REVIEW

Paleontological Evidence to Date the Tree of Life

Michael J. Benton and Philip C. J. Donoghue

Department of Earth Sciences, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

The role of fossils in dating the tree of life has been misunderstood. Fossils can provide good "minimum" age estimates for branches in the tree, but "maximum" constraints on those ages are poorer. Current debates about which are the "best" fossil dates for calibration move to consideration of the most appropriate constraints on the ages of tree nodes. Because fossil-based dates are constraints, and because molecular evolution is not perfectly clock-like, analysts should use more rather than fewer dates, but there has to be a balance between many genes and few dates versus many dates and few genes. We provide "hard" minimum and "soft" maximum age constraints for 30 divergences among key genome model organisms; these should contribute to better understanding of the dating of the animal tree of life.

Introduction

Calibrating the tree of life has long been the preserve of paleontology but its place has recently been usurped completely by molecular clocks. Fossil data are fundamental to molecular clock methodology, providing the key means of clock calibration, but their commonplace use is far from satisfactory. We consider the utility and qualities of good calibration dates and, on that basis, we propose a number of well-supported dates, and give ages based on the best current information. In doing this, we argue that paleontological data do not provide actual age estimates for divergence events, but they can provide rather precise minimum constraints on the calibration of molecular clocks, and much looser maximum constraints. The evidence of a "hard" lower bound (minimum constraint) and a "soft" upper bound (maximum constraint) provided from paleontology can then be fed into a molecular clock analysis. It is not our aim to determine the actual timing of divergence events as we do not believe that this is possible using paleontological data alone—though paleontological data can be used to test dates estimated using molecular clock methods (e.g., Foote et al. 1999; Tavaré et al. 2002).

Traditionally, very small numbers of calibration dates have been employed and these have been selected for utility and have rarely been defended. The most commonly used calibration node is the mammal–bird divergence, dated at 310 MYA and accepted in some 500 or more publications since 1990. This date was based on the age of the oldest members of the synapsid and diapsid clades (Benton 1990), and yet these basal fossils have been debated, as has the dating of the rocks from which they come. Recently, authors have suggested an age range from 330 to 288 MYA at most (Lee 1999; Reisz and Muller 2004; van Tuinen and Hadly 2004). So, which date is to be used, and what does that date really represent?

It is clear that the fossil record cannot be read literally (Darwin 1859). There are many gaps, and many organisms, and indeed whole groups of poorly preservable organisms that have never been preserved and are doubtless lost for ever (Raup 1972). Some have even gone so far as to suggest

that the fossil record is almost entirely an artifact of the rock record, with appearances and disappearances of fossil taxa controlled by the occurrence of suitable rock units for their preservation (Peters and Foote 2001, 2002), or the matching rock and fossil records controlled by a third common cause (Peters 2005). However, the widespread congruence between the order of fossils in the rocks and the order of nodes in cladograms (Norell and Novacek 1992; Benton et al. 2000) indicates that the order of appearance of lineages within the fossil record is not a random pattern. Furthermore, a fossil of any age demonstrates the divergence of its lineage, and so provides an absolute constraint on the temporal dimension of the tree of life.

Traditionally, calibration dates have been assumed to indicate the timing of an evolutionary divergence event, as a basis for inferring rates of functionally equivalent amino acid or nucleotide substitution (in proteins or genes, respectively), from which the timing of other lineage-splitting events may be deduced (Zuckerkandl and Pauling 1965). However, paleontological data can provide good estimates only for minimum constraints on the timing of lineage divergence events (Benton and Ayala 2003; Hedges and Kumar 2004; Reisz and Muller 2004). Note that relaxed-clock methods can often require at least one point calibration or hard maximum constraint in order for the algorithm to converge on a unique solution. So, debates about the superiority of one "calibration" date or another are irrelevant in the context of a search for the most appropriate distribution of dates and minimum and maximum constraints—the only bad dates are those that predate the evolutionary event upon which they are supposed to provide a minimum constraint.

Deviations from the molecular clock may occur because of changes in selective pressures and mutation rates, and this requires that molecular clock analyses rely upon a law of large numbers in which an average rate may be derived from a data set that is sufficiently large (Rodríguez-Trelles et al. 2003). It is still debated whether an analysis based on many genes and few dates or few genes and many dates is preferable. However, multiple calibration points are particularly helpful in relaxed-clock methods where the rate is allowed to vary among branches in the tree; multiple calibrations throughout the tree act as anchor points, allowing the method to estimate the patterns and degree of rate variation more accurately. Good estimates of rate variation are required from the well-calibrated regions of the tree so that the pattern can be extrapolated to other parts of the tree that

Table 1
Constraints on Calibration Dates for Branching Points in the Tree of Life

Node	Equivalent to Clade	Age-Indicative Fossil	Minimum Age Constraint		Maximum Age Constraint		Evidence
			Youngest Date (MYA)	Recommended Date (MYA)	Oldest date (MYA)	Recommended Date (MYA)	
Human–chimp	Homini–*Pan*	*Sahelanthropus*	6.5	6.5	10	10	Biostratigraphy
Human–macaque	Hominoidea–Cercopithecoidea	*Proconsul*	23.5 ± 0.5	23.0	33.8 ± 0.1	33.9	Biostratigraphy
Mouse–rat	*Mus* lineage–*Rattus* lineage	*Progonomys*	11.0	11.0	12.3	12.3	Magnetostratigraphy
Rabbit–mouse	Glires	*Heomys*	61.7 ± 0.2	61.5	99.6 ± 0.9	100.5	Biostratigraphy
Human–mouse	Archonta–Glires (Euarchontoglires)	*Heomys*	61.7 ± 0.2	61.5	99.6 ± 0.9	100.5	Biostratigraphy
Dog–cat	Caniformia–Feliformia	*Tapocyon*	43 ± 0.2	42.8	63.6 ± 0.2	63.8	Bio/Magnetostraigraphy
Dog–horse	Carnivora–Perissodactyla	*Tetraclaenodon*	62.5 ± 0.2	62.3	70.6 ± 0.6	71.2	Bio/Magnetostratigraphy
Cow–sheep	Bovinae–Antilopinae	*Eotragus*	18.3	18.3	28.4 ± 0.1	28.5	Biostratigraphy
Cow–pig	Ruminantia/Tylopoda–Suiformes	*Mixtotherium*	48.5 ± 0.2	48.3	53.5	53.5	Biostratigraphy
Cow–dog	Ferungulata	Zhelestidae	96.2 ± 0.9	95.3	112 ± 1	113	Biostratigraphy
Human–cow	Euarchontoglires–Laurasiatheria	Zhelestidae	96.2 ± 0.9	95.3	112 ± 1	113	Biostratigraphy
Human–armadillo	Boreoeutheria–Xenarthra	Zhelestidae	96.2 ± 0.9	95.3	112 ± 1	113	Biostratigraphy
Tenrec–elephant	Afrosoricida/Tubulidentata–Paenungulata	*Phosphatherium*	48.6 ± 0.2	48.4	112 ± 1	113	Biostratigraphy
Human–tenrec	Boreoeutheria/Xenarthra–Afrotheria	Zhelestidae	96.2 ± 0.9	95.3	112 ± 1	113	Biostratigraphy
Opossum–kangaroo	Ameridelphia–Australidelphia	*Pucadelphys*	61.7 ± 0.2	61.5	70.6 ± 0.6	71.2	Biostratigraphy
Human–opossum	Eutheria–Metatheria	*Eomaia*	124.6 ± 0.01	124.6	136.4 ± 2.0	138.4	Direct date
Human–platypus	Theriimorpha–Australosphenida	*Phascolotherium*	166.5 ± 4.0	162.5	189.6 ± 1.5	191.1	Biostratigraphy
Chicken–zebrafinch	Galloanserae–Neoaves (Neognathae)	*Vegavis*	66	66	85.8 ± 0.7	86.5	Biostratigraphy
Emu–chicken	Palaeognathae–Neognathae (Neornithes)	*Vegavis*	66	66	85.8 ± 0.7	86.5	Biostratigraphy
Bird–crocodile	Avemetatarsalia/Ornithodira–Crurotarsi	*Vjushkovisaurus*	237 ± 2.0	235	249.7 ± 0.7	250.4	Biostratigraphy
Crocodile–lizard	Archosauromorpha–Lepidosauromorpha	*Protorosaurus*	260.4 ± 0.7	259.7	299 ± 0.8	299.8	Biostratigraphy
Mammal–bird	Sauropsida–Synapsida (Amniota)	*Hylonomus*	313.4 ± 1.1	312.3	328.8 ± 1.6	330.4	Biostratigraphy
Human–toad	Reptiliomorpha–Batrachomorpha	*Lethiscus*	332.4 ± 2.0	330.4	348 ± 2.1	350.1	Biostratigraphy

NOTE.—Branching points are indicated for key species, and their larger clade equivalences. The oldest and youngest dates are given, based on the literature, and on the *Cambridge 2004* timescale (Gradstein et al. 2004). The youngest date is given for the minimum age constraint, and the oldest for the maximum age constraint, based on the date of the geological formation containing the age indicative fossil. The recommended dates are the youngest possible (i.e., minimum) date for the minimum constraint, and the oldest possible (i.e., maximum) for the maximum constraint.

are poorly calibrated. Furthermore, molecular clock analyses are rarely, if ever, framed around the availability of reliable calibration dates. Rather, they are characterized by scientifically interesting questions and the availability of appropriate sequence data (Hedges and Kumar 2004). Together, these facts require that well-researched calibration dates are available for the majority of available sequence data and, to this end, we provide detailed assessments of the paleontological data constraining the timing of lineage splits between the main genomic models.

Minimum Constraints on Divergence Dates

The indicated range of minimum branching dates (table 1) reflects both uncertainty in the dates (stratigraphic error) as well as the inferred duration of the fossiliferous unit. Such a small range of dates, less than 1% in many cases, may seem startlingly low, but current geological timescales (Gradstein et al. 2004) offer that level of precision. The quoted age range does not incorporate an estimate of uncertainty about whether the oldest fossil really belongs to the clade or about whether the clade might have originated much earlier. The date arose from a 2-step process: 1) Which is the oldest relevant fossil within the clade in question? 2) What is the best current age estimate for the geological formation that includes that fossil?

The first step relied on our reading of current paleontological data, and wide consultation on each date with relevant experts. We excluded all uncertain or scrappy fossils, and retained only those for which there is definitive anatom-

ical evidence of one or more apomorphies of the clade in question. In all cases, the date is sought for branching between 2 extant species, and so we pursued each of the 2 lineages back to the point at which they shared their last common ancestor, based on current phylogenetic evidence. Having 2 lineages meant, we could select the older of the 2 oldest fossils (table 1).

The second step is to date the geological formation in which the oldest fossil, or fossils, occurs, or occur. The identity of that geological formation is clear in all cases—the earliest members of the Zebrafish (ostariophysean) and Pufferfish (euteleost) lineages, for example, both date from the lithographic limestones of the Obere Solnhofener Schichten of southern Germany. A geological formation is a well-constrained succession of rocks with a clearly marked base and top. In most cases, there is an extensive biostratigraphic literature devoted to establishing the relative age of the unit in question. For the Solnhofen lithographic limestones, ammonites and other fossils place the unit in the lower Tithonian stage (zeta 2a zone) of the Upper Jurassic. That is a relative age, refined to a zonal level that may be less than 1 Myr in duration. Absolute chronostratigraphic ages are then assigned by reference to the international standard, with precise ages established by radiometric methods. The zeta 2a zone is part of the *Hyboniticeras hybonotum* ammonite zone, the base of which coincides with the base of the normal-polarity Chron M22An magnetozone that is dated at 150.8 MYA ± 0.1 Myr (Ogg 2005); a minimum constraint on its age can be derived from the base of the succeeding, *Semiformiceras darwini* ammonite

zone that coincides approximately with the M22n Chronozone, dated at 149.9 MYA ± 0.05 Myr (Ogg 2005). This is the current best estimate of the minimum date of divergence of the Zebrafish and Pufferfish genomes. Here, and in our tabulation of divergence dates, we provide minimum constraints. However, we provide the full range of error for those who wish to perpetuate the use of paleontological dates as direct substitutes for divergence times.

The Nature of Minimum Constraints and the Need for Maximum Constraints

Some molecular clock analyses have been calibrated using a single fossil-based date that was assumed to have no error, or with an error distributed symmetrically on either side and with uniform probability between the minimum and maximum bounds and zero probability that the date falls outside the interval (Hedges and Kumar 2004). However, fossil calibrations are minimum dates that provide asymmetrical constraints, below which probability drops immediately to zero, but above which probability decays more gradually, and probability densities can be modeled in a variety of ways to reflect the quality of fossil calibrations (Hedges and Kumar 2004; Kumar et al. 2005; Drummond et al. 2006). Drummond et al. (2006) outline a number of parametric probability distributions for the ages of nodes, including normal, lognormal, exponential, and uniform distributions, that may be used as priors in Bayesian treatments of relaxed-clock models of sequence evolution. The shape of the probability distribution selected can then reflect current biological understanding of the shape of the base of a clade.

Probability distributions of potential ages for the origin of a clade between the maximum and minimum constraints may be modeled to reflect the postulated shape of the base of the clade in question. Paleontologists have described long, thin, spindle-shaped clades and short, fat clades (Gould et al. 1977). Empirical observations suggest that all clades, whatever their shape, expand from one species to many following a logistic curve (Gould et al. 1977; Sepkoski 1996; Tavaré et al. 2002). There may be a long or short initial phase when diversity is low, and then species are added until some kind of "equilibrium" clade species richness is achieved. The logistic model is in line with expectations from ecological models such as the Lotka-Volterra models of competition and the island biogeography model (MacArthur and Wilson 1967; Rosenzweig 1995). If the logistic model is appropriate, then the initial tail, whether long or short, would generally fall outside the maximum constraint if that were set as a 95% confidence interval.

The ends of such distributions have been termed "hard" and "soft" bounds (Hedges and Kumar 2004; Yang and Rannala 2006). A "hard bound" is absolute, and the date cannot fall beyond it, whereas a soft bound is not, and divergence dates could lie beyond it, to a degree that is dependent upon the probability density modeled. The probability density may be entirely arbitrary, or informed predictions about the shape and extent of the probability tail leading from the hard bound may be made based on the nature of the paleontological data (Hedges and Kumar

2004; Barnett et al. 2005; Yang and Rannala 2006). "Soft bounds" for maximum age constraints allow paleontologists to propose short, but realistic, time extensions below the oldest known fossil in a group; if the maximum age constraint is a hard bound, that estimate has to be very large in some cases just to allow for the faintest possibility of a very ancient fossil. Thus, soft bounds provide not only a means of reflecting the nature of the fossil record beyond providing a minimum date but they also lend themselves well to relaxed-tree algorithms in which some age constraints may be better than others, but which are good and which are bad is not known a priori. In the context of parametric probability distributions, the minimum and maximum constraints could be equated with 95% lower and upper limits, and this would allow the placement of a curve and its mean; we use the terms maximum and minimum constraint bounds for the moment because they could then be set as 99%, 95%, or 90% confidence limits for example.

A number of approaches may be taken in determining soft bounds. One approach is to consider all possible sources of error in estimating the maximum date of origin of a clade of which there are 5 broad categories of error: 1) phylogenetic topology, 2) fossil record sampling, 3) identification, 4) correlation (relative dating), and 5) exact age–date assignment (absolute dating). These errors are nonadditive but some (e.g., phylogenetic topology) may be difficult to constrain. Another approach is to model diversification pattern and preservation probability (Foote et al. 1999; Tavaré et al. 2002). Phylogenetic bracketing has also been used to provide a maximum constraint on divergence events, by bracketing the next node below and above (Reisz and Muller 2004; Müller and Reisz 2005), and even conflated with estimates of errors on each of these dates (van Tuinen and Hedges 2001; van Tuinen and Hadly 2004). However, although this method may be beguiling, all nodes used to constrain the timing of divergence are subject to the usual uncertainties of dating fossil occurrences. There is no reason why the date of the node below should be related in any way to the date of origin of the next clade above.

