

Supplementary Materials for

Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms via heterochrony

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The PDF file includes:

Supplementary Text

Fig. S1. Paleogeographic map during early Late Cretaceous times (~95 to 90 Ma ago).

Fig. S2. Stratigraphic column of the Cenomanian-Turonian Churuvita Group in the studied area.

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Fig. S7. ML topology with the nine major brachyuran sections and podotremous brachyuran families, including Callichimaeridae n. fam.

Fig. S8. Bayesian majority-rule consensus topology of the post-burnin sample of trees for fossil and extant podotremous brachyuran families, including Callichimaeridae n. fam.

Table S1. List of characters for phylogenetic analysis.

Table S2. Superfamilies and families of anomuran and brachyuran crabs included in the phylogenetic analysis.

References (80–146)

Other Supplementary Material for this manuscript includes the following:

(available at advances.sciencemag.org/cgi/content/full/5/4/eaav3875/DC1)

Data file S1 (.nex format). Data matrix for phylogenetic analysis.

Data file S2 (.obj format). Printable 3D model file of *Callichimaera perplexa* n. gen. n. sp.

Movie S1 (.mp4 format). Dorsoventral view 3D reconstruction of *Callichimaera perplexa* n. gen. n. sp.

Movie S2 (.mp4 format). Side view 3D reconstruction of *Callichimaera perplexa* n. gen. n. sp.

Supplementary Text

Geographical, geological, and paleontological context

The type series of *Callichimaera perplexa* was collected in lower Upper Cretaceous marine rocks of the Churuvita Group, cropping out near Pesca, Department of Boyacá, Eastern Cordillera of Colombia (fig. S1), 150 km northeast of Bogotá, and 50 km southeast of Villa de Leyva (also spelled Villa de Leiva). The upper Cenomanian–lower Turonian Nocuatá Section is approximately 95 m thick, and includes the uppermost part of the Churuvita Formation at the base (Segments A and B) and the lowermost part of the San Rafael Formation at the top (Segment C) (fig. S2). Segment A (28 m) is composed at the base of 15.5 m of gray shales, and light-gray, micaceous, fossiliferous claystones. Three crustacean taxa, including *Callichimaera*, constitute the dominant macrofaunal elements, with occasional occurrence of scattered fish remains, small ammonites, ammonite aptychi, and small lingulid brachiopods. *Callichimaera* is the largest arthropod element from this faunule, reaching a maximum carapace length of ~15 mm, while the associated shrimp reach ~10 mm in length, and the cumaceans ~5 mm in length (fig. S3). The uppermost portion of Section A (12.5 m) is covered/weathered. The overlying Segment B is composed of 11 m of silty sandstones, and thick beds of white–yellowish, slightly micaceous sandstones, representing the last occurrence of coarse–grained deposits along the section. Segment C lies above these thick layers of sandstone and is composed of ~56 m of gray fossiliferous shales with occasional indurated, gray, fossiliferous shale beds in the lower portion, interbedded at the top with fine–grained, silty sandstone lenses and non–calcareous nodules (fig. S2). Its lowermost portion (~25 m) is covered/weathered. The uppermost Segment C (~31 m) contains invertebrate assemblages typical of the lower–middle Turonian San Rafael and La Frontera formations in Colombia (80–83) and of the Eagle Ford Group equivalent strata in Coahuila, Mexico (81, 84). Abundant globulose foraminifera, teleostei fish remains, ammonites such as *Hoplitoides* spp., *Collingnoniceras* sp., *?Coilopoceras* sp., and *?Romaniceras* sp. (Etayo–Serna, personal communication, 2011), abundant decapod crustaceans such as *Cenomanocarcinus* sp. (5, 41, 81, 85), and several decapod remains under study also occur within Section C (fig. S3).

The Churuvita Formation has been dated as Cenomanian, and the San Rafael Formation as lower to middle Turonian in age, using ammonites and foraminifera (83, 86–88). Throughout the late

Cenomanian–early Turonian, the rocks cropping out at the Nocuatá Section were deposited in the eastern margin of a NNE–SSW aligned epicontinental sea, limited to the west by a volcanic arc–trench–system (part of what is today the Central Cordillera), and to the east by the Guayana Craton (89), covering most of what is today the emerged Colombian Andes Eastern Cordillera (82, 90, 91) (fig. S1). A regional transgressive surface indicates the end of relatively shallow–water, coarse clastic sedimentation during the Cenomanian and the initiation of deeper–water, fine–grained sedimentation at the beginning of the Turonian (80, 82, 92).

The additional non-type material of *Callichimaera perplexa* was collected in lower Upper Cretaceous marine rocks of the Frontier Formation, Colorado Group, exposed just north of the Cumberland Gap, Southwestern Wyoming Province on the eastern edge of the Green River Basin, U.S.A., ~150 km northeast of Salt Lake City, Utah. The Frontier Formation is composed of five members; Chalk Creek, Coalville, Allen Hollow, Oyster Ridge and Dry Hollow members, and is comprised mostly of sandstones, shales and siltstones of both marine and non-marine origin. It is underlain by the Albian Aspen shale and overlain by the Coniacian-Santonian Hilliard Shale. The specimens were found in the light-grey shale of the middle portion of the Allen Hollow Member, in association with bivalves, lingulid–like brachiopods, undetermined algae, and scattered fish remains. Merewether *et al.* (93) placed the base of the Allen Hollow Member at the beginning of the mid Turonian. Exact dating of the Allen Hollow Member has not been done; however, the underlying Coalville Member was dated to 91.1 Ma and the lower part of the overlying Hilliard Shale Formation at 88.9 Ma (94). Based on the stratigraphy of the area, the date of the Allen Hollow Member would be closer to 91.1 Ma considering there are two other interfering members.

Systematic paleontology

Arthropoda von Siebold, 1848

Decapoda Latreille, 1802 (95)

Brachyura Latreille, 1802 (95)

Callichimaeroida section. nov.

Included superfamily. Callichimaeroidea fam. nov.

Diagnosis. As for superfamily (see main text).

Callichimaeroidea superfam. nov.

Included families. Callichimaeridae fam. nov.; tentatively Retrorsichelidae Feldmann, Tshudy, and Thompson, 1993 (see main text).

Diagnosis. See main text.

Callichimaeridae fam. nov.

LSID. urn:lsid:zoobank.org:act:A5D6688D-756B-4FB7-8098-5EB066C38383

Included Genus. *Callichimaera* gen. nov.

Diagnosis. As for type genus and species (see main text).

***Callichimaera perplexa* gen. et sp. nov.**

LSID. urn:lsid:zoobank.org:act:CD4585D1-B198-45E6-8485-45F94167BDEE

LSID. urn:lsid:zoobank.org:act:650E5046-C4FC-4485-A3B5-254DE785F80B

Figs 1–3; fig. S4

Diagnosis. See main text.

Description. Dorsal carapace: Small, elongate, fusiform, longitudinally sub-ovate in outline, with maximum width two-thirds maximum length of carapace, widest at posterior two-fifths carapace length at level of sternite 5; cervical groove distinct, well developed, ending at anterolateral margin, shallow antero-distally and more pronounced mesially, interrupted axially by a short mesial longitudinal ridge; branchiocardiac groove distinct, shallow at middle portion of carapace, more pronounced toward the anterolateral margin; dorsal carapace finely granulated;

two short, parallel postrostral ridges arise at base of rostrum and deflect posterodistally, apparently continuing longitudinally as pre-cervical ridges separating the protogastric and mesogastric regions; longitudinal axial ridge prominent, more or less continuous, extending from mesogastric region, beginning approximately at first anterior quarter of carapace length and extending to cardio-intestinal region, interrupting the cervical groove axially and bearing a row of few low-relief tubercles along its length; unornamented lateral branchial ridges present. Rostrum longer than wide, bifid, sub-square, with sides almost parallel, depressed axially, broader at the base, representing one-tenth the maximum carapace length; fronto-orbital margin short, about one-third maximum carapace length; absence of true orbits, augenrest, and orbital fissures, bearing only one short, blunt spine-like protuberance at mid-orbit. Anterolateral margin sinuous, poorly defined, bearing one short, blunt spine-like protuberance at end; posterolateral margin convex at middle portion of carapace and straight posteriorly; posterior margin concave, slightly less than half the maximum carapace width.

