Chapter 10

The origin and early evolution of chordates: molecular clocks and the fossil record

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ABSTRACT

Evolutionary biology abounds with theories and scenarios for the origins of the major chordate clades but little attempt has been made to constrain knowledge over the dating of these evolutionary events. The fossil record of early chordates, including stem-gnathostomes and basal crown-gnathostomes, as well as the sister-clade Ambulacraria (Hemichordata plus Echinodermata), is critically re-evaluated. This is achieved through both qualitative and quantitative assessment of the fit of phylogenetic hypotheses to stratigraphic range data, and through assessment of the internal consistency of stratigraphic range data. The results suggest that the fossil record of early chordates is of variable quality; the fossil record of basal chordates appears to be a poor reflection of their evolutionary history, while the fossil record of many stem-gnathostomes, such as conodonts and heterostracans, appears to be very good, albeit poorly understood in places. Thus, palaeontological data provide little constraint on the origin of chordates, craniates, and vertebrates, other than to indicate that these clades were established by 530 Ma. The origin of total-group Gnathostomata has a well-supported fossil estimate of 495 Ma, a date which falls within the error calculations of published molecular clock estimates. The origin of crown-gnathostomes is dated at 457 Ma using the fossil record, with a confidence interval extending to 463 Ma, implying an incomplete record; this lies just outside molecular estimates (e.g. 528 Ma ± 56.4 myr). Finally, the fossil record suggests the divergence of actinopterygians and sarcopterygians at 425 Ma, with a very narrow confidence interval (+ 580 Ka) and falls within molecular estimates (450 Ma ± 35.5 myr). Thus, where internal assessments of palaeontological data imply a good record there is correlation with molecular clock estimates, and where these assessments suggest a poor record there is poor correlation. Where correlation occurs we may assume that our estimates are a good reflection of the true time of divergence of the various clades, and where there is conflict we must assume nothing. We note that even where corroborarion between datasets occurs, error bars on divergence times remain too coarse to attempt correlation to evolutionary events in other clades, and extrinsic events in Earth history.

The data

The nearest living relatives of the巡航类 chordates are a clade comprising two of the most plesiomorphic groups that has historically been placed within the tunicates and echinoderms. The next most closely related vertebrates, the living jawed vertebrates, and the two most closely related clades are one of the two most closely related clades are one of the two most closely related clades. These taxa are phylogenetically possible to produce a complete phylogeny without recourse to molecular or fossil calibration. However, the origin of the taxon that includes these taxa is not well understood, leading to the classification of the phylum Chordata. For instance, the classification of the phylum Chordata

The problem

It is of course anthropocentric bias, but the nature of the evolutionary and environmental events surrounding the origin and early evolution of the phylum Chordata
are some of the most extensively researched problems in evolutionary biology. Theories that have sought to account for these events are contingent upon shifts in calibration of the geological timescale, a fossil record that is dynamic both in terms of new discoveries and reinterpretation of the phylogenetic affinities of old finds and, more recently, the introduction of molecular clock estimates for the times of divergence of living clades. It is therefore not surprising that many such hypotheses have fallen purely because events once thought to be coeval are revealed not to be so. But with so many lines of evidence, many of which are independent, there remains the possibility that conflict may give way to consilience, rather than merely to compromise. Recent advances have resulted in a considerable fleshing out of the early fossil record of chordates (Sansom et al. 2001; M.P. Smith et al. 2001, 2002), the geological timescale is now more finely calibrated than at any time in the past (e.g. Remane 2000), and there is an ever increasing database of molecular sequences for analysing evolutionary relationships and sampling for molecular clock analyses. With these developments, understanding the events surrounding the origin and early evolution of the chordate phylum may now prove more tractable than at any time previously.

The data

The nearest living relatives of the chordates are the echinoderms and hemichordates and, together, these three phyla comprise the Deuterostomia. Living invertebrate chordates are a very depauperate group in comparison with their vertebrate relatives, comprising two or three groups depending upon how the Vertebrata are defined. The most plesiomorphic groups are the tunicates and cephalochordates, and although there has historically been a great deal of prevarication surrounding their interrelationships, the tunicates are now widely recognized as the most basal group of living chordates. The next most inclusive clade, Craniata, includes only the hagfishes in addition to the vertebrates, which are in turn composed of the lampreys plus the Gnathostomata (living jawed vertebrates). Gnathostomes, in turn, are composed of chondrichthians, and the two most derived groups, the actinopterygians and sarcopterygians, which includes the lineage leading to tetrapods.

These taxonomic groups are defined solely on the basis of living taxa, and so it is possible to provide molecular estimates for the divergence of the various groups without recourse to the fossil record for anything other than internal and/or external calibration. However, the divergence of the various lineages does not equate to the origin of the taxonomic groups, at least not in the sense that most biologists understand these taxa. This is because most of these groups also include fossil taxa, with varying degrees of taxonomic diversity and disparity, which are part of the lineage leading to the crown-group of living taxa, but do not possess the full suite of anatomical characteristics necessary for inclusion within the crown-group (Jefferies 1979). For instance, the extinct osteostracans are a group of jawless vertebrates that share a number of derived characters with gnathostomes that they do not share with lampreys. Hence, osteostracans are resolved as more closely related to gnathostomes than lampreys and represent part of the lineage leading to gnathostomes after its divergence from that last common ancestor shared with lampreys. However, since they lack jaws, osteostracans cannot be considered part of the group ‘Gnathostomata’ as perceived by most biologists. Current hypotheses of early vertebrate relationships
tenuous and limiting interpretations. Many phylogenetic theory identify the still poorly known extraxial rather than the lampry rays, flooring plating, and tissues akin to the edrioasteroids Mooy 2001; Mooi and Arkansas is the sister-group to the echinoderm stem-group. We should remember that the assumption of a tree-like structure works would lead to great uncertainty. We will discuss the evolutionary history of echinoderms in more detail later (Mooi 1988a,b, 1990).

The fossil record of chordates and their near relatives

Echinoderms

The earliest putative echinoderms are both Neoproterozoic in age. Subsequent to its description, Tribarchidium (Glaessner and Wade 1966) has generally been excluded from contention as an echinoderm (e.g. Wills and Sepkoski 1993), but debate concerning the affinities of Arkarua (Gehling 1987) continues. Budd and Jensen (2000) have argued that data in support of echinoderm affinity for the latter taxon are

Hemichordates

The early fossil record extends back to the late Archaean and fishless Cambrian. The discussion is of Yunnanozoon (Arduini et al. 1996a), an assumed original and most proximate ancestor to both the chordates and the echinoderms (e.g. Dzik 1995, 1999; Chatterton 1996a), whilst the discovery of craniane (Chen et al. 1996b), and jawless vertebrates, like the Cheung 1996b).
tenuous and limited exclusively to the presence of pentameral symmetry. More recent interpretations of echinoderm skeletal homologies following the extraxial-axial theory identify many more echinoderm synapomorphies and synapomorphies in the still poorly known anatomy of Arkarua. These include a body wall dominated by extraxial rather than axial components, upwardly-oriented perforate extraxial and axial rays, flooring plates that follow the ocular plate rule, and a disc-shaped morphology akin to the edrioasteroids (David and Mooi 1998; Mooi and David 1997, 1998; Mooi 2001; Mooi pers. comm. 2002). The logical extension of this argument is that Arkarua is the sister-taxon to all other echinoderms, representing the only member of the echinoderm total-group to lack a stereom skeleton plesiomorphically. However, it should be remembered that all identified homologies are contingent upon the a priori assumption of an echinoderm affinity for Arkarua and alternative phylogenetic frameworks would lead to a very different interpretation of homologies. Thus, although we will discuss the implications of a Neoproterozoic echinoderm record for the evolutionary history of chordates, this record should not be considered beyond reproach.

Echinoderms are well represented amongst Early Cambrian faunas (see e.g. Smith 1988a,b, 1990), but the precise affinity of these taxa remains the subject of wide-ranging debate. The helicoplacoids are generally considered stem-group echinoderms, slightly more derived than Arkarua, but the phylogenetic position of Camptostroma, the edrioasteroids, and the carpoids remains contentious, with some authors placing them in stem-echinoderm positions, and others resolving them as members of the echinoderm crown-group; see Smith (1984, 1988a,b, 1990), Sumrall (1997) and David and Mooi (1999; Mooi and David 1998; David et al. 2000) for the different arguments, and Mooi (2001) for a compilation of trees reflecting the different hypotheses.

**Hemichordates**

The early fossil record of hemichordates is limited in large part to the pterobranchs and extends back to the Middle Cambrian (Bengtson and Urbanek 1986; Durman and Sennikov 1993); the record of enteropneusts does not extend beyond the Jurassic (Arduini et al. 1981). These data are widely accepted, but the earliest possible record is of Yunnanozoon from the Lower Cambrian Chengjiang Lagerstätten of China. The original and most valid interpretation of this organism to date is as a metazoan of unknown affinity (Hou et al. 1991). Yunnanozoon has subsequently been described both as a chordate (Chen et al. 1995; Dzik 1993) and as a hemichordate (Shu et al. 1996a), whilst the suspiciously similar Haikouella has also been described as a ctenostome (Chen et al. 1999). The mélange of characters exhibited by Yunnanozoon (e.g. Dzik 1995) may indicate a more appropriate placement in the deuterostome stem-group.

