PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Wolfe JM, Breinholt JW, Crandall KA, Lemmon AR, Lemmon EM, Timm LE, Siddall ME, Bracken-Grissom HD. 2019 A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proc. R. Soc. B* **286**: 20190079.
http://dx.doi.org/10.1098/rspb.2019.0079

Received: 16 January 2019
Accepted: 1 April 2019

Subject Category:
Genetics and genomics

Subject Areas:
taxonomy and systematics, genomics, evolution

Keywords:
Decapoda, Pancrustacea, Crustacea, phylogenomics, anchored hybrid enrichment, systematics

Authors for correspondence:
Joanna M. Wolfe
e-mail: jowolfe@g.harvard.edu
Heather D. Bracken-Grissom
e-mail: hbracken@fiu.edu

Electronic supplementary material is available online at http://dx.doi.org/10.6084/m9.figshare.c.4462862.

THE ROYAL SOCIETY PUBLISHING

A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans

Joanna M. Wolfe[1,2,3], Jesse W. Breinholt[4,5], Keith A. Crandall[6,7], Alan R. Lemmon[8], Emily Moriarty Lemmon[9], Laura E. Timm[10], Mark E. Siddall[1] and Heather D. Bracken-Grissom[10]

[1]Division of Invertebrate Zoology and Sackler Institute of Comparative Genomics, American Museum of Natural History, New York, NY 10024, USA
[2]Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA
[3]Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
[4]Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA
[5]RAPiD Genomics, Gainesville, FL 32601, USA
[6]Computational Biology Institute, The George Washington University, Ashburn, VA 20147, USA
[7]Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20012, USA
[8]Department of Scientific Computing, Florida State University, Dirac Science Library, Tallahassee, FL 32306, USA
[9]Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA
[10]Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA

JMW, 0000-0001-6708-8332; JWB, 0000-0002-3867-2430; KAC, 0000-0002-0836-3389; EML, 0000-0001-5911-6102; LET, 0000-0002-7285-0261

Comprising over 15 000 living species, decapods (crabs, shrimp and lobsters) are the most instantly recognizable crustaceans, representing a considerable global food source. Although decapod systematics have received much study, limitations of morphological and Sanger sequence data have yet to produce a consensus for higher-level relationships. Here, we introduce a new anchored hybrid enrichment kit for decapod phylogenetics designed from genomic and transcriptomic sequences that we used to capture new high-throughput sequence data from 94 species, including 58 of 179 extant decapod families, and 11 of 12 major lineages. The enrichment kit yields 410 loci (greater than 86 000 bp) conserved across all lineages of Decapoda, more clade-specific molecular data than any prior study. Phylogenomic analyses recover a robust decapod tree of life strongly supporting the monophyly of all infraorders, and monophyly of each of the reptant, 'lobster' and 'crab' groups, with some results supporting pleocyemate monophyly. We show that crown decapods diverged in the Late Ordovician and most crown lineages diverged in the Triassic–Jurassic, highlighting a cryptic Palaeozoic history, and post-extinction diversification. New insights into decapod relationships provide a phylogenomic window into morphology and behaviour, and a basis to rapidly and cheaply expand sampling in this economically and ecologically significant invertebrate clade.

1. Introduction

Decapod crustaceans, broadly categorized into 'shrimp', 'lobsters' and 'crabs', are embedded in the public consciousness due to their importance as a global food source worth over $24 billion [1]. Several ornamental species are popular in the pet trade [2], and crayfish may be promising models for cancer and ageing research [3]. Furthermore, decapods are a major faunal

component of a bewildering variety of global habitats: open ocean, seafloor vents and seeps, caves, coral reefs, mangroves and estuaries, intertidal mud and sand, freshwater streams and lakes, semi-terrestrial locations and in symbiosis with other animals (figure 1). Decapods have diversified over the course of 455 million years, with over 15 000 living and 3000 fossil species recognized in approximately 233 families [4,5]. Despite the economic and ecological significance of the clade, higher-level phylogenetic relationships among decapods have proven recalcitrant.

The majority of work is restricted to studies using morphology [6–8], up to nine targeted mitochondrial and nuclear genes [5,9–18], and complete mitogenomes of 13 genes [19,20]. Mitogenomic data can be problematic for reconstructing ancient nodes [21], and indeed, deeper relationships receive poor support [20]. As part of a larger analysis, decapods were included in a recent transcriptomic study [22], but with limited taxon sampling within the order. This plurality of results, several based on the same underlying data [21], has reported conflicting deep relationships among decapods. Without a robust phylogeny, comparative inferences about morphology, development, ecology and behaviour are limited.

Herein, phylogenomic sequencing of nuclear genes is leveraged for the first time in decapods, using anchored hybrid enrichment (AHE), a technique previously applied to vertebrates [23], plants [24] and clades of terrestrial arthropods that have diverged at least 100 Myr more recently than decapods [25–27]. AHE targets conserved coding regions that are flanked by less conserved sequence regions, with the goal of optimizing phylogenetic informativeness at multiple levels of divergence [23]. Unlike popular transcriptomic approaches, AHE does not require fresh or specially preserved tissues (critical as many lineages are rare, confined to the deep sea and/or have complicated life histories). Instead, AHE allows the use of ethanol-preserved specimens; however, prior genomic and/or transcriptomic data are required to determine genomic target regions.

Here, we combine new genomic and transcriptomic sequences to build AHE probes spanning all of Decapoda, sequenced for 86 species and seven outgroups. The enrichment kit we constructed can easily be used by the systematics community for future studies of decapod evolution. Ours is the first example of a strongly supported phylogenomic analysis including almost all major decapod lineages, and the largest dataset yet compiled for this group. With the inclusion of 19 vetted fossil calibration points, we also present the first divergence time analysis incorporating a well-supported topology for the entire decapod clade.

2. Methods

(a) Probe design

Target AHE loci were identified using our previous workflows [25–27] (electronic supplementary material, figure S1). Targets were based on genomic resources from 23 decapod species (electronic supplementary material, table S1), including new genomic data from nine species (approx. 6–31× coverage; electronic supplementary material, table S2) and four new transcriptomes (electronic supplementary material, tables S3 and S4). Best-matching reads were identified in the two highest-recovery taxa (table 1, refsA), as well as reference sequences from the red flour beetle *Tribolium castanaeum* [25,27], resulting in 823 preliminary AHE target sequences. As in [25], we screened exemplar transcriptomes from five major decapod lineages (table 1, refsB) for the best-matching transcript, and aligned in MAFFT v7.023 [28], requiring representation in at least four of the lineages and resulting in 352 final AHE targets.

We used additional genomic resources (electronic supplementary material, table S1) to build alignments from six major lineages representing the diversity of decapods (Achelata, Anomura, Astacidea, Brachyura, Caridea, Dendrobranchiata). Raw reads from these species were mapped to the references above to extend probes into flanking regions [25]. For each combination of target region and major lineage, an alignment containing all recovered sequences was created in MAFFT. We identified and masked intronic and repetitive regions, based on the best-matching genomic region in the published red cherry shrimp (*Neocaridina denticulata*) genome [29]. Probes were tiled at 4× density across all sequences in each alignment and divided into two Agilent SureSelect XT kits (electronic supplementary material, table S5).

(b) Anchored hybrid enrichment sequencing and dataset assembly

From the Florida International Crustacean Collection, 89 species of decapods and seven additional crustaceans were selected for AHE sequencing (electronic supplementary material, table S6). High molecular weight DNA was extracted from gills, legs or pleon tissue using the DNeasy Blood and Tissue Qiagen Kit following the manufacturer's protocols. A post-extraction RNase Treatment was performed on all samples to remove RNA contamination. AHE libraries were prepared from DNA extracts [23], pooled and sequenced in a single Illumina HiSeq2500 lane with 2 × 150 paired end reads. Due to high divergence across Decapoda, we screened resulting AHE data for single-copy exons in the reference genome of the Chinese mitten crab, *Eriocheir sinensis* [30]. A total of 675 exons were identified with approximately 40% coverage across AHE sequenced taxa (as the 352 final AHE targets included non-coding regions, there are thus more exons than final targets). The *E. sinensis* amino acid sequences for these 675 exon-based reference loci were used for iterative baited assembly (IBA) and orthology screening following Breinholt *et al*. [26], except where noted in electronic supplementary material, Extended Methods S1f–g.