Ventral Carapace: Thoracic sternum wide anteriorly, narrow posteriorly; sternites 1 to 4 forming an elongated sternal crown; sternites 1 to 3 distinct, fused, forming a triangle, with straight, convergent anterolateral margins, nearly as long as sternite 4; sutures 1/2 and 2/3 not clear; gynglimes present laterally between sternites 3 and 4, where Mxp3 articulates; sternite 4 sub-quadrate, slightly wider than long, width one-fourth carapace width, length one-eighth carapace length, not mesially depressed or furrowed, lateral margins smoothly concave, anterior portion nearly equal to posterior, strongly concave posterior margin mesially; suture 3/4 distinct only laterally; sternite 5 the broadest sternite, maximum width anteriorly, more than two-thirds maximum carapace width, maximum length near sternum axis, one-fourth the maximum carapace length, depressed mesially by linea media, with lateral margins straight, convergent posteriorly, and bearing long and prominent longitudinal ridge on each side, which extend along position of maximum length, parallel to main axis; suture 4/5 complete, rather well defined by a deep sinuous groove, with anterior mesial portion of sternite 5 articulating into sternite 4 posterior margin concavity; sternite 6 very different in shape outline and in size from sternites 5 and 7, maximum width at anterior portion, approximately half maximum carapace width, maximum length approximately one-sixth carapace length, strongly depressed mesially by a deep cleft, occasionally bearing a subtle ridge on each side, almost parallel to main axis, with anterior margin irregular, extending obliquely posteriorly from main axis, producing a sinuous concavity

posteriorly near where sternite 5 longitudinal ridge ends, and describing a convex, arcuate loop ending at lateral margin, which is straight, converging posteriorly, suture 5/6 complete, well defined by a deep groove; sternite 7 reduced, different in shape and size from sternites 5 and 6, maximum width at posterior portion, nearly parallel to carapace posterior margin, approximately one-sixth maximum carapace width, maximum length near carapace axis, approximately one-seventh carapace maximum length, inverted V-shaped, strongly depressed mesially, with margins diverging posteriorly, suture 6/7 complete, well defined by a deep groove; sternite 8 not clearly recognized in the material studied. Thoracic gonopores not present in males or females. Linea anomura or linea brachyura apparently missing.

Pleon: Symmetrical, short, lacking articulated rings and uropodal plates, sexually dimorphic. Female pleonites sub-rectangular in outline, pleonite 1 to 3 exposed dorsally, pleonite 1 reduced, pleonites 2 to 5 similar in shape and size, epimeres with a longitudinal depression, separated from the tergum; each pleonite bearing dorsal axial tubercle that may be distinctly spiniform in small specimens; in one specimen, pleonal somite 4 tergum bearing a notch, extending anterolaterally to postero-mesial portion; pleonites and telson preserved in a few specimens, pleonite 5 similar in shape to pleonites 2-4 but smaller; pleonite 6 with a concave posterior margin articulating with telson; telson short, wider than long, strongly convex anteriorly. Female pleopods 2-5 present, small, slender, similar in shape and size. Male pleonites narrower than females, pleonite 6 and telson exposed ventrally in one male specimen; pleonite 6 longer than wide, semi-rectangular in outline, posteriorly arcuate, concave, articulating with telson; telson small, lanceolate, longer than wide, approximately two-thirds as long as pleonite 6 length. Male first two pairs of pleopods (gonopods) slender and slightly arched, highly sclerotized; pleopods 3-5 absent.

Eyes: Very large (each nearly 15% the length of carapace, or 25% the width of carapace), approximately as long as wide, round to semi-ovate in outline, always exposed and lacking any protective structure; compound eye facets predominantly hexagonal and in hexagonal arrangements through most of the outer-middle portion, although in one specimen (Fig. 2G) the proximal portion of the cornea bears squarish facets in orthogonal packing; three retinal layers are recognizable in one specimen; eyestalk short and stout, one-third the length of eye.

Cephalic appendages: first and second antennae (antennula and antenna s.s., respectively) short and slender, between the eyes, antenna as long as eye maximum length, first segment broad, one-fourth the length of rostrum.

Oral appendages: Third maxillipeds pediform, articulating with a gynglimes on postero–distal portion of sternite 3; endognath ischium elongate, semi–rectangular in outline, as long as sternite 4 width, two–fifths as wide as long, bearing a crista dentata armored with four to five small, acute, evenly spaced spines on internal margin; merus elongate, semi–quadrate in outline, slender, somewhat shorter than ischium, more than twice as long as broad; palp (carpus–dactylus) slightly shorter than ischium + merus, directed forward; merus of endognath never reaching anterior carapace, ischium + merus length approximately one–fifth carapace maximum length; exognath slender, nearly as long as endognath ischium, as wide as one–third endognath ischium width, with nearly straight outer margin; endognath of second maxilliped very small, pediform; mandibulae as long as half the endognath ischium length, robust, slightly asymmetrical in shape, but similar in size, left mandible describing a concave curvature on occlusal surface slightly different from the right mandible.

Pereopods: Chelipeds (P1) isochelous, ischio–merus semi–rectangular, about one–fourth as long as carapace length; carpus sub–trapezoidal, as long as two–thirds the length of merus; propodus–carpus articulation subparallel to merus long axis; propodus height as long as ischio–merus length, with a blunt tooth–like projection at outer distal corner, close to articulation with dactylus; manus stout and inflated, about two times carpus width, often tuberculate; pollex three times longer than carpus, broad, deflected $\sim 90^\circ$ with respect to propodus length axis, with 10 to 15 small, sharp, and irregular, well–developed denticles on occlusal surface, and distal denticle upturned; dactylus slender, with distal denticle downturned, slightly shorter than fixed finger, smooth edentulous occlusal surface, except for occasional one or two small, fine denticles near junction with propodus. Pereopod 2 (P2) the longest of all pereopods, usually as long as, or slightly longer than, maximum carapace length; coxa semi–rectangular in outline, long, articulating laterally with sternite 5; basis poorly defined, apparently small, with a slender condyle that articulates with coxa; ischio–merus subrectangular, slightly convex forward, bearing a small spine at upper distal margin, close to articulation with carpus; carpus length one–third the length of ischio–merus, trapezoidal in outline, narrow at articulation with merus, may bear small spines on outer margin; propodus elongate, ovoid, twice the length of carpus, or two–thirds as long as ischio–merus length, may be serrated, sometimes with one to three small, acute, spiniform projections at anterior edge close to articulation with dactylus, narrow at articulation with carpus; dactylus broadly lanceolate, as long as propodus, narrow at articulation with

propodus; P2 segments bearing a fine rim of evenly spaced setal pits; P3 almost identical in shape and size to P2, but slightly shorter, coxa articulating laterally with sternite 6, and bearing a small, slender and acute posterior coxal spine. Pereopods 4 to 5 similar in shape and very different in shape and size from P2–P3; P4 slender, half the length of P2–P3, with a median carina along all sclerites; ischio–merus subrectangular, often finely granulated, broader posteriorly; carpus half the size of ischio–merus, subquadrate, narrow at articulation with merus; propodus subrectangular, one–third longer than carpus length, and similar in size to ischio–merus; dactylus sharp, slender and acute, similar in length to propodus, but two–thirds the width, weakly serrate, narrow at articulation with propodus. Pereopod 5 the smallest pereopod, one–third length of P3, slender, with median carina along all the segments, similar in shape to P4 but considerably smaller and carried subdorsally; coxae and basi not recognized; ischio–merus fused, sub–perpendicular to main carapace axis, as long as P4 dactylus; carpus length half the ischio–merus length, narrow at junction with ischio–merus; propodus as long as ischio–merus length, narrow at junction with carpus; dactylus slender and acute, as long as propodus (modified from 21).

Supplementary systematic remarks

To assess the phylogenetic position of *Callichimaera* among false and true crabs, we used a dataset modified from (10), and incorporated new taxa and morphological information from additional works (e.g., 6, 56, 58–60, 96). Our modified data matrix incorporates 85 adult morphological characters and 42 terminals: 5 outgroups (*Astacidea*, †*Platykotta*, *Galathea*, *Chiostylus*, and *Blepharipoda*) and 37 ingroups, including *Callichimaera* (figs S5–S8; Supplementary Dataset S1; Supplementary Tables S1–S2). Some dromiacean taxa included in (10), i.e., bucculentids, longodromitids, lecythocarids, as well as *Viaiidae* (97), and the family *Paranecrocarcinidae* (98, 99), were excluded due to the high percentage of missing characters, which did not help resolve the topology. Taxa in Supplementary Table S2 were scored in the matrix at the family level, to convey the morphological diversity seen among brachyuran clades and to examine the combination of plesiomorphic and apomorphic character states seen in *Callichimaera*.