**Chordates**

Fossil representatives have been claimed for all living groups of invertebrate chordates and jawless vertebrates as far back as the Early Cambrian. Putative fossil tunicates include Cheungkongella (Shu et al. 2001a), *Palaeobotryllus* (Müller 1977), and Peltocystis (Jeffries et al. 1996). Putative acraniate chordates include Lagynocystis (Jeffries 1973), Pikaia (Conway Morris 1979), Yunnanozoon (Chen et al. 1995;
Dzik (1995), and Cathaymyrus (Shu et al. 1996b). Possible fossil representatives or close relatives of the living jawless vertebrates include the Cambrian taxa Haikouella (Chen et al. 1999; but see above), Myllokunmingia and Haikouichthys (Shu et al. 1999), and the Carboniferous taxa Gilpichthys and Pipiscius (Bardack and Richardson 1977), Mayomyzon (Bardack and Zangerl 1968, 1971), Myxinikela (Bardack 1991, 1998), and Hardistiella (Janvier and Lund 1983; Lund and Janvier 1986), as well as a number of mitrates such as Mitrocystites (Jeffries 1967) and Placocystites (Jeffries and Lewis 1978).

In addition, there are a wide variety of fossil jawless vertebrates characterized by an extensively developed dermal 'armour' and historically grouped together as the 'ostracoderms'. These include the anaspid, galeaspids, heterostracans, osteostracans, and thelodonts (see Janvier 1996b for an introduction to these various groups). Amongst the jawed vertebrates, there are also a number of large groups that have no living representatives, principally including the placoderms and acanthodians. There is also a swath of basal chondrichthians, actinopterygians, and sarcopterygians that belie the apparent disparity of their living relatives.

The phylogenetic relationships of living and extinct chordates and their near relatives

To compare palaeontological and molecular estimates for the time of divergence of the various chordate clades it is necessary to resolve the phylogenetic relationships of the living and fossil groups of chordates and their near relatives; palaeontological estimates can then be provided through calibration of the resulting phylogeny to the stratigraphic occurrence of the various groups within the geological timescale.

The calcichordate–stylophoran problem

No discussion of early chordate evolution would be complete without a consideration of the 'calcichordates'. Jeffries (1967 et seq.) identifies an extinct group of calcite-plated invertebrates, otherwise interpreted as basal echinoderms (Stylophora; e.g. Ulbaghs 1968; Paul and Smith 1984), as paraphyletic suites of lineages that interleave the stems of extant echinoderms, cephalochordates, tunicates, and vertebrates. This theory has been criticized on many grounds. Amongst the most substantive of these, independent phylogenetic analyses resolve tunicates as basal chordates (Garcia-Fernández and Holland 1994) rather than as the sister-group to the vertebrates, which is a requirement of the 'calcichordate' hypothesis (Jeffries 1986). Furthermore, independent phylogenetic analyses (Peterson 1995) recognize that the corunite and mitrate 'calcichordates' share a number of potential homologies that may only be rejected by weighting other characters that are deemed on the basis of the calcichordate theory to be of greater phylogenetic significance (Ruta 1999). This appears to preclude not only the calcichordate theory, but also Gee's compromise hypothesis that the 'calcichordates' are a paraphyletic ensemble of basal deuterostomes, some of which are more closely related to one or more phyla, than are others (Gee 2001; although it does not preclude the possibility that they are basal deuterostomes). Thus, the stylophorans are not germane to understanding the timing of chordate diversification and we will not discuss them further.

Morphological

The interrelationships controversy since the relative relationship of extinct, possible solutions have been inferred by far application of cyclobranchial for both hypotheses.

The hypothesis of early chordate divergences estimates of divergence, the analysis underlines groups of investigation. Chengjiang Launched Figure 10.2 and

Molecular analysis

In contrast to the resolution of chordates of incomplete resolution. (Suzuki et al. 1999), vocal support for this hypothesis. Similarly, small sample size the living jawed vertebrates support for molecular clock analysis of RNA. Mallatt and Sepkoski partitioned interordinal incompleteness for both hypotheses.

Resolution of the phylogenetic understanding of chordates is currently limited. However, both hypotheses are intermediate taxa, the fossil record is too fragmentary to detect a difference between the two. The phylogenetic relationships among chordate divergences are not yet resolved, as inferred from molecular clocks.
Morphological analysis

The interrelationships of both living and fossil chordates have been the subject of controversy since the origin of systematic classification. Much debate has centred on the relative relationships of the living jawless vertebrates, the hagfishes and lampreys, to living jawed vertebrates, and the implications that this has for the interrelationships of extinct groups of jawless vertebrates and invertebrate chordates. All three possible solutions to the problem of hagfish–lamprey–jawed vertebrate interrelationships have been proposed, but of these, cyclostome monophyly (hagfish, lamprey jawed vertebrate) and cyclostome paraphyly (hagfish, lamprey jawed vertebrate) have received by far the most attention. Although morphological data were formerly interpreted to support cyclostome monophyly (e.g., Stensiö 1927, 1968; Yalden 1983), the application of phylogenetic systematics to the same dataset led to a revised interpretation of cyclostome paraphyly (Løvtrup 1977; Janvier 1996a, 1981; Hardisty 1982; Forey 1984), a view that is still defended by morphologists (e.g., Janvier 1998; Donoghue et al. 2000; Donoghue and Smith 2001). We will consider the implications of both hypotheses in assessing the completeness of the chordate fossil record.

The hypothesis of relationships that we have adopted to provide palaeontological estimates of divergence times for the various chordate clades is a development of the analysis undertaken by Donoghue et al. (2000), to include the recently discovered groups of invertebrate chordates and basal vertebrates from the Lower Cambrian Chengjiang Lagerstätte. The results of this extended analysis are presented in Figure 10.2 and the codings for additional taxa are included in Appendix 10.1.

Molecular analysis

In contrast to morphological datasets, analyses of molecular datasets universally resolve the living jawless vertebrates as monophyletic. Although phylogenetic analysis of incomplete mitochondrial datasets resolved hagfishes and lampreys as paraphyletic (Suzuki et al. 1995), analysis of the entire mitochondrial genome provides unequivocal support for the monophyly of hagfishes and lampreys (Delarbret et al. 2002). Similarly, small datasets of nuclear DNA have provided support for the paraphyly of the living jawless vertebrates (Suzuki et al. 1995), but larger datasets provide strong support for monophyly (Goodman et al. 1987; Kuraku et al. 1999; Hedges 2001). Analysis of RNA also strongly supports cyclostome monophyly (Stock and Whitt 1992; Mallatt and Sullivan 1998; Mallatt et al. 2001), although analysis of RNA datasets partitioned into small- and large-subunit components provides conflicting support for both hypotheses (Zrzavý et al. 1998).

Resolution of the interrelationships of hagfishes and lampreys is critical to understanding character evolution at the origin of vertebrates and gnathostomes. However, both groups have a comparable fossil record, and there are no known intermediate taxa with a fundamentally earlier or later first appearance in the fossil record than sister and ingroup clades (the reality is quite the opposite). Thus, the difference between the two most likely resolutions of hagfish–lamprey–jawed vertebrate interrelationships is not critical to our understanding of the timing of early chordate diversification or the relationship between the fossil record and molecular clocks.
Stratigraphic analysis

Although stratigraphic range data are often taken at face value in attempts to calibrate molecular clocks and phylogenetic trees, and to provide palaeontological estimates for the divergence times, various techniques exist to provide confidence limits on the first and/or last appearance of taxa based upon the quality of the intervening record. The chief method for this is gap analysis which was originally developed to provide confidence limits on stratigraphic range data in local sections (Marshall 1990), but can be (Marshall 1990) and has been (Bleiwiss 1998) applied to global datasets provided that the distribution of fossil-bearing horizons within the observed range is random. The technique provides a means of determining limits of probability on how far outside the known stratigraphic range of a taxon the true first (and/or last) appearance might occur – this is proportional to the density with which the taxon has been found throughout its known stratigraphic range (Marshall 1990). It follows that the greater the number of horizons from which the taxon has been recorded, the less likely it is that the true range lies far beyond the limits of the known range, and vice versa. Gap analysis calculates, at a given level of confidence (e.g. 95 or 99 per cent), an interval within which the true end point (appearance or disappearance) of a stratigraphic range lies (Marshall 1990). At its simplest, the calculation assumes constant fossil recovery potential, but techniques have been developed to incorporate various forms of facies preservation (Marshall 1997).

We have calculated confidence limits for each of the major clades of jawed vertebrates as presented in Table 10.1.

Assessing confidence limits

Ghost lineages

Following the principle that all lineages have an evolutionary history, we consider when they diverged from each other. It is possible to infer the ranges of sister taxa from the range of its sister taxon, e.g. as calculated by Gauthier et al. (1988). This technique is useful when a clade is poorly sampled or unsampled, and can also provide useful limiting assumptions about the direction of evolution.

Table 10.1 Confidence limits

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sil n'</th>
<th>Ord n'</th>
<th>95 per cent confidence interval</th>
<th>99 per cent confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myxinoida</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Petromyzontida</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conodontia</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arandaspidia</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heterostraci</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anaspidia</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thelodontia</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galeaspidia</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osteostraci</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Placoderms</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chondrichthyans</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acanthodians</td>
<td>n'</td>
<td>n</td>
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<td></td>
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<tr>
<td>Actinopterygians</td>
<td>n'</td>
<td>n</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sarcopterygians</td>
<td>n'</td>
<td>n</td>
<td></td>
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</tbody>
</table>

*Sil n' is the number of confidence intervals.
*Ord n' is the number of 99 per cent confidence intervals.
*The fossil record observations are based on.
Table 10.1  Confidence intervals calculated on the basis of the internal relationships of the pleons included in the main analysis.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Base</th>
<th>Top</th>
<th>Sil P &gt; 0.95</th>
<th>Sil P &gt; 0.99</th>
<th>Ord n</th>
<th>Ord P &gt; 0.95</th>
<th>Ord P &gt; 0.99</th>
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<td>6080</td>
<td>30400</td>
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<td>Placoderms</td>
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<td>418</td>
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</table>

*Sil n* is the number of records within the interval Cambrian–Silurian, and ‘Sil P > 0.95’ and ‘Sil P > 0.99’ are 95 and 99 per cent confidence intervals on the first appearance of the pleon, respectively, based upon the Cambrian–Silurian interval.