(c) Phylogenomics

The main data matrix used for phylogenetic analysis comprised 410 exon-based loci with at least 60% of the taxa represented in each locus (electronic supplementary material, figure S2). We inferred phylogenetic relationships using several methods (electronic supplementary material, Extended Methods S1i–j). Bayesian inference was conducted on amino acid matrices with PhyloBayes v. 3.3f [31] using the CAT-GTR+G substitution model. Maximum-likelihood analyses used IQ-TREE v. 1.6.3 [32] on 149 best-fitting partitions identified by PartitionFinder [33]. Coalescent methods were applied with gene trees inferred in IQ-TREE as inputs to estimate the species tree in ASTRAL-III v. 5.6.1 [34].

(d) Divergence time estimation

We identified 19 fossil calibrations across Decapoda, based on best practices [35] (electronic supplementary material, Extended Data S2 and table S7). All internal calibrations used soft bounds with 5% of the probability distribution allowed outside of the input ages. We applied a γ-distributed root prior based on crown Eumalacostraca [35] with a mean age of 440 Ma and s.d. 20 Myr. Divergence times were estimated in PhyloBayes using a fixed topology from our preferred tree (figure 2), the

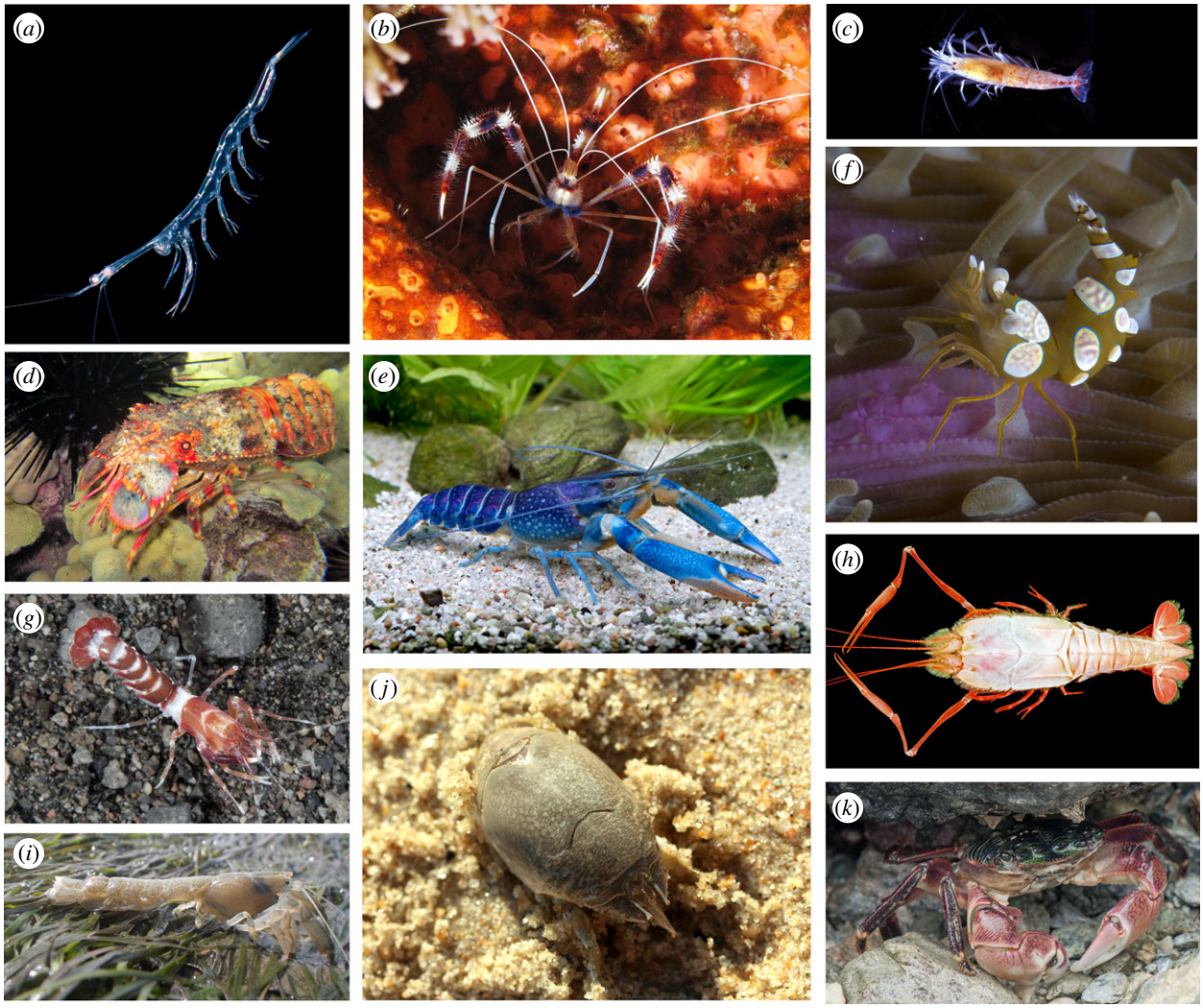

Figure 1. Representatives of major decapod lineages. (*a*) *Lucifer* sp. (southeast Florida, USA) (Dendrobranchiata); (*b*) *Stenopus hispidus* (Komodo, Indonesia) (Stenopodidea); (*c*) *Procaris chacei* (Bermuda) (Procarididea); *(d) Arctides regalis* (Maui, Hawaii, USA) (Achelata); (*e*) *Cherax quadricarinatus* (aquarium specimen) (Astacidea); (*f*) *Thor amboinensis* complex (Ternate, Indonesia) (Caridea); (*g*) *Axiopsis serratifrons* (Bali, Indonesia) (Axiidea); (*h*) *Stereomastis sculpta* (specimen ULLZ 8022) (Polychelida); (*i*) *Upogebia* cf. *pusilla* (Arcachon Bay, France) (Gebiidea); (*j*) *Emerita talpoida* (Westerly, Rhode Island, USA) (Anomura); (*k*) *Pachygrapsus crassipes* (Catalina Island, California, USA) (Brachyura). Photo credits: (*a*) L. Ianniello; (*b*) A. Vasenin, licence CC-BY-SA; (*c*) T. M. Iliffe; (*d*,*k*) J. Scioli; (*e*) C. Lukhaup; (*f*) C. H. J. M. Fransen; (*g*) A. Ryanskiy; (*h*) D. L. Felder; (*i*) X. de Montaudouin; (*j*) J. M. Wolfe. (Online version in colour.)

CAT-GTR+G substitution model on the top 50 loci [36], both the autocorrelated CIR and uncorrelated UGAM clock models, and two runs of four MCMC chains each.

3. Results and discussion

(a) Target capture success

We successfully sequenced targeted regions from 94 species representing 11 of 12 major decapod lineages. We attempted to include *Neoglyphea inopinata*, one of only two living members of Glypheidea (deep sea lobsters with a diverse fossil record); however, multiple attempts to extract DNA from the limited tissue available to us did not render high-quality genomic extractions (however, see [19] for mitogenome data). All other taxa we sequenced were successful, producing an average of 3 299 141 reads, with an average of 332 exon-based loci and range of 57–405 exon-based loci across samples (electronic supplementary material, figure S2 and table S8). The final 410 exon-based loci ranged from 66 to 1683 bp with a total alignment length of 86 322 bp (table 2). Our probes were effective across Decapoda, yielding more than 350 exon-based loci in all major lineages except Procarididea. Using our enrichment kit (probe sequences available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k7505mn [37]), it will be possible for the community to easily sequence the same loci for large-scale phylogenomics spanning any decapods of interest.

