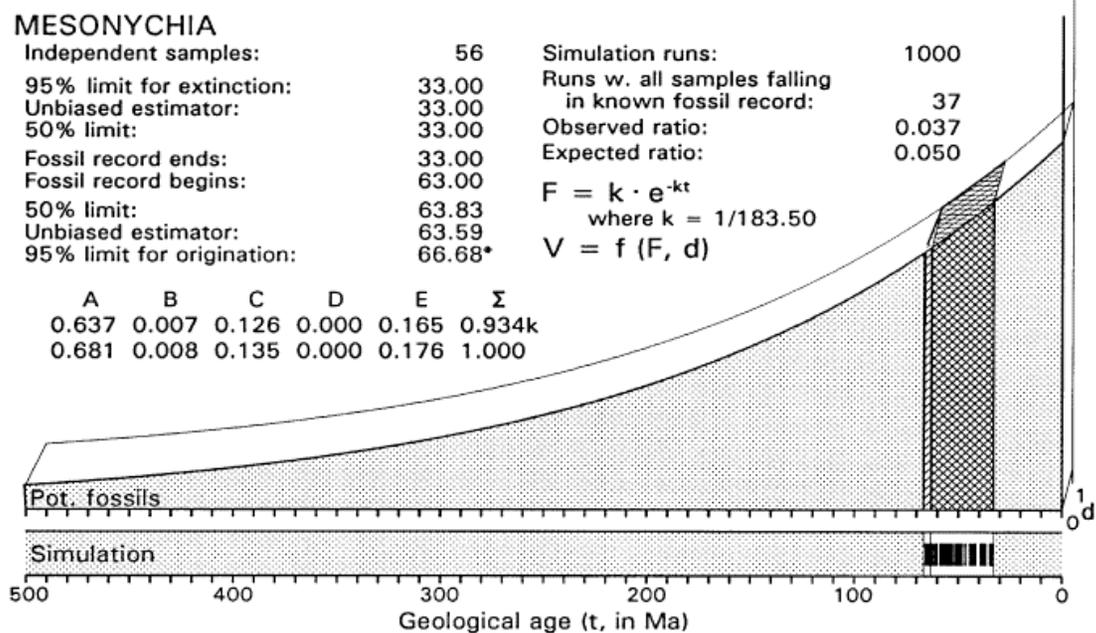
A	B	C	D	E	$\Sigma$
0.694	0.004	0.058	0.000	0.178	0.934k
0.742	0.005	0.062	0.000	0.191	1.000



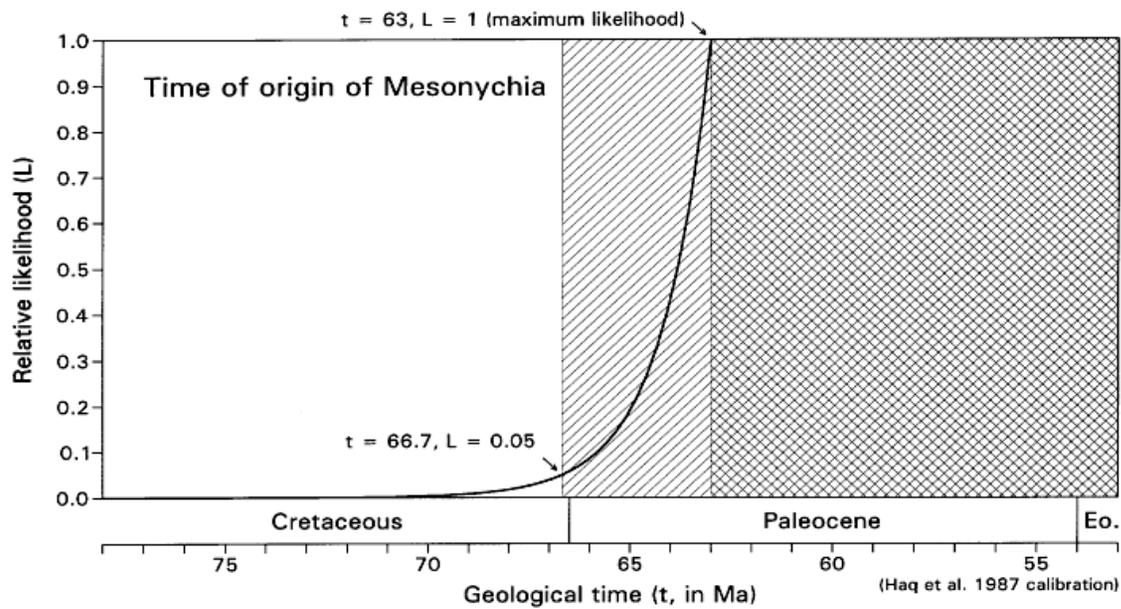
**Figure 5.** Likelihood function for the time of origin of Archaeoceti, calculated as shown in [Table 2](#) (but with a 0.0001 increment of origination volume). Note that maximum likelihood here ( $L = 1$ ) corresponds to the time  $t = 49.5$  Ma when the fossil record of Archaeoceti begins.  $L = 0.05$  (the critical likelihood  $\lambda$  employed here) when  $t$  is about 51.6 Ma. Given present evidence, there are about 2 chances in a thousand that archaeocetes existed and will be found as fossils at the Paleocene-Eocene boundary, and 6 chances in a billion that archaeocetes existed and will be found as fossils at the Cretaceous-Paleocene boundary.