*Ord n* is the number of records within the interval Cambrian–Ordovician, and ‘Ord P > 0.95’ and ‘Ord P > 0.99’ are 95 and 99 per cent confidence intervals on the first appearance of the pleon, respectively, based upon the Cambrian–Ordovician interval.

The fossil record of hagfishes and lampreys is limited to the Carboniferous and, as a result, the confidence interval calculations are based on their full stratigraphic range, rather than limited to the pre-Devonian as are the other calculations.

Incorporate variable recovery potential that may result, for example, from biases in facies preservation arising from changes in relative sea level (Holland 1995, 2000; Marshall 1997; Tavaré et al. 2002).

We have calculated 95 and 99 per cent confidence limits for the fossil record of each of the main groups of fossil and living vertebrate chordates and jawless and jawed vertebrates using the combined micro- and macrofossil record. The values are presented in Table 10.1 and are graphically expressed in Figure 10.3.

Assessing congruence between cladograms and stratigraphy

Ghost lineages and their conceptual efficacy

Following the principle that sister taxa are derived from common ancestors and, thus, have an evolutionary history that can be traced back to the point in time at which they diverged from their latest common ancestor, an assessment of the completeness of the fossil record of a taxon can be achieved through comparing the stratigraphic ranges of sister taxa. The inferred range extension of a taxon based on the longevity of its sister taxon is known as a ‘ghost lineage’ or ‘ghost range’, a concept introduced by Gauthier et al. (1988) and developed by Norell (1992) amongst others. The technique is useful because it provides a means of inferring the existence of unsampled or unsampleable taxa, but it relies upon a number of important and potentially limiting assumptions. First, it must be assumed that the cladogram is a faithful reflection of evolutionary relationships. Second, all the taxa in the cladogram must be...
monophyletic, since the inclusion of paraphyletic taxa (e.g. ancestors) will lead to an incorrect inference of a ghost lineage (Wagner 1998; Paul, Chapter 5).

Although many of the nodes in the tree presented in Figure 10.2 are relatively weakly supported, the overall structure of the tree is well supported. The second assumption is also justified in that taxa used in the analysis have been scrutinised through character analysis and all exhibit identifiable synapomorphies (e.g. Janvier 1996b). The results of this analysis indicate that although the fossil record of most groups of stem-gnathostomes does not begin until the Silurian, all have ghost ranges that extend a considerable way downwards into the Ordovician (Figure 10.4). This is surprising given the relatively reduced state of the fossil record in the earlier skeleton and...
surprising given that these organisms have an extensive mineralized component to their skeleton and, thus, might be expected to have a much better fossil record.

**Cladogram fit to stratigraphy**

Calibrating cladograms to time and inferring ghost lineages provides a useful visual assessment of the completeness of the fossil record. However, the rigour of this technique has been extended through the application of a number of metrics that assess different aspects of the relationship between tree structure and stratigraphic data. These include the Stratigraphic Consistency Index (SCI; Huelsenbeck 1994), which compares the number of stratigraphically consistent cladogram nodes to the total number of cladogram nodes. The Relative Completeness Index (RCI; Benton and Storrs 1994) attempts to measure the overall level of inconsistency in a tree by quantifying the ghost range implied as the difference between the age of origin of branches subtending sister taxa, divided by the observed range length, and expressed as a percentage. A third metric, the Gap Excess Ratio (GER; Wills 1999) combines aspects of both SCI and RCI, expressing the sum of inferred ghost lineages across a tree as a fraction of the total range of possible ghost lineage values based on a common stratigraphic dataset. Other metrics have been devised but they have not been widely applied, either
without reason (as in the case of the Manhattan Stratigraphic Measure (Siddall 1998), or because of concerns regarding their efficacy, such as Spearman Rank Correlation (SRC; Gauthier et al. 1988; Norell and Novacek 1992).

The SRC has been criticized regarding its appropriateness (Huelsenbeck 1994), its contingency upon temporal spacing (Benton and Storrs 1994; Hitchin and Benton 1996), and the procedural requirement of altering the cladogram before analysis (trees must be pruned for analysis and so more balanced trees must be pruned a priori precluding the full analysis; Huelsenbeck 1994). Neither are the SCI and RCI metrics free of potential artefact. The SCI is handicapped by tree balance such that only fully imbalanced trees can achieve the full theoretical range of values 0.00–1.00; perfectly balanced trees also have theoretical maximum SCI score of 1.00, but the minimum value achieved is 0.50 (Siddall 1996, 1997; Wills 1999). The SCI is also affected by the temporal distribution of first occurrences such that if they are all contemporaneous the SCI will equal 1.00, regardless of tree balance; if no first appearances are contemporaneous, the range of SCI is again contingent upon tree balance such that perfectly balanced trees will have a SCI of 0.50, while fully pruned trees yield the full range of SCI scores (Wills 1999). The effect of tree balance on the RCI is more complex. A perfect RCI score of 100 per cent is possible only if the first appearance of all taxa is contemporaneous and fully pruned trees fulfilling these stratigraphic requirements will always achieve this score. However, other topologies may not be able to achieve a perfect RCI score even if the component taxa meet these stratigraphic requirements (Wills 1999). The GER controls for the distribution of range data and is also sensitive to tree balance. However, by randomly reassigning the stratigraphic range data over the tree it is possible to assess whether stratigraphy–cladogram congruence is significantly better than random, while holding the potential biases (stratigraphy, taxon number, tree balance) constant (Wills 1999). Permutation tests can also be applied to SCI calculation and the degree to which these metrics deviate from random provides a measure of confidence in their significance (Wills 1999).

The SCI, RCI, and GER (as well as permutation tests for significance of these indices) were calculated for the overall tree and for the internal record of each of the plesions in the overall tree, using Ghosts 2.3 (Wills 1999) and the results are presented in Table 10.2. Dates for chronostratigraphic boundaries used in the stratigraphy file for the program were obtained from Tucker and McKerrow (1995), Gradstein and Ogg (1996), Saylor et al. (1998), Tucker et al. (1998), Cooper (1999), Encarnación et al. (1999), Knoll (2000), and Remane (2000). Internal relationships of the plesions used in the analysis are presented in Appendix 10.2; the full data matrix, as well as the associated stratigraphy files and the occurrence data on which the cladogram–stratigraphy correlation metrics are based, are available from the senior author upon request.

Results: internal assessment of the quality of the early chordate fossil record

The combined results of the analyses outlined above are presented in Figure 10.5 and imply that, overall, the fossil record of early chordates is much better than has been suggested previously. The SCI analysis indicates that approximately two-thirds of the cladogram nodes are consistent with stratigraphic data, and the RCI and GER analyses both reveal that the analyses of the relationships of chordate invertebrate clades to groups to groups and between the Earth in the (hagfishes). They are entirely soft-bodied slow. However, which possesses no anatomy. Again, offer conflicting evidence that our knowledge confidence the 346 kyr of the 532 kyr bracket of 532 resolution wi
The origin and early evolution of chordates

Table 10.2 Cladogram–stratigraphy metrics calculated using Ghosts (Wills 1999) for the plesions included in the main analysis based upon hypotheses of relationships included in the appendix

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>SCI</th>
<th>SCI sig</th>
<th>RCI</th>
<th>Gmin</th>
<th>Gmax</th>
<th>MIG</th>
<th>GER</th>
<th>GER sig</th>
</tr>
</thead>
<tbody>
<tr>
<td>Echinodermata</td>
<td>16</td>
<td>0.5</td>
<td>0.95</td>
<td>81.319555</td>
<td>349</td>
<td>1552</td>
<td>705</td>
<td>0.70407</td>
<td>0.975</td>
</tr>
<tr>
<td>Chordata</td>
<td>18</td>
<td>0.6875</td>
<td>0.99</td>
<td>94.803759</td>
<td>141</td>
<td>1569</td>
<td>282</td>
<td>0.901261</td>
<td>0.99</td>
</tr>
<tr>
<td>Conodontata</td>
<td>37</td>
<td>0.685714</td>
<td>0.99</td>
<td>65.305011</td>
<td>177</td>
<td>2358</td>
<td>437</td>
<td>0.779852</td>
<td>0.99</td>
</tr>
<tr>
<td>Anaspida</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>-33.333333</td>
<td>15</td>
<td>60</td>
<td>60</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Heterostraci</td>
<td>18</td>
<td>0.625</td>
<td>0.99</td>
<td>47.826867</td>
<td>67</td>
<td>965</td>
<td>132</td>
<td>0.927617</td>
<td>0.99</td>
</tr>
<tr>
<td>Thelodontida</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>48.076923</td>
<td>24</td>
<td>54</td>
<td>54</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Galeaspida</td>
<td>7</td>
<td>0.461538</td>
<td>0.8766</td>
<td>35.97561</td>
<td>33</td>
<td>346</td>
<td>105</td>
<td>0.769968</td>
<td>0.99</td>
</tr>
<tr>
<td>Osterostraci</td>
<td>25</td>
<td>0.5</td>
<td>0.435</td>
<td>63.186813</td>
<td>46</td>
<td>214</td>
<td>134</td>
<td>0.47619</td>
<td>0.94</td>
</tr>
<tr>
<td>Placodermi</td>
<td>22</td>
<td>0.55</td>
<td>0.713</td>
<td>61.977186</td>
<td>36</td>
<td>400</td>
<td>200</td>
<td>0.70896</td>
<td>0.99</td>
</tr>
<tr>
<td>Chondrichthyes</td>
<td>14</td>
<td>0.5</td>
<td>0.606</td>
<td>72.643375</td>
<td>140</td>
<td>552</td>
<td>415</td>
<td>0.332524</td>
<td>0.736</td>
</tr>
<tr>
<td>Acanthodii</td>
<td>8</td>
<td>0.5</td>
<td>0.525</td>
<td>66.924565</td>
<td>61</td>
<td>282</td>
<td>171</td>
<td>0.502262</td>
<td>0.75</td>
</tr>
<tr>
<td>Actinopterygi</td>
<td>15</td>
<td>0.230769</td>
<td>0.681</td>
<td>-97.321429</td>
<td>356</td>
<td>777</td>
<td>442</td>
<td>0.795724</td>
<td>0.99</td>
</tr>
<tr>
<td>Basal Synapsida</td>
<td>13</td>
<td>0.727273</td>
<td>0.975</td>
<td>80.96</td>
<td>61</td>
<td>462</td>
<td>107</td>
<td>0.868287</td>
<td>0.5</td>
</tr>
<tr>
<td>Basal Diapsida</td>
<td>8</td>
<td>0.83</td>
<td>1</td>
<td>40.3</td>
<td>61</td>
<td>241</td>
<td>74</td>
<td>0.927782</td>
<td>0.5</td>
</tr>
</tbody>
</table>