In seeking to determine a maximum age constraint on the origin of a clade, there is merit in modeling diversification pattern and preservation probability and in phylogenetic bracketing, but neither can ever provide a definitive answer. In practice, the degree of precision provided by some of these approaches is false and is beyond that needed to attain computational feasibility in constraining molecular clock analyses. For the moment, we prefer to use a combined, but intuitive, approach.

Our method uses aspects of phylogenetic bracketing and stratigraphic bounding, namely a consideration of the absence of fossils from underlying deposits. The line of reasoning is broadly the following: 1) the maximum age constraint for the origin of a clade will be older than the oldest definitive fossil in the clade; 2) older fossils that might belong to the clade, or to its stem lineage, can hint at (but never prove) a downward time extension; 3) older fossils in clade C, the nearest outgroup (fig. 1) could also hint at (but never prove) a downward time extension; and 4) an older fossil deposit that ought to contain fossils of the clade in question, but does not, can mark an ultimate maximum bound. We do not, here, guarantee that
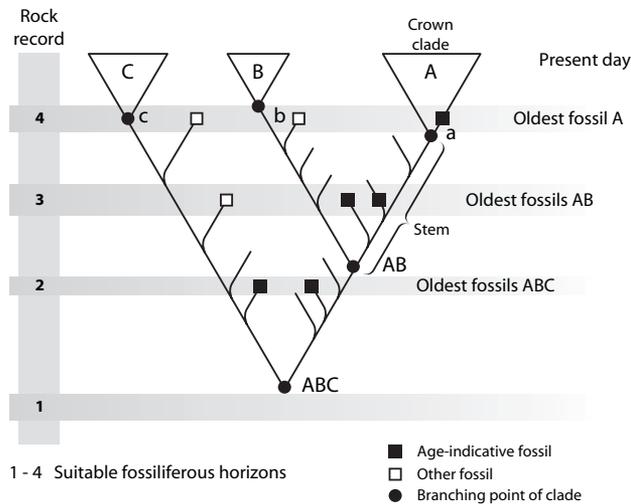
FIG. 1.—Definitions of terms in assigning fossils to clades. The crown clade consists of all living species and their most recent common ancestor, and this is preceded by a stem lineage of purely fossil forms that are closer to their crown clade than to another crown clade. The divergence or splitting point between a species in clade A and a species in clade B is the point AB. This is older than the points of origin of crown clades A and B (indicated as points a and b). Fossils may belong to a crown clade or to a stem lineage, and cladistic evidence should indicate which. Four fossiliferous horizons are indicated, the source of all relevant fossils. Fossiliferous horizon 1 that contains no fossils assignable to the clade ABC marks a maximum constraint (soft bound) on the age of the clade. Fossiliferous horizon 2 marks a maximum constraint on the age of clade AB. Minimum constraints are indicated by the 'oldest fossils' for ABC, AB, and A.
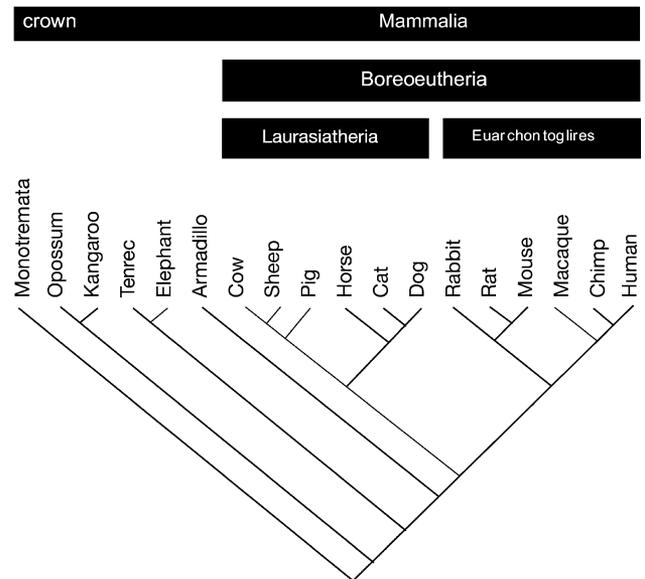
FIG. 2.—Outline relationships of the major clades of mammals, incorporating key genomic organisms. Major clades are named, and numbered nodes correspond to the text.

an older fossil will never be found, but the likelihood is low, and this will be reflected in the probability density (Yang and Rannala 2006). Probability densities have been used in deriving the confidence interval either with (Yang and Rannala 2006) or without (Kumar et al. 2005) the assumption of a molecular clock. The probability density can be modeled accurately on the basis of recovery potential functions that incorporate data on ecological distribution conflated with data on facies variation, outcrop exposure, and even taphonomic controls provided by anatomically similar organisms (Holland 1995; Marshall 1997). Alternatively, the probability density may be entirely arbitrary, for example, described by a lognormal distribution; even such simple models can be readily adapted to approximate reality by, for instance, using fossil and lithostratigraphic data to inform the position of the mean.

We emphasize finally that minimum and maximum constraints on calibration dates should be fully substantiated so that if any of the variables change, such as recently with the publication of the new geological timescale (Gradstein et al. 2004), with a shift in phylogenetic hypothesis, or the discovery of an older member of the clade, the impact of the change upon the calibration date is obvious and may be refined. Thus, minimum age constraints should be justified on the basis of a phylogenetic hypothesis, with reference to the oldest integral member of the clade—on which the date is ultimately based, the justification for its membership of the clade, the means by which the correlation is achieved to a section in which a chronostratigraphic date may be obtained, and

the source of the chronostratigraphic date. Maximum age constraints should likewise be justified on the basis of a phylogenetic hypothesis, with reference to fossils belonging to outgroups and to putative stem groups, and to the next oldest fossil horizon that lacks relevant fossils.

Our proposed calibrations are justified below and summarized in table 1 and figure 8.

Dating Divergences among Mammals

Eighteen mammalian genomes have been sequenced, or are in progress (August 2006; http://www.ensembl.org/index.html), namely human (*Homo sapiens*), chimp (*Pan troglodytes*), macaque (*Macaca mulatta*), mouse (*Mus musculus*), rat (*Rattus norvegicus*), rabbit (*Oryctolagus cuniculus*), dog (*Canis familiaris*), cat (*Felis catus*), horse (*Equus caballus*), pig (*Sus scrofa*), sheep (*Ovis aries*), cow (*Bos taurus*), armadillo (*Dasypus novemcinctus*), tenrec (*Echinops telfairi*), African elephant (*Loxodonta africana*), kangaroo (*Macropus eugenii*), opossum (*Monodelphis domestica*), and platypus (*Ornithorhynchus anatinus*). These 18 consist of 1 monotreme (the platypus), 2 marsupials (the opossum and kangaroo) and 15 placental mammals, members of the clade Eutheria. According to current molecular and morphological phylogenies (Madsen et al. 2001; Murphy et al. 2001; Huchon et al. 2002; Springer et al. 2003; Benton 2005), the Eutheria fall into 3 main clades, Afrotheria, Xenarthra, and Boreoeutheria. The 12 placental mammals include 2 afrotherians (tenrec and elephant), 1 xenarthran (armadillo), and the remaining 9 belong to Boreoeutheria that fall into 2 clades, the Laurasiatheria, containing the orders Artiodactyla (pig, cow, and sheep), Perissodactyla (horse), and Carnivora (dog and cat), and the Euarchontoglires, containing the orders Primates (macaque, chimp, and human), Lagomorpha (rabbit), and Rodentia (mouse and rat).

The tree of 18 major mammalian groups (fig. 2) then contains 17 branching points: 7 within major clades (opossum–kangaroo, cow–sheep, cow–pig, cat–dog, human–chimp, human–macaque, mouse–rat) and the other 10 between orders or higher clades, namely human–mouse (i.e., Primates–Rodentia), rabbit–mouse (i.e., Glires), horse–dog (i.e., Perissodactyla–Carnivora), cow–dog (i.e., Ferungulata), human–cow (i.e., Euarchontoglires–Laurasiatheria), human–armadillo (i.e., Boreoeutheria–Xenarthra), tenrec–elephant (i.e., Afrotheria), human–tenrec (i.e., Boreoeutheria–Xenarthra–Afrotheria), human–opossum (i.e., Eutheria–Marsupialia), and human–platypus (i.e., Theria–Monotremata). Other pairings of taxa could be selected, but they are synonymous with 1 of these 10 (e.g., rat–cow is the same as human–cow; dog–opossum is the same as human–opossum).

These 17 branching points will be considered in order (see fig. 2).

Human–Chimp

The dating of the chimp–human split has been discussed for nearly a century. Early paleontological estimates, up to the 1970s, placed the branching point deep in the Miocene, at perhaps 20–15 MYA, but this was revised dramatically upward to about 5 MYA by early molecular studies (Sarich and Wilson 1967), and estimates as low as 2.7 MYA have been quoted (Hasegawa et al. 1985). Paleontological evidence for the branching point was distinctly one-sided until recently, since the only fossils fell on the human line, and so the question of the date of divergence of humans and chimps became synonymous, for paleontologists, with the date of the oldest certain hominin (species on the human, not chimp, line). The recent discovery of the first chimpanzee fossils (McBrearty and Jablonski 2005) does not change much, as they are dated as 545,000 years old at most.

The date of the oldest hominin has extended backward rapidly in the last 25 years. Until 1980, the oldest fossils were gracile and robust australopithecines from 3 MYA. The discovery of "Lucy", now termed *Praeanthropus afarensis* in Ethiopia (Johanson and Taieb 1976) extended the age back to 3.2 MYA at most. Then, 2 further hominin species pushed the age back to over 4 Myr: *Ardipithecus ramidus* from rocks dated as 4.4 MYA from Ethiopia (White et al. 1994) and *Praeanthropus anamensis* from rocks dated as 4.1–3.9 MYA from Kenya (Leakey et al. 1995). More recent finds, remarkably, have pushed the dates back to 6 Myr: *A. ramidus kadabba* from Ethiopia (5.8–5.2 MYA; Haile-Selassie 2001), *Ororrin tugenensis* from Kenya (c. 6 MYA; Senut et al. 2001), and *Sahelanthropus tchadensis* from Chad (6–7 MYA; Brunet et al. 2002). The last 2 taxa have proved highly controversial, with claims that one or other, or both, are not hominin, but ape like. However, the majority view is that *Sahelanthropus* at least is hominin (Wood 2002; Cela-Conde and Ayala 2003), and so its date becomes crucial.

Dating of the *Sahelanthropus* beds in Chad is not direct. Biostratigraphic evidence from mammals in particular, but with cross-checking from fish and reptile specimens, indicates that the unit is definitely late Miocene (i.e., older

than 5.33 MYA), and it is older than the Lukeino Formation of Kenya, the source of *Orrorin* (dated at 6.56–5.73 MYA from Ar/Ar dates on volcanic layers; Deino et al. 2002), and may be equivalent to the lower fossiliferous units of the Nawata Formation at Lothagam (dated as 7.4–6.5 MYA; Vignaud et al. 2002). This might suggest a date for the sediments containing *Sahelanthropus* of 7.5–6.5 MYA, based on biostratigraphy and external dating. Thus, we determine a 6.5-MYA age for the minimum constraint on the human–chimp split. Kumar et al. (2005) have recently calculated a range of ages for the human–chimp divergence of 4.98–7.02 MYA; their minimum constraint (4.98 MYA) is younger than the oldest fossils (*Orrorin, Sahelanthropus*). However, paleoanthropogists generally accept that *Sahelanthropus* and *Orrorin* were both bipedal, upright forms, and until both are rejected by consensus view of their anatomy, we retain them as the oldest valid hominins.

A soft maximum constraint on the human–chimp divergence is hard to place because the immediate outgroups (gorilla, orang, and gibbons) lack convincing fossil records. Some late Miocene ape fossils, such as *Gigantopithecus* and *Sivapithecus* may be stem-orangs. Nonetheless, a range of such apes, *Ankarapithecus* from Turkey (10 MYA), *Gigantopithecus* from China (8–0.3 MYA), *Lufengopithecus* from China (10 MYA), *Ouranopithecus* from Greece (10–9 MYA), and *Sivapithecus* from Pakistan (10–7 MYA) give maximum ages of 10 MYA, early in late Miocene, and these deposits have yielded no fossils attributable to either chimps or humans. This is taken as the soft maximum constraint on the human–chimp divergence.

Human, Chimp–Macaque

The human–macaque split is equivalent to the branching of Old World monkeys (Cercopithecoidea) and apes (Hominoidea), which together form the clade Catarrhini.

The oldest cercopithecoids are *Victoriapithecus macinnesi* from Kenya, and 2 species of *Prohylobates* from Libya and Egypt. Miller (1999) surveyed all fossils of these 2 genera, and compared ages of their respective deposits. The oldest cercopithecoid fossil is a tooth identified as *Victoriapithecus* sp. from Napak V, Uganda (c. 19 MYA), followed by *Prohylobates tandyi* from Moghara, Egypt (18–17 MYA) and *Prohylobates* sp. from Buluk, Kenya (>17.2 MYA), *P. simonsi* from Gebel Zelten, Libya (c. 17–15 MYA), and *V. macinnesi* from Maboko, Kenya (ca. 16–14.7 MYA). MacLatchy et al. (2003) report an even older cercopithecoid, a fragment of a maxilla from the Moroto II locality in Uganda, that has been radiometrically dated to be older than 20.6 MYA ± 0.05 Myr (Gebo et al. 1997).

The oldest hominoids include *Morotopithecus*, also from the Moroto II locality in Uganda (Gebo et al. 1997). Young and MacLatchy (2004) determined that this taxon is a hominoid, located in the cladogram above the gibbons, and so not the most basal member of the group. Because of incompleteness of the material, Finarelli and Clyde (2004) are less certain of its phylogenetic position, but *Morotopithecus* is certainly a catarrhine. Even older is the first record of the long-ranging hominoid genus *Proconsul* from Meswa Bridge in Kenya, biostratigraphically constrained to c. 23.5 MYA (Pickford and Andrews 1981; Tassy and Pickford

1983). Even older is the purported hominoid *Kamoyapithecus* from the Eragaliet Beds of the Lothidok Formation of Kenya, dated at 24.3–27.5 MYA (Boschetto et al. 1992), but the material is insufficient to determine whether it is a hominoid or a catarrhine, possibly lying below the human–macaque split (Finarelli and Clyde 2004).

So, the minimum constraint on the human–macaque split is 23.5 MYA, based on the oldest record of *Proconsul*, or perhaps 23.5 MYA ± 0.5 Myr, based on biostratigraphy and external dating.

The soft maximum constraint is based on members of the stem of Catarrhini, namely the families Propliopithecidae (*Propliopithecus*, *Aegyptopithecus*) and Oligopithecidae (*Oligopithecus*, *Catopithecus*) that are basal to the cercopithecoid--hominoid split (Rasmussen 2002). These are represented in particular from the rich Fayûm beds in Egypt, dated as early Oligocene (33.9–28.4 MYA ± 0.1 Myr), and so 28.3 MYA, deposits that have produced many primate, and other mammal, fossils, but no hint of a crown-group catarrhine.

Mouse–Rat

The mouse (*M. musculus*) and rat (*R. norvegicus*) are both the members of the subfamily Murinae within the family Muridae, members of the larger clade of muroid rodents. The Old World rats and mice are hugely diverse, with over 500 species, and they appear to have radiated relatively rapidly in Europe, Africa, Asia, and Australia.

The phylogeny of all genera within Murinae has not been determined, so the location of the split between *Mus* and *Rattus* is somewhat speculative at present. However, all current morphological and molecular phylogenies (Michaux et al. 2001; Jansa and Weksler 2004; Steppan et al. 2004; Chevret et al. 2005) indicate that *Mus* and *Rattus* diverged early in the evolution of Murinae, but not at the base of the divergence of that clade. A lower limit to the mouse–rat divergence is indicated by the oldest known murine fossil, *Antemus chinjiensis* from the middle Miocene Chinji Formation of Pakistan, dated at about 14.0–12.7 MYA on the basis of magnetostratigraphy and radiometric dating (Jacobs and Flynn 2005).

