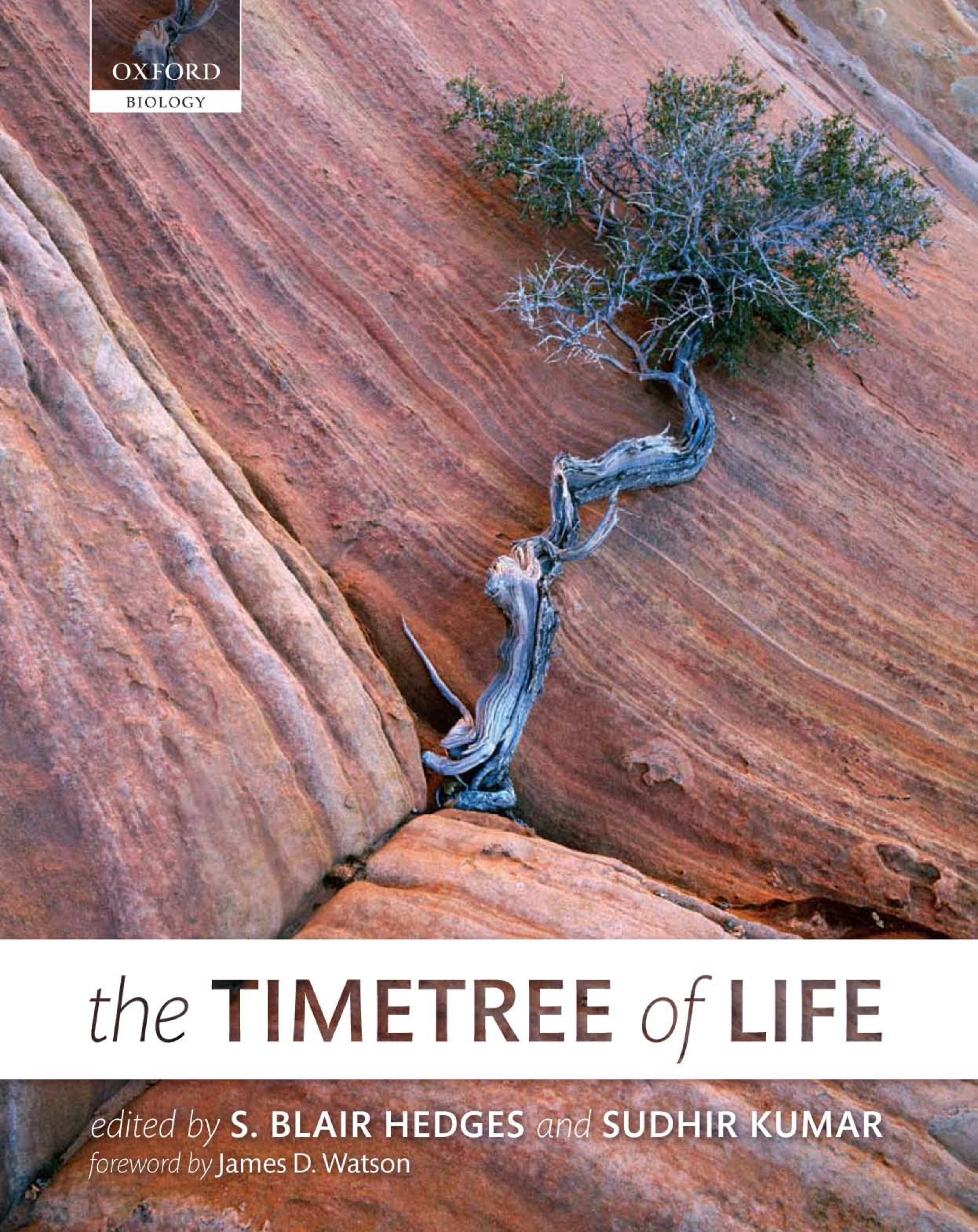

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Crabs, shrimps, and lobsters (Decapoda)

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Abstract

Decapoda is the most diverse and species-rich Crustacean order. The 15,000 decapod species are organized in ~170 families, including ~20 known only from fossils. Their relationships are largely unresolved, but molecular phylogenies support the recognition of two suborders and seven infraorders of decapods. Molecular time estimates using multiple fossil and geological calibrations indicate that the first divergences among living decapods occurred in the early Silurian, ~430 million years ago (Ma). Diversification was rapid, resulting in lineages representing all infraorders by the Carboniferous, 325 Ma.