'\(n\)' is the number of terminal taxa that the metrics are based upon. 'SCI' is the Stratigraphic Consistency Index (Pielou 1974). 'SCI sig' is the significance that the SCI value is better than random. 'RCI' is the Relative Completeness Index (Benton and Storr 1994). 'Gmin' and 'Gmax' are the minimum and maximum possible summation of the temporal ranges of the terminal taxa included in the analysis based upon a rearrangement of the terminals such that they achieve best- and worst-possible fit to stratigraphy. 'MIG' is the Minimum Implied Gap based upon the given topology of relationships and stratigraphic data. 'GER' is the Gap Excess Ratio (Wills 1999) and 'GER sig' is the significance that the RCI and GER values are better than random. The basal synapsid and diapsid metrics were calculated as part of a study by Benton and colleagues, including Benton and Hitchin (1996), and further details can be found at the following url: <http://palaeo.gly.gla.ac.uk/cladestrat/ reptiles.html>.

\(a\) Based on the hypothesis of relationships from Modesto (1995, fig. 19A).
\(b\) Based on the hypothesis of relationships from de Braga and Reisz (1995, fig. 6).

analyses both indicate that the record is approximately complete. Permutation tests reveal that these values are not significantly worse than random \((P > 0.99)\). However, analyses of the stratigraphic data and their correlation to cladograms of the internal relationships of the operational taxa indicate that the quality of the record varies from group to group. For instance, the fossil record of the living jawless vertebrates and invertebrate chordates is so poor that at 95 per cent confidence the first appearance of these groups can only be constrained within an interval that predates the origin of the Earth in some groups (lampreys), and the origin of the universe in others (hagfishes). This is not an altogether surprising result given that these organisms are entirely soft-bodied and the chances of their preservation in the fossil record are very low. However, the same cannot be said for taxa more derived than lampreys, all of which possess a mineralized, and therefore readily fossilizable, component to their anatomy. Again, the fossil record of these groups is of variable quality and the metrics offer conflicting interpretations of the dataset. For instance, confidence limits suggest that our knowledge of the conodont fossil record is very mature; at 95 per cent confidence the first appearance of the group suggests that it lies within a bracket of 346 kyr of the first stratigraphic appearance, and at 99 per cent confidence, within a bracket of 532 kyr of this datum, both of which are beyond the limits of stratigraphic resolution within this interval.
The GER value is less supportive, but nevertheless indicates that the cladogram–stratigraphy correlation is close, within 0.77 of a tree constructed solely on the basis of stratigraphic order of appearance. However, the other cladogram–stratigraphy metrics suggest that the record is only moderately complete; the SCI indicates that only two-thirds of the cladogram nodes are stratigraphically consistent and the RCI suggests that the known record is only two-thirds complete. All values achieve 99 per cent confidence that they are no worse than random. Taking another example of the better groups, assessments of the heterostracan fossil record have also yielded conflicting results; at 95 per cent confidence, the bracket on first appearance is only 278 kyr, and 432 kyr at 99 per cent confidence. This compares well with the GER which indicates that cladogram–stratigraphy correlation is within 0.92 of a tree perfectly concordant to the stratigraphic data. However, the SCI and RCI metrics tell a very different story; less than two-thirds of cladogram nodes are stratigraphically consistent and the heterostracan fossil record represents less than half of the hypothesized evolutionary history of the group.

Although both examples show the same conflicting pattern between metrics, they probably result from two different artefacts in the datasets. Knowledge of the intrarelationships of conodonts is at a relatively immature stage and all existing schemes are based on significantly dated and are not a better method of dating the published ghost groups. Polytomies have thus, ghost ranges lower than minimum tracans have been used. G et al. 1991; J astronomy and stratigraphy correlation are depressed by Genetic analyses of correlation likely, based on a method of trees. GER value proposed is record than does not provide very well arising from relationships in both Conodonts via molecular studies, vertebrates, are often in record that exists for groups that mean that implied diverse, placoderms, provide importance of the correlation in that is at ≤0.5 for the is internally not at 95 per cent is random, although the same confidence values suggest to cladograms, although clad that correlated low corroborated for example, calculation is only 9 of the narrow interval of fossil record of would mean of conflicting results in a br Inverse correlation between placoderms and the understood, fossil records.
are based on stratophenetic analysis of the dataset. It is surprising, therefore, that there is not a better tree–stratigraphy correlation. However, in the process of converting the published phylogeny (Sweet 1988, and in Sweet and Donoghue 2001), some 'hard' polytomies have been converted to 'soft' polytomies for the purposes of analysis and, thus, ghost ranges have been artificially extended and statistical scores are artificially lower than might be expected. On the other hand, the intrarelationships of heterostracans have been analysed independently of stratigraphic data (Bleck 1984; Bleck et al. 1991; Janvier and Bleck 1993; Janvier 1996b) and although the cladogram–stratigraphy correlation of well-understood groups is good, the SCI and RCI metrics are depressed because many taxa are too poorly known to be included in phylogenetic analyses and have, thus, been placed in a soft polytomy in the most derived position likely, based on character distribution across existing trees. However, given the method of tree construction, it is likely that the short confidence interval and high GER value provide a better assessment of the completeness of the heterostracan fossil record than do the SCI and RCI metrics. In short, the fossil record of both groups is probably very complete but relatively poorly understood, the lack of understanding arising from poor quality data in heterostracans and from poorly resolved relationships in both groups (cf. Benton et al. 1999).

Conodons and heterostracans are important for providing constraints on molecular estimates for the divergence of the living jawless vertebrates and jawed vertebrates, and it is therefore a happy coincidence that they appear to possess a fossil record that exhibits internal consistency. Assessments of the quality of the record of groups that might constrain the divergence of crown-group jawed vertebrates suggest that implied divergence dates may be less reliable. Groups such as the osteostracans, placoderms, and chondrichthyans bracket this diversification event, and potentially provide important upper bounds on divergence timing. However, cladogram–stratigraphy correlation in these groups is poor, generally at a level of 50 per cent for the SCI, at ≤ 0.5 for the RCI (except placoderms which appear to have a fossil record that is internally more consistent), and with a GER = 0.3–0.5; SCI values do not pass a 95 per cent confidence test to determine whether they are not significantly worse than random, although GER and RCI values are generally no worse than random at the same confidence level. Positive correlation between high and low GER and SCI values suggests that poor cladogram–stratigraphy correlation does not arise solely from cladogram inaccuracy, which would normally produce an inverse correlation, although cladogram inaccuracy is possibly an important factor. It is more likely that correlated low GER and SCI values reflect a genuinely poor fossil record and this is corroborated by relatively long confidence intervals on stratigraphic occurrence data in, for example, chondrichthyans, which have a confidence bracket of 1.8 myr. However, this calculation is based on the compilation of Ordovician and Silurian occurrences, only 9 of the 67 of which are Ordovician, and these occurrences are limited to a narrow interval in the Caradoc (Harding Sandstone and its equivalents). Thus, the fossil record of this group appears to be particularly intermittent early on, and a reassessment of confidence limits on first appearance based upon the Ordovician record alone results in a bracket of over six million years. The same situation is true of thelodonts. Inverse correlation between low SCI (P > 0.95) and high GER (P < 0.95), as in the placoderms and actinopterygians, probably results from a good, but poorly understood, fossil record. The fossil record of placoderms is rich, but attempts to resolve the
relationships of the group have thus far proved only variably successful (e.g. Goujet and Young 1995; Goujet 2001). The fossil record of actinopterygians is more gap than record, hence the strongly negative RCI ($P < 0.99$), but the sum of implied ghost ranges is very low compared with the maximum, and very close to the minimum possible by optimizing stratigraphic fit/discordance to the tree (GER 0.79; same $P$ as for RCI).

**Problems with assessing the quality of the record**

There are two potential problems with regard to this analysis, one relating to the analysis itself, and the second relating to potential artefact in the dataset. First, there is a very poor correlation, absolutely and proportionally, between the confidence intervals on each of the groups, which are derived from internal assessments of the quality of the record within each of the plesions, and the inferred ghost lineages, which are based on analysis at plesion level (compare Figures 10.4 and 10.5). Paul (1998) suggested that this may be an appropriate means of identifying ghost lineages that are an artefact of cladistic methodology, rather than reflecting a true gap in the temporal record of a lineage. We outlined earlier why we think that our analysis is not subject to this kind of artefact (plesions are monophyletic).