The oldest fossil example of *Mus* dates from 7.3 MYA, a specimen of *Mus* sp. from locality Y457 in the Siwaliks (Jacobs and Flynn 2005). Fossils of *Rattus* are not known until the latest Pliocene and the Pleistocene of Thailand (Chaimanee et al. 1996) and China (Zheng 1993), no more than 3 MYA.

The divergence of the 2 lineages leading to *Mus* and *Rattus* was stated to be 14–8 MYA by Jacobs and Pilbeam (1980), in a first review of the fossil evidence. This range was narrowed down at its older end to 12 MYA in subsequent studies (Jaeger et al. 1986; Jacobs and Downs 1994), based on the first appearance of the fossil genus *Progonomys*, early members of which were assumed to include the common ancestor of *Mus* and *Rattus*. The 12 MYA figure has most commonly been selected as the mouse–rat calibration point, but dates in the range from 16 to 8.8 MYA have been used in recent molecular studies.

In a thorough review of the fossil evidence, Jacobs and Flynn (2005) show that records of *Progonomys* in the Si-

walik succession extend from 12.3 to 8.1 MYA, with the later forms (10.4–8.1 MYA) assumed to lie on the *Mus* lineage. The extinct genus *Karnimata* (11.1–6.4 MYA) is interpreted as a member of the lineage leading to *Rattus*. The oldest record (11.1 MYA) is uncertain, but the next (at 10.4 MYA) is unquestionable. The early species, *Progonomys hussaini* (11.5–11.1 MYA) is interpreted as an undifferentiated basal murine antedating the common ancestor of *Mus* and *Rattus* by Jacobs and Flynn (2005), and so they place the *Progonomys–Karnimata* split (equivalent to the *Mus–Rattus* split) at not much beyond 11 MYA, "although it may be younger." The dating is based on detailed field stratigraphic study of the long Siwaliks sedimentary sequence, with dating from magnestostratigraphy and radiometric dating (Johnson et al. 1985; Barry et al. 2002). The soft maximum constraint on this date is taken as the oldest record of *Progonomys* at 12.3 MYA.

Rabbit–Mouse, Rat

The rabbit–mouse basal node is synonymous with the clade Glires, comprising orders Rodentia plus Lagomorpha. The date would have been assumed traditionally to lie at 65 MYA, or younger, marking the time of purported placental mammal radiation after the extinction of the dinosaurs.

There have never been any records of Cretaceous rodent fossils, even though some molecular studies have placed the origin of the order deep within the Cretaceous. The oldest fossil rodents are known with confidence from the Thanetian (late Paleocene, 58.7–55.8 MYA), members of the family Ischyromidae from North America and Europe (Stucky and McKenna 1993), after which the clade expanded enormously to its present huge diversity. An older putative rodent might be *Heomys*, a eurymylid from the Danian (early Paleocene, 65.5–61.7 MYA) of China (McKenna and Bell 1997). The eurymylids may not be proper rodents, but members of a larger including clade Simplicidentata, or they may fall outside Simplicidentata, but within Glires, as outgroup to rodents and rabbits (Asher et al. 2005). Either way, the oldest members of Glires are post-Cretaceous in age (<65 MYA). Whether the Late Cretaceous zalambdalestids are related to Glires or not (see below) is irrelevant to this node.

The oldest lagomorphs are somewhat younger. Stucky and McKenna (1993) indicate several Eocene rabbits from the Lutetian: *Lushilagus* from China, *Procaprolagus* from Canada, and *Mytonolagus* from the United States. Meng and Wyss (2005) note an older possible lagomorph, *Mimotona* from the early to late Paleocene (Doumu Formation, Nonshangian, Qianshan Basin, China), the same unit that yielded the putative earliest rodent *Heomys*.

The minimum constraint on the age of clade Glires, and so for the rabbit–mouse split, is 61.7 MYA. The nearest outgroups of Glires (Meng and Wyss 2005) and forms such as *Pseudictops*, *Anagale*, and *Hyopsodus* are later Paleocene than *Heomys*, and so of little assistance in indicating a possible soft maximum constraint. The next outgroups, possibly the zalambdalestids, set a much older soft maximum constraint of 99.6 MYA ± 0.9 Myr to 96.2 MYA ± 0.9 Myr.

Human, Chimp, Macaque–Rabbit, Mouse, Rat

The human–mouse split is synonymous with the latest branching point between the mammalian orders Primates and Rodentia. Both orders are members of the clade Euarchontoglires. Euarchontoglires is composed of 2 clades, the Archonta and the Glires, and Primates belongs to the former, Rodentia to the latter. Thus, the human–mouse split becomes synonymous with the origin of Euarchontoglires.

Traditionally, this branching point would have been set at 65 MYA, the beginning of the Paleogene (base of Cenozoic, base of Tertiary), and corresponding to the extinction of the dinosaurs and the beginning of the radiation of placental mammal orders. This view has been challenged since 1995 as a result of 2 factors: 1) the discovery of major supraordinal clades within Eutheria, as noted earlier and 2) the repeated discovery from molecular analyses that the eutherian orders and the larger clades might have their origin at some point in the Cretaceous, whether rather early (Hedges et al. 1996; Janke et al. 1997) or rather later, and more in line with the fossils (Murphy et al. 2001; Arnason et al. 2002; Springer et al. 2003), evidence perhaps of a rapprochement between molecular and paleontological evidence (Archibald 2003; Benton and Ayala 2003).

There are no confirmed fossils of Primates or Rodentia in the Cretaceous (i.e., >65 MYA). An isolated tooth from the latest Cretaceous Hell Creek Formation (c. 67 MYA) of North America was assigned to the plesiadapiform taxon *Purgatorius*, and has been cited as the oldest primate (Van Valen and Sloan 1965). However, the phylogenetic position of the plesiadapiforms is debated—they were probably close relatives of primates, but not primates proper (Bloch and Boyer 2002). Further, the single tooth is arguably too little evidence for a firm record (Archibald 2003). The oldest confirmed primates are from the Paleocene–Eocene transition, some 55 MYA (Bloch and Boyer 2002), and the oldest plesiadapiform is *Subengius* from the late Paleocene of China (Smith et al. 2004). It comes from the Nomogen Formation, assigned to the Gashatan Land Mammal Age (latest Paleocene, 57–56 MYA).

As noted above, the oldest fossil rodents are known with confidence from the Thanetian (late Paleocene, 58.7–55.8 MYA), members of the family Ischyromidae from North America and Europe (Stucky and McKenna 1993), after which the clade expanded enormously to its present huge diversity.

Some Cretaceous fossils might be relevant to the node at the base of Euarchontoglires, however: the zalambdalestids, a group of small, long-legged jumping mammals known from excellent fossils from the Late Cretaceous of Mongolia and Central Asia (Kielan-Jaworowska et al. 2000; Archibald et al. 2001). They have been assigned numerous phylogenetic positions, but were found to be outgroup of rodents and rabbits, either members of the clade Glires or close to it (Archibald et al. 2001). Until recently, the zalambdalestids from the Bissekty Formation of Dzharakuduk, Kyzylkum Desert, Uzbekistan, were the oldest known of this clade, but they are now thought to come from the older Khodzhakul Formation at Sheikhdzheili, Kyzylkum Desert, Uzbekistan. There are 3 sets of localities in the Kyzylkum Desert that have yielded mammals. Based on biostratigraphic studies of intercalated marine units with invertebrate fossils (Averianov 2000; Archibald et al. 2001; Archibald 2003), these 3 local faunas are early Cenomanian (about 97 MYA), late Turonian (about 90 MYA), and possibly Coniacian (about 87 MYA). The age of the Khodzhakul Formation is particularly crucial: a reworked, early placenticeratid ammonite from the base of the formation suggests an early Cenomanian age, whereas an inoceramid bivalve from just above the Khodzhakul Formation suggests a late Cenomanian age (Averianov and Archibald 2005). So, the oldest zalambdalestids are from the early Cenomanian that corresponds to 99.6 MYA ± 0.9 Myr to 96.2 MYA ± 0.9 Myr.

This phylogenetic position has been challenged (Meng et al. 2003; Asher et al. 2005), and these authors place zalambdalestids outside the clade Placentalia, and certainly below Afrotheria in the cladogram of mammals. In this view, zalambdalestids would say nothing about the date of origin of either Glires or Euarchontoglires, both of which would revert to minimum origin dates of basal Paleocene (61.7 MYA). For the present, and until the contradictory views (Archibald et al. 2001; Meng et al. 2003; Asher et al. 2005) are resolved, we take a conservative view and place a minimum constraint on the human–mouse split in the early Paleocene, at 61.7 MYA. The soft maximum constraint is based on the assumption that zalambdalestids are close to Glires that corresponds to 99.6 MYA ± 0.9 Myr to 96.2 MYA ± 0.9 Myr. This soft maximum constraint is a long time before the minimum constraint.

Dog–Cat

The dog–cat split is equivalent to the branching point between the clades Caniformia (dogs, bears, raccoons, and seals) and Feliformia (cats, mongooses, and hyaenas), the major subdivisions of the Order Carnivora (Flynn and Wesley-Hunt 2005).

The oldest carnivores are members of the families "Miacidae" (paraphyletic) and Viverravidae, known from the early Paleocene onward (Stucky and McKenna 1993), but these lie outside the Caniformia–Feliformia clade (Flynn and Wesley-Hunt 2005), and so cannot provide a minimum date for the dog–cat split.

The oldest caniforms are amphicyonids such as *Daphoenus* and canids such as *Hesperocyon*, known first from the earliest Duchesnean North American Land Mammal Age (NALMA) that corresponds to magnetochron 18N, and is dated as 39.74 MYA ± 0.07 Myr, based on radiometric dating of the LaPoint Tuff (Robinson et al. 2004). *Tapocyon* may be an even older caniform; it comes from the Middle Eocene, Uintan, dated as 46–43 MYA (Wesley and Flynn 2003), although Flynn and Wesley-Hunt (2005) place this taxon outside the Carnivora.

The oldest feliforms may be the nimravids, also known first from the White River carnivore fauna of the Chadronian NALMA, with uncertain records extending to the base of that unit (Hunt 2004). The earliest Chadronian corresponds to the top of magnetochron 17N, and an age of 37.2–36.7 MYA (Hunt 2004; Prothero and Emry 2004).

Flynn et al. (2005) suggest a caniform–feliform split around 50 Myr, but the evidence at present suggests a

minimum constraint of 43 MYA, based on magnetostratigraphy and radiometric dating of the Uintan NALMA. The soft maximum constraint is based on the occurrence of the oldest stem carnivores (miacids, viverravids) in the Torrejonian NALMA of the early Paleocene (see dog–horse below), so 63.8 MYA.

Dog, Cat–Horse

The dog–horse split is equivalent to the branching point between the orders Carnivora and Perissodactyla, that together form an unnamed clade. The minimum age will be determined from the oldest member of the carnivore and perissodactyl lineages.

Flynn et al. (2005) and others, have modified the meaning of Carnivora so that it is restricted by them to the crown clade consisting of Caniformia + Feliformia. They rename the more inclusive clade traditionally called Carnivora as Carnivoramorpha. They rename the more inclusive clade traditionally called Carnivora as Carnivoramorpha. The oldest carnivoramorphans are the viverravids. The oldest generally accepted viverravid is *Protictis* from the Fort Union/Polecat Bench Formation, assigned to the basal Torrejonian (To1) NALMA, and dated as 63.6–62.5 MYA (Lofgren et al. 2004). If *Ravenictis* from Canada is also a carnivoramorphan (Flynn 1998), and that is debated (Flynn and Wesley-Hunt 2005), it extends this date back to at least the Puercan (Pu2), 65.4–64.3 MYA $\pm$ 0.3 Myr. Most authors also agree that the extinct group Creodonta is sister group to Carnivoramorpha (Flynn and Wesley-Hunt 2005), and these date back to the Thanetian, 58.7–55.8 MYA $\pm$ 0.2 Myr, younger than the oldest carnivormorphans.

The oldest perissodactyl is represented by fragmentary teeth that resemble the brontotheriid *Lambdotherium* from the late Paleocene site of Bayan Ulan in China (Beard 1998), but the perissodacyl lineage may be extended further back in time. Among basal outgroups of Perissodactyla, Hooker (Hooker 2005) includes the phenacodont "condylarths" such as *Ectocion*, *Phenacodus*, and *Tetraclaenodon*. These all extend back into the Paleocene, and the oldest is *Tetraclaenodon*, known first from the basal Torrejonian (To1) of North America, the same age as the oldest creodont (above).

This places the dog–horse split minimally at the basal Torrejonian, and so 62.3 MYA. The soft maximum constraint is determined from the diverse fossiliferous units of similar facies in the North American Maastrichtian (70.6 MYA $\pm$ 0.6 Myr to 65.5 MYA $\pm$ 0.3 Myr) that have not produced remains identifiable to Carnivoramorpha or Perissodactyla, or to the stem lineages or either, providing a date of 71.2 MYA.

Cow–Sheep

The branching between the cow (*Bos*) and sheep (*Ovis*) is an intrafamilial split within the family Bovidae. *Bos* is a member of the Tribe Bovini and *Ovis* is a member of the Tribe Caprini that belong, respectively, to the subfamilies Bovinae and Antilopinae (Hassanin and Douzery 1999), although the monophyly of Antilopinae is questioned (Fernandez and Vrba 2005). These 2 subfamilies comprise the family Bovidae, so the cow–sheep split corresponds to the point of origin of the extant Bovidae.

Fernández and Vrba (2005) point to a major series of splits within Bovidae, that gave rise to the major subfamilies 25.4–22.3 MYA, and they link this to a major climatic change at the Oligocene/Miocene boundary. This date is, however, not based directly on fossil evidence, but upon a number of best-fitting dates from published morphological and molecular phylogenies.

A number of putative late Oligocene bovids (Stucky and McKenna 1993) have since been rejected. The oldest putative bovid was *Palaeohypsodontus zinensis* from the Oligocene of the Bugti Hills, Bolochistan, Pakistan, and the early Oligocene of Mongolia and China. This is identified as a ruminant, and was formerly at times assigned to Bovidae. However, it lacks unequivocal anatomical features of Bovidae, and is currently excluded from that family (Metais et al. 2003; Barry et al. 2005).

Fossil bovids may be identified in the fossil record by the presence of horn cores. The oldest such records, ascribed to *Eotragus*, come from the Early Miocene of Western Europe and Pakistan. For example, *Eotragus noyi* from the base of the terrestrial sequence on the Potwar Plateau is dated at approximately 18.3 MYA (Solounias et al. 1995).

Eotragus is attributed to Boselaphini, a tribe within the subfamily Bovinae consisting of the nilgai and other 4-horned antelopes. The oldest members of Antilopinae appear to come from the middle Miocene of 3 continents: *Caprotragoides* from Asia (India and Pakistan), *Tethytragus* from Europe (Spain and Turkey), and *Gentrytragus* from Africa (Kenya and Saudi Arabia), all dated at approximately 14 MYA (Vrba and Schaller 2000). The oldest firmly dated bovid then places the minimum constraint on the origin of the family at 18.3 MYA, and we set the soft maximum constraint as late Oligocene, the time of putative bovid fossils, so 28.5 MYA.

Cow, Sheep–Pig

The cow–pig split is equivalent to the major division in Artiodactyla between Ruminantia-Tylopoda and Suiformes. The oldest artiodactyls, such as *Diacodexis* from the Early Eocene of North America, fall outside this clade.

The oldest member of the Ruminantia-Tylopoda clade, the cows, deer, and camels, is the family Mixtotheriidae, represented by the single genus *Mixtotherium* (Theodor et al. 2005). The oldest records of *Mixtotherium* are from the Early Eocene (McKenna and Bell 1997), from the Cuisian mammalian fauna of France and Spain (Savage and Russell 1983). The Cuisian mammal age is the upper part of the Ypresian stage, equivalent to the Grauvian European Land Mammal Age (MP 10), dating from 51.0 to 48.5 MYA $\pm$ 0.2 Myr (Gradstein et al. 2004).