The majority of nodes were congruent across different analyses, albeit with different levels of support (figure 2; electronic supplementary material, figures S3–S10), demonstrating that our large dataset is mostly cohesive and can resolve deep splits. We use the results from Bayesian inference with the CAT-GTR + G amino acid substitution model as the 'best' topology (figure 2, first support square). This topology does not precisely match any previous result [18,19,21]. We include this tree over the Bayesian recoded topology (electronic supplementary material, figure S4) because it had more nodes resolved, with higher support. Nucleotide analyses (electronic supplementary material, figures S7–S10) were not preferred because of both saturation in our data (electronic supplementary material, figure S11) and disagreement among results of different analyses [38].

Table 1. Genomes and transcriptomes used for preliminary probe design.

major lineage	genus	species	refsA	refsB	type	source
Dendrobranchiata	*Litopenaeus*	*vannamei*		x	transcriptome	NCBI PRJEB5112
Caridea	*Lysmata*	*wurdemanni*		x	transcriptome	new
Astacidea	*Cherax*	*quadricarinatus*		x	transcriptome	NCBI PRJNA255337
Astacidea	*Homarus*	*americanus*		x	transcriptome	new
Astacidea	*Procambarus*	*clarkii*	x		genome	new
Anomura	*Coenobita*	*clypeatus*	x		genome	new
Anomura	*Paralithodes*	*camtschaticus*		x	transcriptome	new
Brachyura	*Mithraculus*	*sculptus*		x	transcriptome	new

(b) Deep evolutionary history of decapods

Monophyly of Decapoda is supported in amino acid analyses (figure 2); some nucleotide results find *Lucifer* (an epipelagic dendrobranchiate shrimp; figure 1*a*) experiencing long-branch attraction towards outgroups. The most classical division in decapods, between suborders Dendrobranchiata (most food shrimp/prawns) and Pleocyemata (all other decapods), is supported by the unrecoded amino acid matrices (pp = 0.97/bootstrap = 83%; figure 2; electronic supplementary material, figure S3), and contradicted by all others. The alternative hypothesis recovered is the natant (shrimp-like) decapods, with Dendrobranchiata, Stenopodidea, Procarididea and Caridea forming a clade (electronic supplementary material, figures S4–S6), sometimes with less than 50% support (electronic supplementary material, figures S8 and S9). We tentatively support Dendrobranchiata and Pleocyemata, similar to transcriptomic results [22]. The polarity of the major characters separating these two clades, the lecithotrophic free-living nauplius larva in dendrobranchiates (as opposed to the egg-nauplius in pleocyemates), and brood care with eggs attached to the pleopods in pleocyemates, depends on whether Euphausiacea (krill) are most closely related to decapods, which we did not test. If euphausiids are the sister group of decapods, then pleocyemates have lost the free-living nauplius [39]; otherwise, the free-living nauplius is convergent in euphausiids and dendrobranchiates [40].

Within Pleocyemata, all infraorders receive full support for their monophyly (figure 2). A single origin of the reptant or 'crawling/walking' decapods (Achelata, Polychelida, Astacidea, Axiidea, Gebiidea, Anomura and Brachyura) is strongly supported. Numerous morphological characters have suggested monophyly of Reptantia, such as a dorsoventrally flattened pleon, calcified body, anterior articulation of the mandibles formed by an elongated molar process, anteroposteriorly rotated walking legs, a short first pleomere and spermatozoa with at least three nuclear arms [6]. Monophyly of Reptantia is concordant with most previous results [21], and almost certainly includes Glypheidea [19].

Our posterior age estimate for the root of crown Decapoda (mean in the Late Ordovician at 455 Ma, 95% CI 512–412 Ma; figure 3) was substantially older than most previous estimates [5,9,11,13,41], which largely fixed crown decapods in the Devonian. Our data include non-decapod outgroups, and the more crownward position of the Devonian calibration fossil *Palaeopalaemon newberryi* within Reptantia [35,42], resulting in older ages for deeper nodes.

(c) Evolutionary history of shrimp

Dendrobranchiate relationships are consistent (figure 2), except the aforementioned long-branch attraction of *Lucifer* to outgroups. Amino acid results place this perplexing decapod with Sergestidae (pelagic shrimp), as suggested by morphological analysis, especially spermatophore morphology [43]. Crown dendrobranchiates diverged in the Late Devonian (figure 3), with the two main clades Sergestoidea and Penaeoidea both diverging in the Pennsylvanian (approx. 100 Myr prior to previous estimates [44]). Although our mean posterior age of crown Penaeidae (134 Ma) is younger than the phylogenetically justified Late Jurassic crown fossil *Antrimpos speciosus* [44], which we did not use as a calibration, our 95% CI encompasses the fossil age of 151 Ma.

Among the pleocyemate shrimps, a sister group relationship between Stenopodidea (cleaner/boxer shrimp) and (Procarididea + Caridea) is strongly supported (figure 2); similar topologies have been found from molecules and morphology [7,10,22]. The sister group relationship of Procarididea (anchialine shrimp) and Caridea is supported by four-gene molecular analyses, the extended second pleurite overlapping the first and third somites, phyllobranchiate gills and the form of the telson and uropods [5,45].

Within Caridea, we sampled eight families, compared with a maximum of 27 families in previous studies [17,46]. Our results are broadly concordant within the limits of the taxa we sequenced, producing a strongly supported backbone topology upon which future studies can build. The deepest split within carideans was between Atyidae (freshwater shrimp) and all others (figure 2). Support for an alternative deep split of Atyidae and Oplophoridae from all other carideans was in some cases weak (electronic supplementary material, figures S8 and S10), or a polytomy (electronic supplementary material, figures S5 and S6). We support findings that the traditional concept of 'Alpheoidea' (snapping shrimp and allies) is not monophyletic and contains Palaemonidae (approx. 200 genera [17,46]). This larger Alpheioidea + Palaemonidae clade contains the majority of caridean diversity, possibly including Amphionidacea [18]. We inferred younger posterior ages (figure 3) for the Procaridea-Caridea split (Pennsylvanian), and crown Caridea (Late Triassic), compared with previous analyses [5,47].

(d) Evolutionary history of lobsters

Few previous analyses (from six or fewer nuclear genes [10,15,16]) have recovered monophyly of the overall lobster