The second problem relates to the dataset and has implications for the analysis of confidence intervals and, in turn, their degree of fit to ghost lineages. The calculation of classic confidence intervals assumes that fossil recovery potential is random. Testing this assumption is very difficult when dealing with global compilations of palaeontological data and probably represents the greatest limitation upon the extension of confidence intervals to global datasets. Nevertheless, there is some evidence to suggest that there are two significant biases in the dataset, indicating that the existing dataset is not a random sample of the fossil record. First, the vast majority of known occurrences are from northern Europe, the USA, and South-East Asia, compared with a global fossil collection bias for north-west Europe and North America (e.g. Smith 2001). Although there are numerous fossil records from North America as a whole, the vast majority of taxonomic treatments of North American faunas (especially Arctic Canada) are new taxa, suggesting that although the North American record is being recovered rapidly, it has been sampled only sparsely to date (using the collecting curve analogy we remain on the steep component of the curve). A bias against collecting central Asian faunas appears to be supported by records of spot occurrences in terranes such as Tuva (Afanassieva and Janvier 1985). A virtual absence of ‘ostracoderm’ faunas, bar thelodonts, from Gondwana after the Ordovician may also suggest a dearth of collecting. However, many basins have been densely sampled, particularly for conodont biostratigraphy, to little avail (the exception to this being the enigmatic pituriaspids; Young 1991). It would appear that the absence of records from this interval does reflect the real absence of most ‘ostracoderm’ groups in Gondwana during this time (for further discussion see Smith et al. 2002). Thus, there is a systematic bias in the sampling of geographical regions, but some gaping holes in the regional distribution of fossil sites result from primary signal rather than an absence of sampling.

Another source of evidence supporting a non-random fossil record stems from the fact that the distribution of many, or even most, groups was facies controlled. Given the differential preservation potential of faecies with sea level change, it would be expected that the recovery of fossil taxa would improve by removing a genetic bias, the effect of a non-random geographic data matrix. This requires abandoning the assumption that $P = 1$ (Holland 1982; Strauss and Holland 2001). Potential functions are in Table 3.4 (Holland 1995). In some cases it may be possible to estimate the proportion that is signal.

Our attempts at estimating confidence intervals failed because a regression model of the position of each of the groups was not possible with the fossil occurrence data. In future occurrences can function as an additional data set to implement. Many of these types of groups exhibit an enigmatic distribution (see Donoghue et al. 2002) and would benefit at both the taxonomic level and the level of the recovery potential. This method to testing the effect of a non-random fossil recovery potential can be an important tool to test a eustatic sea level change hypothesis for the near future. Future data sets will be required to observed else where, and the additional occurrence of further facies had no impacts on eustatic episodes. Thus, we suggest that we may consider such relationships are to be revised down the line. Here we note that the

**Comparison of models**

**Origin of character**

Inferences regarding the origin of character provide a problem of figuring out the origin of character against absence of our
that the recovery potential and, thus, the stratigraphic distribution of facies-controlled fossil taxa would be similarly affected (Holland 1995). While the only recourse to removing a geographical collecting bias is systematic sampling of unsampled regions, the effect of a non-random record upon the calculation of confidence intervals on stratigraphic data may be readily overcome, at least in principle. This is achieved through abandoning the uniform recovery potential assumption of classic confidence limits (Paul 1982; Strauss and Sadler 1989; Marshall 1990) and replacing it with a fossil recovery potential function that reflects secular bias resulting from, for example, sea level change (Holland 1995; Marshall 1997). Devising this function can be non-trivial, but in many cases it may be simplified on the basis that it is only change with stratigraphic position that is significant (Marshall 1997).

Our attempts to implement the ‘generalized’ method of calculating confidence intervals failed on a number of counts. First, the method requires that the stratigraphic position of each fossil occurrence is known with a degree of precision that is not possible with the global dataset of early vertebrates; the stratigraphic position of some occurrences cannot be resolved even to series level. Second, fossil recovery potential functions are incalculable at the taxonomic level at which our analysis has been undertaken. Many of the component lineages (e.g. heterostegans and osteostracans) exhibit an ecological shift through time and phylogeny (Bleek and Janvier 1991; Smith et al. 2002) and so it would have been necessary to divide plesios into much lower taxonomic levels for which fossil recovery potential curves could be produced and implemented. The conflation of these two variables precluded analysis of the entire dataset. As a fallback, and given that it is the time of first appearance of groups that is germane to this study, it was our intention to confine application of the generalized method to the pre-Silurian record alone. This objective is more easily achieved because the secular distribution of vertebrates is much better constrained for the Cambro-Ordovician (mainly because the records are entirely marine), and the ecologies of taxa are less complex than for post-Ordovician vertebrates. However, while it is possible to derive fossil recovery probabilities for each lineage, the calculation of fossil recovery potential functions is precluded by almost total absence of agreement over a eustatic sea level curve for the interval. While we intend to remedy this problem in the near future, it is beyond the scope of the present study. In the interim, we have observed elsewhere (Sansom et al. 2001; Smith et al. 2002) that intracontinental occurrences of Ordovician vertebrates in Laurentia are confined to eustatic highstand episodes. Thus, although it has not proved possible to quantify confidence intervals that consider systematic bias in groups that have their first records in the Ordovician, we may conclude that the base range of the Ordovician groups (bar conodonts) would be revised downwards. To provide constraint on the lower limit of first appearance we note that the absence of records from preceding highstand episodes is significant.

Comparison of molecular and fossil estimates

Origin of chordates, craniates, and vertebrates

Inferences regarding the time of origin of these clades are hampered by the perennial problem of first appearances clustering in the Attabanian (mid-Early Cambrian). The absence of outgroup representatives of greater age precludes further interpretation
beyond the conclusion that representatives of these clades are observed, or can be inferred to have been present, at this time (530 Ma). There are two reasons for equivocation over this date. First, putative echinoderms remain known from the Proterozoic (e.g. Arkama Gehling 1987), possibly providing evidence for a chordate ghost lineage extending back to the Neoproterozoic. Second, the fossil record of these groups is so poor that internal assessments of confidence limits ($P > 0.95$) place a bracket on the evolutionary origin of the cephalochordates, hagfishes and lampreys that is sufficiently broad to encompass any hypothesis that is compatible with their origin within the constraints provided by the origin of the Earth and/or Universe, as well as some that are not. Thus, without recourse to negative evidence, the fossil record is mute with regard to a judicious lower constraint on the timing of origin of chordates, craniates, and vertebrates.

The absence of firm palaeontological data is unfortunate because molecular estimates for the diversification events are strongly discordant with the available evidence (Figure 10.6), although molecular estimates also differ from one another by just as great a degree. The earliest molecular estimate for the divergence of chordates from their sister clade, the Ambulacaria (echinoderms plus hemichordates), is 1001 Ma (Wray et al. 1996), while the latest is 590 Ma (Feng et al. 1997). The average estimate is 722.75 Ma with a standard deviation of 192 myr ($n = 4$). The time of divergence of craniates and acraniates has been addressed in only two analyses, yielding estimates of 760 Ma (Feng et al. 1997) and 695 Ma (Chen et al. 1997). These are non-independent estimates by Hedges (2001), who became aware of much as 100 Ma. Indeed, these analytical techniques are questionable or inadequate or insufficiently calibrated. The date for the divergence of chordates (Kumar and Hedges 1997) is derived from a date that does not utilize the molecular calibration. The divergence is in sequences that Feng et al. (2001) uses can be obtained. Kumar et al. (1998) then dated a date for Hedges (2001) and a date for the divergence of Hedges (1997) has, in effect, from a molecular-ontological data.

No molecular studies of cranates and -acraniates and -hagfishes and -lampreys. In the molecular study by Feng et al. (2001) used a slightly younger date of 849 ± 36.8 Ma for the divergence of cranates and acraniates, which might suggest a slightly younger date for the divergence of chordates and cephalochordates. The overall scale of divergence of cephalochordate, hagfish, and lamprey (Kumar and Hedges 1997) is 50 Ma and 46 Ma, which might indicate two occurrences of divergences of cranates and acraniates, with a slightly younger date for the divergence of cranates and acraniates.

Overall, in evo-devo, the molecular estimates of divergence of cephalochordates and cephalochordates from the origin of the Earth and/or Universe, as well as some that are not. Thus, without recourse to negative evidence, the fossil record is mute with regard to a judicious lower constraint on the timing of origin of cephalochordates, cranates, and cephalochordates.

The absence of firm palaeontological data is unfortunate because molecular estimates for the diversification events are strongly discordant with the available evidence (Figure 10.6), although molecular estimates also differ from one another by just as great a degree. The earliest molecular estimate for the divergence of cephalochordates from their sister clade, the Ambulacaria (echinoderms plus hemichordates), is 1001 Ma (Wray et al. 1996), while the latest is 590 Ma (Feng et al. 1997). The average estimate is 722.75 Ma with a standard deviation of 192 myr ($n = 4$). The time of divergence of cranates and acraniates has been addressed in only two analyses, yielding estimates of 760 Ma (Feng et al. 1997) and 695 Ma (Chen et al. 1997). These are non-independent estimates by Hedges (2001), who became aware of much as 100 Ma. Indeed, these analytical techniques are questionable or inadequate or insufficiently calibrated. The date for the divergence of cephalochordates (Kumar and Hedges 1997) is derived from a date that does not utilize the molecular calibration. The divergence is in sequences that Feng et al. (2001) uses can be obtained. Kumar et al. (1998) then dated a date for Hedges (2001) and a date for the divergence of Hedges (1997) has, in effect, from a molecular-ontological data.

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estimates of 700 Ma (Nikoh et al. 1997) and 751 Ma (Hedges 2001). These analyses are non-independent in that the sequences used by Nikoh et al. (1997) were also used by Hedges (2001), but yielded results from individual sequences that differ by as much as 100 Ma that can be accounted for by differences in calibration dates and analytical techniques (Hedges 2001). The calibration points used by both analyses are questionable in that they use molecular estimates and, thus, do not provide an adequate or independent test of molecular clock theory. Furthermore, the calibration date for the divergence of arthropods and vertebrates (700 Ma) used by Nikoh et al. (1997) is derived from Dayhoff (1978) who provided no form of substantiation for a date that does not accord with any palaeontological data. In addition, the use of molecular calibration points in this analysis appears to render the analytical argumentation circular since the molecular calibration points are applied to molecular sequences that were used in calculating the molecular estimate. Specifically, Hedges (2001) uses calibration points derived from Kumar and Hedges (1998; and Wang et al. 1998) that are based, in part, upon aldolase and TPI, which are analysed in Hedges (2001). Given that the only palaeontological calibration point used by Kumar and Hedges (1998) is the bird–mammal divergence date of 310 Ma, Hedges (2001) has, in effect, calibrated multiple times, directly and indirectly, using a single palaeontological datum.