Crustaceans comprise the fourth most species-rich group of metazoans on the planet, following insects, chelicerates, and mollusks. But in terms of morphological diversity (disparity), they are unrivaled (see *1, 2*). Foremost among the crustaceans in number and diversity are the decapods. With over 15,000 described species they include those crustaceans most familiar to the general public—shrimp, lobsters, crabs (Fig. 1), and crayfish—but also lesser known and unusual groups (*3*).

The most recent classification (*2*) partitions ~62,000 species of extant Crustacea among 849 families (compared to 874 families for all 1.6 million species of insects). Approximately 152 of those extant families belong to the Decapoda with another 20 families known only from fossils, an enormous assemblage that has been called "the pinnacle of crustacean evolution." More than six new families of decapods have been recognized since 2001 from both extant (e.g., *4, 5*) and extinct (e.g., *6, 7*) groups. Thus, ~18% of all described crustacean families belong to the decapods. Additionally, some 91 decapod families contain fossil taxa, including 27 known only from fossils (*8*).

Decapods inhabit a broad diversity of ecological niches, including marine waters, deep-sea vents, estuaries, freshwater, caves, and terrestrial ecosystems. Accordingly, they are the subject of more published papers and controversy than all other crustacean groups combined, due in part to their species richness, economic importance, and ecological and morphological diversity (*1*). Indeed, the decapods have served as model organisms (including physiology, development, behavior, and morphology) for over a century (*2*).

Decapoda is a clearly defined taxon that is generally regarded to be monophyletic within the Class Malacostraca. The decapods are usually divided into two suborders: Dendrobranchiata containing seven families and the more diverse Pleocyemata encompassing seven infraorders: Stenopodidea (two families), Caridea (37 families), Astacidea (seven families; clawed lobsters and crayfish), Thalassinidea (12 families; mud shrimp), Achelata, (five families; spiny lobsters), Anomala (16 families; hermit crabs, king crabs), and the Brachyura (93 families; true crabs). However, debate continues concerning general classification of the decapods (*3–7*) and specific arrangements of families within infraorders (see discussion in Martin and Davis (*1*)). Classification

Fig. 1 A land crab (*Geocarcinus* sp.) from Santa Cruz de Barahona, Dominican Republic. Credit: A. Sanchez.