The superfamilies Homolodromioidea (100), Konidromitoidea (10) and Glaessneropsoidea (101), differ from *Callichimaeroidea* in the possession of subchelate P4 and P5, eyes protected by well-

defined orbits and an augenrest (except in Glaessneropsoidea) and bearing square facets in orthogonal packing, a subhepatic region that is usually inflated, the postcervical groove usually present, the pleon bearing uropods or uropodal plates, and pleon in males close to the coxae (10, 100, 102, 103). Similarly, the superfamily Dromioidea (104), is distinguished by its well-developed orbits, the inflated subhepatic regions, usually developed postcervical groove, a narrow sternum bearing sternal projections, the presence of a sterno-coxal depression, pleonite 6 usually bearing triangular epimeres, the possession of uropodal plates, and last pair of pereopods usually prehensile, carried subdorsally (10, 105-111). Furthermore, the possession of small mxp3 coxae that never touch, sternites 1-3 distinct ventrally, and the absence of a postcervical groove (except for Diaulacidae (106), and Xandarocarcinidae (10)), ensures a separate phylogenetic affiliation from the most primitive brachyurans. Callichimaeridae can also be differentiated from Homoloida by the lack of an evident ‘linea’ (often referred to as ‘linea homolica’), the characteristic ‘homolid press-button’ (absent in Mithracitidae (102)), a telson projecting between the coxae of maxillipeds, the absence of an augenrest (except in Latreillidae (112)), and the lack of sterno-coxal and sterno-pleonal depressions (10, 12, 102, 113).

Third maxillipeds equipped with serrated or spinose ischium (*crista dentata*) are known from adult and juvenile forms among many brachyuran and non-brachyuran decapods, including, but not exclusive to, some astacideans (e.g., 114, 115), achelates (e.g., 116, 117), anomurans (e.g., 118-121), and early-diverging brachyurans (e.g., 109, 122, 123). Nonetheless, whether the spiniform structures found in some eubrachiurans (e.g., 12, 124-126) is homologous with the ‘*crista dentata*’ sensu stricto is unclear (1). Scholtz and McLay (12) stated that: “the *crista dentata* (...) is a plesiomorphic reptant character that is present in the homolodromioids, dromiids, dynomenids, and homolids (except latreilliids)”, but lost once in the most recent common ancestor of the clade that unites Raninoida, Cyclodorippoida, and Eubrachiura. The *crista dentata* present in *Callichimaera* possesses four to five acute spines, positioned in the inner border of the mxp3 ischium (Fig. 1C). *Crista dentata* and mxp3 bearing a long palp are the plesiomorphic conditions for Decapoda, but absent in higher podotremes and Eubrachiura. The dorsal carapace of *Callichimaera* superficially resembles that of *Probeebei* (127), a hermit crab that has become secondarily carcinized and has a sub-symmetrical pleon. Yet, it differs dramatically from *Callichimaera* in the possession of a long triangular rostrum, extremely enlarged antennae, broad branchial chambers, strong spinose ornamentation in the carapace and

legs, the broad pleon bearing well-developed uropods, which are absent in *Callichimaera*, the very narrow sternum with the coxae of the pereopods in close contact with each other axially, and the chelate P5. These are typical paguroid features missing in *Callichimaera*.

Precise phylogenetic placement of *Callichimaera* within Brachyura is problematic because of a) its ‘chimaeric’ nature and b) possession of multiple distinctive characters typical of several fossil and extant early-branching and ‘higher’ Brachyura clades (main text, Figs. 1–4, Supplementary Fig. 4), but not collectively seen in any one taxon. These characters of *Callichimaera* include, but are not restricted to:

- i) A carapace outline with broad branchial regions and a dorsal pattern of longitudinal keels and grooves that is more reminiscent of some lobsters and palaeocorystid crabs, respectively (light grey, Fig. 4A), than it is of most anomurans or brachyurans.
- ii) A third maxilliped that bears a *crista dentata* (red, Fig. 2b), the ancestral condition for larval decapods and adult lobsters, most anomurans, early-branching brachyurans like Homolodromioidea, and most Homoloidea. The alternate character state of an operculiform third maxilliped shielding the buccal frame is present in two clades: the ‘higher’ Dromioidea, and more inclusive podotreme brachyurans plus Eubrachyura.
- iii) Spanner-like chelipeds similar to those seen burrowing groups like Hippoidea (Anomura), *Retrorsichela* (doubtfully Anomura, most likely within Callichimaeroidea superfam. Nov.), and Raninoidea (Brachyura) (yellow, Fig. 4A–B).
- iv) The shape, size, position, and function of paddle-like limbs, e.g., *Callichimaera*’s flattened pereopods 2–3 (P2–P3), which are highly variable among anomurans and brachyurans. In hippoids and raninoids, the pereopods are specialized digging tools, while in brachyurans such as Portunoidea, Orithyoidea, some Calappoidea (i.e., Matutidae), and some extinct Necrocarcinoidea (i.e., *Cenomanocarcinus*), they likely facilitate both swimming and digging (green, Fig. 4A–B). *Callichimaera* possesses reduced P4–P5 (blue, Fig. 4A–B), which occur in some anomurans (e.g., Paguroidea, or hermit crabs), some podotreme brachyurans (e.g., Homolodromioidea, Cyclodorippoidea), and early-branching eubrachyurans (e.g., Dorippoidea), but mostly with claw-like modifications to grab or grasp, absent in the new taxon.

- v) A symmetrical pleon, unlike that of hermit crabs but as in most Brachyura, it lacks articulating rings between pleonites (purple, Fig. 4A–B). The presence of uropods or uropodal plates at the posterior end of the pleon is plesiomorphic for Decapoda (shrimps, lobsters, anomurans and early-branching brachyuran clades have them), but these are absent in *Callichimaera*, and the most inclusive podotreme clades plus Eubrachyura.
- vi) A puzzling sternal configuration due to the dissimilarity in shape and size of its sternites. The large S5–S6 vaguely resemble those of *Heikeopsis* (Eubrachyura: Dorippoidea), and †*Retrorsichela*, previously included in Anomura: Galattheoidea, but herein tentatively transferred to Brachyura: Callichimaeroidea superfam. nov. (orange, Fig. 4B), although the sternal configuration in *Callichimaera* remains unmatched among crustaceans (6).
- vii) Pediform mouthparts with *crista dentata*, the marked difference between legs P2–P3 and legs P4–P5, the unusual pattern of sternal sutures, the shape and size of the sternites, and the orbital and optical configuration, are all inconsistent with diagnostic characters for the more inclusive podotreme clades (e.g., Raninoidea, Cyclodorippoidea) and Eubrachyura (Fig. 5).
- viii) Finally, large eyes lacking true orbits and orbital fissures that also occur in some ancient brachyurans such as *Ekalakia* (Dromiacea: Glaessneropsidae), and several homoloids (dark grey, Fig. 4A–B).