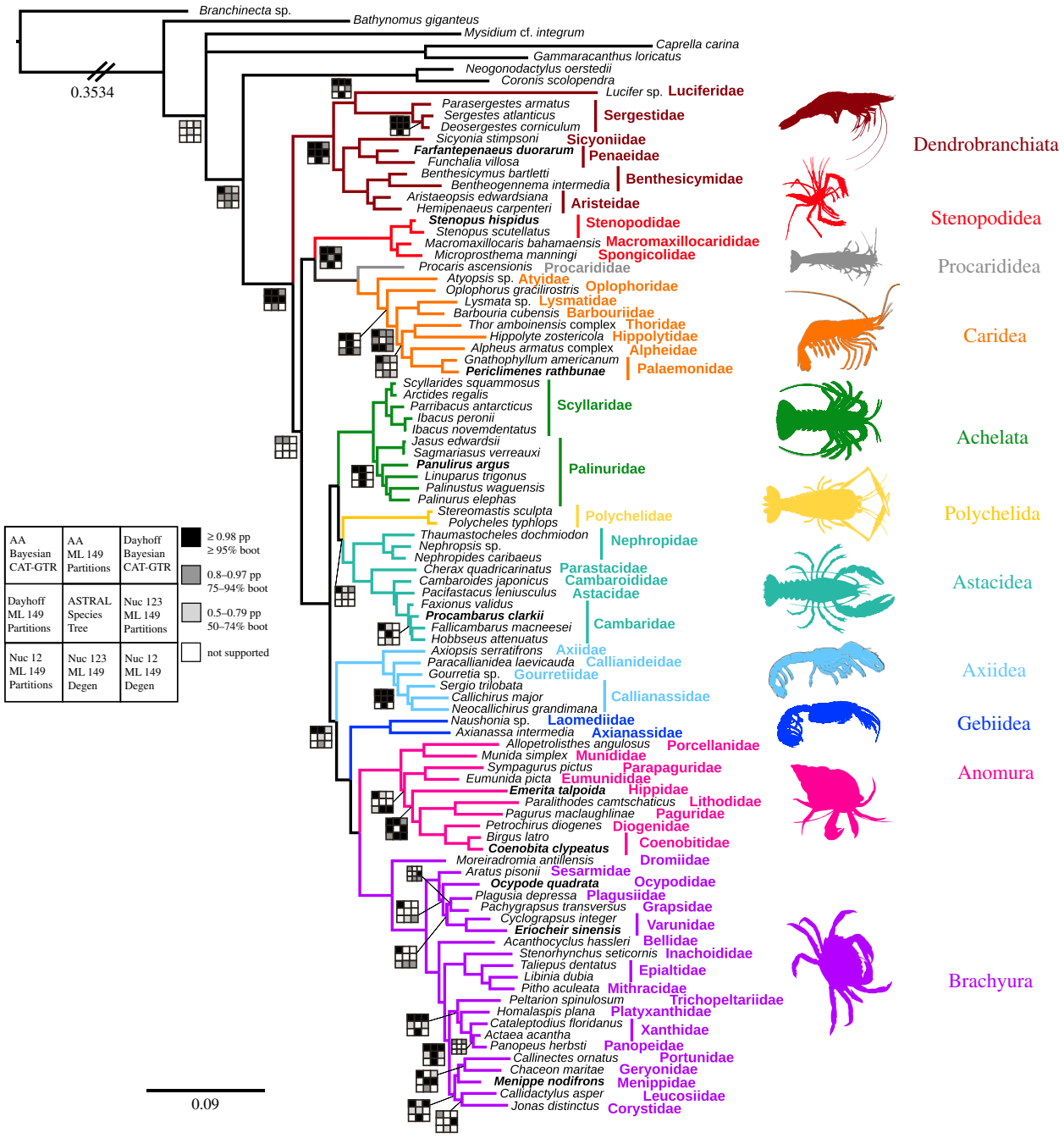

Figure 2. Phylogenetic hypothesis for Decapoda based on the topology from the Bayesian CAT-GTR+G analysis. Unlabelled nodes are considered strongly supported. Nodes where at least one analysis rejected the depicted topology are illustrated with rug plots showing the support values from each analysis. In rug plots, the illustrated topology is first row, first column. All alternative topologies are visualized as electronic supplementary material, figures S3–S10. Species used for probe design by shotgun whole genome sequencing in bold text. Organism silhouettes are from PhyloPic (phylopic.org). (Online version in colour.)

body plan, which receives full support in all our analyses (figure 2). The relationships among lobster infraorders, however, are poorly resolved. Amino acid analyses suggest a sister group relationship between Polychelida (blind deep sea lobsters) and Astacidea (clawed lobsters and crayfish), some with less than 80% support (electronic supplementary material, figures S3 and S6). Recent mitogenomic work shows Glypheidea intervening as the sister group of Polychelida [19,20] within a paraphyletic lobster grouping. It is difficult to predict how the addition of Glypheidea would affect our topology, as it is possible that the mitochondrial grouping results from long-branch attraction (both Glypheidea and Polychelida have species-poor crown groups and morphologically diverse stem groups that pre-date their crowns by greater than 150 Myr [14,48]).

Achelata, with the crown members united by their unique phyllosomal larval stage, are monophyletic (figure 2). Of the two constituent families, Scyllaridae (slipper lobsters) are monophyletic in all analyses. Palinuridae (spiny lobsters), however, are paraphyletic in some analyses (electronic supplementary material, figures S4, S7 and S10). Based on monophyletic Palinuridae (figure 3), their crown divergence occurred in the Late Triassic, and crown Scyllaridae in the Early Cretaceous (87 Myr younger than [14]). These age estimates pre-date the wealth of Jurassic and Cretaceous fossil achelatan larvae [49], implying bizarre stem-group representatives may have persisted throughout the Mesozoic alongside the crown. Our phylogenetic results also support the division of Palinuridae into distinct clades of Silentes and Stridentes, the latter bearing an enlarged antennular

Table 2. Data matrix statistics.

matrix	no. exon-based loci	no. amino acids	no. base pairs	average locus length (aa or bp, respectively)	% informative sites	% missing data	% GC content
amino acid	410	28 774	n/a	70	27	20	n/a
amino acid Dayhoff-6 recoding	410	28 774	n/a	70	14	20	n/a
amino acid top 50	50	5994	n/a	120	39	25	n/a
nucleotide	410	n/a	86 322	210	48	20	48.6
nucleotide positions 1 + 2	410	n/a	57 548	140	24	20	45.8
nucleotide Degen recoding	410	n/a	86 322	210	11	20	45.2
nucleotide Degen positions 1 + 2	410	n/a	57 548	140	17	20	43.8

plate used in sound production in adults [14,50]. The palinurid genera that are close to Scyllaridae in alternative results are the included members of Silentes, further supporting the auditory behaviour of Stridentes as a clade apomorphy, having diversified in the Jurassic.

Relationships within Astacidea were similar to a combined Sanger sequencing and taxonomic synthesis approach [51,52]. Crown Astacidea diverged in the Pennsylvanian, and crown Nephropidae ('true' lobsters) diverged in the Early Jurassic (figure 3). The split between Southern Hemisphere crayfish (Parastacidae) and Northern Hemisphere crayfish occurred in the Middle Triassic around 241 Ma, prior to the breakup of Pangaea [14].

(e) Evolutionary history of mud/ghost shrimp

The mud/ghost shrimps Axiidea and Gebiidea (formerly Thalassinidea) are not monophyletic [53]. Most of our amino acid analyses produce a paraphyletic mud shrimp group (figure 2), with limited but clear support for Axiidea as the sister group to the Gebiidea and Meiura clade (i.e. the 'Monochélie', or Monochelia, of de Saint Laurent [54], which is strongly supported herein). There is precedent for our mud shrimp and crab clade based on morphology [6], Sanger [13] and mitogenomic results [19]. The alternative hypothesis is mud shrimp polyphyly, with Axiidea as sister group to the lobster clade (electronic supplementary material, figures S5, S7 and S8). The loss of chelae on pereiopods posterior to the first was proposed as convergent in Meiura and members of Gebiidea [6]; our topology suggests that this character is the eponymic synapomorphy of the Monochelia [53,54]. Our divergence time analysis suggests that the mud shrimp + crab clade diverged in the Late Devonian (figure 3), with crown Monochelia diverging in the Mississippian, and both crown Axiidea and crown Gebiidea in the Late Triassic. These posterior age estimates are older than previous studies [13] or a literal interpretation of the fossil record [55].

(f) Evolutionary history of crabs

The sister group relationship between Anomura ('false' crabs) and Brachyura (true crabs), forming together the Meiura, is strongly supported (figure 2). This is important because several Sanger analyses [5,9,12,15,18] purported to refute meiuran monophyly. Several synapomorphies have been proposed, such as a short asymmetric flagella on the antennule, bent exopods on the maxillipeds and fusion of ganglia [6]. Carcinization, the overall crab-like body plan including a flattened carapace with lateral margins, fused sternites and strongly bent pleon [56] has been suggested as a developmentally co-opted trait of Meiura with a 'tendency' to evolve repeatedly [57]. Our topology suggests at least three separately carcinized clades in Anomura, and one in Brachyura; however, increased taxon sampling will complicate character distribution [13,56] and introduce secondary losses [58,59].