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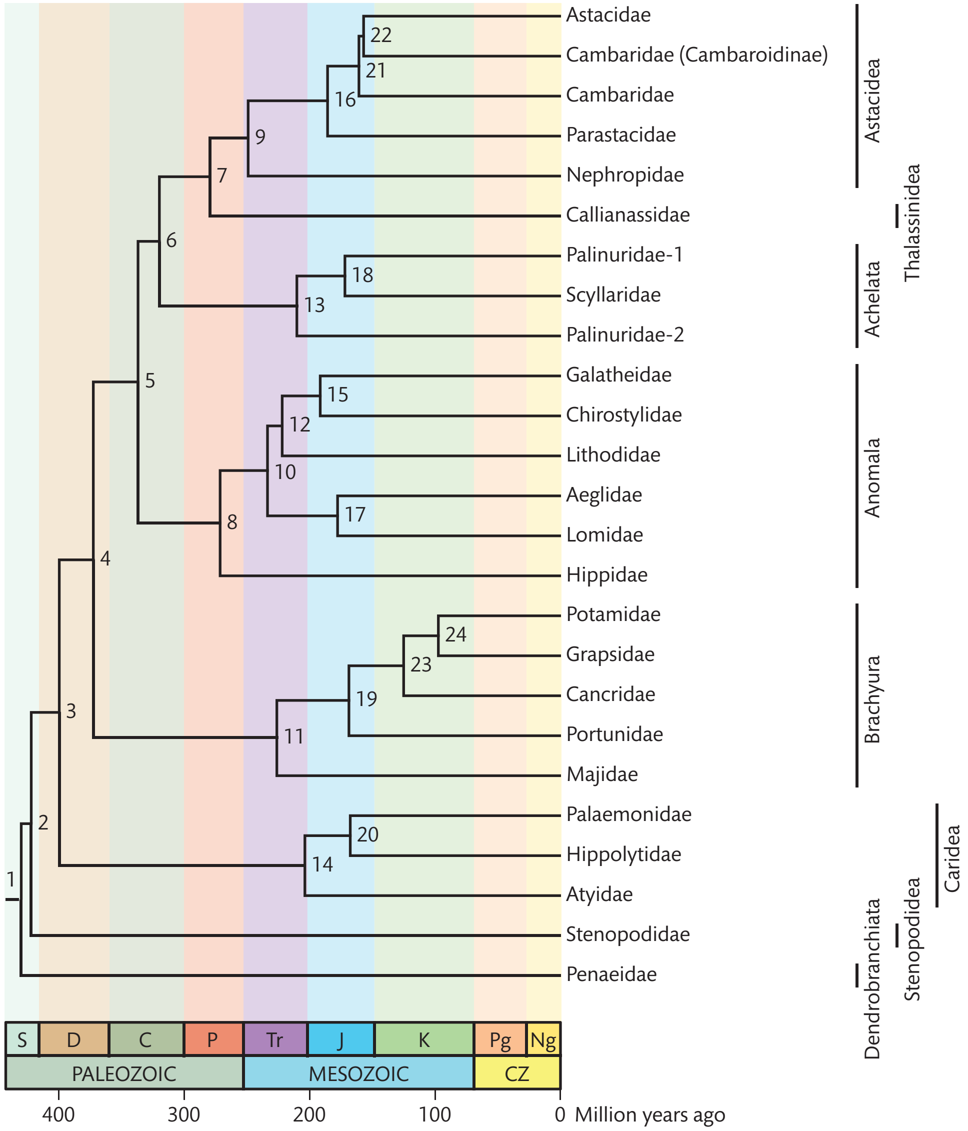

Fig. 2 A timetree of crabs, shrimps, and lobsters (Decapoda). Divergence times are shown in Table 1. *Abbreviations*: C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), Ng (Neogene), P (Permian), Pg (Paleogene), S (Silurian), and Tr (Triassic). Palinuridae-1 (*Panulirus regius*); Palinuridae-2 (*Jasus edwardsii*).

within the Decapoda is highly unstable with further rearrangements proposed recently (*4*). Brusca and Brusca (*8*) summarize nicely the classification schemes for the Decapoda: "Rearrangement of the subtaxa within this order is a popular carcinological pastime, and the classification is far from being stable."

There are as many phylogenetic hypotheses concerning the relationships among the higher decapods as there are experts with opinions (*6*), with no consensus in sight. Historically, the decapod crustaceans were divided into two groups based on mode of locomotion: the Natantia ("swimming" lineages) and the Reptantia ("crawling" lineages) (*9*). However, the "Natantia" was recognized early as paraphyletic and accordingly the Decapoda were reorganized into the Suborders Dendrobranchiata (penaeoid shrimp and their relatives) and Pleocyemata (all other decapods) by Burkenroad (*10, 11*). This taxonomic restructuring is supported by several defining morphological characters (i.e., dendrobranchiate gill structure and pleocyemate brooding of eggs on the female's pleopods) and phylogenetic studies showing the "natant" decapods to be a paraphyletic assemblage

Table 1. Divergence times (Ma) and their credibility intervals (CI) among crabs, shrimps, and lobsters (Decapoda).