The chimaeric nature of *Callichimaera* is due to a combination of primitive and derived traits that place it in an intermediate position between the oldest groups of true crabs (i.e. Dromiacea and Homoloida), and all of the more derived podotreme and sternitreme clades (Fig. 5, figs. S5–S7). *Callichimaera* fills a major gap in crab evolution, and bring extra support to the hypothesis that podotreme brachyurans do not represent a monophyletic assemblage but a rather a diverse evolutionary grade. The phylogenetic proximity of several of the more inclusive podotreme clades to the highly derived Eubrachyura led us to recognize an unnamed and unranked monophyletic clade comprised by the most inclusive lineages of extant brachyurans and their fossil relatives — i.e., Raninoidea (Cyclodorippoidea + (Eubrachyura)), and a stem-group formed by extinct lineages, e.g., Etyoidea, Torynommoidea, Dakoticancroidea (figs. S5–S7), sharing apomorphies not seen, in whole or in part, among less inclusive crab clades. The adult morphological characters that support this clade include a) the presence of truly operculiform maxillipeds 3, b) the palp of maxillipeds 3 articulating in the same plane as the rest of the

operculum, c) the lack of true crista dentata on the inner margin of the ischium in maxillipeds 3 (homoplasious in latreilids), and d) the presence of well-defined orbits (homoplasious in dromioids). These apomorphic traits strongly differ from the plesiomorphic conditions seen among the less inclusive brachyuran clades Homolodromioidea, most Dromioidea, Homoloidea, and Callichimaeroidea n. superfam. However, the presence of hexagonal shaped facets in adults of *Callichimaera*, suggestive of apposition eyes, is a feature shared with more inclusive brachyurans than to dromiacean-like and homoloidean-like lineages. Yet, at this point we cannot say whether the retention of larval apposition eyes into adulthood was already present in the most recent common ancestor for Callichimaeroidea and the most inclusive podotremes + Eubranchyura, or whether it happened independently in some or all of these groups.

Additional remarks

Although *Callichimaera* strongly resembles the late larval (megalopa) stage of some crabs, both the overall body size and several key anatomical features of larger individuals indicate that they were mature adults. The megalopa larvae of brachyuran crabs tend to measure ~1-2 mm carapace width on average (128). The size of megalopae varies little within a species; even the very large megalopae of the Dungeness crab, which have been reported to vary significantly in size, nonetheless vary only slightly (2.2-4.5 mm CW) (129). While megalopae size is positively related adult size (128), and there are some examples of exceptionally large megalopa, even the megalopae of the giant Japanese spider crab *Macrocheira kaempferi* (adult leg span up to ~4 m) — the largest living arthropod — measures only ~2 mm carapace width (130). Further, when megalopa size is corrected for adult size there is no significant difference in size among brachyuran families (128). Among anomurans, the megalopa of the large robber or coconut crab *Birgus latro* (adult leg span up to ~1 m), reaches ~4 mm (131), as also do the megalopae of pagurids like *Dardanus* and some parapaguroid hermit crabs (132). *Callichimaera* specimens are two to eight times larger than the largest known living and fossil megalopa larvae, and comprise a larger range of sizes than typical crab megalopae do (see Fig. 3D, G–I). Also, crab larvae swim by either beating the maxillipeds 1–2 (zoeae stages) — usually aided by the pleon — or by biramous pleopods on the pleonal segments or pleonites 2–5 (megalopa) (39, 132). Instead, *Callichimaera* swam presumably by motion of its strongly flattened pereopods P2–P3,

which are unknown in fossil or extant crab megalopae. Furthermore, sexual dimorphism in crabs does not become evident until several molts beyond metamorphosis into the first juvenile crab stage, usually around crab stage 6 or 7 (133-138). Crab megalopae of most anomurans, dromiaceans, homoloidans, raninoidans, and several eubrachyurans (calappids, corystids, etc.) lack the primary and secondary sexual traits seen in early to adult crab stages (43), and have either fully developed uropods or relicts of uropodal plates. The *Callichimaera* specimens found to date do not possess uropods or uropodal remains, and several of the most well-preserved specimens show sexually dimorphic characteristics such as sclerotized gonopods and dimorphic pleonites (Fig. 3); sexual traits never seen in megalopa larval stages.

Callichimaeridae fam. nov., from the upper Cenomanian of Colombia, adds to the growing evidence that the tropics may have acted as a cradle of crab diversification since at least the Early Cretaceous (139). Recent discoveries from northern South America represent either the oldest, or one of the oldest fossil records for several ancient crab families and superfamilies, including the oldest Orithopsidae (58, 60, 99, 140, 141) (superfam. Necrocarcinoidea), Palaeocorystidae (58) (superfam. Palaeocorystoidea), Diaulacidae (142) (superfam. Dromioidea), and the oldest members of the section Eubrachyura, or 'higher' true crabs (superfam. Dorippoidea, and possibly Portunoidea) (141, 143). Also, other findings include some of the oldest Cenomanocarcinidae (85) (superfam. Necrocarcinoidea), and Mithracitidae (144) (superfam. Homoloidea). Together, these occurrences suggest that many brachyuran crab clades previously considered to have originated at higher latitudes (145, 146) might have had their origins in tropical to subtropical regions.

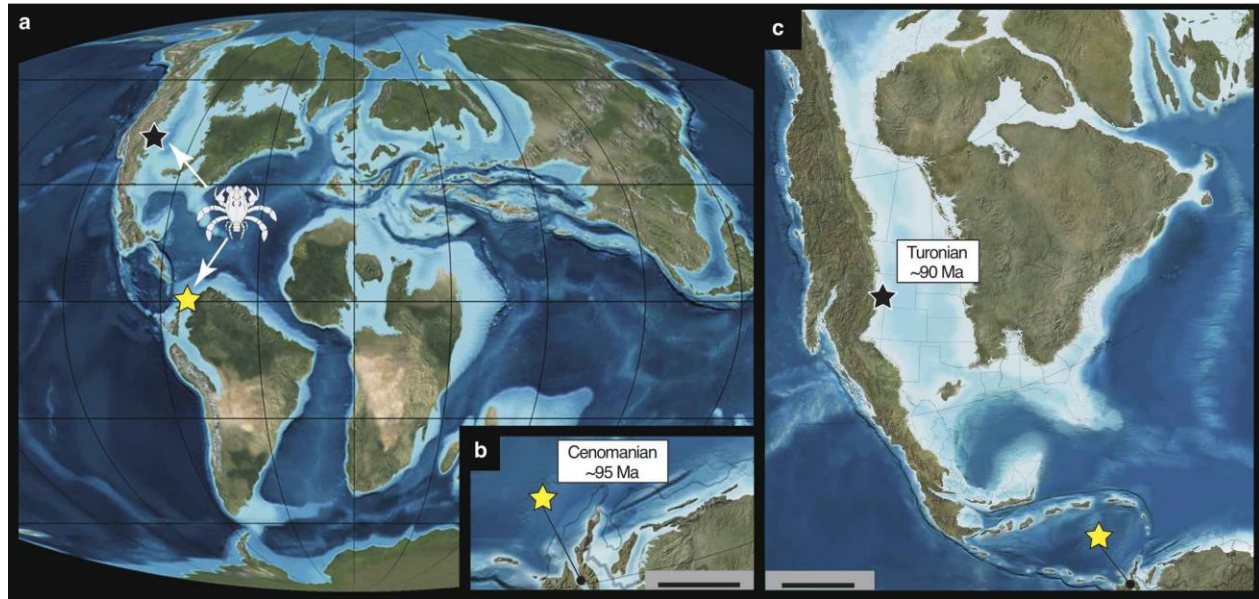


Fig. S1. Paleogeographic map during early Late Cretaceous times (~95 to 90 Ma ago). (a) localities where the holotypes and paratypes (Colombia, yellow star; USA, black star) of *Callichimaera perplexa* gen. et sp. nov. were discovered. (b) Close-up showing the tropical South American type locality of *Callichimaera*, Upper Churuvita Formation (~95 Ma), Boyacá, Colombia. (c) Close-up showing the North American locality, Frontier Formation (~90 Ma), Wyoming, USA. (Base maps modified from <http://cpgeosystems.com>, data retrieved August 20, 2015. Paleomaps copyright and courtesy: Ron Blakey). Scale bars: b, 500 km; c, 1000 km.