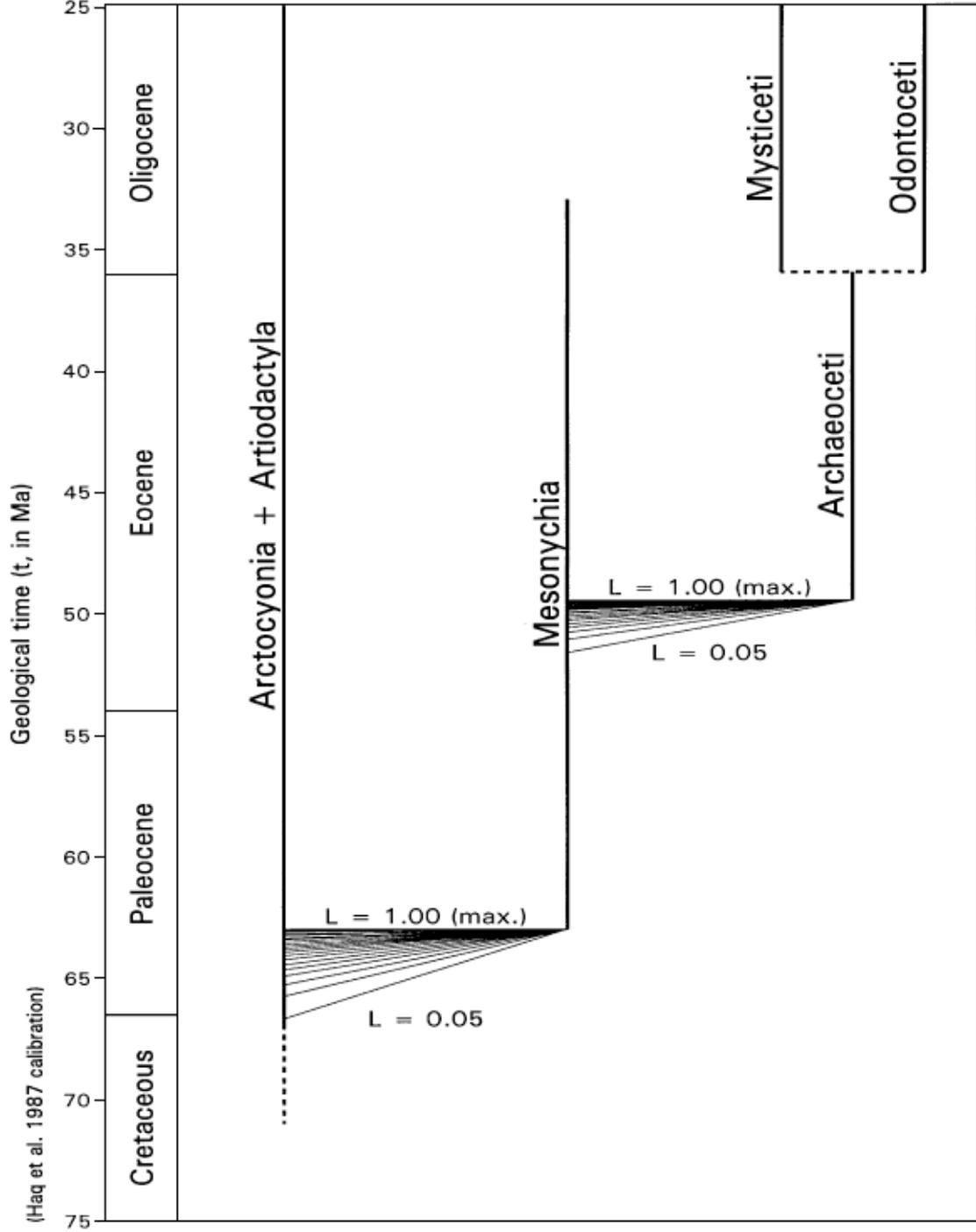
**Figure 6.** Graphical model for analysis of the time of origin of Mesonychia, assuming that all uncertainty is in the left or origination tail of the confidence interval (compare work sheet in [Table 4](#)). Sample space is three-dimensional as in [Figure 4](#). The sample space shown here reflects the exponentially declining availability of older fossil-bearing sedimentary rocks at the earth's surface ( $F$ ), and diversification of Mesonychia at a constant rate in the  $d$  dimension from the time they are first inferred to have existed until they are first found as fossils. Simulation built into the analysis tests analytical assumptions by repeatedly drawing samples of size  $n = 56$  from  $B + C$  (or ETD) and counting the number of times all fall in  $C$  (or OTD) in 1000 trials (one sample is shown in simulation bar at bottom of figure). All samples drawn from  $B + C$  fell in  $C$  in 37 of 1000 simulation trials, which is close to the 50/1000 times expected with a critical likelihood  $\lambda = 0.05$ .