Within Anomura, we recover support for Hippidae (mole crabs) as the sister group of 'Paguroidea' (king crabs and most hermit crabs; figure 2) rather than the outgroup to all other anomurans [13,60]. Precedent for a sister group relationship of Hippidae to Paguroidea comes from mitochondrial gene rearrangements [57], the shape of the carapace and sternites [61] and characters of the foregut ossicles [62]. As in past molecular-only results [13,60],

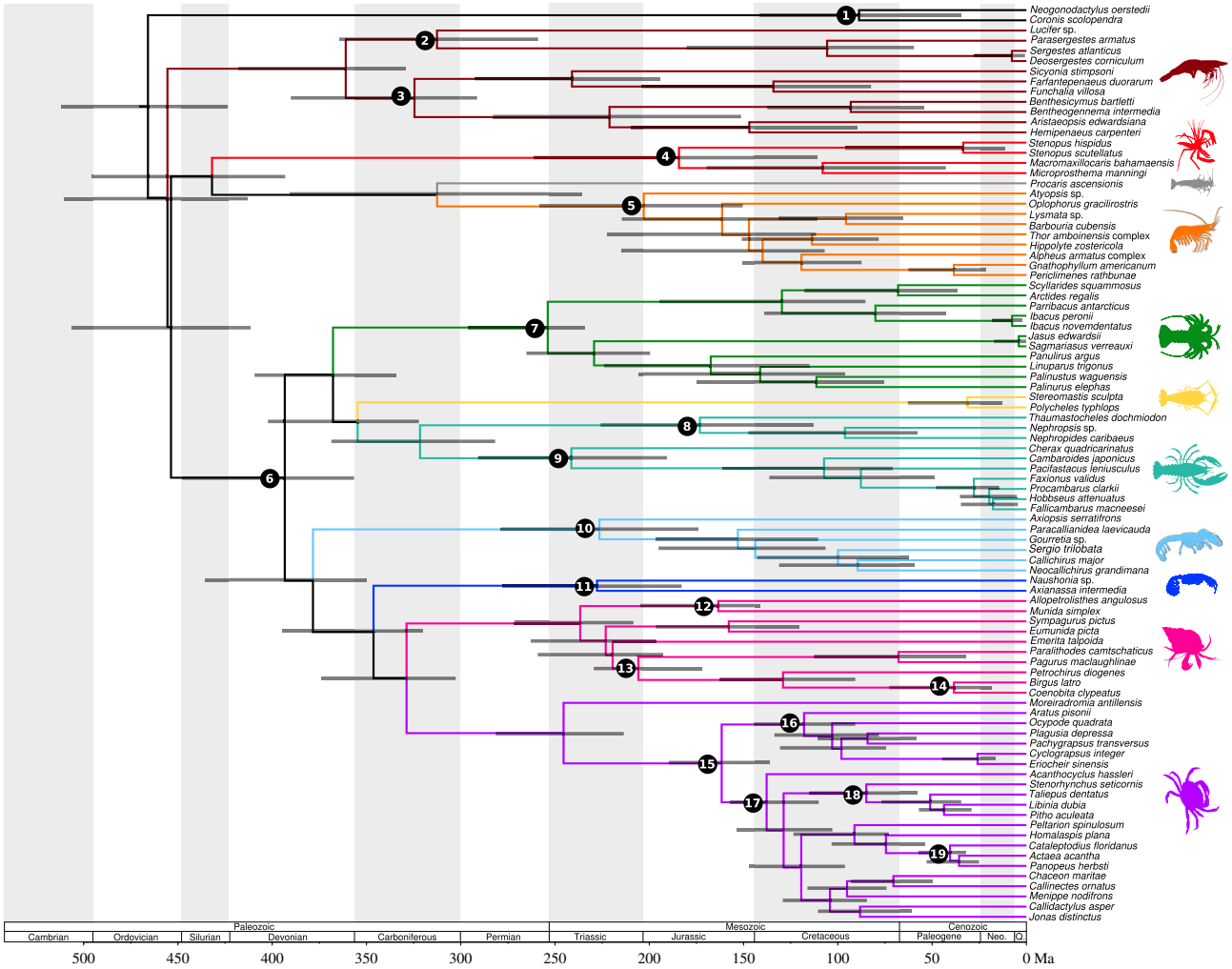

Figure 3. Divergence time estimates for Decapoda based on the topology in figure 2. Posterior ages were estimated in PhyloBayes using the CAT-GTR+G substitution model, the CIR clock model and a γ distributed root prior of 440 Ma $\pm$ 20 Myr. Horizontal shaded bars represent 95% confidence intervals. Numbered circles represent nodes with fossil calibrations. (Online version in colour.)

Parapaguridae are more closely related to Eumunididae (squat lobsters), rendering hermit crabs polyphyletic with potentially convergent evolution of asymmetrical pleons [60]. Recent mitogenome research [20] displayed dramatically different relationships among Anomura, including hermit crab polyphyly, but mitochondrial data are weaker for deep splits, as they represent a single locus. Posterior divergence estimates (figure 3) from crown Anomura to crown Paguroidea span a narrow interval of about 22 Myr in the Late Triassic, with each node about 20 Myr older than previous estimates [13]. We recover these posterior ages based on only soft maximum priors (i.e. not minima) from the Late Triassic *Platykotta akaina* [13], as it may be placed outside the meiuran crown group [63]. We also observe a conflicting split between Galatheoida and all other anomurans (figure 2), where preferred analyses support previous molecular-only results [13,58]. These relationships could be clarified by sampling additional squat lobster and hermit crab groups.

Our analyses strongly support the traditional morphological divisions within Brachyura (figure 2), with podotremes (represented by Dromiidae, or sponge crabs; gonopores located on the pereiopod coxa) as the deepest split in the Late Triassic (figure 3), and eubrachyurans divided into Thoracotremata (gonopores on the sternum) and Heterotremata (female gonopores on the sternum, male gonopores on the coxa). Each of the two eubrachyuran branches diverged in the Early Cretaceous, with diversification among families mainly in the Late Cretaceous. Within Thoracotremata, all our results reject monophyletic Grapsoidea (figure 2). The focal tree supports Sesarmidae as outgroup to other families; otherwise, it is either Plagusiidae (electronic supplementary material, figures S3–S5) or Varunidae (electronic supplementary material, figure S6). Within Heterotremata, we recover support for several clades that have been previously defined [11], at least within our taxon sampling: Majoidea (spider and decorator crabs: Epialtidae, Inachoididae and Mithracidae), Xanthoidea (mud crabs: Panopeidae and Xanthidae) and Portunoidea (swimming crabs: Portunidae and Geryonidae). Within Majoidea, the family Epialtidae is paraphyletic with respect to Mithracidae, suggesting continued evaluation of larval morphology [11,64,65]. This is the best-supported region of the heterotreme tree. As we only sampled 19 of 96 total brachyuran families, important AHE target taxa include Raninidae, Cyclodorippidae, and Homolidae (all podotremes), Gecarcinidae and Pinnotheridae (pea crabs, within thoracotremes), primary freshwater heterotremes [11] and xanthoid relatives.

(g) Divergence times

We present the posterior age results from divergence time analysis using the CIR clock model (figure 3). Unlike in

broader studies of arthropods [66], posterior credibility intervals were similar for many deep nodes regardless of which clock model we applied (electronic supplementary material, figures S12–S13), although the CIR model was more precise overall than UGAM. The posteriors hewing close to the effective prior are not necessarily problematic [66–68]. Similarities between effective prior and posterior distributions are also present for nodes we did not explicitly calibrate (electronic supplementary material, figure S13b), though they are free to vary according to the birth-death tree prior. This effect is less pronounced for non-reptantian nodes, which have scant fossil information and essentially uniform maxima [69].

Overall, our divergence time estimates imply a significant cryptic history for decapods (figure 3), which may motivate revision of Palaeozoic fossils that have been suggested as decapods [63,70–72], in a more explicit phylogenetic framework. We infer a lack of cladogenesis among the deep lineages during the Permian, followed by diversification in most crown groups in the Triassic. Although molecular data alone cannot accurately estimate diversification [73], it is striking that our divergence time analysis infers the modern decapod clades replaced ecological roles following the largest mass extinction 251 Ma, and became important members of the Modern evolutionary fauna [74]. Moreover, the most species-rich lineages, Caridea, Anomura and Brachyura, each show deep divergences during the Jurassic and family-level diversification in the Cretaceous, concurrent with the radiation of modern reef-building corals [75], a major habitat and source of biodiversity for these crustaceans [76,77].