No molecular estimates have been calculated for the divergence of invertebrate craniates and vertebrates. This is because molecular phylogenies consistently resolve hagfishes and lampreys as monophyletic and, hence, there is no distinction between craniates and vertebrates within the field of molecular systematics. However, Hedges (2001) used a subset of his data to provide an estimate for the divergence of hagfishes and lampreys within the context of cyclostome monophyly and arrived at a date of 499 ± 36.8 Ma, using the lamprey–gnathostome molecular estimate of 564 Ma (Kumar and Hedges 1998) as the calibration point. For once, palaeontological data indicate two older spot dates (530 Ma on Myllokunmingia and Haikouichthys) with a slightly younger and better-constrained date of 495 Ma bracketing the molecular estimates and falling well within the standard error on the molecular estimate.

Overall, in consideration of the origin of chordates and divergence of the lower chordate groups, there is poor correlation both between molecular and palaeontological estimates and between molecular estimates that are based upon different datasets. Thus, in the absence of any independent constraint that the fossil record may otherwise afford, it would be dangerous to conclude anything other than the fact that chordates, craniates, and vertebrates had diverged by 530 Ma. Furthermore, given the low stochastic value of the calculated error limits on published molecular clock studies, there can be no confidence that the origin of the clade was not significantly before such estimates, based on molecular data alone.

**Origin of gnathostomes**

Although there is little temporal constraint on the origin of vertebrates afforded by the fossil record, internal assessments of the consistency of the record point to a dramatic increase in the quality of the record after the divergence of the lineages leading to lampreys and living jawed vertebrates (crown-gnathostomes). This coincides with the appearance of mineralized skeletonization within the gnathostome
stem-lineage. The fossil record of conodonts exhibits remarkable internal consistency and the first appearance of this basal member of the gnathostome stem-lineage affords an inferred 495 Ma constraint on the latest possible date for divergence, with a confidence bracket of just 346 kyr ($P > 0.95$; and only 532 kyr with $P > 0.99$). The absence of a sister taxon with even an approximately comparable fossil record precludes the possibility that this date can be corroborated through inference of a ghost lineage. The absence of a stepwise geological appearance of successive sister taxa within the sister clade to the Conodonts is problematic; the conodont fossil record implies a significant ghost lineage amongst many of these groups. This signal is in agreement with internal assessments of the quality of the record of these groups (which conclude that it is a poor reflection of the evolutionary history of these groups), the fact that all well-known taxa fall within known clades within the stem-lineage (rather than as individual plesions on the stem-lineage), and knowledge of a large number of vertebrate remains of this age that cannot be assigned to known groups (e.g. Sansom et al. 2001).

Only two molecular clock analyses have addressed the lamprey–gnathostome divergence. Wray et al. (1996), who famously estimated the divergence of Bilateria at 1200 Ma, estimated the divergence of lampreys and gnathostomes at 599 Ma, while Kumar and Hedges (1998) suggested a date of 564 Ma. The entire analysis undertaken by Wray et al. (1996) was reanalysed and robustly criticized by Ayala et al. (1998), who revised upwards all the divergence estimates. This is in accordance with the analysis undertaken by Kumar and Hedges (1998) which, given the enormity of the dataset, must be considered the most robust analysis undertaken to date. Despite the poor internal support for palaeontological dating of the origin of gnathostomes, the average date given by Kumar and Hedges (1998; 559 Ma) corresponds well to the palaeontological estimate, at least when considered within the context of a standard error of ±74.6 myr on the molecular estimate which encompasses an interval extending from the earliest Ordovician to the Neoproterozoic (484.4–633.6 Ma).

### Origin of crown-group gnathostomes

Inference of the time of origin of crown-gnathostomes is complicated by equivocation over the affinity of shark-like microremains from the Late Ordovician and early Silurian (for a discussion see Janvier 1998; Sansom et al. 2000, 2001; Smith et al. 2002). These scales are identified as chondrichthians (total-group Chondrichthyes) on the basis that they possess neck canals and exhibit rigidly patterned areal growth, at present a chondrichthyan synapomorphy and sympleiomorphy, respectively. However, it is not known whether the inclusion of these taxa renders the group paraphyletic or, indeed, whether these characters are exclusive to crown-gnathostomes; only further resolution of the anatomy of these taxa will lead to a resolution of their precise placement within total-group gnathostome systematics. In the meantime, all available evidence suggests that they are representatives of total-group Chondrichthyes and, thus, crown-gnathostomes; by inference they place a lower constraint on the divergence of crown-gnathostomes at 457 Ma, but with a confidence interval extending to 463.4 Ma ($P > 0.95$; accepting the confidence interval based upon the Ordovician record alone).

A molecular clock analysis of Osteichthyes, as presented by Kumar and Hedges (1998), indicated a mid-Ordovician geological estimate of divergence, with the lower bound of the 95% confidence interval not overlap.

### Origin of actinopterygians

The earliest actinopterygian fossils (thanks, again, to L. H. Huxley 1968; Gross 1980) have been interpreted as a confidence interval for the true range of divergence of the early Devonian sarcopterygian clade (Zhu and Schultze 1993), and it is likely that the true range of divergence of the sarcopterygian clade is considerably lower. However, given the remarkable consistency of the molecular clock, there is very little influence on the molecular estimate of the origin of the sarcopterygian clade (430–450 Ma).

Kumar and Hedges (1998) also suggested that clades within the actinopterygian clade are Ordovician (445–485 Ma), and that the paleontological and molecular estimates do not necessarily converge on the origin of the sarcopterygian clade.

### Discussion

Correspondence between molecular and palaeontological estimates is very variable. Molecular estimates are not necessarily informed upon internal palaeontological and phylogenetic relationships between sarcopterygian and gnathostome actinopterygians, and there is a priori no reason to expect a baseline set of internal relationships that are discordant.

Where there is discordance, it is difficult to disambiguate the source of divergence outside of correspondence upon negative
A molecular estimate for the time of divergence between Chondrichthyes and Osteichthyes, and hence, the time of origin of crown-gnathostomes, was calculated by Kumar and Hedges (1998) at 528 ± 56.4 Ma, encompassing an interval from the mid-Ordovician (471.6 Ma) to late Neoproterozoic (584.4 Ma). The palaeontological estimate derived from a literal reading of the record (457 Ma) narrowly misses the lower bound on the bracket provided by the molecular estimate. Confidence limits provided by the Ordovician record alone extend the predicted first appearance closer to the lower bound on the molecular estimate, but the two do not overlap.

**Origin of actinopterygians and sarcopterygians**

The earliest actinopterygian remains are dated at 425 Ma, and are part of a rich record (thanks, again, to the application of micropalaeontological techniques; e.g. Schultzze 1968; Gross 1969; Märs 1986; Fredhöl 1988a,b). This confers a remarkably short confidence interval (425.58 Ma at \( P > 0.95 \)) on first appearance. The record of pre-Devonian sarcopterygians is much poorer, with only a single known fossil horizon (Zhu and Schultzze 1997). With such a poor record, the obvious implication is that the true range extends much further back than present evidence indicates. This is supported by the observation that these occurrences were palaeogeographically remote from each other. However, this earliest sarcopterygian record (423 Ma) is remarkably consistent with the extent of the range of actinopterygians such that there is very little inferred ghost lineage. Thus, we accept 425.58 Ma as a firm lower bound on the origin of crown-osteichthyan and the divergence of two osteichthyan clades.

Kumar and Hedges’ (1998) estimate for the divergence of the two extant osteichthyan clades is 450 Ma ± 35.5 myr, encompassing an interval extending from earliest Ordovician (485.5 Ma) to Early Devonian (419.5 Ma). This compares well with the palaeontological estimate, although internal assessments of the quality of the record, particularly of sarcopterygians, suggest that palaeontological data may eventually converge on the mid-range of this molecular estimate.

**Discussion**

Correspondence between molecular clock estimates for the timing of divergence and palaeontological data indicating the minimum possible date for divergence is very variable. There is a clear correspondence between molecular and palaeontological estimates where there is a *priori* evidence for confidence in the fossil record based upon internal assessments of its quality based upon stratigraphic data alone and the relationship between stratigraphic data and cladogram structure (e.g. the lamprey-gnathostome and actinopterygian–sarcopterygian divergences). Concomitantly, where there is a *priori* evidence for a lack of confidence in the quality of the record on the basis of internal assessments, the molecular and palaeontological estimates are in discord.

Where there is disagreement between palaeontological and molecular estimates it is difficult to reconcile which dataset provides the best approximation of true time of divergence of a particular clade. Palaeontological estimates are limited by their reliance upon negative evidence and although quantitative methods are being developed to
assess the plausibility of range extensions in the face of sampled, but barren time intervals (Weiss and Marshall 1999), they are at present limited by the assumptions on which they are based, many of which are extremely controversial. On the other hand, given that it is difficult to reconcile between competing molecular estimates, it is not surprising that it is difficult to arbitrate between palaeontological and molecular estimates. This is partly because, as scientific theories, molecular clock calculations are extremely poorly formulated and, thus, are difficult to test. In many instances, one molecular hypothesis is preferred over another on the basis that it is derived from the greatest dataset, relying upon a law of large numbers approach to molecular clock mechanics (cf. Rodríguez-Trelles et al., Chapter 1,); rather than a neutrality theory basis (Zuckerkandl and Pauling 1962, 1965). Thus, they are testable only by other molecular clock calculations, based upon larger, more universal datasets and/or the falsification or augmentation of calibration points. Smith and Peterson (2002) have suggested an explanation for the discrepancy between molecular and palaeontological temporal divergence estimates, arguing that they reflect two quite distinct events, with molecular clocks estimating the time of origin of a clade, and palaeontological estimates recording the diversification of the clade, which they equate to the origin of the total-group and origin of the crown-group — placing undue weight on the evolutionary significance of crown-groups. This follows the widespread assumption that most molecular clock estimates pertain to total-group divergence, but total-groups and crown-groups are hierarchical such that one taxon’s total-group is the next more inclusive taxon’s crown-group and vice versa. Thus, there is no better correlation between molecular and palaeontological estimates for the origin of crown-groups than total-groups, and the rapprochement fails.