**Figure 7.** Likelihood function for the time of origin of Mesonychia, calculated as shown in [Table 4](#) (but with a 0.0001 increment of origination volume). Note that maximum likelihood here ( $L = 1$ ) corresponds to the time  $t = 63$  Ma when the fossil record of Mesonychia begins.  $L = 0.05$  (the critical likelihood  $\lambda$  employed here) when  $t$  is about 66.7 Ma.



**Figure 8.** Range chart of Arctocyonia (extinct) + Artiodactyla (extant), Mesonychia (extinct), and Archaeoceti (extinct) + Mysticeti/Odontoceti (both extant). Spectra of reasonable likelihoods (0.05 less than or equal to  $L$  less than or equal to 1.00) for the time of origin of Mesonychia from Arctocyonia + Artiodactyla and the time of origin of Archaeoceti from Mesonychia, are shown in the context of condylarthran, artiodactyl, and cetacean phylogeny (phylogenetic relationships follow [Van Valen 1966](#), [1971](#), [1978](#); [Rose 1996](#); [Geisler and O'Leary 1997](#); and others). From a paleontological point of view the origin of Cetacea is constrained by fossils to lie within the interval from 49.5 to about 51.6 Ma (early Eocene). From a neontological point of view the divergence time of Cetacea and Artiodactyla is constrained by fossils to lie within the interval from 63 to about 66.7 Ma (early Paleocene to latest Cretaceous).







**Table 1.** Independent records of archaeocete Cetacea. Records from different geological formations are considered independent; records from the same geological formation are considered independent if they come from different states, provinces, or countries.