4. Conclusion

Our well-resolved dated phylogeny may inform comparative evolutionary topics, such as the evolution of visual systems in deep sea and cave environments [51,78], evolution of major body plan features [13,56,79], the role of symbiosis [80,81], evolution of behaviour [82], macroevolutionary trends through time [76,83], conservation biology and vulnerability to climate change [41,84] and more. Our new enrichment kit permits an inexpensive expansion of taxon sampling across Decapoda, via our large-scale matrix of loci conserved across 450 Myr, to accelerate discoveries in a fascinating invertebrate clade.

Data accessibility. Extended methods and fossil calibrations, electronic supplementary material, figures S1–S13 and tables S1–S8 are available as electronic supplementary material. Raw reads are available in the NCBI BioProject: PRJNA508807. Assemblies, probe sequences, matrices and tree files data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k7505mn [37]. Scripts for this paper are available at https://github.com/jessebreinholt/proteinIBA.git.

Authors' contributions. H.D.B.-G. and K.A.C. conceived the project, J.M.W., K.A.C., M.E.S. and H.D.B.-G. acquired samples, L.E.T. and H.D.B.-G. extracted DNA, J.M.W. and M.E.S. extracted RNA, A.R.L. and E.M.L. developed probes and conducted sequencing, J.W.B. developed, assembled, screened orthologues and produced matrices, J.W.B. and J.M.W. conducted phylogenetic analysis, J.M.W. vetted fossil constraints, performed divergence time analyses and wrote the manuscript with input from all authors.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by: AMNH Gerstner Scholarship and Lerner-Gray Fellowship (J.M.W.), NSF-EAR 1615426 (J.M.W.), NSF-DEB 1556059 (H.D.B.-G.) and Florida International University.

Acknowledgements. We thank Mercer Brugler, Jorge Perez-Moreno, Shaina Simon and Juliet Wong for assistance with extractions, and Michelle Kortyna, Sean Holland and Ameer Jalal for assistance with probe design and data collection. We acknowledge use of the Engaging Cluster at MGHPCC. This is contribution no. 127 for the Center for Coastal Oceans Research in the Institute for Water and Environment, Florida International University.

References

1. Bondad-Reantaso MG, Subasinghe RP, Josupeit H, Cai J, Zhou X. 2012 The role of crustacean fisheries and aquaculture in global food security: past, present and future. *J. Invertebr. Pathol.* **110**, 158–165. (doi:10.1016/j.jip.2012.03.010)
2. Calado R, Lin J, Rhyne AL, Araujo R, Narciso L. 2003 Marine ornamental decapods—popular, pricey, and poorly studied. *J. Crustacean Biol.* **23**, 963–973. (doi:10.1651/C-2409)
3. Vogt G. 2018 Investigating the genetic and epigenetic basis of big biological questions with the parthenogenetic marbled crayfish: a review and perspectives. *J. Biosci.* **43**, 189–223. (doi:10.1007/s12038-018-9741-x)
4. De Grave S *et al.* 2009 A classification of living and fossil genera of decapod crustaceans. *Raffles Bull. Zool.* **21**, 1–109.
5. Bracken HD, De Grave S, Toon A, Felder DL, Crandall KA. 2010 Phylogenetic position, systematic status, and divergence time of the Procaridididea (Crustacea: Decapoda). *Zool. Scr.* **39**, 198–212. (doi:10.1111/j.1463-6409.2009.00410.x)
6. Scholtz G, Richter S. 1995 Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zool. J. Linn. Soc.* **113**, 289–328. (doi:10.1111/j.1096-3642.1995.tb00936.x)
7. Dixon CJ, Ahyong ST, Schram FR. 2003 A new hypothesis of decapod phylogeny. *Crustaceana* **76**, 935–975. (doi:10.1163/156854003771997846)
8. Ahyong ST, O'Meally D. 2004 Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. *Raffles Bull. Zool.* **52**, 673–693.
9. Porter ML, Pérez-Losada M, Crandall KA. 2005 Model-based multi-locus estimation of decapod phylogeny and divergence times. *Mol. Phylogenet. Evol.* **37**, 355–369. (doi:10.1016/j.ympev.2005.06.021)
10. Tsang LM, Ma KY, Ahyong ST, Chan T-Y, Chu KH. 2008 Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Mol. Phylogenet. Evol.* **48**, 359–368. (doi:10.1016/j.ympev.2008.04.009)
11. Tsang LM, Schubart CD, Ahyong ST, Lai JCY, Au EYC, Chan T-Y, Ng PKL, Chu KH. 2014 Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Mol. Biol. Evol.* **31**, 1173–1187. (doi:10.1093/molbev/msu068)
12. Bracken HD, Toon A, Felder DL, Martin JW, Finley M, Rasmussen J, Palero F, Crandall KA. 2009 The decapod tree of life: compiling the data and moving toward a consensus of decapod evolution. *Arthropod. Syst. Phylog.* **67**, 99–116.
13. Bracken-Grissom HD, Cannon ME, Cabezas P, Feldmann RM, Schweitzer CE, Ahyong ST, Felder DL, Lemaitre R, Crandall KA. 2013 A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evol. Biol.* **13**, 128. (doi:10.1186/1471-2148-13-128)
14. Bracken-Grissom HD *et al.* 2014 The emergence of lobsters: phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Syst. Biol.* **63**, 457–479. (doi:10.1093/sysbio/syu008)
15. Toon A, Finley M, Staples J, Crandall KA. 2009 Decapod phylogenetics and molecular evolution. In

Decapod crustacean phylogenetics (eds JW Martin, KA Crandall, DL Felder), pp. 14–23. Boca Raton, FL: CRC Press.