The Suiformes, or pig-like artiodactyls, include extant pigs, peccaries, and hippos, as well as the extinct raoellids and choeropotamids, of which the raoellids extend back to ca. 54 MYA (Theodor et al. 2005). The oldest raoellids include *Khirtharia* and *Indohyus* from the Early Eocene Kuldana Formation of Pakistan, dated to tethyan biozone P10, lower Lutetian, and dated as about 48 MYA (Gingerich 2003).

A confounding factor here is the suggestion that whales may be sister group to hippos (e.g., Ursing and Arnason

1998). So, if hippos are suiforms, are cetaceans also suiforms? In this case, the branching point in question would correspond to the split of whales and hippos. The alternative, and more likely, view (Theodor et al. 2005) is that whales and artiodactyls as a whole are sister groups, forming the larger clade Cetartiodactyla that split some 53.5 MYA (Gingerich 2005). This predates the cow–pig node, however.

So, based on *Mixtotherium* and the Indo-Pakistani raoellids, the cow–pig division is dated minimally at 48 MYA. The soft maximum constraint is selected as the putative date of splitting of Cetartiodactyla, so 53.5 MYA.

Cow, Sheep, Pig–Dog, Cat, Horse

The cow–dog split is equivalent to the branching point between the clades containing the orders Artiodactyla (even-toed ungulates) and Carnivora (flesh-eating placental mammals). This is synonymous with the point of origin of the clade Ferungulata, a clade within Laurasiatheria.

The oldest artiodactyl is *Diacodexis* from the Early Eocene of North America (c. 55 MYA). Artiodactyls are part of a larger clade Cetartiodactyla, with the Cetacea, whales and relatives, and these date back to the Early Eocene as well, at about 53.5 MYA (Theodor e al. 2005). The clade may also include the extinct mesonychids that are known first from the Danian/Thanetian, some 62 MYA (Stucky and McKenna 1993). The oldest carnivoramorphan is the miacoid *Ravenictis* from the Danian (Puercan, early Paleocene) of North America, and several carnivoran families radiated in the mid to late Paleocene of that continent (Meehan and Wilson 2002).

The clade Ferungulata includes also the orders Perissodactyla and Pholidota, but neither of these dates back before the early Eocene. The oldest fossil ferungulates by a long way may be the zhelestids from the Khodzhakul Formation of Dzharakuduk, Kyzylkum Desert, Uzbekistan. These were assigned to Laurasiatheria as basal "ungulatomorphs" (Archibald et al. 2001; Archibald 2003), that is, basal to the hoofed artiodactyls and perissodactyls. Averianov and Archibald (2005) reject Ungulatomorpha, as a polyphyletic group, and place Zhelestidae in Laurasiatheria; (J.D. Archibald, personal communication) further places Zhelestidae within Ferungulata. This then provides a minimum constraint on the human–cow split based on biostratigraphy and external dating evidence. As noted above, the Khodzhakul Formation is dated to the early Cenomanian (99.6 MYA ± 0.9 Myr to 96.2 MYA ± 0.9 Myr), hence 95.3 MYA.

The soft maximum constraint on this, and other basal dates among crown-group placentals, is the series of latest Early Cretaceous localities from North America and Mongolia, dated as Aptian and Albian. The Albian is dated as 112 MYA ± 1 Myr to 99.6 MYA ± 0.9 Myr, providing a date of 113 MYA.

Human, Chimp, Macaque, Rabbit, Mouse, Rat–Cow, Sheep, Pig, Rabbit, Dog, Cat

The human–cow divergence is synonymous with the origin of Boreoeutheria. This clade is composed of the clades Euarchontoglires (human) and Laurasiatheria (cow).

The oldest members of Euarchontoglires were noted above as the zalambdalestids from Uzbekistan, dated at 90–85 MYA (Archibald et al. 2001), although doubt has been expressed about their phylogenetic placement (Asher et al. 2005; Averianov and Archibald 2005).

A number of Late Cretaceous putative laurasiatherians have been cited. Although most orders within Laurasiatheria (Artiodactyla, Cetacea, Carnivora, Perissodactyla, Pholidota, Chiroptera) do not have fossil records older than Eocene or Paleocene, the Lipotyphla, the insectivores, may have Late Cretaceous representatives. McKenna and Bell (1997) reported the oldest lipotyphlan as *Otlestes* from the Cenomanian (99.6–93.5 MYA) of Uzbekistan, but Archibald (2003) regarded it as a basal eutherian, lacking apomorphies of Lipotyphla, or any other modern order. Most recently, Averianov and Archibald (2005) synonymized it with *Bobolestes* (from the same local fauna) and regarded it as a questionable zalambdalestoid. Next in time is *Paranyctoides* from the Turonian (93.4–89.3 MYA) of Asia and the Campanian (83.5–70.6 MYA) of North America, and *Batodon* from the Maastrichtian (70.6–65.5 MYA) of North America, both regarded as lipotyphlans by McKenna and Bell (1997). Archibald (2003) is uncertain, but retains these records pending discovery of further specimens.

More significant though are the zhelestids from the Bissekty Formation of Dzharakuduk, Kyzylkum Desert, Uzbekistan, and the even older Khodzhakul Formation at Sheikhdzhili. Zhelestids are assigned to Laurasiatheria (Archibald et al. 2001; Archibald 2003; Averianov and Archibald 2005; Wible et al. 2005), that is, basal to the hoofed artiodactyls and perissodactyls. Wherever Zhelestidae are assigned in the new conception of Laurasiatheria, they do apparently belong to that clade, and hence they provide a minimum age for the human–cow split based on biostratigraphy and external dating evidence. As noted above, the Khodzhakul Formation is dated to early Cenomanian; hence we propose a minimum constraint of 95.3.

The soft maximum constraint is, as for the cow–dog split above, 113 MYA.

Human, Chimp, Macaque, Mouse, Rat, Rabbit, Dog, Cat, Horse, Pig, Sheep, Cow–Armadillo

The human–armadillo split is equivalent to the origin of the clade comprising Boreoeutheria and Xenarthra. The oldest boreoeutherians are, as already noted, the zalambdalestids and zhelestids from the Khodzhakul Formation of Uzbekistan, dated to early Cenomanian, hence 99.6–96.2 MYA ± 0.9 Myr. The oldest reported xenarthrans are much younger, dating from the Paleocene. *Riostegotherium* is dated as Itaboraian (Rose et al. 2005), equivalent to the later Selandian (61.7–58.7 MYA ± 0.2 Myr).

The minimum constraint for the Boreoeutheria–Xenarthra split is then 95.3 MYA, and the soft maximum constraint is, as for the cow–dog split above, 113 MYA.

Tenrec–Elephant

The tenrec–elephant split represents a deep division within Afrotheria. According to current phylogenies, the tenrec, golden moles (Macroscelidea) and aardvark

(Tubulidentata) may form one clade within Afrotheria, and the elephants, hyraxes, and sirenians form the other, termed Paenungulata. Paenungulata is widely accepted as a valid clade, having been established on morphological characters, and now confirmed by molecular analyses. Many systematists accept a grouping of tenrecs and golden moles in the clade Afrosoricida, and aardvarks may be sister to these, but that is unclear. In any case, the last common ancestor of tenrec and elephant corresponds to the base of crown-clade Afrotheria.

The oldest fossil aardvarks, tenrecs, and golden moles are all Miocene (McKenna and Bell 1997), with a possible older golden mole, *Metoldobotes* from the Late Eocene Jebel Qatrani Formation of Egypt. These are equaled or predated by the oldest paenungulates. The oldest hyraxes are known from the Eocene of North Africa (Gheerbrandt et al. 2005). The oldest sirenians are *Prorastomus* and *Pezosiren* from early middle Eocene of Jamaica (Gheerbrandt et al. 2005). The oldest proboscidean fossils are *Phosphatherium* and *Daouitherium* from Ypresian (lower Eocene) phosphorites of the Ouled Abdoun Basin of Morocco (Gheerbrandt et al. 2005). Extinct putative outgroups of crown-group Paenungulata such as Desmostylia and Embrithopoda (*Arsinoitherium*) are younger, being Oligocene in age, whereas the Anthracobunidae date back to the early Eocene.

At present, no extant clade within Afrotheria or any confirmed extinct afrothere clade predates the Ypresian (early Eocene) dated as 55.8–48.6 MYA ± 0.2 Myr, and this must be used as the basis of a minimum age constraint for the tenrec–elephant split of 48.4 MYA. Further study might reveal that certain Paleocene groups belong within one or other afrothere branch, and that could increase the minimum age constraint.

The maximum constraint is determined as equivalent to the maximum constraint on the age of Boreoeutheria and Xenarthra, because Afrotheria must be at least as old as its sister clades, although the large age extension might in the end consist of stem-afrotherians that do not belong to either the Afrosoricida–Tubulidentata or the Paenungulata clades within Afrotheria, and hence would considerably overestimate the age of the tenrec–elephant split. The soft maximum constraint is then the soft maximum constraint on the age of Boreoeutheria, as noted above, namely 113 MYA.

Tenrec, Elephant–Human, Chimp, Macaque, Mouse, Rat, Rabbit, Dog, Cat, Horse, Pig, Sheep, Cow, Armadillo

The human–tenrec split is equivalent to the origin of the clade comprising Boreoeutheria, Xenarthra. and Afrotheria. The oldest boreoeutherians are, as already noted, the zalambdalestids and zhelestids from the Khodzhakul Formation of Uzbekistan, dated to early Cenomanian, hence 99.6–96.2 MYA ± 0.9 Myr. The oldest reported afrotherians are much younger, dating from the Eocene, as just noted. The oldest are *Phosphatherium* and *Daouitherium* from Ypresian (lower Eocene) phosphorites of the Ouled Abdoun Basin of Morocco (Gheerbrandt et al. 2005).

The minimum constraint for the Boreoeutheria/Xenarthra–Afrotheria split is then 95.3 MYA, and the maximum constraint is, as for the cow–dog split above, 113 MYA.

Opossum–Kangaroo

The opossum–kangaroo split is equivalent to the deep divergence among marsupial mammals between the clades Ameridelphia, the South American marsupials, and Australidelphia, the Australian marsupials (Amrine-Madsen et al. 2003; Nilsson et al. 2004). There are older marsupials from the Mid to Late Cretaceous, but these lie outside the split between the extant clades.

Until recently, the oldest ameridelphians came from the Tiupampa fauna from Bolivia (de Muizon and Cifelli 2000, 2001), type locality of the Tiupampan South American Land Mammal Age, and dated as 60.4–59.2 MYA ± 0.2 Myr (Gradstein et al. 2004), not 64.5–63 MYA, as is sometimes quoted (Nilsson et al. 2004). The fauna contains 11 ameridelphian marsupials, with representatives of several major lineages (didelphimorphs, sparassodonts), so the clade was already moderately diverse by this point. A new find of a possible polydolopimorphian, *Cocatherium*, extends the age back to Danian (Goin et al. 2006). *Cocatherium* is reported from the Lefipán Formation of Chubut, Argentina, a marine unit dated as basal Paleocene (basal Danian). The Late Cretaceous (possibly Campanian) La Colonia and Los Alamitos faunas do not contain marsupials, and the Laguna Umayo fauna (sometimes dated as latest Cretaceous) has been said to contain dental remains of the didelphid *Peradectes* in association with dinosaur eggs. However, the unit is now dated as late Paleocene to early Eocene, and it has not yielded dinosaurs. Various Cretaceous marsupials from North America have been included in Ameridelphia from time to time (Kielan-Jaworowska et al. 2005), but this is not supported by current cladistic analysis.

The oldest Australian marsupials are *Thylacotinga* and *Djarthia* from the Early Eocene Tingamarra local fauna from Murgon, Queensland, dated radiometrically at 54.6 MYA ± 0.5 Myr, indicating an Early Eocene age, and supported by biostratigraphy (Godthelp et al. 1999). The Australidelphia date back further because, oddly, within this clade is the South American family Microbiotheriidae (and a putative microbiotheriid has been noted from the Murgon locality). The oldest microbiotheriid is *Khasia* from the Tiupampa fauna of Bolivia.

So, the oldest crown-group marsupial known to date is *Cocatherium*, an ameridelphian that is older than the oldest australidelphian, from the Danian (65.5 MYA ± 0.3 Myr to 61.7 MYA ± 0.2 Myr), providing the minimum constraint of 61.5 MYA on the opossum–kangaroo split.

The soft maximum constraint is determined as 71.2 MYA from the diverse fossiliferous units of similar facies in the North and South American Maastrichtian (70.6 ± 0.6 to 65.5 ± 0.3 MYA) that have not produced remains identifiable to either modern group of marsupials, or to the stem taxa, or either.

Opossum, Kangaroo–Human, Chimp, Macaque, Mouse, Rat, Rabbit, Dog, Cat, Horse, Pig, Sheep, Cow, Armadillo, Tenrec, Elephant

The human–opossum branching point is of course synonymous with the split of marsupials and placentals.

The earliest unequivocal marsupial dental fossils come from the mid Cretaceous of North America. The oldest of these is *Kokopellia juddi* reported (Cifelli 1993) from the Mussentuchit Member, in the upper part of the Cedar Mountain Formation, Utah, that is dated as middle to late Albian on the basis of bivalves and palynomorphs, and a radiometric date of 98.37 MYA ± 0.07 Myr was obtained from radiometric dating of zircons in a bentonitic clay layer. This suggests that the Mussentuchit Member extends to the Albian/Cenomanian boundary (99.6 MYA ± 0.06 Myr), but that the bulk of the unit is late Albian. Even older is the boreosphenidan *Sinodelphys szalayi* from the Yixian Formation, Liaoning Province, China, that is placed phylogenetically closer to marsupials than to placentals by Luo et al. (2003). This then has taken the root of the marsupial clade back to 125 Myr.

The oldest placentals were also, until recently, restricted to the mid and Late Cretaceous (Stucky and McKenna 1993), but subsequent finds have pushed the age back step-by-step deeper into the Early Cretaceous. First were *Prokennalestes trofimovi* and *P. minor*, reported from the Höövör beds of Mongolia (Kielan-Jaworowska and Dashzeveg 1989), and dated as either Aptian or Albian. Then came *Montanalestes keeblerorum* (Cifelli 1999) from the Cloverly Formation (late Aptian to early Albian, c. 100 MYA). Then, *Murtoilestes abramovi* was named (Averianov and Skutschas 2001) from the Murtoi Svita, Buryatia, Transbaikalia, Russia, being dated as late Barremian to middle Aptian (say, 128–120 MYA). These 3 taxa were based on isolated jaws and teeth. These were all topped by the spectacular find of *Eomaia scansoria* in the Yixian Formation of Liaoning Province, China (Ji et al. 2002), a complete skeleton with hair and soft parts preserved. Dating of the Jehol Group of China has been contentious, with early suggestiuons of a Late Jurassic age for some or all of the fossiliferous beds. Biostratigraphic evidence now confirms an Early Cretaceous (Barremian) age, with several radiometric dates, using different techniques, on 3 tuff layers that occur among the fossil beds of 124.6 MYA ± 0.1 Myr, 125.0 MYA ± 0.18 Myr, 125.2 MYA ± 0.9 Myr (Zhou et al. 2003). This gives an encompassing age designation of 125.0 MYA ± 0.7 Myr for the span of the 3 tuff layers, and for the fossiliferous beds of the Yixian Formation, based on direct dating. Thus, we conclude a minimum constraint of 124.3 MYA.

The soft maximum constraint is set by older fossiliferous beds with fossil mammals, but not placentals or marsupials, or members of the stem groups of either clade. For example, an older therian, neither marsupial nor placental, is *Vincelestes* from the La Amarga Formation of Argentina, dated as Hauterivian (136.4 MYA ± 2.0 Myr to 130.0 MYA ± 1.5 Myr. Thus, our soft maximum constraint is 138.4 MYA. Beds of similar age in North America and Europe have also produced such basal therians that are neither marsupials nor placentals according to present evidence.

Platypus–Opossum, Kangaroo, Human, Chimp, Macaque, Mouse, Rat, Rabbit, Dog, Cat, Horse, Pig, Sheep, Cow, Armadillo, Tenrec, Elephant

The base of the crown clade of modern mammals, marking the split between Monotremata, represented by the platypus, and Theria, represented by the human, might have a number of positions, depending on how many of the extinct Mesozoic mammal groups are included in the clade.