<b>Country/State</b>	<b>Formation</b>	<b>Age</b>	<b>Ref.</b>
<b>North America</b>			
1. Canada (B.C.)	Nootka Conglomerate	L. Eocene	Kellogg (1936)
2. U.S.A. (N. Car.)	Castle Hayne	L. Eocene (Bart.-Priab.)	Kellogg (1936)
3. U.S.A. (S. Car.)	Harleyville Formation	M. Eocene (Bartonian)	Sanders (1974)
4. U.S.A. (S. Car.)	Santee Limestone	M. Eocene (E. Bart.)	Albright (1996)
5. U.S.A. (Georgia)	Twiggs Clay	L. Eocene (L. Priab.)	Case (1975)
6. U.S.A. (Georgia)	Barnwell Sand	L. Eocene (Bart.-Priab.)	Cooke and Shearer (1918)
7. U.S.A. (Georgia)	Clinchfield	L. Eocene (L. Bart.)	Westgate (1994)
8. U.S.A. (Georgia)	McBean	M. Eocene (E. Bart.)	Petkewich and Lancaster (1984)
9. U.S.A. (Florida)	Ocala Limestone	L. Eocene (L. Bart.-Priab.)	Morgan (1978)
10. U.S.A. (Alabama)	Jackson/Ocala	L. Eocene (L. Bart.-Priab.)	Kellogg (1936)
11. U.S.A. (Miss.)	Yazoo	L. Eocene (L. Bart.-Priab.)	Daly (1992)
12. U.S.A. (Miss.)	Moodys Branch	M. Eocene (M. Bart.)	Dockery (1974)
13. U.S.A. (Ark.)	Jackson	L. Eocene (Priabonian)	Palmer (1939)
14. U.S.A. (Tenn.)	Jackson	L. Eocene (Priabonian)	Corgan (1976)
15. U.S.A. (Louis.)	Cook Mountain	M. Eocene (E. Bart.)	Maher and Jones (1949)
16. U.S.A. (Louis.)	Jackson	L. Eocene (L. Bart.-Priab.)	Lancaster (1986)
17. U.S.A. (Texas)	Yegua (basal)	M. Eocene (E. Bart.)	Ball (1931)
18. U.S.A. (Texas)	Cook Mountain	M. Eocene (L. Lut.)	Gimbrede (1962)
<b>Europe</b>			

19. England	Middle Headon Beds	L. Eocene (L. Priab.)	Hooker et al. (1980)
20. England	Barton Clay	M. Eocene (Bartonian)	Hooker et al. (1980)
21. Germany	Braunschweig Phosphates	L. Eocene (reworked)	Kuhn (1935)
22. Italy	Not reported	M. to I. Eocene	Pilleri and Cig.-Ful. (1989)
23. Spain	Not reported	M. to I. Eocene	Pilleri (1989)
<b>Asia</b>			
24. India (Kutch)	Gypsiferous Clay	M. Eocene (Lutetian)	Kumar and Sahni (1986)
25. India (Kutch)	Chocolate Limestone	M. Eocene (Lutetian)	Kumar and Sahni (1986)
26. India (Kashmir)	Subathu	E.-M. Eocene	Kumar and Sahni (1985)
27. Pakistan (Punj.)	Drazinda	M. Eocene (Lutetian)	Gingerich et al. (1995b)
28. Pakistan (Punj.)	Domanda	M. Eocene (Lutetian)	Gingerich et al. (1994)
29. Pakistan (Punj.)	Habib Rahi	M. Eocene (Lutetian)	Gingerich (1991)
30. Pakistan (Punj.)	Kuldana	E. Eocene (L. Ypr.)	West (1980)
31. Pakistan (NWFP)	Kuldana	E. Eocene (L. Ypr.)	Gingerich and Russell (1981)
<b>Africa</b>			
32. Egypt (Fayum)	Qasr el-Sagha	L. Eocene (M.-L. Priab.)	Stromer (1903)
33. Egypt (Fayum)	Birket Qarun	L. Eocene (E. Priab.)	Andrews (1906)
34. Egypt (Fayum)	Gehannam	M. Eocene (L. Bart.)	Gingerich (1992)
35. Egypt (E. desert)	Mokattam	M. Eocene (L. Lut.?)	Blanckenhorn (1900)
36. Egypt (Cairo)	Mokattam	M. Eocene (Lut.-E. Bart.)	Fraas (1904)
37. Nigeria	Ameki	M. Eocene (Lutetian)	Andrews (1919)
38. Senegal	Not reported	M. to I. Eocene	Elouard (1981)
39. Togo	Kpogamé Phosphates	M. Eocene (L. Lut.)	Gingerich et al. (1992)
<b>Australia</b>			
40. New Zealand	Opuha River Sandstone	M. to I. Eocene	Fordyce (1985)
41. New Zealand	Waihao Greensands	L. Eocene	Fordyce (1985)
<b>Antarctica</b>			