16. Bybee SM, Bracken-Grissom HD, Hermansen RA, Clement MJ, Crandall KA, Felder DL. 2011 Directed next generation sequencing for phylogenetics: an example using Decapoda (Crustacea). *Zool. Anz.* **250**, 497–506. (doi:10.1016/j.jcz.2011.05.010)
17. Aznar-Cormano L, Brisset J, Chan T-Y, Corbari L, Puillandre N, Utge J, Zbinden M, Zuccon D, Samadi S. 2015 An improved taxonomic sampling is a necessary but not sufficient condition for resolving inter-families relationships in Caridean decapods. *Genetica* **143**, 195–205. (doi:10.1007/s10709-014-9807-0)
18. De Grave S, Chan T-Y, Chu KH, Yang C-H, Landeira JM. 2015 Phylogenetics reveals the crustacean order Amphionidacea to be larval shrimps (Decapoda: Caridea). *Sci. Rep.* **5**, 17464. (doi:10.1038/srep17464)
19. Tan MH, Gan HM, Dally G, Horner S, Moreno PAR, Rahman S, Austin CM. 2018 More limbs on the tree: mitogenome characterisation and systematic position of 'living fossil' species *Neoglyphea inopinata* and *Laurentaeglyphea neocaledonica* (Decapoda: Glypheidea: Glypheidae). *Invertebr. Syst.* **32**, 448–456. (doi:10.1071/IS17050)
20. Tan MH, Gan HM, Lee YP, Linton S, Grandjean F, Bartholomei-Santos ML, Miller AD, Austin CM. 2018 ORDER within the chaos: insights into phylogenetic relationships within the Anomura (Crustacea: Decapoda) from mitochondrial sequences and gene order rearrangements. *Mol. Phylogenet. Evol.* **127**, 320–331. (doi:10.1016/j.ympev.2018.05.015)
21. Timm L, Bracken-Grissom HD. 2015 The forest for the trees: evaluating molecular phylogenies with an emphasis on higher-level Decapoda. *J. Crustacean Biol.* **35**, 577–592. (doi:10.1163/1937240X-00002371)
22. Schwentner M, Richter S, Rogers DC, Giribet G. 2018 Tetraconatan phylogeny with special focus on Malacostraca and Branchiopoda: highlighting the strength of taxon-specific matrices in phylogenomics. *Proc. R. Soc. B* **285**, 20181524. (doi:10.1098/rspb.2018.1524)
23. Lemmon AR, Emme SA, Lemmon EM. 2012 Anchored hybrid enrichment for massively high-throughput phylogenomics. *Syst. Biol.* **61**, 727–744. (doi:10.1093/sysbio/sys049)
24. Léveillé-Bourret É, Starr JR, Ford BA, Lemmon EM, Lemmon AR. 2017 Resolving rapid radiations within angiosperm families using anchored phylogenomics. *Syst. Biol.* **67**, 94–112. (doi:10.1093/sysbio/syx050)
25. Hamilton CA, Lemmon AR, Lemmon EM, Bond JE. 2016 Expanding anchored hybrid enrichment to resolve both deep and shallow relationships within the spider tree of life. *BMC Evol. Biol.* **16**, 212. (doi:10.1186/s12862-016-0769-y)
26. Breinholt JW, Earl C, Lemmon AR, Lemmon EM, Xiao L, Kawahara AY. 2018 Resolving relationships among the megadiverse butterflies and moths with a novel pipeline for anchored phylogenomics. *Syst. Biol.* **67**, 78–93. (doi:10.1093/sysbio/syx048)
27. Haddad S, Shin S, Lemmon AR, Lemmon EM, Svacha P, Farrell B, Ślipiński A, Windsor D, McKenna DD. 2018 Anchored hybrid enrichment provides new insights into the phylogeny and evolution of longhorned beetles (Cerambycidae). *Syst. Entomol.* **43**, 68–89. (doi:10.1111/syen.12257)
28. Katoh K, Standley DM. 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780. (doi:10.1093/molbev/mst010)
29. Kenny N *et al*. 2014 Genomic sequence and experimental tractability of a new decapod shrimp model, *Neocaridina denticulata*. *Mar. Drugs* **12**, 1419–1437. (doi:10.3390/md12031419)
30. Song L *et al*. 2016 Draft genome of the Chinese mitten crab, *Eriocheir sinensis*. *GigaScience* **5**, 5.
31. Lartillot N, Rodrigue N, Stubbs D, Richer J. 2013 PhyloBayes MPI: phylogenetic reconstruction with infinite mixtures of profiles in a parallel environment. *Syst. Biol.* **62**, 611–615. (doi:10.1093/sysbio/syt022)
32. Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ. 2015 IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **32**, 268–274. (doi:10.1093/molbev/msu300)
33. Lanfear R, Calcott B, Ho SYW, Guindon S. 2012 PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* **29**, 1695–1701. (doi:10.1093/molbev/mss020)
34. Zhang C, Sayyari E, Mirarab S. 2017 ASTRAL-III: increased scalability and impacts of contracting low support branches. In *RECOMB international workshop on comparative genomics*, pp. 53–75. Cham, Switzerland: Springer.
35. Wolfe JM, Daley AC, Legg DA, Edgecombe GD. 2016 Fossil calibrations for the arthropod Tree of Life. *Earth Sci. Rev.* **160**, 43–110. (doi:10.1016/j.earscirev.2016.06.008)
36. Smith SA, Brown JW, Walker JF. 2018 So many genes, so little time: a practical approach to divergence-time estimation in the genomic era. *PLoS ONE* **13**, e0197433. (doi:10.1371/journal.pone.0197433)
37. Wolfe JM, Breinholt J, Crandall KA, Lemmon AR, Lemmon EM, Siddall ME, Timm LE, Bracken-Grissom HD. 2019 Data from: A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. Dryad Digital Repository. (doi:10.5061/dryad.k7505mn)
38. Gillung JP *et al*. 2018 Anchored phylogenomics unravels the evolution of spider flies (Diptera, Acroceridae) and reveals discordance between nucleotides and amino acids. *Mol. Phylogenet. Evol.* **128**, 233–245. (doi:10.1016/j.ympev.2018.08.007)
39. Jirikowski GJ, Richter S, Wolff C. 2013 Myogenesis of Malacostraca—the 'egg-nauplius' concept revisited. *Front. Zool.* **10**, 76. (doi:10.1186/1742-9994-10-76)
40. Jirikowski GJ, Wolff C, Richter S. 2015 Evolution of eumalacostracan development—new insights into loss and reacquisition of larval stages revealed by heterochrony analysis. *EvoDevo* **6**, 4. (doi:10.1186/2041-9139-6-4)
41. Davis KE, Hill J, Astrop TI, Wills MA. 2016 Global cooling as a driver of diversification in a major marine clade. *Nat. Commun.* **7**, 13003. (doi:10.1038/ncomms13003)
42. Jones WT, Feldmann RM, Hannibal JT, Schweitzer CE, Garland MC, Maguire EP, Tashman JN. 2018 Morphology and paleoecology of the oldest lobster-like decapod, *Palaeopalaemon newberryi* Whitfield, 1880 (Decapoda: Malacostraca). *J. Crustacean Biol.* **38**, 302–314. (doi:10.1093/jcbiol/ruy022)
43. Vereshchaka AL. 2017 The shrimp superfamily Sergestoidea: a global phylogeny with definition of new families and an assessment of the pathways into principal biotopes. *R. Soc. open sci.* **4**, 170221. (doi:10.1098/rsos.170221)
44. Robalino J, Wilkins B, Bracken-Grissom HD, Chan T-Y, O'Leary MA. 2016 The origin of large-bodied shrimp that dominate modern global aquaculture. *PLoS ONE* **11**, e0158840. (doi:10.1371/journal.pone.0158840)
45. Fransen C, De Grave S. 2009 Evolution and radiation of shrimp-like decapods: an overview. In *Decapod crustacean phylogenetics* (eds JW Martin, KA Crandall, DL Felder), pp. 246–259. Boca Raton, FL: CRC Press.
46. Bracken HD, De Grave S, Felder DL. 2009 Phylogeny of the infraorder Caridea based on mitochondrial and nuclear genes (Crustacea: Decapoda). In *Decapod crustacean phylogenetics* (eds JW Martin, KA Crandall, DL Felder), pp. 281–305. Boca Raton, FL: CRC Press.
47. Davis KE, De Grave S, Delmer C, Wills MA. 2018 Freshwater transitions and symbioses shaped the evolution and extant diversity of caridean shrimps. *Commun. Biol.* **1**, 16. (doi:10.1038/s42003-018-0018-6)
48. Audo D, Schweigert G, Saint Martin J-P, Charbonnier S. 2014 High biodiversity in Polychelida crustaceans from the Jurassic La Voulte-sur-Rhône Lagerstätte. *Geodiversitas* **36**, 489–525. (doi:10.5252/g2014n4a1)
49. Haug JT, Audo D, Charbonnier S, Haug C. 2013 Diversity of developmental patterns in achelate lobsters—today and in the Mesozoic. *Dev. Genes Evol.* **223**, 363–373. (doi:10.1007/s00427-013-0452-x)
50. Patek SN, Oakley TH. 2003 Comparative tests of evolutionary trade-offs in a palinurid lobster acoustic system. *Evolution* **57**, 2082–2100. (doi:10.1111/j.0014-3820.2003.tb00387.x)
51. Stern DB, Breinholt J, Pedraza-Lara C, López-Mejía M, Owen CL, Bracken-Grissom H, Fetzner JW, Crandall KA. 2017 Phylogenetic evidence from freshwater crayfishes that cave adaptation is not an evolutionary dead-end. *Evolution* **71**, 2522–2532. (doi:10.1111/evo.13326)
52. Crandall KA, De Grave S. 2017 An updated classification of the freshwater crayfishes (Decapoda: Astacidea) of the world, with a complete species

list. *J. Crustacean Biol.* **37**, 615–653. (doi:10.1093/jcbiol/rux070)