As noted above, the oldest marsupial, *Sinodelphys*, and the oldest placental, *Eomaia*, take the age of Theria back to about 125 MYA. *Vincelestes* from the La Amarga Formation of Argentina, as noted above, is dated as Hauterivian, and takes the age of Theria back to 136.4 MYA ± 2.0 Myr to 130.0 MYA ± 1.5 Myr.

According to a widely accepted cladogram of Mesozoic mammals (Luo et al. 2002, 2003; Kielan-Jaworowska et al. 2005), the Theria are part of a larger clade Theriimorpha that includes further extinct clades: Triconodonta, Multituberculata, Symmetrodonta, and Dryolestoidea. Most of these originated in the Late Jurassic, but triconodonts and dryolestoids began earlier, in the Middle Jurassic. Basal triconodonts include *Amphilestes* and *Phascolotherium* from the Stonesfield Slate, referred to the *Procerites progracilis* zone of the lower part of the middle Bathonian stage on the basis of ammonites (Boneham and Wyatt 1993), and so dated as 166.9 to 166.5 MYA ± 4.0 Myr (Gradstein et al. 2004). Tooth-based mammal taxa from the Early Jurassic of India (*Kotatherium*, *Nakundon*) and North America (*Amphidon*) that have been ascribed to Symmetrodonta (e.g., Asher et al. 2005) are not convincingly members of the clade (Averianov 2002), and so are ignored here. The oldest dryolestoid appears to be *Amphitherium*, also from the Stonesfield Slate.

The oldest monotremes are *Steropodon* and *Kollikodon* from the Griman Creek Formation, Lightning Ridge, South Australia, and dated as middle to late Albian, 109–100 MYA. *Teinolophos* is from the Wonthaggi Formation, Flat Rocks, Victoria, and is dated as early Aptian, 125–121 MYA.

In the new cladistic view (Luo et al. 2002, 2003; Kielan-Jaworowska et al. 2005), the Ausktribosphenida from Gondwana are immediate sister group of Monotremata, forming together the Australosphenida. Oldest are *Asfaltomylos* from the late Middle Jurassic (Callovian) Cañadon Asfalto Formation of Cerro Condor, Argentina (Rauhut et al. 2002), and *Ambondro* from the upper part of the Isalo "Group" (Middle Jurassic, Bathonian) of Madagascar (Flynn et al. 1999). The position of the Madagascar find in the Bathonian is uncertain, so the age range is 167.7 MYA ± 3.5 Myr to 164.6 MYA ± 4.0 Myr.

The human–platypus split is then dated on the oldest theriimorph from 166.9 to 166.5 MYA ± 4.0 Myr, similar in age to the less well-dated oldest australosphenidan. If the Theriimorpha–Australosphenida cladistic hypothesis of Luo et al. (Luo et al. 2002, 2003; Kielan-Jaworowska et al. 2005) is incorrect, and monotremes and therians form a clade exclusive of all extinct groups, the human–platypus split date could be as young as 130 MYA, the minimal age of the therian *Vincelestes*.

If this date is not too ancient, a soft maximum constraint can be considered. The sister group of Australosphenida + Theriimorpha is Docodonta, and the oldest docodonts are from the Bathonian of Europe, with a possible earlier form from the Kota Formation of India. Further outgroups, Morganucodontidae, *Sinoconodon*, and *Adelobasileus*,
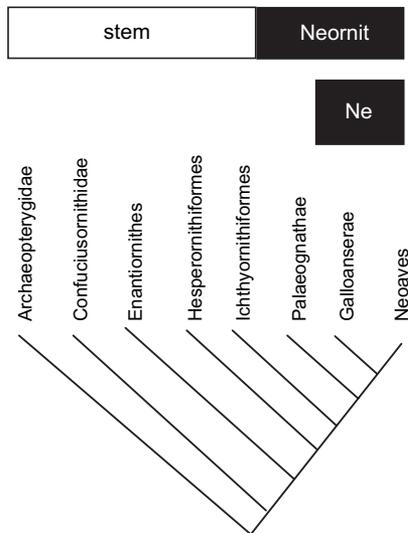
Fig. 3.—Outline relationships of the major clades of birds. Abbreviations: Ne, Neognathae; Neornith, Neornithes.

are known from the Late Triassic and Early Jurassic. The Kota Formation and several other units from other parts of the world that have yielded fossil mammals, but nothing assignable to the Australosphenida or Theriimorpha, date to the later half of the Early Jurassic, equivalent to the Pliensbachian and Toarcian stages (189.6 MYA ± 1.5 Myr to 175.6 MYA ± 2.0 Myr), and so 191.1 MYA should be used as a maximum constraint.

Birds and Reptiles

Only 2 divergence dates will be presented for birds, partly because there has been less gene sequencing than for mammals, but also because most details of the branching pattern of the tree of extant birds are still disputed (Cracraft et al. 2004; Dyke and Van Tuinen 2004). The selected divergence dates are between Galloanserae and Neoaves within Neognathae (the chicken–zebrafinch split) and between Palaeognathae and Neognathae within Neornithes (the emu–chicken split). The cladogram (fig. 3) is based on a consensus of recent work (Chiappe 2002; Cracraft et al. 2004).

Chicken–Zebrafinch

The phylogeny of major groups of modern flying birds (clade Neognathae) has been hard to resolve. Recent morphological and molecular analyses now agree on a deep divergence between the clade Galloanserae, comprising Galliformes (chickens and game birds) and Anseriformes (ducks) on the one hand, and Neoaves (all other flying birds) on the other (Cracraft et al. 2004; Dyke and Van Tuinen 2004).

The oldest purported galloanserine is *Teviornis gobiensis*, a presbyornithid anseriform from the Gurilyn Tsav locality of Mongolia (Kurochkin et al. 2002). Sediments here come from the lower portion of the Nemegt Horizon, at the base of the Nemegt Formation. The Nemegt Formation is assigned to the early Maastrichtian (Lillegraven and McKenna 1986), dated as 70.6 MYA ± 0.6 Myr to 69.6

MYA ± 0.6 Myr. Doubt has been cast, however (Clarke and Norell 2004), on whether *Teviornis* is a neognath, letalone a galloanserine, so the next youngest purported neognath should be selected until this issue is clarified. A further latest Cretaceous anseriform is *Vegavis iaai* from lithostratigraphic unit K3 of Vega Island, Antarctica, dated as mid to late Maastrichtian, c. 68–66 MYA (Clarke et al. 2005). The oldest galliform fossil that can be identified with confidence is much younger, Early Eocene (Dyke and Van Tuinen 2004).

The oldest neoavian is debated, with dozens of records of gaviiforms, pelecaniforms, charadriiforms, procellariiforms, and psittaciforms from the latest Cretaceous (most are close to the Cretaceous Tertiary boundary, 65.5 MYA; Dyke 2001; Hope 2002). The most complete fossil is *Polarornis gregorii*, described as a loon (gaviiform) from the Lopez de Bertodano Formation of Seymour Island, Antarctica (Chatterjee 2002). This stratigraphic unit is dated as mid to late Maastrichtian on the basis of microplankton (Pirrie et al. 1997), so 69.6–65.5 MYA ± 0.3 Myr. Dyke and Van Tuinen (2004) indicate some doubt about the taxonomic assignment of the specimen and about its geological provenance.

Even if the various neoavian specimens fall close to the Maastrichtian–Danian boundary, and if there is some doubt about *Polarornis* and *Teviornis*, the galloanserine record of *Vegavis* is older, and dates the minimum constraint on chicken–zebrafinch divergence at 66 MYA, on the basis of biostratigraphy and indirect dating.

The soft maximum constraint is based on older birdbearing deposits that match some at least of the facies represented in the late Maastrichtian, that are broadly from the shallow marine to coastal belt. Fossil birds, most notably, hundreds of specimens of *Hesperornis*, *Baptornis*, and *Ichthyornis* (members of the clades Ichthyornithiformes and Hesperornithiformes, both outgroups to Neornithes) have been recovered in abundance from the Niobrara Chalk Formation of Kansas and neighboring states, dated as Santonian (85.8–83.5 MYA ± 0.7 Myr), and so 86.5 MYA.

Emu–Chicken, Zebrafinch

The divergence of emu and chicken is synonymous with the deep divergence between clades Palaeognathae (the ratites, or flightless birds) and the Neognathae (all other, flying, birds).

The oldest palaeognaths are the lithornithids, a family known from the Paleocene and Eocene of North America. A putative latest Cretaceous lithornithid was reported by Parris and Hope (2002) from the New Jersey greensands. The age of these deposits has been much debated (Dyke and Van Tuinen 2004), and they fall either below or above the KT boundary (65.5 MYA ± 0.3 Myr). An older specimen might be mistakenly assigned here: the pelvis of a large flightless bird, *Gargantuavis philoinos*, reported (Buffetaut and Le Loeuff 1998) from the base of the Marnes de la Maurines Formation, in association with dinosaurs of late Campanian to early Maastrichtian aspect. These authors were clear that *Gargantuavis* was not a palaeognath, and suggested that it might be related to the nonneornithine *Patagopteryx*.

As just noted, the oldest confirmed neognath fossil is the anserfirom *Vegavis* from 66 MYA, and this has to be the minimum constraint on the divergence date for palaeognaths and neognaths. The maximum constraint is currently the same as for the chicken–zebrafinch split above, namely the clades Ichthyornithiformes and Hesperornithiformes of the Niobrara Chalk Formation, dated as Santonian (85.8–83.5 MYA ± 0.7 Myr), and so 86.5 MYA.

Crocodile–Emu, Chicken, Zebrafinch

The most recent common ancestor of crocodiles and birds was an archosaur that lay at the deep junction of the 2 major clades within Archosauria: Avemetatarsalia/Ornithodira, the "bird" line and Crurotarsi, the "crocodile" line (Gauthier 1986; Sereno 1991; Benton 1999). These 2 clades together form the Avesuchia (="crown-group Archosauria").

The basal crurotarsans are the poposaurid *Bromsgroveia* from the Bromsgrove Sandstone Formation of England, and the "rauisuchians" *Wangisuchus* and *Fenhosuchus* from the Er-ma-Ying Series of China, *Vjushkovisaurus* from the Donguz Svita of Russia, and *Stagonosuchus* and "*Mandasuchus* from the Manda Formation of Tanzania (Benton 1993). All these records are dated as Anisian, but at present it is hard to be more precise. This gives an age range of 245 MYA ± 0.5 Myr to 237 MYA ± 2.0 Myr.

The basal avemetatarsalian is *Scleromochlus* from the Carnian of Scotland, but older relatives are *Marasuchus*, *Lagerpeton*, and *Pseudolagosuchus* from the Chañares Formation of Argentina, dated as Ladinian, so 237 MYA ± 2.0 Myr to 228.0 MYA ± 2.0 Myr.

The minimum constraint on the divergence date for birds and crocodiles then falls at the top of the Anisian (245 MYA ± 1.5 Myr to 237 MYA ± 2.0 Myr), and so 246.5 MYA.

The soft maximum constraint may be assessed from the age distribution of immediate outgroups to Avesuchia, the Proterochampsidae, Euparkeriidae, Erythrosuchidae, and Proterosuchidae (Gauthier 1986; Sereno 1991; Benton 1999). Numerous fossil sites from around the world in the Olenekian, the stage below the Anisian, have produced representatives of these outgroups, but not of avesuchians, and so the Olenekian (249.7 MYA ± 0.7 Myr to 245 MYA ± 1.5 Myr), and so 250.4 MYA.

Lizard–Crocodile, Emu, Chicken, Zebrafinch

The clades Crocodylia (modern crocodiles and extinct relatives) and Squamata (modern lizards and snakes and their extinct relatives) are members, respectively, of the larger clades Archosauromorpha and Lepidosauromorpha (fig. 4). The ultimate split between crocodilians and lizards then is marked by the split between those 2, and they, together with a number of basal outgroups, form the major clade Diapsida. Through a series of cladistic analyses (Benton 1985; Evans 1988; Gauthier et al. 1988; Laurin 1991; Laurin and Reisz 1995; deBraga and Rieppel 1997; Dilkes 1998), the topology of the basal region of the cladogram around the split of Archosauromorpha and Lepidosauromorpha has been agreed (although some higher parts of
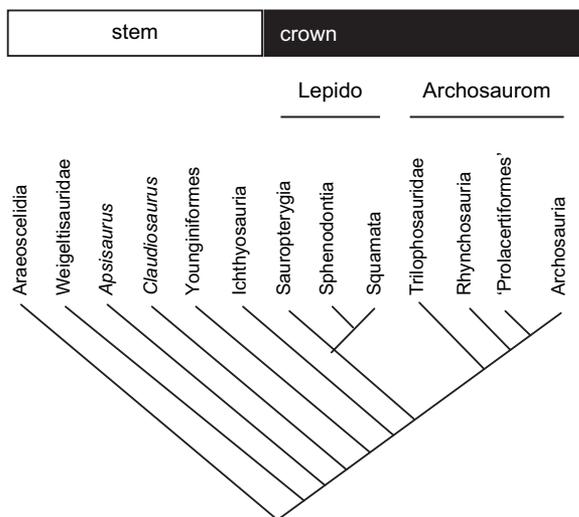

Fig. 4.—Outline relationships of the major clades of Diapsida. Abbreviations: Archosaurom, Archosaurmorpha; Lepido, Lepidosauromorpha.

the cladogram are still much debated, especially the placement of Sauropterygia and Ichthyosauria).

The most ancient archosauromorph is the "prolacertiform" *Protorosaurus speneri* from the Kupferschiefer of Germany and the Marl Slate of NE England (Evans and King 1993). Both geological units are correlated with each other on independent geological evidence, and defined as the basal unit of the Zechstein 1 (EZ1; Werra Folge) depositional cycle. The 2 units were generally assigned to the Kazanian (e.g., Benton 1993, p. 695), but subsequent stratigraphic revisions have shown that the Zechstein falls above the Illawarra Reversal, which is at the Wordian–Capitanian boundary, and the Zechstein I contains fossils characteristic of the Capitanian (Gradstein et al. 2004). It is unclear how much of the Capitanian is represented by the Zechstein, but it probably represents the upper part, so 263.8–260.4 MYA ± 0.7 Myr.

The most ancient lepidosauromorph is debated–Benton (1993, p. 688) indicated that *Saurosternon bainii*, sole representative of the Saurosternidae, may be the oldest, but he was uncertain. Other authors (Gauthier et al. 1988; Clark and Hernandez 1994; Reynoso 1998) were more convinced that this is a true lepidosauromorph. The doubt arises because the taxon is based on a single partial skeleton lacking the skull. *Saurosternon* is from the *Cistecephalus* or *Dicynodon* Assemblage zone of South Africa (Hancox and Rubidge 1997) equivalent to the uppermost Wuchiapingian or Changhsingian, respectively, perhaps some 257–251 MYA. If *Saurosternon* is not a lepidosauromorph, the next possibility would be a sauropterygian. The uncertainty here is whether sauropterygians are lepidosauromorphs—the group was unplaced phylogenetically for some time, but deBraga and Rieppel (1997) and others have made a strong case that these marine reptiles are unequivocal lepidosauromorphs. Benton (1993, p. 70) listed 2 Lower Triassic (Scythian) sauropterygians, *Corosaurus* and *Placodus*, but the dating of both is uncertain. *Corosaurus* is from the Alcova Limestone Member of the Chugwater Formation

in Wyoming, formerly assigned to the Middle or Upper Triassic, but noted as Lower Triassic by Storrs (1991). The precise age is hard to pin down. The Lower Triassic *Placodus* is from the Obere Buntsandstein of Pfalz, Germany, a unit dated as spanning the Olenekian–Anisian boundary, and ranging in age from 246 to 244 MYA ± 1.5 Myr.

Based on the oldest neodiapsid, *Protorosaurus*, the minimum constraint on the divergence of crocodilians and lizards is 259.7 MYA.