42. Seymour Island

La Meseta

L. Eocene(?)

Borsuk-Bialynicka (1988)

**Table 2.** Work sheet for likelihood estimation of the time of origin of Archaeoceti. The fossil record of archaeocetes begins at about 49.5 Ma and ends at about 36 Ma, an interval of about 13.5 m.y. ([Haq et al. 1987](#) temporal calibration). There are 42 independently-sampled fossil localities known from sites on six continents ([Table 1](#)). Analysis here takes account of exponentially decreasing area of sedimentary rocks of older ages exposed at the earth's surface and linear diversification through the inferred temporal range of archaeocetes before their earliest fossil record (see [Fig. 4](#)). Interpolated 50% and 5% likelihood limits for the time of origin of mesonychians are shown in bold face. Results are not accurate to more than one decimal place and must be interpreted in context of the particular temporal calibration used to quantify the geological time scale (50.0 and 51.6 Ma are both late early Eocene).

1.	2.	3.	4.	5.	6.	7.	8.	9.
0.0000	49.5000	0.0000	0.0583	0.0000	36.0000	1.0000	1.0000	1.0000
---	<b>49.9869</b>	---	---	---	---	---	---	<b>0.5000</b>
0.0010	49.9899	0.0010	0.0583	0.0000	36.0000	0.9831	0.4979	0.4979
0.0020	50.4698	0.0020	0.0583	0.0000	36.0000	0.9668	0.2508	0.2508
0.0030	50.9498	0.0030	0.0583	0.0000	36.0000	0.9511	0.1278	0.1278
0.0040	51.4297	0.0040	0.0583	0.0000	36.0000	0.9358	0.0658	0.0658
---	<b>51.6352</b>	---	---	---	---	---	---	<b>0.0500</b>
0.0050	51.9196	0.0050	0.0583	0.0000	36.0000	0.9210	0.0343	0.0343

Volume quotient is the fossil record volume (C here and in Fig. 4) divided by the sum of the hypothesized origination volume plus the fossil record volume (B + C here and in Fig. 4). Exponentiated quotient is  $(B / (B + C))^n$  where  $n$  is the number of independent samples drawn from B + C and falling in C (here  $n = 42$ ).

**Table 3.** Independent records of Mesonychia (here Mesonychidae plus Hapalodectidae). Records from different geological formations are considered independent; records from the same geological formation are considered independent if they come from different states, provinces, or countries.