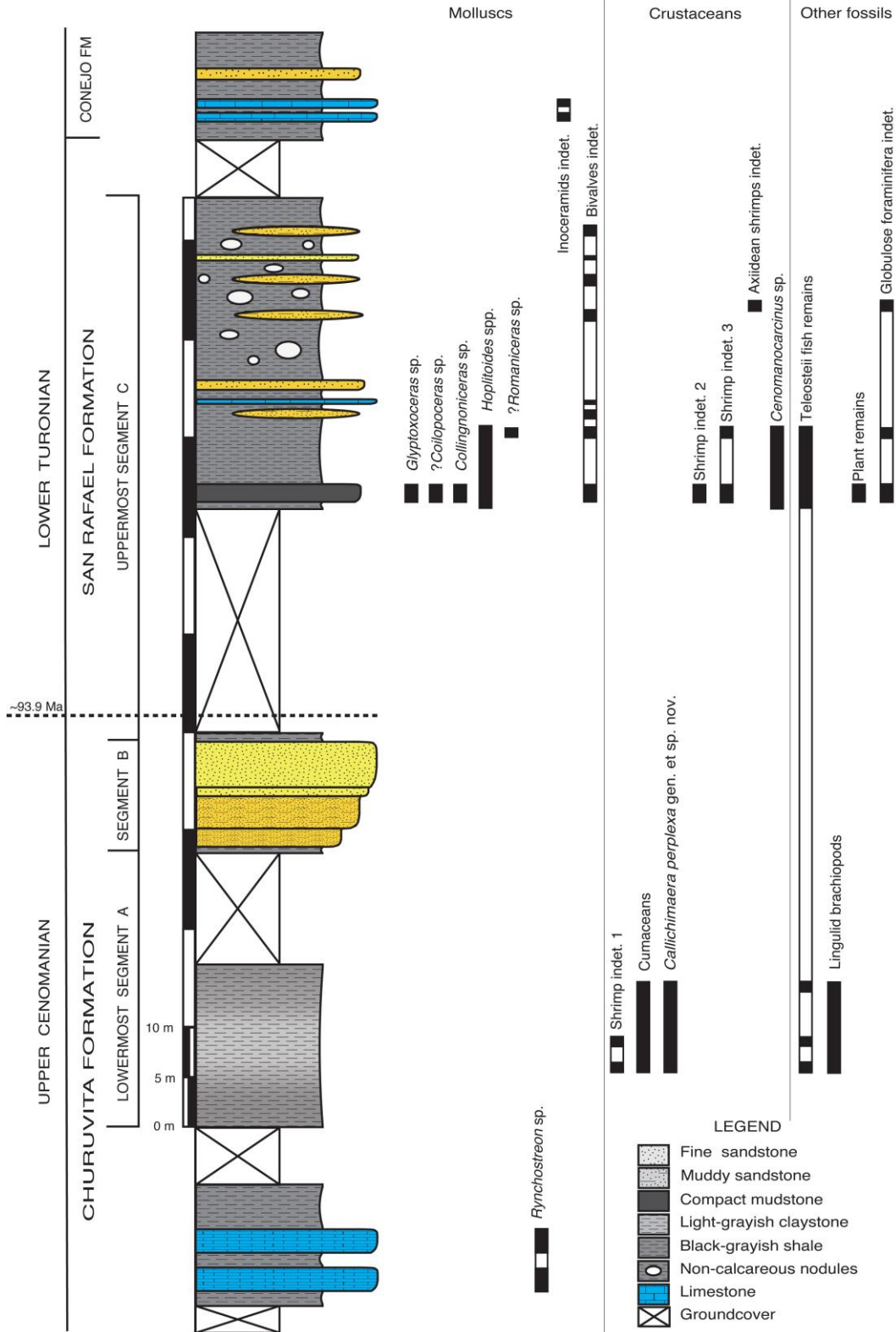


Fig. S2. Stratigraphic column of the Cenomanian-Turonian Churuvita Group in the studied section. Section outcropping at the Nocuatá Section, Department of Boyacá, Colombian Eastern Cordillera. For each taxon, black and white columns indicate where macrofossils were recovered or not along the section, respectively. Dashed line indicates the tentative Cenomanian–Turonian boundary (~93.9 Ma).

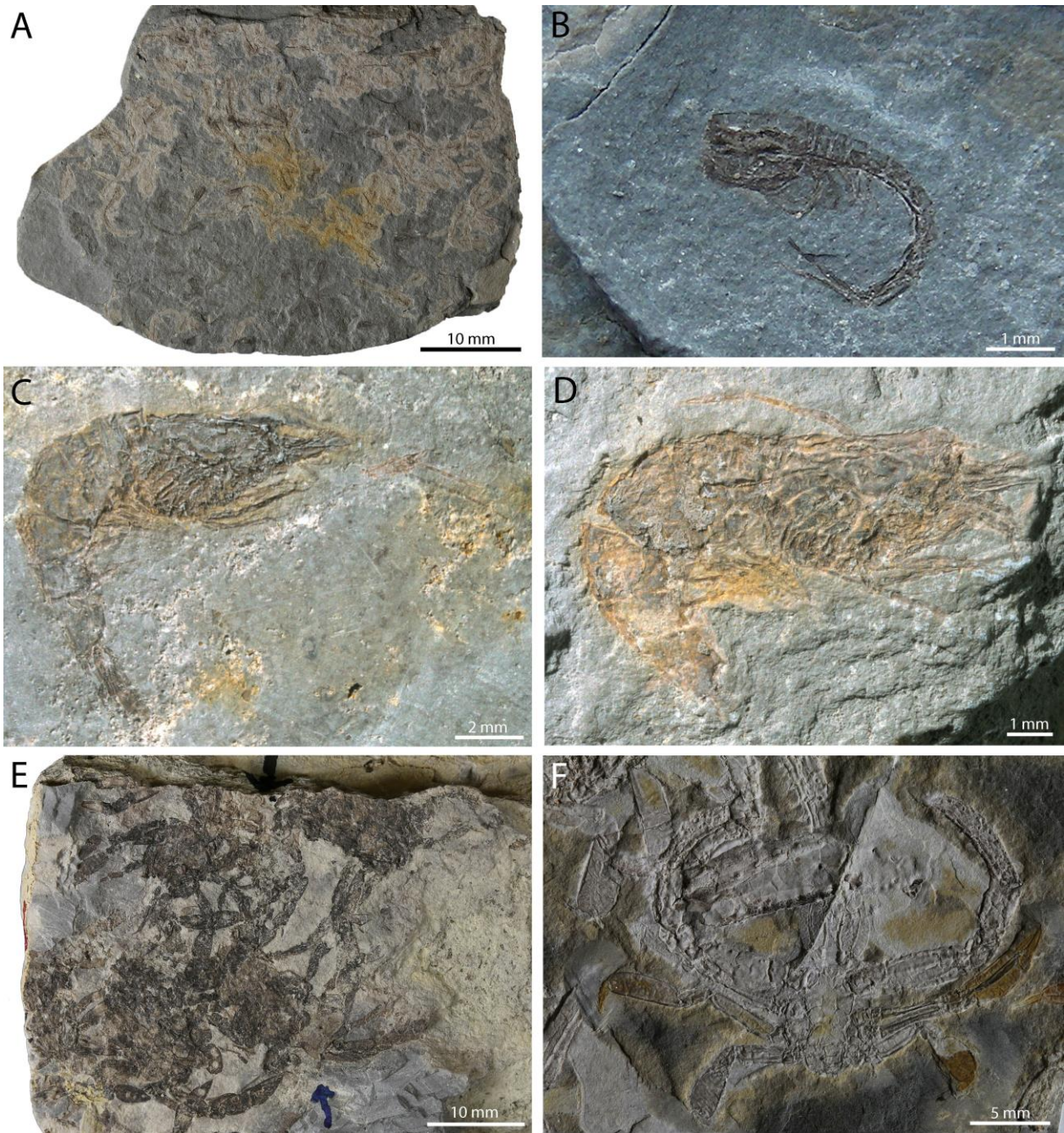


Fig. S3. Crustacean-dominated faunule at the studied section. (A) Cumacean-rich surface showing the high density and random orientation of cumaceans specimens associated with *Callichimaera perplexa* gen. et sp. nov. (B) cumacean specimen showing details of the carapace, thoracopods, and pleon. (C–D) unidentified shrimps. (E) *Callichimaera*-rich surface, showing several overlapping individuals with appendages. (F) *Cenomanocarcinus* sp. ventral view of specimen, from crab-rich surfaces of the San Rafael Formation, lower-mid Turonian. Photos by J. Luque.