In order to establish the soft maximum constraint on this divergence, outgroups to Neodiapsida are considered. Ichthyosauria are known first in the Early Triassic, younger than the minimum age constraint. Younginiformes and *Claudiosaurus* are of similar age to *Protorosaurus*, or younger. Next oldest is *Apsisaurus* from the Archer City Formation of Texas, dated as Asselian (299–294.6 MYA ± 0.8 Myr) (Benton 1993), and so 299.8 MYA. This is a long way below the minimum age constraint, but there is a well-known "gap" in suitable fossiliferous formations through the Mid Permian.

Basal amniotes and tetrapods
Bird–Mammal

The ultimate divergence date between birds and mammals has been quoted many times as 310 MYA, generally tracing back to Benton (1990), who in fact gave the age as 305 MYA. van Tuinen and Hadly (2004) trace the history of estimates of this date in molecular analyses, and they quote a range of estimates from 338 to 247 MYA, with a preference for the 310 MYA date on the basis of reassessment of the Late Carboniferous timescale.

This estimate has been criticized for being used without error bars (Graur and Martin 2004; van Tuinen and Hadly 2004), for being based on uncertain fossils and hence too old (Lee 1999), for being misdated (Reisz and Muller 2004; van Tuinen and Hadly 2004), and for being poorly bracketed by outgroups above and below (Reisz and Muller 2004) and Müller and Reisz (2005) indeed argue that this calibration point should no longer be used because it is so problematic, but others (Hedges and Kumar 2004; van Tuinen and Hadly 2004) reasonably point out that there is a demand to use this date because of the volume of sequence data for mammals and birds, and the need to use a member of one or other clade as an outgroup in many studies.

The ultimate ancestor of birds and mammals has to be tracked back to the base of the Synapsida and Sauropsida, the larger clades that include mammals and birds, respectively (fig. 5). These 2 clades together make up Amniota, the clade containing all tetrapods other than amphibians, and the relationship of major groups is agreed by most (e.g., deBraga and Rieppel 1997; Reynoso 1998; van Tuinen and Hadly 2004; Benton 2005). The question of the ultimate bird–mammal split becomes synonymous then with dating the origin of the clade Amniota.

The oldest identified synapsid is *Protoclepsydrops* from the Joggins Formation of Joggins, Nova Scotia. The age of the Joggins Formation has been much debated, and figures in the range from 320 to 305 MYA have been cited recently. Reisz and Müller (2004) indicate an age of
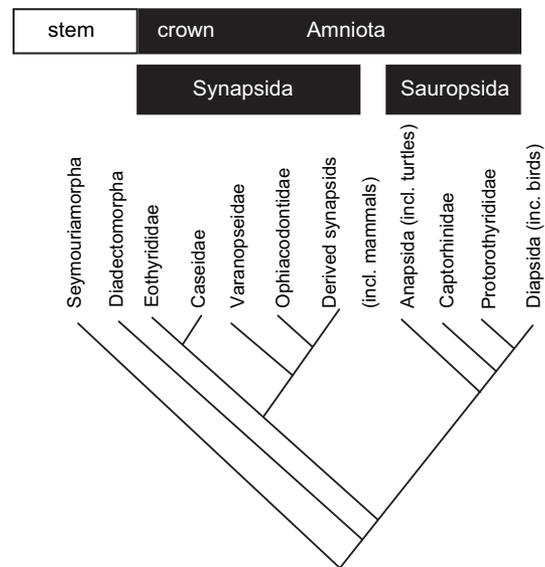

Fig. 5.—Outline relationships of the major clades of Amniota.

316–313 MYA, whereas van Tuinen and Hadly (2004) settle for 310.7 MYA ± 8.5 Myr. Detailed field logging and biostratigraphy (Dolby 1991; Calder 1994; Falcon-Lang et al. 2006) confirm that the Joggins Formation falls entirely within the Langsettian European time unit, equivalent to the Westphalian A, and roughly matching the Russian Cheremshanian, in the later part of the Bashkirian stage. Earlier dates for these units were equivocal (Menning et al. 2000), but Gradstein et al. (2004) date the Langsettian as 314.5–313.4 MYA ± 1.1 Myr.

Protoclepsydrops has been classed as an ophiacodontid, not a member of the basalmost synapsid families—Eothyrididae, Caseidae, or Varanopseidae—whose basal members, if ever found, might be of the same age or older. *Protoclepsydrops haplous* is known from one incomplete partial skeleton and skull (Reisz 1972), but the remains are fragmentary; even the identification of these remains as a synapsid has been questioned (Reisz 1986; Reisz and Modesto 1996). Lee (1999) used this uncertainty to reject *Protoclepsydrops* as informative in this discussion, and to look at the next oldest synapsids, such as *Echinerpeton* and *Archaeothyris* from the Morien Group of Florence, Nova Scotia (Myachkovian, upper Moscovian, 307.2–306.5 MYA). Because each retained only one synapomorphy of Synapsida, Lee (1999) rejected them, and moved up to more complete material of basal synapsids from some 288 MYA. van Tuinen and Hadly (2004) rejected *Protoclepsydrops* as a useful marker of the bird–mammal split, but accepted *Archeothyris* as reasonable, with a date of 306.1 MYA ± 8.5 Myr.

The earliest member of the other branch, the Sauropsida (sometimes called Eureptilia, or Reptilia) is less contentious. *Hylonomus*, also from the Joggins Formation at Joggins, Nova Scotia, is a member of Protorothyrididae (Carroll 1964; Gauthier et al. 1988; Laurin and Reisz 1995), part of the stem to Diapsida, and the oldest known member of the clade. The clade Captorhinidae is more basal than Protorothyrididae, but the oldest captorhinid is

younger—*Romeria primus* from the Moran Formation of Texas (Early Permian, Sakmarian, c. 294–284 MYA; Benton 1993). Lee (1999) cast doubt on the assignment on *Hylonomus* to the sauropsid clade, and preferred to redate that branch also to some 288 MYA.

Lee's (1999) proposal would move the mammal–bird split date from somewhere around 310 MYA to 290 MYA, whereas van Tuinen and Hadly (2004) settled for 305 MYA as a minimal date. However, Reisz and Müller (2004) and van Tuinen and Hadly (2004) suggested that Lee was wrong to cast doubt on nearly all the Carboniferous synapsids and sauropsids—many are diagnostic of one or other group. More importantly though, Reisz and Müller (2004) pointed out that the question of dating the ultimate bird–mammal split is synonymous with dating the origin of Amniota. So, it may be uncertain whether *Protoclepsydrops* is a synapsid, and *Hylonomus* is not a diapsid, and one could debate the phylogenetic position of Protorothyrididae, but all these taxa are diagnostically members of Amniota, so the origin of Amniota happened before the age of the Joggins Formation of Nova Scotia.

The minimum constraint on the mammal–bird split, equivalent to the minimum age of the origin of clade Amniota corresponds to the age of the Joggins Formation. This is 314.5–313.4 MYA ± 1.1 Myr, a date based on biostratigraphy (palynology) and exact dating from elsewhere, conferring a minimum constraint of 312.3 MYA.

The soft maximum constraint on the bird–mammal split is based on the next richly fossiliferous units lying below these horizons. The first is the East Kirkton locality, source of a diverse fauna of batrachomorphs and reptiliomorphs (see human–toad split below), but that has hitherto not yielded anything that could be called either a diapsid or a synapsid. Further, fossiliferous sites of similar facies lie below the East Kirkton level, and they have not yielded reptile remains. We take the age of the fossiliferous Little Cliff Shale of the East Kirkton locality (Brigantian; 328.8–326.4 MYA ± 1.6 Myr) as the basis for the soft maximum age constraint of 330.4 MYA.

Toad–Bird, Mammal

The African clawed toad (*Xenopus laevis*) is a representative of modern Amphibia (the clade Lissamphibia, including frogs and toads, salamanders, and caecilians), and the human–toad split is equivalent to the deep branching point between Amphibia and Amniota. Within crown Tetrapoda, this is the split of Batrachomorpha (extant lissamphibians and extinct relatives) and Reptiliomorpha (extant amniotes and their extinct relatives) (fig. 6).

The oldest batrachomorph is *Balanerpeton woodi*, a basal temnospondyl from the East Kirkton locality in Scotland. Another putative basal batrachomorph is *Eucritta melanolimnetes*, from the same location, described as a possible baphetid (Clack 1998), but possibly a batrachomorph (Ruta et al. 2003). The fossils come from the Little Cliff Shale, a unit within the East Kirkton Limestone, a subdivision of the Upper Oilshale Group of the Midland Valley of Scotland. The fossil beds are ascribed to the Brigantian (D2; lower portion) of the Viséan stage, based on biostrati-
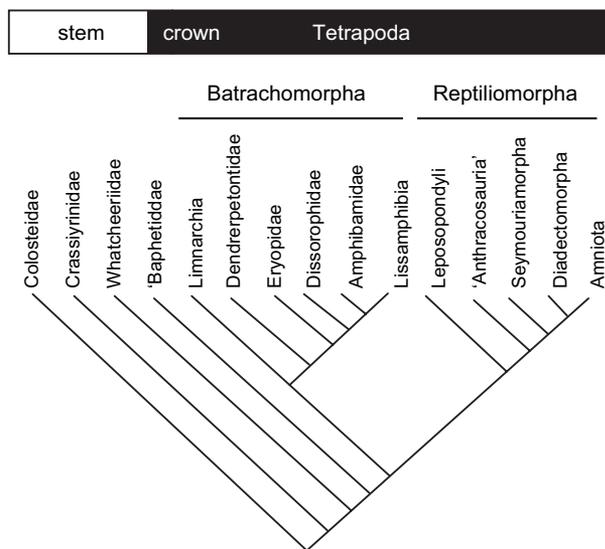

FIG. 6.—Outline relationships of the major clades of Tetrapoda.

graphic comparisons of the fossil plants, pollen, and bivalves with the rich records of Lower Carboniferous sites throughout Europe (Rolfe et al. 1993). The Brigantian regional stage is dated from 328.8 to 326.4 MYA ± 1.6 Myr.

The oldest reptiliomorphs are the basal lepospondyl *Westlothiana lizziae*, and the aïstopod *Lethiscus stocki* (Ruta et al. 2003). *Westlothiana* and *Lethiscus* are both from the Viséan. *Westlothiana* comes from the East Kirkton locality, and is dated at 327.6 MYA ± 2.8 Myr (see above). *L. stocki* is from the Wardie Shales, part of the lower Oil Shale Group, near Edinburgh, and dated as older than the East Kirkton locality (Rolfe et al. 1993). The Wardie Shales are assigned to the Holkerian regional stage on the basis of fossil fishes and palynomorphs (Paton et al. 1999), dated as 339.2–332.4 MYA ± 2.0 Myr.

van Tuinen and Hadly (2004) reviewed the amphibian–amniote divergence date in detail, but assigned the Wardie Shales to the Asbian, the stage above the Holkerian, and so came to an age of 332.3 MYA. Further, they used radiometric dates from Menning et al. (2000) that have been revised in Gradstein et al. (2004). Our minimum constraint on the human–toad divergence is 330.4 MYA, based on *Lethiscus*, and biostratigraphic placement of the Wardie Shales Formation, with radiometric dating of the Holkerian from elsewhere.

The soft maximum constraint is harder to determine because most of the close outgroups to the batrachomorph–reptiliomorph clade are known only from younger deposits: the oldest baphetids and crassigyrinids are from the Brigantian (Benton 1993), the oldest colosteids from the Asbian (Benton 1993). The whatcheeriids *Whatcheeria* and *Pederpes*, from North America and Europe, respectively, are older, however, and dated to the Ivorean regional North American stage, and so 348–345.3 MYA ± 2.1 Myr. These horizons are underlain by further units of Famennian age, dated as 374.5 MYA ± 2.6 Myr to 359.2 MYA ± 2.5 Myr, with basal tetrapods known

from several continents, but no batrachomorphs or reptiliomorphs. We choose the whatcheeriids as marking the soft maximum constraint, even though they are phylogenetically more distant from crown Tetrapoda than baphetids and colosteids—but the latter 2 are younger than *Lethiscus*. Thus, we propose a date of 350.1 MYA as a soft maximum constraint.

Dating Divergences among Basal Vertebrates and Other Metazoans

Takifugu–Tetraodon

Following the phylogenetic scheme of Holcroft (2005), this divergence event represents the origin of crown-group Tetraodontidae. *Archaeotetraodon winterbottomi* has been identified as a member of this clade on the presence of numerous tetraodontid synapomorphies, including the presence of 11 caudal fin rays, 18 vertebrae, broadened neural and haemal spines and an absence of ribs (Santini and Tyler 2003). It has been recorded from the Pshekhsky Horizon, in the lower part of the Maikop Formation of the north Caucasus, Russia (Tyler and Bannikov 1994), making it the earliest known member of Tetraodontidae (Santini and Tyler 2003). The lower part of the Maikop Formation has been widely quoted as Lower Oligocene (Tyler and Bannikov 1994; Gürgey 2003), although evidence is rarely presented in support of this.

Leonov et al. (1998) provide evidence on the age of the Pshekhsky Horizon on the basis of planktic and benthic foram, nannoplankton and dinocyst biostratigraphy. The base of the Pshekhsky Horizon coincides with the base of range of the *Globigerina tapuriensis* that belongs to the Zone P18 of the Paleogene planktic foram zonation scheme (Spezzaferri and Silva 1991). The base of P18 equates to the base of the Oligocene that has been dated at 33.90 MYA ± 0.1 Myr (Luterbacher et al. 2004). The top of the Pshekhsky Horizon coincides approximately with the first appearance of the nannoplanton species *Sphenolithus predistentus*, and the base of NP23, a Paleogene Nannoplankton zone (Leonov et al. 1998). The latter has been dated at 32.25 MYA (Luterbacher et al. 2004), the errors on which are negligible, though there will be an inherent uncalculated error on the biostratigraphic correlation to the Caucasus.

Thus, paleontological evidence on the divergence of the lineages leading to *Takifugu rubripes* and *Tetraodon nigroviridis* provides a minimum constraint of 32.25 MYA. Relationships within Tetraodontiformes have been approached from anatomy and molecular phylogenetics, but remain poorly constrained. Nonetheless, the oldest records for the potential sister clades are all of Eocene age and among them, the oldest record is provided by the balistid *Moclaybalistes danekrus*, known from the Lower Eocene Mo-Clay (Fur/Ølst) Formation, that has been dated using magnetostratigraphy and biostratigraphy using nannoplankton, dinoflagellate, and pollen zones (Willumsen 2004). The base of the Ølst Formation coincides with the base of dinoflagellate Zone 6 and the base of the *Apectodinium augustum* zone that coincides with the base of the Eocene. A soft maximum constraint on the split of *T. rubripes* and *T. nigroviridus* can thus be obtained from the age of the base of the Eocene that has been dated at 55.8 MYA ± 0.2 Myr (Luterbacher et al. 2004), thus 56.0 MYA.

Stickleback–Takifugu, Tetraoodon

This divergence event represents the split between Gasterosteiformes and Tetraodontiformes within Percomorpha. The oldest member of Gasterosteiformes is *Gasterorhamphosus zuppichinii* from Calcare di Mellissano, near Nardò, Lecce, Apulia southeastern Italy (Sorbini 1981), that is believed to be Campanian (Late Cretaceous) in age (Patterson 1993). This is younger than the oldest known member of the tetraodontiform lineage, *Plectocretacicus clarae*, the earliest stem-tetraodontiform, from the Cenomanian (Upper Cretaceous) of Hakel, Lebanon (Sorbini 1979; Tyler and Sorbini 1996). The age of the lithographic limestones at Hakel is derived from the occurrence of *Mantelliceras mantelli* and the benthic foraminifer *Orbitulina concava* (Hückel 1970). The stratigraphic range of *O. concava* ranges from Late Albian to Early Cenomanian (Cherchi and Schroeder 2004), whereas *M. mantelli* is more restricted temporally, and falls fully within the range of *M. mantelli*, defining the basal ammonite zone of the Cenomanian. The base of the *M. mantelli* zone is well dated on the basis of Ar–Ar and cycle stratigraphy at 99.1 ± 0.4 MYA (Obradovich et al. 2002). Ogg et al. (2004) provide a date of 97.8 MYA for the top of the *M. mantelli* zone; errors on the timescale on surrounding zonal boundaries are 0.9 Myr. Thus, the minimum age of the divergence of Atherinomorpha and Percomorpha can be based on the age on the minimum age of the Lithographic Limestones of Hakel that would be 96.9 MYA.