Country/State	Formation	Age	Ref.
<b>North America</b>			
1. Mexico (B. Cal.)	Tetas de Cabra	Early Eocene (Wasatchian)	Novacek et al. (1991)
2. USA (Colorado)	Huerfano	Middle Eocene (Bridger.)	Robinson (1966)
3. USA (Colorado)	Wasatch	Early Eocene (Wasatchian)	McKenna (1960)
4. USA (Colorado)	DeBeque	Late Paleocene (Clarkfork.)	Kihm (1984)
5. USA (Colorado)	San Jose	Late Paleocene (Tiffanian)	Granger (1917)
6. USA (Montana)	Fort Union	Late Paleocene (Clarkfork.)	Simpson (1929)
7. USA (Montana)	Tongue River	Late Paleocene (Tiffanian)	Zhou (1995)
8. USA (Montana)	Lebo	Middle Paleocene (Torrejon.)	Simpson (1937)
9. USA (New Mexico)	San Jose	Early Eocene (Wasatchian)	Cope (1874)
10. USA (New Mexico)	Nacimiento	Middle Paleocene (Torrejon.)	Osborn and Earle (1895)
11. USA (Texas)	Comena	Middle Eocene (Uintan)	Gustafson (1986)
12. USA (Texas)	Devils Graveyard	Middle Eocene (Uintan)	Gustafson (1986)
13. USA (Utah)	Duchesne River	Late Eocene (Duchesnian)	Peterson (1931)
14. USA (Utah)	Uinta	Middle Eocene (Uintan)	Osborn (1895)
15. USA (Wyoming)	Washakie	Middle Eocene (Bridgerian)	Cope (1872b)
16. USA (Wyoming)	Bridger	Middle Eocene (Bridgerian)	Cope (1872a)

17. USA (Wyoming)	Aycross	Middle Eocene (Bridgerian)	Bown (1982)
18. USA (Wyoming)	Wasatch	Early Eocene (Wasatchian)	Gazin (1952)
19. USA (Wyoming)	Wind River	Early Eocene (Wasatchian)	Matthew (1909)
20. USA (Wyoming)	Willwood	Early Eocene (Wasatchian)	Osborn and Wortman (1892)
21. USA (Wyoming)	Fort Union	Late Paleocene (Tiffanian)	Rose (1981)

### Europe

22. Belgium	Landen	Early Eocene (Sparnacian)	Russell (1982)
23. France (Hérault)	Marnes Jaunes et Rouges	Middle Eocene (Lutetian)	Stehlin (1926)
24. France (Marne)	Lignites de Soissonais	Early Eocene (Sparnacian)	Lemoine (1891)
25. France (B. Rhône)	Lentille de Marne	Early Eocene (Sparnacian)	Godinot et al. (1987)
26. France (H. Seine)	Argile Plastique	Early Eocene (Sparnacian)	Boule (1903)
27. France (Marne)	Conglomérat de Cernay	Late Paleocene (Thanetian)	Lemoine (1891)
28. Spain (Lérida)	Tremp or Montañana	Middle Eocene (Lutetian)	Crusafont and Golpe (1968)
29. Spain (Huesca)	Tremp or Montañana	Early Eocene (Cuisian)	Crusafont and Golpe (1973)

### Asia

30. China (Anhui)	Tujinshan	Late Paleocene (Nongshanian)	Zhou et al. (1995)
31. China (Anhui)	Shuangtasi	Late Paleocene (Nongshanian)	Yan and Tang (1976)
32. China (Guangdong)	Nongshan	Late Paleocene (Nongshanian)	Wang (1976)
33. China (Guangdong)	Shanghu	Middle Paleocene (Shanghuan)	Chow et al. (1973)