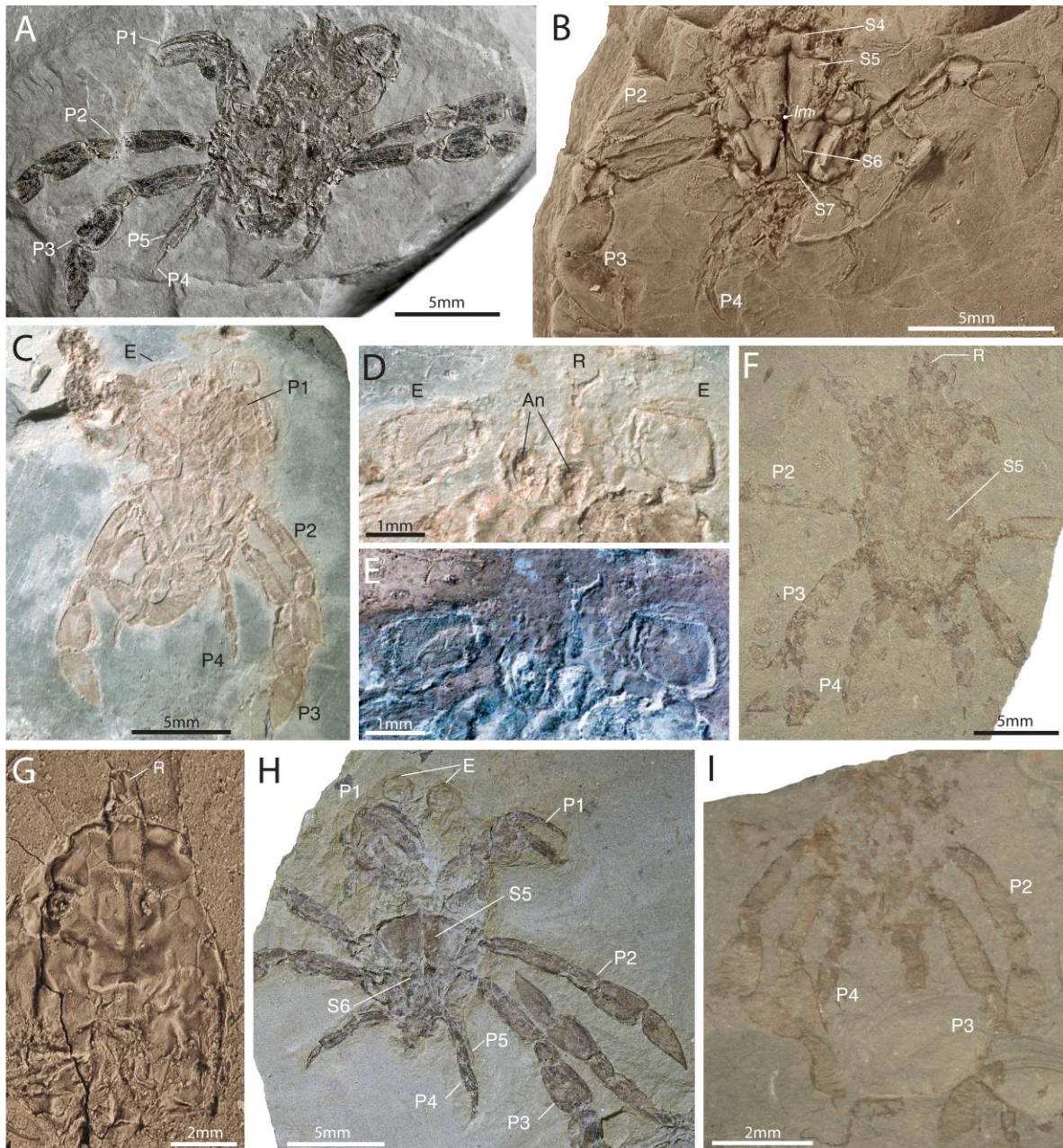


Fig. S4. Additional dorsal, ventral, and appendicular features in *Callichimaera perplexa* n. gen. n. sp., from the mid-Cretaceous of Colombia and the United States. (A) Paratype UN-DG-CR-003, showing all the legs and chelipeds (collector: D. Schonwalder). (B) Paratype IGM p881216, ventral view, showing the thoracic sternum and legs P2–P4. (C) Paratype 320005-081, showing details of the pereopods, sternum, and eyes; (D) Close-up of large compound eyes bearing small hexagonal facets; (E) inverted colors of (D) highlighting the shape of the eye and eye facets. (F) Non-type specimen USNM 605049, showing legs P2–P4, sternal plates, and rostrum. (G) Paratype IGM p881204, dorsal counterpart showing the fine granulation at the median portion of the carapace. (H) Paratype MUN-STRI 27044-02 (see Fig. 2A–B), a well-preserved specimen in ventral view bearing all limbs, sternites, mouthparts and eyes. (I) Non-type specimen USNM 605051, showing the paddle-like legs typical of *Callichimaera perplexa* n. gen. n. sp. All the paratypes are from the Cenomanian–Turonian Churuvita Group of Colombia; non-type specimens (F, I) are from the Turonian Frontier Formation of USA. Abbreviations: An: bases of antennae; lm: linea media; P1: cheliped or claw; P2–P5: pereopods or walking legs 2 to 5; R: rostrum; S1–S7: sternites 1 to 7. All specimens photographed dry; specimens in B, G coated with ammonium chloride; specimens in A, C–F, H–I uncoated. Photos by J. Luque.

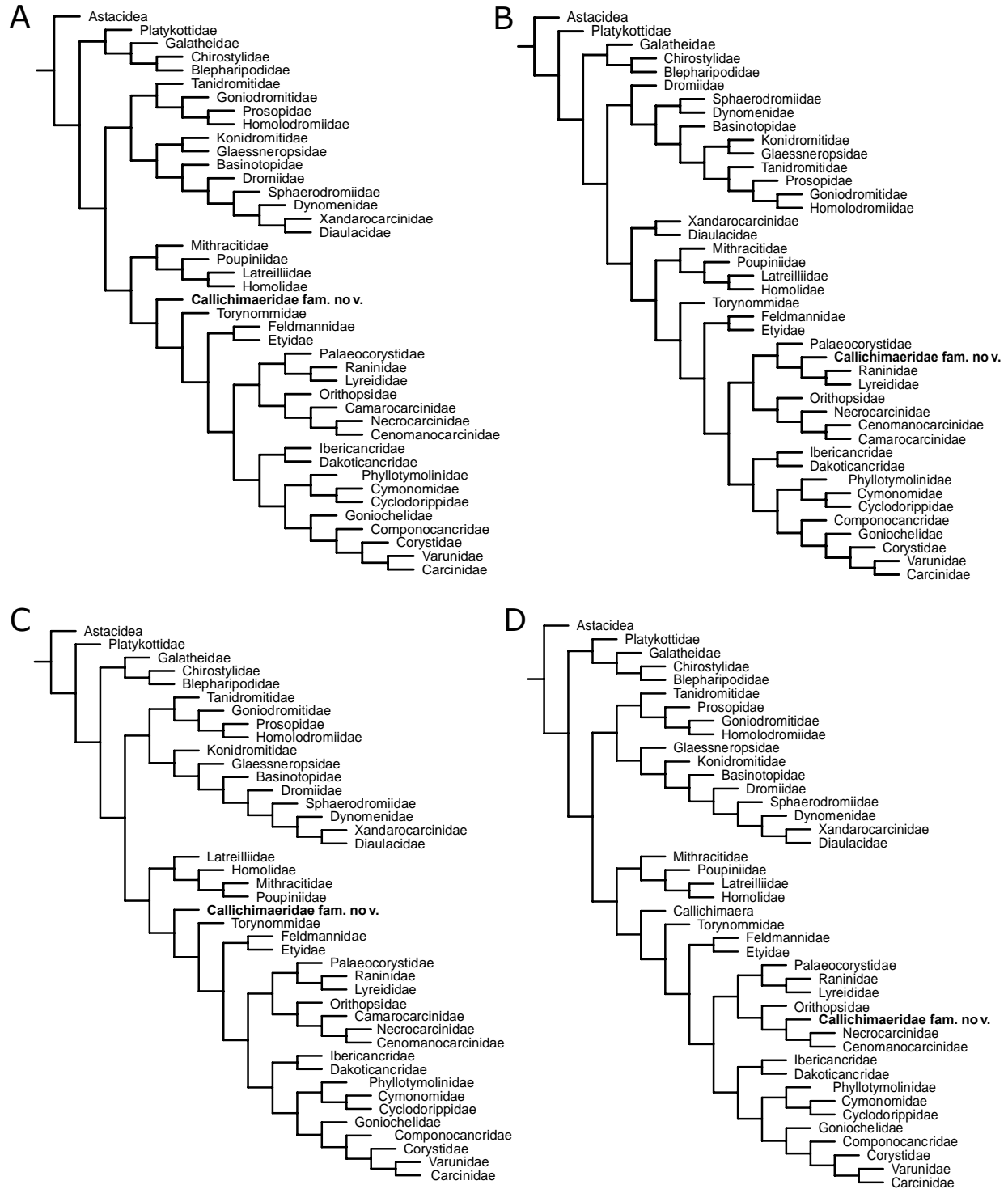


Fig. S6. Results of equally weighted and IWMP analyses. A) equally-weighted parsimony: single most parsimonious tree: Tree length (TL)= 203 steps; consistency index (CI)= 0.528; retention index (RI)= 0.796. (B–D) Implied-weights maximum parsimony (IWMP) topologies: (B) concavity value K=3; (C) concavity value K=6; (D) concavity value K=12. Analyses performed in TNT v.1.5.