Timetree		Estimates			
Node	Time	Ref. (*12*)(a)		Ref. (*12*)(b)	
		Time	CI	Time	CI
1	430.0	437	515–394	423	448–398
2	422.0	423	499–385	421	439–403
3	399.5	417	491–381	382	395–369
4	372.0	385	450–360	359	–
5	336.0	358	420–323	314	325–303
6	318.5	341	402–301	296	309–283
7	278.0	325	384–280	231	–
8	270.0	309	372–261	231	244–218
9	247.0	278	330–235	216	221–211
10	231.5	272	334–220	191	201–181
11	224.0	254	317–203	194	–
12	220.0	255	317–202	185	194–176
13	208.0	239	310–174	177	192–162
14	201.5	263	322–217	140	146–134
15	189.0	215	275–164	163	173–153
16	183.0	181	185–172	185	–
17	175.0	244	306–191	106	–
18	169.0	201	270–139	137	147–127
19	166.0	225	288–172	107	118–96
20	165.0	224	280–177	106	–
21	158.0	164	179–154	152	–
22	154.0	156	167–152	152	–
23	122.0	199	264–140	45	–
24	94.0	149	225–77	39	41–37

Note: Node times in the timetree represent the mean of time estimates from different studies. The divergence times estimated from the TK method incorporating calibrations as minimum ages (a) and the AHRS method using calibrations as fixed ages (b) are shown.

(*12–14*). Most of the studies investigating relationships among the major decapod lineages have been based on morphological characters, which due to the extreme diversity of form, makes it difficult to discern homologous relationships among features in a standard morphological analysis (*15*).

Moreover, there has been surprisingly little molecular phylogenetic study of ordinal-level relationships in this group. Those molecular studies that have been completed have focused on only part of the order (i.e., the "Natantia") and have not included adequate taxon sampling within the Reptantia to evaluate the relationships of the major infraorders (*12, 16*). However, two recent phylogenetic studies have included all the infraorders within the Reptantia, but produced contradictory results. One based solely on molecular data, such as *16S* mtDNA, *18S* and *28S* rDNA, and histone 3 (*H3*) (*5*) and the other combining molecular (*16S* mtDNA, *18S* and *28S* rDNA) and morphological (105 characters) data (*4*). Clearly, work must be done to reconcile these alternative views. Both studies lacked broad taxonomic sampling across the decapod families. A recent study introducing two new nuclear genetic markers for decapod systematics provides yet another view of relationships among the major lineages (*17*). In this latest study with more taxon sampling, Tsang *et al.* (*17*) found the Thalassinidea to be polyphyletic. They found the Stenopodidea and Caridea to form a clade, contrary to Porter *et al.* (*5*) and Ahyong and O'Meally (*4*). The remaining relationships are quite disparate amongst these three latest studies. Like most systematic controversy, this diversity of opinion stems from lack of sufficient characters coupled with inadequate taxon sampling and a disregard for the geologic history of the groups.

The Porter *et al.* (*5*) study was the only study to include fossil calibration points and estimate divergence times among the major lineages. Of course, this may well be premature given the instability of relationships at the moment. Nevertheless, because this is the only study with calibration points and divergence time estimates, we take our divergence estimates from it. The decapod fossil record is continually being updated and reclassified, due to new discoveries of both fossil (*18*) and trace fossil evidence (*19*) and because many fossils are described from incomplete specimens causing uncertainty as to their phylogenetic affinities. Consequently, where possible, fossil references for this study were taken from species where descriptions were based on nearly complete specimens or where recent phylogenetic studies have placed fossil species relative to extant groups (*20–23*). Additionally, the fossils selected for calibration points were chosen based on the precision of the estimated date of the oldest known representative for particular clades, across several levels of divergence relative to the taxa sampling of our phylogeny. Based on these factors and the ages of fossils relative to their placement on the phylogeny, a set of seven fossils were used as calibrations in our analyses (*5*). Additionally, because the Bayesian method chosen for divergence time estimation (see later) requires at least one calibration to consist of an upper limit (maximum age), we set the split between the crayfish Superfamilies Astacoidea and Parastacoidea as an upper limit of 185 Ma based on the splitting of Pangea (*24*). Decapoda divergence times were estimated using the Bayesian method of Thorne and Kishino (*25*) (referred to as TK) and the likelihood heuristic rate-smoothing algorithm (AHRS) of Yang (*26*).