Even when palaeontological and molecular estimates are comparable, molecular clock analyses consistently yield a date that is considerably older than the palaeontological data indicates (except in the instance of the hagfish–lamprey divergence estimate within the context of cyclostome monophyly). Thus, the fossil record of early chordate evolution is either consistently missing the early history of various chordate clades or molecular clock dates consistently overestimate the true time of cladogenesis. To some extent this should be expected. First, because no one argues that the earliest fossil record equates to the origin of a clade; there is a cryptic evolutionary history to all clades, the critical issue is the temporal extent of this period of unrecorded evolutionary history. Second, in a strict interpretation of molecular clock theory, such calculations estimate the time of divergence based on a fossil record comparable with that on which the ‘clock’ is calibrated, not the true time of origin of a clade and, hence, it has been argued that molecular clock estimates should be conservative. All of the clades in our analysis exhibit stratigraphy–cladogram congruence metrics that are worse than the fossil record of the calibration point on which most molecular clocks are calibrated, the divergence of bird–mammal lineages at 310 Ma (Table 10.2; but see Lee 1999; it should also be noted that although the basal synapsid and diapsid fossil records perform well in the SCI and GER indices, it is likely, given the patchy nature of the record – betrayed by the particularly low RCI for the diapsid lineage – that confidence intervals on the stratigraphic range data for the various plesions would be extensive).

However, there is some circumstantial evidence to suggest that the fossil record of early vertebrates, and total-group gnathostomes in particular, may be more reliable than we would expect from the occasionally poor correspondence of the chronology of the fossil record and the first appearance of the divergence of clades (they are base-inflation corrected, but we have not hold true to the assumption that they will only be a problem where there is a non-evolutionary signal). On the one hand, with high fidelity sequence data, phylogenies consistently come out with the expected non-mutually exclusive alone and the asymmetrical, but diverse clades found at the upper end of the divergence of a clade of divergence of higher order clades (Holland 2001) and even the few fossil calibration dates and internal calibration hypotheses at a date. This material for an asymptomatic (1998); although the fossil record of divergence times is clearly younger than the very oldest dates, they are not the origin of crown-groups.

The alternative view of the fossil record is that the fossil record is resolutely interpreted, in a traditional and/or stem-centric way (Sloan et al. 1996; Gaskill et al. 2000). As the examination of the fossil record and its vertebrate diversity has focused on the veracity of their assignment (see Chapter 9).

The other aspect of the palaeontological data, that it is also informative about, by inference, the history of assembly and the biology of the history that spectacularly indicates, even when it coincides with evidence for evolution, to the gnathostome clade (see also Sansom et al. 1994), and provides evidence for a Late Cambrian radiation (see Back et al. records of other groups, about the time of a secular basal agnathans, rather than imperfections in palaeontology (see Holland 1995).
than we would otherwise assume. This stems from the rather surprising degree of correspondence between molecular estimates and palaeontological data, at least in terms of the chronologically consistent ordering of palaeontologically based estimates for the first appearance of successive extant clades. While molecular estimates for the divergence of successive clades have to be chronologically consistent, by definition (they are based upon a direct extrapolation from a hierarchical dataset), the same does not hold true for the fossil data. Indeed, the temporal distribution of fossil remains will only be chronologically consistent if their ordering reflects the hierarchy of evolutionary relationships – which they will do only if the fossil record is preserved with high fidelity. There is also evidence to suggest that molecular clocks may consistently overestimate the date of divergence of clades. This can occur for two non-mutually exclusive reasons. First, constraints on molecular clock estimates are asymmetrical, i.e. they are bound to be non-negative but there are no such constraints at the upper end of the spectrum (Rodríguez-Trelles et al. 2002). Second, overestimation of divergence times arises from the accumulating inaccuracy associated with extrapolating farther and farther from the calibration date (Springer 1997; Nei et al. 2001) and especially concerns analyses that use single internal palaeontological calibration dates, although it also affects analyses that use multiple external and/or internal calibration dates that are derived from a single palaeontological calibration date. This may be a particular weakness of the analysis by Kumar and Hedges (1998); although encompassing by far the greatest number of sequences in calculating divergence times (658), very few of these were used in calculating the timing of the very oldest divergence events (13 for the origin of jawed vertebrates, 15 for the origin of crown-gnathostomes, 44 for the origin of crown-ostechthysans).

The alternative view, that the fossil record of early chordates is particularly poor, is reflected by the fact that plesiomorphic chordate and deuterostome anatomies have been the subject of debate for over a century and yet the subject remains resolutely intractable. In addition, very few stem-chordates, stem-ambulacrarians, and/or stem-deuterostomes have been identified from the fossil record (e.g. Jeffries et al. 1996; Gee 2001; Shu et al. 2001b) and none (arguably) have escaped critical examination (Ruta 1999; Lacalli 2002). Finally, questions of chordate, craniate, and vertebrate divergence timings cannot be resolved in isolation while debate over the veracity of the Cambrian ‘explosion’ continues (e.g. Smith 1999; Budd & Jensen, Chapter 9).

The other molecular estimate that exhibits poor correspondence to palaeontological data, the divergence of crown-gnathostomes, predicts a Late Cambrian event and, by inference, a hitherto unrecorded interval of crown-gnathostome evolutionary history that spans the Late Cambrian–Middle Ordovician. Significantly, this interval coincides with recent discoveries of a swath of new vertebrate taxa, which are assignable to the gnathostome total-group, but no further, based upon the available evidence (Sansom et al. 2001). It is quite possible that these new taxa include further Ordovician representatives of crown-gnathostomes (e.g. Skutschys Smith and Sansom 1997). The Late Cambrian–Middle Ordovician gap in the record overlaps well with gaps in the records of other groups, for example, the echinoderms (Smith 1988a). This hints at a secular bias in the fossil record as a whole that probably reflects the fact that imperfections in the fossil record are rooted in imperfections in the rock record (cf. Holland 1995, 2000; Smith 2001; A.B. Smith et al. 2001).
Implications for established hypotheses and scenarios

Understanding early chordate evolution using an incomplete fossil record

If nothing else, molecular clocks have provided the stimulus for palaeontologists to look at their datasets anew and provide justification for cherished methodologies. This, in turn, has provided the impetus for the development of old and new methods for assessing the completeness of the fossil record. These internal assessments provide a means of determining degrees of confidence in subsets of a dataset, provide cautionary limits in reading the evolutionary history of particular clades, and provide predictions in our attempts to recover missing components of the record.

The greatest concern of palaeontologists with regard to the mismatch of molecular clocks and the fossil record may be that it indicates not only that the fossil record is substantially incomplete but also, critically, that it is the initial period of the evolutionary history of these clades that is missing. In such a case, would not the usefulness of the fossil record, in uncovering the sequences of character change between extant clades, be compromised? The simple answer to this question is no. The chief value of the fossil record is that it reduces error in inferring the sequence of character changes that underlie the establishment of living clades – this has been integral to testing and rejecting models such as, for example, the origin of paired appendages within vertebrates (Coates 1994). Whether or not we have a complete sample of the anatomical designs that have been realized is not relevant; with the fossil record we have a more complete, and continually expanding, understanding of chordate evolution than would be possible using only the living biota. Furthermore, fossils help to prevent the identification of homoplasy as homology in living members of distantly related groups, and identify homologies that might not otherwise be recognized because of the hundreds of millions of years of evolutionary change that has occurred subsequent to the divergence of the clades.

Our understanding of early chordate evolution may well be incomplete but it does not follow that it is incorrect. Further attempts to reconcile the fossil record with the living biota will lead to further refinement not only to the temporal scale of early chordate evolution but also to our understanding of the sequence of character changes that shaped all subsequent events in chordate phylogeny.

Neoproterozoic refugia and the origin of vertebrates

One inevitable development of molecular clock estimates is that attempts are being made to link intrinsic evolutionary change to extrinsic environmental factors. For instance, van Tuinen et al. (1998) proposed that the origin of ratites is not just coincident with, but inextricably linked to, the separation of Africa and South America during the Early to mid-Cretaceous (see Cracraft 2001 for an excellent analysis). More recently, Hedges (2001; Chapter 2) proposed that the proximity of the molecular clock estimate for the divergence of crown-vertebrates to radometric dates for the first major Neoproterozoic glaciation (Sturtian; 750–700 Ma) may not be coincidental. It is argued that both the Sturtian and Varanger glaciations (610–570 Ma) would have led to contraction in the topological range of species and, through long-term genetic isolation in small refugia, to considerable speciation. As worthy as this approach may be in demonstrating an integrated approach to the questions of when, where, how, and why vertebrates diversified, this linkage of date, phylogeny, and environment is, at present, unresolved, in part due to the paucity of data (Hedges 2001; Cracraft 2000). Secondly, although there are currently so many hypotheses in circulation, it may be an attempt to make sense of the overwhelming mass of data.

Evolutionary patterns

Although molecular and palaeontological attempts to date extrinsic events may be at least with regard to the timing, it is recognized for many clades that the actual event is but many sce- narios. They are therefore more challenging. For instance, the postulated emergence of eurypterids (Romer 1933) is one of the milestones in the origin of the vertebrates. The relationship between eurypterids and other early aquatic vertebrates now suggests that the Ordovician interval may be more consistent with this event (Hutchinson 1993). Thus, the date of origin may be no longer an evolutionary dead end.