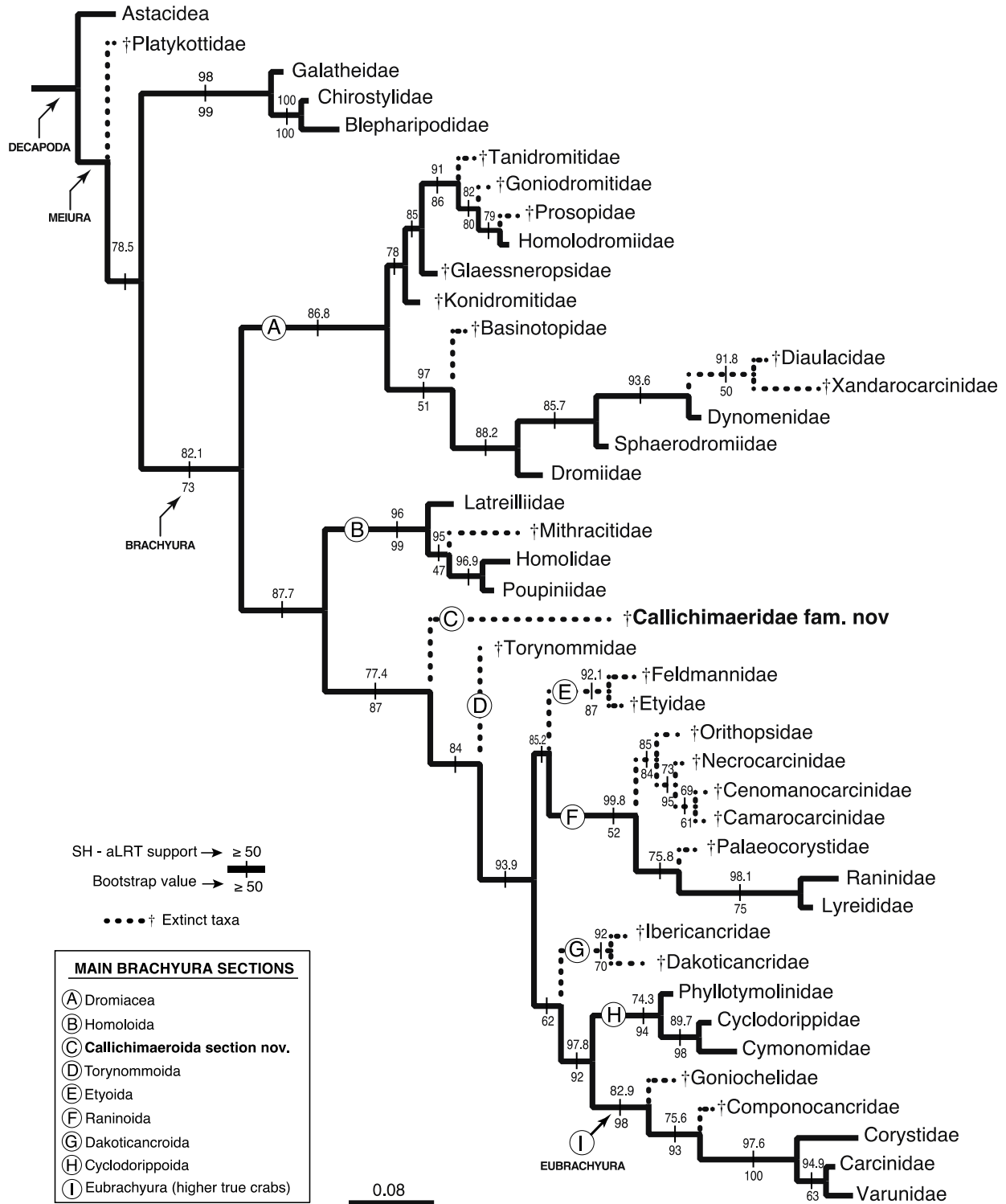


Fig. S7. ML topology with the nine major brachyuran sections and podotremous brachyuran families, including *Callichimaeridae* n. fam. Each capital letter in circle represents one of the nine main sections. Major brachyuran lineages indicated by capital letters A to I. SH-aLRT support values indicated above branches; bootstrap support values indicated below branches. Terminal taxa indicated by a dagger (†) are extinct.

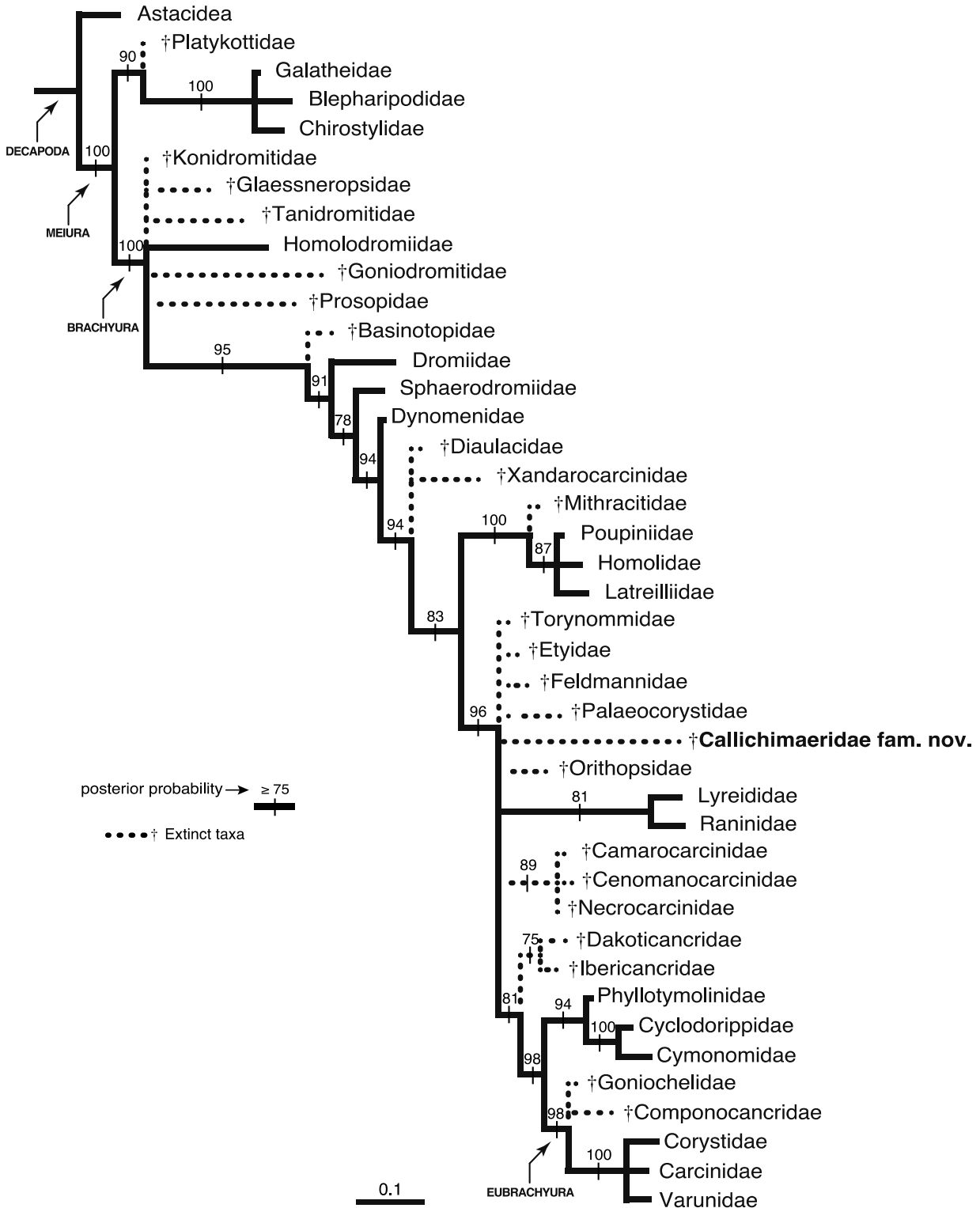


Fig. S8. Bayesian majority-rule consensus topology of the post-burnin sample of trees for fossil and extant podotremous brachyuran families, including *Callichimaeridae* n. fam. Posterior probability support values indicated above branches. Branches with posterior probability support $< 75\%$ are collapsed. Terminal taxa indicated by a dagger (†) are extinct.