The decapod TK chronogram based on the single maximum likelihood topology and treating the calibration points as minimum or maximum ages places the origin of the Dendrobranchiata and Pleocyemata decapod lineages in the early Silurian (437 Ma; Fig. 2). This implies that the stem line of the decapods emerged even earlier; however, we are unable to estimate this age given our taxon sampling.

Based on the molecular timescales, the radiation of the major decapod lineages occurred rapidly. The reptant lineage originated 385 Ma and all of the major reptant infraorders were present by the late Carboniferous, 60 million years later (Fig. 2, Table 1). The radiation of the extant taxa within each infraorder, however, occurred at different periods of time. The natant lineages have an early origin (423–417 Ma), however the caridean Superfamilies Alpheoidea, Atyoidea, and Palaemonoidea radiate in the early Permian (263 Ma). Among the Brachyuran superfamilies sampled, the Majoidea has the oldest lineage (254 Ma). The Achelata originate 341 Ma, with radiation of the extant lineages (Palinuridae and Scyllaridae) occurring as early as 239 Ma. The Thalassinidea appear 325 Ma, with the radiation of the Callianasoidea occurring at least 173 Ma.

The anomalan lineage originated 309 Ma, with the extant superfamilies radiating between 309 and 244 Ma. The Astacidea lineage originated 325 Ma, with the divergence between the astacid lineages (Astacoidea, Parastacoidea) and the Nephropoidea occurring 278 Ma. Within the astacids, the radiation of the Parastacidae (~134 Ma) occurred earlier than the Astacidae (76 Ma) or the Cambaridae (90 Ma). The Nephropidae radiated as early as 140 Ma, with the genus *Homarus* appearing ~19 Ma.

Although Porter *et al.* (*5*) estimated decapod divergence times without assuming a molecular clock and using multiple molecular markers and fossil calibration points, and these estimates appear to be concordant to a large degree with the decapod fossil record, these analyses come with a number of caveats. The first and most obvious concern is the instability of the phylogenetic estimate itself, upon which all the divergence time analyses are contingent. Given the recent and divergent studies on decapod phylogeny, it appears we are still far from consensus on a stable phylogeny to base divergence estimates (*3–5, 17*). Alternative topologies would possibly generate different estimates for the derived nodes of the infraorders, but the two main conclusions of our analyses—that the Decapoda originated in the Silurian (437 Ma) and have experienced a fast radiation with all of the major infraorders present by the late Carboniferous (325 Ma)—would not change. Furthermore, the monophyletic Pleocyemata and the informal "Reptantia" are consistent in all hypotheses of decapod relationships, and therefore the divergence time estimates of these clades (423 and 385 Ma, respectively) can be used as common time points regardless of the particular arrangement of lineages. There are also inaccuracies associated with the fossil record that are not taken into account (*27*). These analyses assumed that the fossil ages are known with no error. Future advances in divergence time estimation methodologies could take advantage of the Bayesian framework to account for uncertainties in topology estimation and fossil dating and use different priors for rates and divergence times, as those included in Aris-Brosou and Yang (*28*). An extension of this Bayesian approach to include multiple genes and calibrations has recently been implemented (*29*).

Rapid diversification and radiation is characteristic of the Crustacea as a whole (*30*), and this is a trend readily apparent in these divergence time estimates of decapod lineages (Fig. 2). Major decapod radiation events have been proposed to have occurred in the Eocene (Brachyura, *15*), the Cretaceous (*31*), and the Triassic (macrurous forms, *15*). The molecular-based divergence time estimates are older than hypotheses based solely on the fossil record, with the radiation of the "natant" infraorders occurring in the Devonian, the reptant infraorders in the Carboniferous (359–299 Ma), Anomalan diversification in the Permian–Triassic (299–200 Ma), and the Callianassoidea and Palaemonoidea in the Cretaceous (146–66 Ma). As decapod paleontological research is a quickly expanding field of research (*31*), it will be most interesting to track the knowledge of decapod fossil date ranges relative to molecular-based divergence time estimations. Indeed, we hope that the above account will stimulate bringing together paleontological and evolutionary studies to shed further light on the divergence times of the decapod lineages.

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