Given that *P. clarae* is also the oldest known percomorph (Patterson 1993), the most appropriate soft maximum bound on the divergence of Gasterosteiformes and Tetraodontiformes would be the earliest euteleost record, provided by taxa such as *Tischlingerichthys viohli* and associated crown-euteleosts from the Tithonian of Solnholfen (Arratia 1997). Acanthopterygians (as are convincing members of any elopocephalan superorders or orders) are entirely absent. The maximum age of the Solnholfen Lithographic limestones (justified below in connection with the Ostariophysean–Euteleost split) is 150.8 MYA ± 0.1 Myr. Thus, a soft maximum constraint for divergence of the gasterosteiform and tetraodontiform lineages is 150.9 MYA.

Medaka–stickleback, Takifugu, Tetraodon

This divergence event represents the split between Atherinomorpha and Percomorpha within Acanthopterygii. The oldest member of Atherinomorpha, based on otoliths of "*Atherinidarum*", from Argile de Gan, Gan, Pyrénées-Atlantiques, France, and has been assigned a Lower Eocene (Ypresian) age (Nolf 1988). The earliest skeletal records are Upper Eocene (Priabonian) (Patterson 1993). The oldest percomorph is the stem-Tetraodontoform *P. clarae* (see above). Thus, the minimum constraint on the divergence of Atheriniomorpha and Percomorpha is the same as for Gasterosteiformes and Tetraodontiformes, 96.9 MYA. Similarly, the soft maximum constraint is 150.9 MYA.

Zebrafish–Medaka, stickleback, Takifugu, Tetraodon

This divergence event represents the splitting of the Ostariophysean and Euteleost lineages.

The earliest ostariophysean is *T. viohli* from the Tithonian of Solnholfen (Arratia 1997). It is recognized on the basis of synapomorphies including the absence of a basisphenoid, and dorsomedial portions of the anterior neural arches expanding and abutting against each other and the posterior margin of the exoccipital.

From the same deposit, Arratia (1997) also described a number of additional taxa (*Leptolepides, Orthogonikleithrus*) that qualify as the earliest record of the euteleost lineage. These were assigned to Salmoniformes. The security of their assignments to these higher level clades within Euteleostei is questionable, although their assignment to the euteleost total group is not, based not least on the presence of enlarged neural arches/spines.

Thus, earliest representatives of both lineages are in precise agreement. However, this should come as no surprise given that they were recovered from the same deposit. Therefore, the fossil date is likely to be a considerable underestimate, subject to lagerstätten effect. There are no earlier records.

The dating of the Solnhofen has been based on ammonite zonation and the Formation is assigned to the ti$_2$ division of the Middle Tithonian, Late Jurassic. The Tithonian is dated as 150.8 MYA ± 4.0 Myr to 145.5 MYA ±4.0 Myr (Gradstein et al. 2004), but the Solnhofen Formation represents just the middle biohorizon of the lowest ammonite zone of the Tithonian (Zeiss 1977), its base intercalated by the first (local) appearances of the ammonites *H. hybonotum* (and *Gravesia*) and *Glochiceras lithographicum* (Barthels et al. 1990). In proposed stratotype sections, the base of the Tithonian is represented by the marked by the simultaneous first appearance of these 2 taxa plus the immediately subsequent appearance of *Gravesia* sp. (Ogg 2005). The base of *H. hybonotum* zone coincides with the base of the normal-polarity Chron M22An that is dated at 150.8 MYA ± 0.1 Myr (Ogg 2005). Given that the Solnhofen Formation falls fully within the *H. hybonotum* zone, it is possible to derive a lower bound on its age from the base of the succeeding, *S. darwini* ammonite zone that coincides approximately with the M22n Chronozone, dated at 149.9 MYA ± 0.05 Myr (Ogg 2005).

Thus, the earliest paleontological evidence and, therefore, a lower bound on the split of *Danio rerio*–*T. rubripes, Tetraodon nigris* can be considered to be 150.8 MYA ±0.1 Myr to 149.9 MYA ±0.05 Myr, giving a minimum date of 149.85 MYA. However, note should be taken of the fact that the co-occurrence of the earliest records of these 2 lineages is an artefact of their presence in a Konservat-lagerstätte. A soft maximum constraint on the divergence of the Ostariophysean and Euteleost lineages is provided by the census of Teleost–total group diversity provided by the assemblages recovered from the many Oxfordian localities in the Cordillera de Domeyko (Arratia and Schultze 1999). Many species are known in conditions of exceptional preservation and these are stem-teleosts; no otophysans or euteleosts are known from here or from older deposits. The base of the Oxfordian (161.2 MYA ± 4.0 Myr; Ogg 2005) can be taken as the soft maximum constraint: 165.2 MYA.
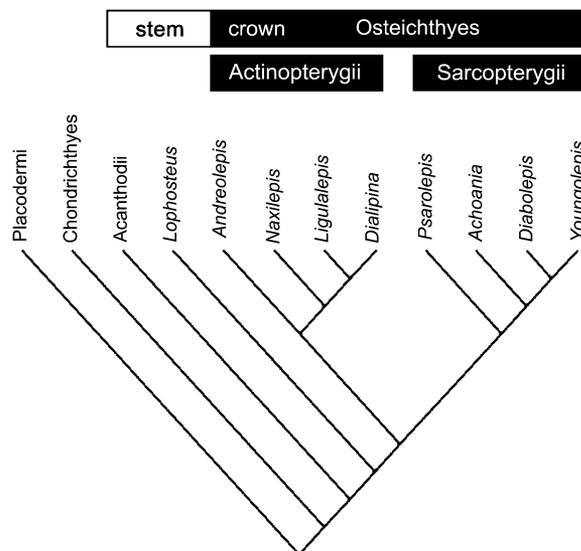

FIG. 7.—Outline relationships of basal members of Osteichthyes.

Zebrafish, Medaka, stickleback, Takifugu, Tetraodon–toad, bird, mammal

This divergence event represents the splitting of Actinopterygii and Sarcopterygii (fig. 7), and so the minimum constraint depends on determining the oldest member of either clade.

The earliest representative of total-group Actinopterygii may be *Andreolepis hedei*, known from microfragments from Gotland, Sweden (Gross 1968; Märss 1986; Fredholm 1988a, 1988b) and elsewhere (Märss 2001). It can be assigned to total-group Actinopterygii on the following synapomorphies: rhomboid scale shape, ganoine-covered scales. The oldest occurrence that is readily constrained is from the lower part of division C of the Hemse Marl at Västlaus, Gotland, Sweden (Fredholm 1988a). Although there are no direct radiometric dates from the Ludlow of Gotland, these sections have been incorporated into a graphic correlation composite standard that incorporates radiometric dates (Kleffner 1995; Fordham 1998). Thus, a date for this occurrence can be established from the composite standard through the line of correlation that equates to 421.75 MYA.

The certainty with which *A. hedei* is assigned to Actinopterygii is obviously less than it might be were it known from articulated remains. However, it is known from a number of skeletal elements (Gross 1968; Janvier 1971, 1978), rather than mere scales, as are the other, slightly younger, early records of Actinopterygii (Schultze 1968; (Wang and Dong 1989).

Naxilepis, although known only from scales (Wang and Dong 1989), possesses a further synapomorphy of total-group Actinopterygii, in addition to those exhibited by *A. hedei*, in the form of a narrow-based dorsal peg and discrete rows of ganoine. The earliest occurrence is from the Miaogao Formation of the Cuifengshan Formation of Quijing District, Yunnan, China, and has been reported to co-occur with the conodont *Ozarkodina crispa* (Wang and Dong 1989; Zhu and Wang 2000) although this has not
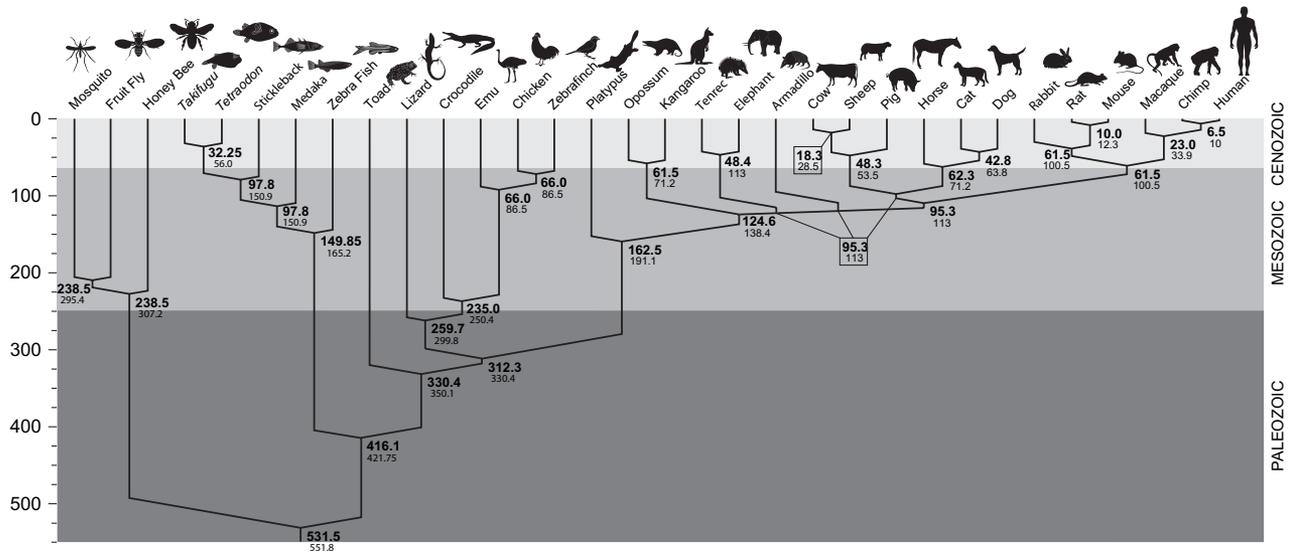
Fig. 8.—Tree of relationships of the key genome model organisms showing minimum (bold) and maximum (roman) fossil-based dates for each branching point. The pattern of relationships is based on a consensus of current views. The minimum age constraints are based on the oldest fossil confidently assigned to either of the 2 sister groups that arise from each branching point. The maximum age constraint is based on bracketing (maximum ages of sister groups) and bounding (age of an underlying suitable fossiliferous formation that lacks a fossil of the clade). Full justification for each minimum and maximum fossil-based age constraint is given in the text, and in tree-based form at http://www.fossilrecord.net.

been substantiated. As below, this constrains the age of the first occurrence of *Naxilepis* between the middle Ludlow and the Ludlow–Pridoli boundary (418.7 MYA).

The earliest macroremains assignable to total-group Actinopterygii are of *Dialipina markae* from the Lochkovian of Siberia (Schultze 1992) that is also know in fully articulated remains from the lower Devonian (Emsian) of the Canadian Arctic (Schultze and Cumbaa 2001). Justification for the Lochkovian age assignment is not clear (Cherkesova 1988).

The earliest record of the sarcopterygian total group is *Psarolepis romeri*, known (in stratigraphic order) from the Yulongsi (Zhu and Schultze 1997), Xishancun (Zhu and Schultze 1997), and Xitun (Yu 1998) members of the Cuifengshan Formation, Quijing District, eastern Yunnan, China (the recently described *Meemania eos* is apparently a more basal member of the sarcopterygian stem but it is known only from the Xitun Member, Zhu et al. 2006). The dating of these occurrences relies primarily upon biostratigraphic dating of a lithostratigraphic correlation of the Yulongsi Member in neighboring Guangxi where the conodont *O. crispa* has been recovered from the middle of the Yulongsi Member (Wang 1981). The lower limit of the stratigraphic range of *O. crispa* is constrained by the Ludlow–Pridoli Boundary (Miller 1995) that has been dated as 418.7 MYA ± 2.7 Myr (Gradstein et al. 2004). In the type Ludlow Series, the upper range limit on *O. crispa* is just a few meters below its lower limit (Miller 1995) (the latest Ludlow and earliest Pridoli are probably unrepresented in the Ludlow type area, Miller et al. 1997). Although it is difficult to provide a direct date on this horizon, zircons from a bentonite 12 m deeper in the type Ludlow section has provided a U-Pb Zircon age of 420.2 MYA ± 3.9 Myr (Tucker and McKerrow 1995). There is a report of *O. crispa* as low as "middle Ludlow" (Viira and Aldridge 1998) although this is just one of a number of

possible interpretations of the conflicting biostratigraphic data. Attempts to directly date the Quijing succession biostratigraphically have yielded the conodont *Oulodus elegans detorta* from the upper part of the Yulongsi Member (Fang et al. 1994). The stratigraphic range of *O. elegans detorta* is confined to its zone which is the ultimate conodont zone of the Silurian (Jeppsson 1988). Thus, direct and indirect biostratigraphic dating is in agreement concerning the age of the middle and upper parts of the Yulongsi Member, indicating that the earliest record of *Psarolepis* is no younger than latest Ludlow (418.7 MYA ± 2.7 Myr) and possibly older than 420.2 MYA ± 3.9 Myr.

Although originally described as a sarcopterygian (Zhu and Schultze 1997; Yu 1998), *Psarolepis* has also been interpreted as stem-Osteichthyes (Zhu et al. 1999; Zhu and Schultze 2001). However, more recent and universal analyses have confirmed its assignment to the sarcopterygian stem lineage (Zhu et al. 2001, 2006).

After *Psarolepis*, the next oldest representatives of total-group Sarcopterygii, *Diabolepis*, *Youngolepis*, and *Achoania* are approximately coeval. They are derived from the Xishancun Member of the Cuifengshan Formation of Quijing District. The Xishancun Member is clearly younger that the underlying Yulongsi Formation, the upper part of which is dated as latest Silurian in age on the occurrence of *O. elegans detorta* (see above), and it has been directly dated as Lochkovian on the basis of ostracode biostratigraphy (Wang and McKenzie 2000).

Outgroups of the Actinopterygii + Sarcopterygii clade may provide evidence for a maximum age constraint. *Lophosteus superbus*, described on the basis of a wide variety of microremains (Gross 1969, 1971) has been considered stem-Osteichthyes (Schultze 1977), although this is poorly substantiated (Janvier 1996; Märss 2001). The earliest occurrence of *L. superbus* is from the Pridoli of Gotland (Gross 1969, 1971), Estonia (Märss 1986), and Latvia (Märss 1986), is later than

the first record of *A. hedei* which, despite concerns over assignment to Actinoptergyii (Janvier 1996), and has not been disputed membership of total-group Osteichthyes. Indeed, some of the evidence on which *Andreolepis* has been assigned to Actinopterygii can be called into question on the basis of the discovery and phylogenetic position of *Meemania*, in which a ganoine-like tissue appears to be present (Zhu et al. 2006). Thus, it is possible that *Andreolepis* presents only osteichthyan symplesiomorphies and that on the basis of the available evidence, it is better assigned to stem-Osteichthyes.

Dating the earliest record of successive sister taxa is complicated by long-standing debate over the relative phylogenetic position and monophyly of the various groups. Acanthodii is generally considered the sister group of Osteichthyes and its earliest record is from the Ashgill of Siberia (Karatajuté-Talimaa and Predtechenskyj 1995). Chondrichthyes is generally accepted as the succeeding sister taxon, the oldest record for which is Caradoc (Sansom et al. 1996), although precious few characters bind these remains to the stem of Chondrichthyes (Donoghue et al. 2003). The oldest placoderms are undescribed forms from the Wenlock of China (Janvier 1996) and Vietnam (Thanh et al. 1997).