53. Poore GCB *et al*. 2014 On stabilising the names of the infraorders of thalassinidean shrimps, Axiidea de Saint Laurent, 1979 and Gebiidea de Saint Laurent, 1979 (Decapoda). *Crustaceana* **87**, 1258–1272. (doi:10.1163/15685403-00003354)
54. de Saint Laurent M. 1979 Vers une nouvelle classification des Crustacés Décapodes Reptantia. *Bulletin de l'Office Nationale de Pêche de Tunisie* **3**, 15–31.
55. Hyžny M, Klompmaker AA. 2015 Systematics, phylogeny, and taphonomy of ghost shrimps (Decapoda): a perspective from the fossil record. *Arthropod Syst. Phylog.* **73**, 401.
56. Keiler J, Wirkner CS, Richter S. 2017 One hundred years of carcinization—the evolution of the crab-like habitus in Anomura (Arthropoda: Crustacea). *Biol. J. Linn. Soc.* **121**, 200–222. (doi:10.1093/biolinnean/blw031)
57. Morrison CL, Harvey AW, Lavery S, Tieu K, Huang Y, Cunningham CW. 2002 Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. *Proc. R. Soc. Lond. B* **269**, 345–350. (doi:10.1098/rspb.2001.1886)
58. Luque J. 2015 A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: frog first or crab first? *J. Syst. Palaeontol.* **13**, 153–166. (doi:10.1080/14772019.2013.871586)
59. Luque J *et al*. 2019 Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms and mode of life via heterochrony. *Sci. Adv.* **5**, eaav3875. (doi:10.1126/sciadv.aav3875)
60. Tsang LM, Chan T-Y, Ahyong ST, Chu KH. 2011 Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. *Syst. Biol.* **60**, 616–629. (doi:10.1093/sysbio/syr063)
61. McLaughlin PA, Lemaitre R. 1997 Carcinization in the Anomura—fact or fiction? I. Evidence from adult morphology. *Contrib. Zool.* **67**, 79–124.
62. Reimann A, Richter S, Scholtz G. 2011 Phylogeny of the Anomala (Crustacea, Decapoda, Reptantia) based on the ossicles of the foregut. *Zool. Anz.* **250**, 316–342. (doi:10.1016/j.jcz.2011.05.006)
63. Hegna TA, Luque J, Wolfe JM. In press. The fossil record of the Pancrustacea. In *Natural history of Crustacea: evolution and biogeography* (eds GCB Poore, M Thiel). Oxford, UK: Oxford University Press.
64. Hultgren KM, Stachowicz JJ. 2008 Molecular phylogeny of the brachyuran crab superfamily Majoidea indicates close congruence with trees based on larval morphology. *Mol. Phylogenet. Evol.* **48**, 986–996. (doi:10.1016/j.ympev.2008.05.004)
65. Windsor AM, Felder DL. 2014 Molecular phylogenetics and taxonomic reanalysis of the family Mithracidae MacLeay (Decapoda: Brachyura: Majoidea). *Invertebr. Syst.* **28**, 145. (doi:10.1071/IS13011)
66. Lozano-Fernandez J *et al*. 2016 A molecular palaeobiological exploration of arthropod terrestrialization. *Phil. Trans. R. Soc. B* **371**, 20150133. (doi:10.1098/rstb.2015.0133)
67. dos Reis M, Thawornwattana Y, Angelis K, Telford MJ, Donoghue PCJ, Yang Z. 2015 Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Curr. Biol.* **25**, 2939–2950. (doi:10.1016/j.cub.2015.09.066)
68. Warnock RCM, Parham JF, Joyce WG, Lyson TR, Donoghue PCJ. 2015 Calibration uncertainty in molecular dating analyses: there is no substitute for the prior evaluation of time priors. *Proc. R. Soc. B* **282**, 20141013. (doi:10.1098/rspb.2014.1013)
69. Brown J, Smith S. 2017 The past sure is tense: on interpreting phylogenetic divergence time estimates. *Syst. Biol.* **67**, 340–353. (doi:10.1093/sysbio/syx074)
70. Schweitzer CE, Feldmann RM. 2005 Decapod crustaceans, the K/P event, and Palaeocene recovery. *Crustacean Issues* **16**, 17. (doi:10.1201/9781420037548.ch2)
71. Gueriau P, Charbonnier S, Clément G. 2014 Angustidontid crustaceans from the Late Devonian of Strud (Namur Province, Belgium): insights into the origin of Decapoda. *Neues Jahrb. Geol. P-A.* **273**, 327–337. (doi:10.1127/0077-7749/2014/0434)
72. Jones WT, Feldmann RM, Schweitzer CE, Schram FR, Behr R-A, Hand KL. 2014 The first Paleozoic stenopodidean from the Huntley Mountain Formation (Devonian–Carboniferous), north-central Pennsylvania. *J. Paleontol.* **88**, 1251–1256. (doi:10.1666/13-059)
73. Marshall CR. 2017 Five palaeobiological laws needed to understand the evolution of the living biota. *Nat. Ecol. Evol.* **1**, 0165. (doi:10.1038/s41559-017-0165)
74. Brayard A *et al*. 2017 Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. *Sci. Adv.* **3**, e1602159. (doi:10.1126/sciadv.1602159)
75. Simpson C, Kiessling W, Mewis H, Baron-Szabo RC, Müller J. 2011 Evolutionary diversification of reef corals: a comparison of the molecular and fossil records. *Evolution* **65**, 3274–3284. (doi:10.1111/j.1558-5646.2011.01365.x)
76. Klompmaker AA, Schweitzer CE, Feldmann RM, Kowalewski M. 2013 The influence of reefs on the rise of Mesozoic marine crustaceans. *Geology* **41**, 1179–1182. (doi:10.1130/G34768.1)
77. Schweitzer CE, Feldmann RM. 2015 Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. *J. Crustacean Biol.* **35**, 633–649. (doi:10.1163/1937240X-00002359)
78. Wong JM, Pérez-Moreno JL, Chan T-Y, Frank TM, Bracken-Grissom HD. 2015 Phylogenetic and transcriptomic analyses reveal the evolution of bioluminescence and light detection in marine deep-sea shrimps of the family Oplophoridae (Crustacea: Decapoda). *Mol. Phylogenet. Evol.* **83**, 278–292. (doi:10.1016/j.ympev.2014.11.013)
79. Kaji T, Anker A, Wirkner CS, Palmer AR. 2018 Parallel saltational evolution of ultrafast movements in snapping shrimp claws. *Curr. Biol.* **28**, 106–113.e4. (doi:10.1016/j.cub.2017.11.044)
80. Klompmaker AA, Boxshall GA. 2015 Fossil crustaceans as parasites and hosts. In *Advances in parasitology* (eds K De Baets, DTJ Littlewood), pp. 233–289. Amsterdam, The Netherlands: Elsevier.
81. van der Meij SET, Fransen CHJM, Pasman LR, Hoeksema BW. 2015 Phylogenetic ecology of gall crabs (Cryptochiridae) as associates of mushroom corals (Fungiidae). *Ecol. Evol.* **5**, 5770–5780. (doi:10.1002/ece3.1808)
82. Chak STC, Duffy JE, Hultgren KM, Rubenstein DR. 2017 Evolutionary transitions towards eusociality in snapping shrimps. *Nat. Ecol. Evol.* **1**, 0096. (doi:10.1038/s41559-017-0096)
83. Klompmaker AA, Schweitzer CE, Feldmann RM, Kowalewski M. 2015 Environmental and scale-dependent evolutionary trends in the body size of crustaceans. *Proc. R. Soc. B* **282**, 20150440. (doi:10.1098/rspb.2015.0440)
84. Owen CL, Bracken-Grissom H, Stern D, Crandall KA. 2015 A synthetic phylogeny of freshwater crayfish: insights for conservation. *Phil. Trans. R. Soc. B* **370**, 20140009. (doi:10.1098/rstb.2014.0009)