34. China (Henan)	Dacangfang	Middle Eocene (Irdinmanhan)	Xu et al. (1979)
35. China (Henan)	Lushi	Middle Eocene (Irdinmanhan)	Chow (1965)
36. China (Hunan)	Lingcha	Early Eocene (Bumbanian)	Ting and Li (1987)
37. China (Hunan)	Zaoshi	Middle Paleocene (Shanghuan)	Wang (1975)
38. China (Jiangxi)	Chijiang	Late Paleocene (Nongshanian)	Zhang et al. (1979)
39. China (Nei Mong.)	Chaganbulage	Early Oligocene (Ergilian)	Qi (1975)
40. China (Nei Mong.)	Ulan Gochu	Early Oligocene (Ergilian)	Szalay and Gould (1966)
41. China (Nei Mong.)	Shara Murun	Late Eocene (Sharamurunian)	Matthew and Granger (1925)
42. China (Nei Mong.)	Ulan Shireh	Middle Eocene (Irdinmanhan)	Szalay and Gould (1966)
43. China (Nei Mong.)	Irdin Manha	Middle Eocene (Irdinmanhan)	Matthew and Granger (1925)
44. China (Nei Mong.)	Arshanto	Middle Eocene (Irdinmanhan)	Qi (1987)
45. China (Nei Mong.)	Nomogen	Late Paleocene (Nongshanian)	Chow and Qi (1978)
46. China (Shaanxi)	Fangou	Middle Paleocene (Shanghuan)	Qi and Huang (1982)
47. China (Yunnan)	Lumeiyi	Middle Eocene (Irdin.-Shar.)	Zheng et al. (1978)
48. China (Yunnan)	Xiangshan	Middle Eocene (Irdin.-Shar.)	Zhang et al. (1978)
49. India (Kashmir)	Subathu	Early to middle Eocene	Ranga Rao (1973)
50. Kazakhstan	Sargamys Svita	Middle Eocene (Irdinmanhan)	Gabunia (1982)
51. Kirgizistan	Alay Svita	Middle Eocene (Irdinmanhan)	Reshetov (Russ. and Zhai 1987)
52. Korea	Hosan coal	Middle to late Eocene	Shikama (1943)
53. Mongolia (Zaal.)	Khaychin Svita	Middle to late Eocene	Dashzeveg (1976)
54. Mongolia (Dorn.)	Unnamed Svita	Middle Eocene	Dashzeveg (Russ. and

		(Irdinmanhan)	Zhai 1987)
55. Mongolia (Omon.)	Naran-Bulak Svita	Late Paleocene (Nongshanian)	Gromova (1952)
56. Mongolia (Omon.)	Khashat Svita	Late Paleocene (Nongshanian)	Szalay and McKenna (1971)

**Table 4.** Work sheet for likelihood estimation of the time of origin of Mesonychia (here Mesonychidae and Hapalodectidae). The fossil record of Mesonychia begins at about 63 Ma and ends at about 33 Ma, an interval of about 30 m.y. (Haq et al. 1987 temporal calibration). There are some 56 independently-sampled fossil localities known from northern continents (Table 3). Analysis takes account of exponentially decreasing area of sedimentary rocks of older ages exposed at the earth's surface and linear diversification through the inferred temporal range of mesonychians before their earliest fossil record (see Fig. 6). Interpolated 50% and 5% likelihood limits for the time of origin of mesonychians are shown in bold face. Results are not accurate to more than one decimal place and must be interpreted in context of the particular temporal calibration used to quantify the geological time scale (63.8 Ma is early Paleocene and 66.7 Ma is very latest Cretaceous).

1.	2.	3.	4.	5.	6.	7.	8.	9.
0.0000	63.0000	0.0000	0.1260	0.0000	33.0000	1.0000	1.0000	1.0000
0.0010	63.5199	0.0010	0.1260	0.0000	33.0000	0.9921	0.6474	0.6474
---	63.8308	---	---	---	---	---	---	0.5000
0.0020	64.0398	0.0020	0.1260	0.0000	33.0000	0.9844	0.4206	0.4206
0.0030	64.5600	0.0030	0.1260	0.0000	33.0000	0.9767	0.2741	0.2741
0.0040	65.0801	0.0040	0.1260	0.0000	33.0000	0.9692	0.1793	0.1793
0.0050	65.6002	0.0050	0.1260	0.0000	33.0000	0.9618	0.1176	0.1176
0.0060	66.1303	0.0060	0.1260	0.0000	33.0000	0.9545	0.0774	0.0774
0.0070	66.6504	0.0070	0.1260	0.0000	33.0000	0.9474	0.0511	0.0511
---	66.6781	---	---	---	---	---	---	0.0500
0.0080	67.1705	0.0080	0.1260	0.0000	33.0000	0.9403	0.0339	0.0339

Volume quotient is the fossil record volume (C here and in Fig. 6) divided by the sum of the hypothesized origination volume plus the fossil record volume (B + C here and in Fig. 6). Exponentiated quotient is  $(B / (B + C))^n$  where  $n$  is the number of independent samples drawn from B + C and falling in C (here  $n = 56$ ).