Similarly, the concomitant origins of tetrapods, the displacement of marine reptiles and the adaptive cryptic history of early tetrapods remain two significant formulations of our understanding which need to be tested via new methods.

The bottom line is that the timing of the early vertebrate radiation, and the speciation associated with it, can be asked, and for this reason we present the available palaeontological and molecular data to test such hypotheses.

Conflict, cooperation, and clade histories

Increase in the number of published papers on the study of interspecific interactions has led to the emergence of the study of conflict, cooperation, and clade histories. The overlap of clades, albeit at different times in clade histories, appear to be more common than expected.
and why vertebrates first evolved, there are two significant problems with regard to this linkage of intrinsic evolutionary and extrinsic environmental factors. First, the nature, timing, and tempo of the Cryogenian period of the Neoproterozoic is utterly unresolved, in terms of the timing, duration, and number of glaciation episodes (Knoll 2000). Second, and more intractably, the standard errors on molecular estimates are currently so vast (and unrealistically conservative) that they render worthless any attempt to match biotic events to radiometrically dated environmental events.

**Evolutionary scenarios based upon palaeontological dating**

Although molecular estimates fail to provide the necessary temporal constraint to underpin attempts to uncover any possible link between intrinsic evolutionary events and extrinsic environmental events, palaeontological data provide no panacea either, at least with regard to the origin and early evolution of vertebrates. It has been recognized for many years that evolutionary history cannot be read directly from the rocks, but many scenarios for the origin of major clades remain current, even though the supporting data have not expanded from those on which they were originally contrived. For instance, Romer's celebrated 'eurypterid influence on vertebrate history' (Romer 1933) is based upon the co-occurrence and vaguely comparable diversity trends of eurypterids and the then earliest skeletonizing vertebrates in the Silurian. Thus, the origin of the skeleton has been attributed to the selection-based effect of predating eurypterids upon early vertebrates. But not only are the earliest known skeletonizing vertebrates now Cambrian in age, and the earliest undisputed 'armoured' vertebrates Ordovician in age, but our phylogenetic tests and internal assessments of the consistency of stratigraphic data both reveal that these lineages probably existed even earlier. Thus, the co-occurrence and evolutionary history of vertebrates and eurypterids is no longer apparent and Romer's evocative theory must finally be laid to rest.

Similarly, it has been argued that the rise of jawed vertebrates and apparently concomitant demise of skeletonizing jawless vertebrates is the result of competitive displacement (for a summary see Purnell 2001). However, our analyses reveal an extensive cryptic history of early jawed vertebrates that has not been considered in the formulation of the theory, or in attempts to test it. Furthermore, it may not be possible to test such hypotheses adequately on the basis of the currently available dataset.

The bottom line with regard to attempts to link intrinsic and extrinsic events in early vertebrate evolution is that although there are many interesting questions that can be asked, it may not be appropriate to try and answer some of them based upon the available palaeontological dataset, and molecular clock analyses do not at present appear to be even close to capable of overcoming these shortcomings.

**Conflict, compromise, or consilience?**

Increase in the application of molecular clock theory has led to a considerable period of introspection amongst the palaeontological community, from which two main camps have emerged. There are those who reject molecular clock estimates outright and contend that only the fossil record can provide reliable estimates for the divergence of clades, albeit minimum estimates for the timing of divergence events (e.g. Conway Morris 1997, 2000; Budd and Jensen 2000). Others have capitulated entirely to molecu-
lar clock estimates, concluding that use of the fossil record is corrupted by its reliance upon negative evidence (Fortey et al. 1996, 1997; Smith 1999; Wills and Fortey 2000; Smith and Peterson 2002). However, neither dataset has a monopoly over the other and, indeed, the two datasets have much mutuality. The inextricable linkage between the fossil record and molecular clock theory is no better exemplified than in the need for palaeontological calibration points in molecular clock analyses, whether they are applied directly or indirectly. Above all, the two databases provide a level of rigour that would not be possible in the absence of one or other dataset, such that molecular clock theory and the fossil record are becoming better understood through reciprocal illumination.

Given the degree of latitude offered by standard error on molecular clock estimates and the lack of internal consistency in the fossil record of early choridates, we are no closer to constraining the times of origin of the chordate, craniate, and vertebrate clades. Indeed, it could be argued that we are even further from providing constrained estimates on the origin of these clades than we were at the outset. Thus, although we understand relatively well what is currently known of early chordate evolution, it appears that what is currently known is by no means all there is to know, and this is particularly the case for the invertebrate choridate, basal vertebrates, and stem-gnathostomes within the Late Cambrian–Middle Ordovician, and lower Silurian intervals. While our knowledge of the invertebrate chordate component of chordate phylodeny will remain contingent upon the chance discovery of fossil remains preserved under exceptional conditions, such a restriction does not obtain for the skeletonizing vertebrates, the remains of which were readily entrained in the fossil record. Targeted examination of previously unsampled environments and palaeogeographical realms will be crucial to resolving the evolutionary history of early vertebrates and stem-gnathostomes in particular. At the same time, development of molecular clock theory, more rigorous composition of molecular clock analyses as scientific hypotheses for testing, and the inclusion of more sequences representative of basal choridates and sister groups are likely to provide better constraints on their time of origin. A more realistic attempt to assess errors on molecular clock estimates is required and this can be developed in hand with more rigorous assessments of the palaeontological data used in calibrating molecular clock analyses. However, unless these errors can be reduced, molecular clock estimates will remain of low practical value; the palaeontological record is imperfect but nevertheless provides the only firm constraint on the timing of clade divergence.

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Appendix 10.1

Codings for taxa augmented to the analysis of Donoghue and Smith (2001):
Appendix 10.2

Tree topologies and occurrence data upon which cladogram-stratigraphy statistics and confidence intervals are based.

Conodonta
((Proconodontus ((Fryxellodontidae Pygodontidae) Cordyloidontidae (Ansellidae (Dapsilodontidae Belodeliidae)))))(Teridontus ((Clavohamulidae (Drepanostontidae (Acanthodontidae Panderodontidae)))))(Rossodus (Multiostodontidae (Periodontidae (Rhipidognathidae (Proniodontidae ((Cytromonodontidae (Chirognathidae Prontiodinidae) Kockelellidae)(Polyplacognathidae (Distomodontidae (Icriodontidae Icriodontidae))))))))))); following Sweet & Donoghue (2001), after Sweet (1988).

Heterostromorphida
(Astraspida (Arandaspidae (Lepidaspidae Teseraspididae Phialaspiformes (Corvaspid/Tolypelepid (Cyaathaspida (Ctenaspidae (Egonaspidae Hibernaspidae) (Siberiapospidae (Amphiaspidinae Olbiaspididae)))))) Anchipteraspidae (Propteraspidae (Protaspidae (Protaspidae Psammosteididae)))); following Novitskaya (1971), Bliek (1984) and Janvier (1996b).

Anaspida
(Pharyngoolepis, Pterygoolepis, Rhyncholepis, Lasiinus, Birkeia)); following Janvier (1996b).

Thelodontii
(Furcasauidiformes (Thelodontids (Loganeillidae Phlebolepidae))); following Donoghue & Smith (2001).

Galeaspida

Osteostraci
(Ateleaspis (Aceraspis (Hirella (Hemiteleaspis (Eiemiclyaspis (Escuminaspidae Tannuaspidae (Cephalaspidae (Mimetaspidae Pattensepidae)))))) (Zenaspidida (Taurusaspis (Hapataspis Benneveaspidae (Hoelaspidae Boreaspidae)))) (Procephalaspis (Auchenaspis (Witaaspis (Thyrasaspis Tremataspidae)))) (Kiaeraspis (Axinaspidae Acrotomaspidae)))); following Janvier (1996b; in press)

Chondrichthyes
(Cladosebacidae (Eugeoneodontida Petalodontida) (Inopterygia (Heleodontidae (Cochlidioidontidae (Echinocideridae Chimeridae)) (Symmoriiidae Stethacanthidae)) (Xenacanthiformes (Ctenacanthus (Hybodontiformes Neoselachii))))); following Janvier (1996b).

Placoderma
((Actinolepida (Phyllolepidida Wuttagoonaspida)) (Phlyctaenii (Gemeundasps (Holoneididae (Buchanosteidae)) (Brachydeiroidea (Coccospidae Camurospidae)) (Dynichthyidae Aspiothoracide)))(Ptyctodontidae Petalichthyidae))
statistics and

(Aansellidae
panoistontidae
(Periodontidae
(Priorniodinidae)
(Pristidae)))))))));

talaspidiformes
(debernaspididae)
nopteraspididae
(1971), Bleck

Donoghue &

Tridensaspidae)
Neodureynaspis
aspida)); fol-

icumaspidae
(Zenaspida
Proeophalasaspis
(Axinaspididae

((Helodontidae
etracanthidae))
following Janvier

(Gemeundaspis
(Coccosteidae
Petalichthyida))

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((Yunnanolepididae (Sinolepidida ((Bothrolepidae Microbrachiidae) (Pterichthyoidea Asterolepidae))) Rhenanida)); following Goujet & Young (1995) and Janvier (1996b).

Acanthodii
(Ischancanthidae (((Climatiidae Gyracanthidae) (Diplacanthidae Culmacanthidae)
(Mesacanthidae (Cheiracanthidae Acanthodidae)))); following Long (1986).

Actinopterygii
(Lophostous (Andreolepis (Naxilepis (Orvikuina (Ligulalepis Dialipina (Cheirolepis
(Polypterus (Osorioichthys (Houdqualepis (Mimia (Moythomasia (Tegeolepis (Stegotrachelus
Kentuckia)))))))))); following Schultze (1992) and Taverne (1997).