Conservative assessments of the age of the earliest remains readily assignable to the actinopterygian and sarcopterygian total groups are in close approximation (421.75 MYA ± 0 Myr vs. 418.7 MYA ± 2.6 Myr, respectively). However, phylogenetic assignment of these microremains rests on 1 or 2 equivocal synapomorphies, and this is insufficient evidence on which to justify constraining molecular clock analyses. Thus, we argue that it is best to rely on the evidence of better-known and better phylogenetically constrained *Psarolepis* to provide a minimum constraint on the divergence of sarcopterygian and actinopterygian lineages. The firmest age dating on the earliest record of *Psarolepis* (based on biostratigraphic correlation) is 418.7 MYA ± 2.7 Myr. Thus, a minimum constraint on the divergence of crown-Osteichthyes should be quoted as 416.0 MYA. A soft maximum constraint could be provided by the age of the earliest record of *A. hedei*, dated at 421.75 MYA.

Fruit fly–Mosquito

This divergence event represents the splitting of Brachycera and Culicomorpha lineages.

The oldest representative of Culicomorpha is *Aenne triassica* from the Late Triassic (Rhaetic) Cotham Member of the Lilstock Formation, Penarth Group at Aust Cliff, near Bristol England (Krzeminski and Jarzembowski 1999). Although this displays chironomid synapomorphies, only the distal half of a wing is preserved. The base of the Cotham Member coincides with the base of SA5n.3r that equates to the E23r reverse polarity magnetozone of the Newark Supergroup (Hounslow et al. 2004), the base of which is estimated at 202 MYA ± 1 Myr on the basis of volcanics in the upper part of the underlying E23 normal-polarity magnetozone (Gradstein et al. 2004). Hounslow et al. (2004) argue that the whole of the Cotham Member equates to the E23r magnetozone, the duration of which is beyond stratigraphic resolution in the current timescale (Gradstein et al. 2004). Thus, we conclude the age of the first possible representative of Culicomorpha to be 202 MYA ± 1 Myr.

The next oldest record is *Aenne liasina* from the Lower Toarcian (Lower Jurassic) of Grimmen, NE Germany (Ansorge 1994), followed by an abundance of other Culicomorpha records in the Lower and Middle Jurassic (Grimaldi and Engel 2005).

The oldest documented representatives of Brachycera are from the Upper Triassic Dan River Group of Virginia (Krzeminski 1992; Krzeminski W and Krzeminski E 2003), although their assignment rests upon precious few and largely inconsistent venation characters (Grimaldi and Engel 2005). There remains an older record of Brachycera, *Gallia alsatica*, from the Grès-à-Voltzia Formation of Arzviller, northeast France (recognized on the basis of the following apomorphies: cell *m3* narrowed distally and Cu and A_1 terminating in one point at the wing margin) (Krzeminski and Evenhuis 2000; Krzeminski W and Krzeminski E 2003). The Grès à Meules facies of the Grès-a-Voltzia Formation, from which these remains are derived, has been dated as Lower Anisian (Papier and Grauvogel-Stamm 1995; Papier et al. 2005), although the evidence on which this is based was not presented. The top of the Lower Anisian is dated as 240.5 MYA, based on proportional scaling of major conodont zones (Ogg 2004) from a graphic correlation global composite standard (Sweet and Bergström 1986), from which an error of ±2.0 Myr is derived. Otherwise, there are convincing records from the Early Jurassic, including the Black Ven Marls (Sinemurian) at the cliff of Stonebarrow Hill near Charmouth, Dorest, England (*turneri-obtusum* zone), 194.1–192.0 MYA (Ansorge and Krzeminski 1994), and the Lower Toarcian (*Harpoceras falciferum* zone) of Dobbertin, Mecklenburg, Germany, 182.7–181.2 MYA (Krzeminski and Ansorge 2000).

The oldest representatives of the clade comprising Culicomorpha and Brachycera are members of grauvogeliid Psychodomorpha, specifically, *Grauvogelia arzvilleriana* from the middle Triassic Grès-a-Voltzia Formation of France (Krzeminski et al. 1994). Crucially, this is neither the most primitive crown-dipteran nor the oldest known total-group dipteran, but the oldest record that falls within the clade circumscribed by *Anopheles* and *Drosophila*, following the phylogenetic scheme presented in Grimaldi and Engel (2005).

Thus, on the record of *G. arzvilleriana* (Krzeminski et al. 1994), its coincidence with the earliest (albeit undocumented) record of Brachycera (Krzeminski and Evenhuis 2000; Krzeminski W and Krzeminski E 2003), and the phylogenetic hypothesis of Grimaldi and Engel (2005), the minimum date for the divergence of the lineages leading to *Drosophila melanogaster* and *Anopheles gambiae*, is 238.5 MYA.

A soft maximum constraint is provided by the insect fauna of Boskovice Furrow, Oboro, Moravia, Czech Republic. A huge diversity of insects has been described from this deposit which is the single most important Paleozoic insect locality in the World (Grimaldi and Engel 2005). No members of the clade circumscribed by Brachycera and Culicomorpha have been described from here or from older deposits. The Oboro fauna has been dated at Early Artinskian (Kukalová-Peck and Willmann 1990) and Sakmarian (Zajic 2000), although only the latter has been substantiated. The base of the Sakmarian has been dated at

294.6 MYA ± 0.8 Myr (Gradstein et al. 2004). Thus, the soft maximum constraint on the divergence of Brachycera and Culicomorpha can be taken as 295.4 MYA.

Honeybee–Fruit fly, Mosquito

This divergence event represents the splitting of the Hymenoptera and Panorpoidea lineages.

The earliest recognized Panorpoidea are the mecopteroids that are interpreted as stem Panorpoidea (or panorpoideans) and are known from records as early as the Permian, the very oldest of which are members of Kaltanidae, interpreted as stem panorpoideans (Willmann 1989).

The earliest recognized Hymenoptera are from the Middle Triassic of Central Asia (Rasnitsyn 1964, 1969), and the Upper Triassic of Australia (Riek 1955), and Africa (Schlüter 2000), all of which are referred to the Archexyelinae within Xyelidae. This difference in first records of Hymenoptera and Panorpoidea has led to the suggestion that putative stem-panorpoideans from the Permian are unified on symplesiomorphies of Panorpoidea + Hymenoptera (Grimaldi and Engel 2005). Thus, the minimum date for the divergence of Hymenoptera and Panorpoidea would be based on the earliest records from the Middle Triassic Madygen Formation of Central Asia (Rasnitsyn 1964, 1969) that is dated as Ladinian and/or Carnian on the basis of palynological data (Dobruskina 1980, 1982). In the absence of greater biostratigraphic control, it is possible only to derive a minimum date from the base of the Norian (base Norian 216.5 MYA ± 2.0 Myr; Ogg 2004) in the absence of better stratigraphic constraint. Thus, a minimum constraining date would be 214.5 MYA.

However, this inconsistency is predicated upon the assumption that Hymenoptera and Panorpoidea are sister taxa, a view that is not universally accepted. Rasnitsyn (2002a), for instance, maintains that Hymenoptera and Panorpoidea are more remotely related, the closest relatives of Panorpoidea being Neuropteroidea and Coleopteroidea (united on modified ovipositor gonapophyses 9 [=dorsal valvula] lost, and the intromittant function transferred to gonocoxa 9 + gonostylus 9 [=Valvula 3]). In this view, Panorpoidea + Neuropteroidea + Coleopteroidea diverged from the lineage leading to Hymenoptera within the paraphyletic order Palaeomanteida, at a time approximating to the Carboniferous/Permian boundary. Unfortunately, the systematics of this group are poorly resolved and it is unclear which represent the earliest members of the either lineages ultimately leading to Panorpiodea and Hymenoptera. The best estimate must be provided by the earliest member of the clade Panorpoidea + Neuropteroidea + Coleopteroidea, but note should be taken of the fact that this date is likely to be extended in light of systematic revision of Palaeomanteida. The oldest known member of Coleoptera is *Pseudomerope gallei*, from the Asselian (299–294.6 MYA ± 0.8 Myr) (Lower Permian) of Říčany, Czech Republic (Kukalová-Peck and Willmann 1990), though the basis of this age assignment is not clear.

The oldest recorded member of this clade appears to be an undescribed member of Coleopteroidea from the Middle Carboniferous Mazon Creek fauna of Illinois, USA (Rasnitsyn 2002b). The Mazon Creek fauna is derived from the Francis Creek Member of the Carbondale Formation in NE Illinois. The Francis Creek Shale Member has been dated as middle Desmoinesian and middle Westphalian D age on the basis of both palynological and paleobotanical data (Pfefferkorn 1979; Wagner 1984; Peppers 1996). This equates to the upper part of the Moscovian stage, the top of which has been dated at 306.5 MYA ± 1.0 Myr on the basis of a graphically correlated composite standard calibrated using radiometric dates (Davydov et al. 2004). The top of the Westphalian D is slightly older at 307.2 MYA (Davydov et al. 2004). Thus, within the phylogenetic milieu that posits that Hymenoptera are not immediate sister taxa (Rasnitsyn 2002a), the minimum date on the divergence of these 2 clades is 307.2 MYA.

In conclusion, however, it must be emphasized that Hymenoptera and Panorpoidea are conventionally viewed as sister taxa. Nevertheless, a minimum date for divergence of 214.5 MYA, post dates the minimum date of is 238.5 MYA for the divergence of the lineages leading to *D. melanogaster* and *A. gambiae*. *Apis mellifera* falls outside this clade and so in the absence of better constraint over the interrelationships of Diptera and Hymenoptera, a minimum date for their divergence can be taken as 238.5 MYA. A soft maximum constraint can be provided by the less likely hypothesis that Panorpoidea are more closely related to Neuropteroidea and Coleopteroidea, using the oldest record of this clade, described above as 307.2 MYA.

Bird, Mammal, Toad, Fish–Fruit Fly, Mosquito, Honeybee

This divergence event represents the splitting of crown-Bilateria and the divergence of deuterostome and protostome lineages.

The oldest possible record of chordates dates from the Lower Cambrian Yu'anshan Member of the Heilinpu Formation (Chengjiang Biota) of Yunnan Province, South China, from which the remains of putative tunicates (Shu et al. 2001a; Chen et al. 2003), cephalochordates (Chen et al. 1995; Shu et al. 1996), and even vertebrates (Shu et al. 1999; Holland and Chen 2001; Hou et al. 2002; Mallatt and Chen 2003; Shu 2003; Shu et al. 2003a) have been described. The problem with many of these records is that the characters defining clades at this deep level within phylogeny are largely cytological or embryological—not the kinds of characters that are preserved under even the most exceptional circumstances (Donoghue and Purnell 2005). Furthermore, both the living and fossil organisms are entirely soft-bodied and so precious few characters are preserved. And of these, many have been resolved to be deuterostome symplesiomorphies, rather than chordate or vertebrate synapomorphies, with the recognition that echinoderms and hemichordates are sister taxa (Gee 2001; Donoghue and Purnell 2005). Thus, *Yunnanozoon* and *Haikouella*, thought by some to represent early craniates (Holland and Chen 2001; Mallatt and Chen 2003), are interpreted by others as basal (perhaps even stem-) deuterostomes (Budd and Jensen 2000; Shu et al. 2001b; Donoghue et al. 2003; Shu 2003; Shu and Conway Morris 2003; Shu et al. 2003b, 2004). Records of early tunicates (Shu et al. 2001a; Chen et al. 2003) have been questioned and the earliest unequivocal remains are Triassic in age (Varol and Houghton 1996). The putative vertebrates *Zhongjianichthys*, *Myllokunmingia*, and *Haikouichthys*

(Shu et al. 1999, 2003a; Hou et al. 2002; Shu 2003) exhibit convincing vertebrate apomorphies, and these provide the best constraint on the minimum date of divergence of vertebrates and chordates. There are contemporaneous records of more primitive deuterostomes, with the identification of vetulicystids as stem-echinoderms (Shu et al. 2004) and vetulicolians as stem-deuterostomes (Shu et al. 2001b, 2004; Shu 2003), although the veracity of the phylogenetic assignments of these taxa is a matter of some controversy (Lacalli 2002; Smith 2004; Briggs et al. 2005). Earlier records of possible deuterostomes include *Arkarua* from among the enigmatic ediaracan biota (Gehling 1987). Although support for the identification of *Arkarua* as an echinoderm has found support from embryological homologies (Mooi 2001), all rests ultimately upon the presence of pentameral symmetry that is not enough to rest an extension of tens of millions of years to a minimum date for divergence of deuterostomes and Bilateria upon. Thus, the vertebrates *Zhongjianichthys*, *Myllokunmingia*, and *Haikouichthys* (Shu et al. 1999, 2003a; Hou et al. 2002; Shu 2003) provide the best evidence for the minimum date of divergence of deuterostomes.

The earliest evidence for the origin of arthropods is *Rusophycus*-like trace fossils from the Upper Nemakit-Daldynian (early Tommotian) of Mongolia (Crimes 1987; Budd and Jensen 2003). However, there are still older representatives of the protostome lineage, further constraining the time of divergence of the Human and fruit fly genomes, as well as the genomes of all integral taxa. The oldest of these is probably the mollusc *Latouchella* from the middle *Purella* Biozone, Nemakit-Daldynian, of Siberia (Khomentovsky et al. 1990; Budd and Jensen 2003). There are a number of candidate crown-bilaterians among the ediacaran biota, among which a molluscan affinity for *Kimberella* has been most cogently argued (Fedonkin and Waggoner 1997). However, the evidence has not withstood scrutiny (Budd and Jensen 2000) and it is certainly insufficient to justify its use as a constraint on molecular clock analyses of metazoan evolution.

Thus, the minimum constraint on the divergence of crown-Bilateria is provided by the vertebrates *Zhongjianichthys*, *Myllokunmingia*, and *Haikouichthys*—the minimum age of the Yu'anshan Member of the Heilinpu Formation, and the age of the first appearance of *Latouchella*—which can be best constrained by the age of the top of the Nemakit-Daldynian.

The age of the Chengjiang biota remains equivocal because, although its local stratigraphic assignment to the *Eoredlichia wutingaspis* Biozone is well constrained and long established (Hou et al. 2004), how this correlates to better dated sections is not clear, not least because the fauna is largely endemic. The Heilinpu Formation belongs to the Qiongzhu stage that is considered to be Atdabanian in age. Thus, a minimum constraint may be provided by the age of the top of the Atdabanian, for which a 518.5 MYA is provided in the latest timescale (Shergold and Cooper 2004). It should be noted, however, that this estimate is stratigraphically, relatively remote from the nearest geochronological-derived date, and contingent upon the questionable conclusion that the Qiongzhu and Atdabanian are time equivalent.

The boundary between the Nemakit-Daldynian and the succeeding Tommotian stage remains equivocal and so a more reliable minimum constraint might be provided by the current best estimate for the base of the Tommotian that is 531.5 MYA (Shergold and Cooper 2004). Thus, on the basis of the available paleontological, stratigraphic, and chronological data, the best minimum constraint for the divergence of crown-Bilateria is 531.5 MYA.

Providing soft maximum bounds on the timing of crown-bilaterian divergence is extremely contentious. Nevertheless, following the same criteria used to provide constraints on other divergence events, it is possible to constrain the timing of crown-bilaterian divergence on the occurrence of older lagerstätten that preserve only records of earlier branching lineages. Inevitably, these records are represented by the Ediacaran faunas, the interpretation of which is extremely contentious, though there is increasing agreement that crown-bilaterians are not represented among them (Budd and Jensen 2000; Shu et al. 2006). Thus, the youngest, most completely sampled Ediacaran assemblage may be used to provide the maximum constraint on the divergence of crown-Bilateria. This is the Doushantuo Formation that provides a sampling of Ediacaran diversity in a number of facies and through a number of modes of exceptional preservation (Yuan et al. 2002; Xiao et al. 2005); although a number of candidate bilaterians have been described from this deposit (Chen et al. 2000, 2002, 2004a, 2004b), these have not withstood scrutiny (Xiao et al. 2000; Bengtson 2003; Bengtson and Budd 2004; Raff et al. 2006; Donoghue et al. 2006; Hagadorn et al. 2006). The top of the Doushantuo Formation has been dated as 551.1 MYA ± 0.7 Myr (Condon et al. 2005). Thus, a soft maximum constraint on the divergence of crown-Bilateria may be taken as 551.8 MYA.

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