Supporting Tables

Table S1. List of characters for phylogenetic analysis. Modified and expanded after (10), and include 85 adult morphological characters scored for 42 decapod terminals, including *Callichimaera perplexa* gen. et sp. nov.

1. Carapace proportions: elongate (0); as long as wide or wider (1)
2. Anterolateral margins: indistinct (0); distinct (1)
3. Spines or teeth on anterolateral margins: absent (0); present (1)
4. Carapace with well differentiated anterolateral and posterolateral margins: absent (0); present (1)
5. Posterolateral margins: rounded, not defined (0); defined (1)
6. Spines on posterolateral margin: absent (0); present (1)
7. Posterior margin: concave (0); straight to convex (1)
8. Reentrants on posterior margin: absent (0); present (1)
9. Orbit: not defined (0); defined (1)
10. Augenrest: absent (0); present (1)
11. Augenrest, if present: shallow (0); deep (1)
12. Inner orbital angle: not defined (0); defined (1)
13. Upper orbital fissures: absent (0); present (1)
14. Number of orbital fissures, if present: one (0); two (1)
15. Sub-hepatic swelling: present (0); absent (1)
16. Antennal groove: present (0); absent (1)
17. Cervical groove: distinct (0); indistinct (1)
18. Postcervical groove well-developed: present (0); absent (1)
19. Branchio-cardiac groove: distinct (0); indistinct (1)
20. Longitudinal ridge or tubercles on branchial region: absent (0); present (1)
21. Cervical or branchio-cardiac groove: reaching ventral carapace (0); ending at anterolateral margin or before reaching it (1)
22. Intestinal region: narrow, limited by branchio-cardiac grooves (0); wide (1)
23. Lateral lineae: absent (0); present (1)
24. Epistomial spine: absent (0); present (1)
25. Buccal cavern: wide (0); elongated, triangular (1)
26. Thoracic sternum: narrow (0); wide (1)
27. Sternites 1-3: indistinct ventrally (0); distinct ventrally (1)
28. Posterior sternites: wide (0); narrow, reduced (1)
29. Lateral position of posterior sternites: not visible (0); visible (1)
30. Episternites: not clearly defined (0); clearly defined by grooves (1)
31. Episternites 4-5: process-like (0); wide (1)
32. Suture 4-5: only lateral position (0); distinct axially (1)

33. Suture 5-6: only lateral position (0); distinct axially (1)
34. Suture 6-7 as seen externally on thoracic sternum: incomplete (0); complete (1)
35. Sternite 4 with anteriorly protruded plate: absent (0), present (1)
36. Median line on sternite 8: absent (0); present (1)
37. Sterno-coxal depression: present (0); absent (1)
38. Sterno-pleonal depression in male: absent (0); present (1)
39. Sterno-pleonal cavity in male: absent (0); present (1)
40. Homolid press-button: absent (0); present (1)
41. Sella turcica: absent (0); present (1)
42. Spermatheca: absent (0); present (1)
43. Spermatheca, if present: paired (0); united (1)
44. Spermatheca position, if present: around level of pereopod 3 coxa (0); much anterior to pereopod 3 coxa (1)
45. Aperture of spermatheca, if present: with margins not raised (0); raised (1)
46. Pleon: not folding (0); folding (1)
47. Pleonal somites: visible dorsally (0); not visible (1)
48. Pleonal pleura: well developed (0); reduced (1)
49. Articulating rings of pleon: present (0); absent (1)
50. Fusion of pleonal somites and telson in male: absent (0); present (1)
51. Pleonal locking: absent (0); present (1)
52. Pleonal locking, if present: coxal spine (0); sternal lobe or double peg (1)
53. Pleonal somite 6 with triangular lateral lobes: present (0); absent (1)
54. Socket on pleonal somite 6: absent (0); present (1)
55. Telson of male: elongate, much longer than wide (0); about as long as wide or wider than long (1)
56. Anterior end of telson, if folding present, between third maxillipeds: present (0); absent (1)
57. Conspicuous uropodal remains: absent (0); present (1)
58. If uropodal remains present: well developed uropods (0); uropodal plates (1)
59. Male gonopore position: coxal (0); sternal (1)
60. Female gonopore position: coxal (0); sternal (1)
61. Renal opening of 2nd antennal coxa with beak-like structure: absent (0); present (1)
62. Maxilliped 3: pediform (0); operculiform (1)
63. Maxilliped 3 much longer than wide: present (0); absent (1)
64. Maxilliped 3 with two planes: absent (0); present (1)
65. Maxilliped 3 with crista dentata: present (0); absent (1)
66. Maxilliped 3 coxae: large, touching each other (0); small, not touching each other (1)
67. Palp of maxilliped 3 merus: distal position (0); inner-mesial position (1)
68. Palp of maxilliped 3 merus: different plane (0); same level to merus (1)
69. Pereopods 2-4 form: normal (0); wide, flattened (1)
70. Pereopod 5 hidden in gill chamber: absent (0); present (1)

71. Coxa of all pereopods at same level: present (0); absent (1)
72. If not all coxae of pereopods at same level: only P5 dorsal (0); P4-P5 dorsal (1)
73. Pereopod 2: chelate (0); simple (1)
74. Pereopod 3: chelate (0); simple (1)
75. Pereopod 4: simple (0); chelate (1)
76. Pereopod 5: simple (0); chelate (1)
77. Pereopods size normal: present (0); absent (1)
78. If not all pereopods normal: only P5 reduced (0); P4 and P5 reduced (1)
79. Coxae of pereopods: elongate, large (0); short (1)
80. Male coxa P5: not modified (0); modified (1)
81. Male coxa P5: penial tube absent (0); penial tube present (1)
82. Pleopods on segments 3-5 in male: present (0); absent (1)
83. Male second pleopod with well-developed exopod: present (0); absent (1)
84. External shape of eye facets: squarish (0); hexagonal (1)
85. Linea anomalica: absent (0); present (1)

Table S2. Superfamilies and families of anomuran and brachyuran crabs included in the phylogenetic analysis. Systematic arrangement following largely (4, 9, 10). Taxa indicated by † are known as fossil and extant. Taxa indicated by †† only known from fossils.

- Infraorder Astacidea † Latreille, 1802
 Superfamily Nephropoidea † Dana, 1852
Nephropidae † Dana, 1852
Homarus † Weber, 1795 [*H. americanus* H. Milne Edwards, 1837 (in 1834-1840)]
- Infraorder Anomura † MacLeay, 1838
 Superfamily Eocarcinoidea Withers, 1932
Platykottidae †† Chablais, Feldmann and Schweitzer, 2011
Platykotta †† Chablais, Feldmann and Schweitzer, 2011 [*P. akaina* Chablais et al., 2011]
- Superfamily Galatheoidea † Samouelle, 1819
Chirostylidae † Ortmann, 1892a
Chirostylus Ortmann, 1892a [*C. sp.*]
Galatheidae † Samouelle, 1919
Galathea † Fabricius, 1793 [*G. sp.*]
- Superfamily Hippoidea † Latreille, 1825a
Blepharipodidae † Boyko, 2002
Blepharipoda † Randall, 1840 [*B. liberata* Shen, 1949]
- Infraorder Brachyura † Linnaeus, 1758
Podotreme grade
 Section Dromiacea † de Haan, 1833
 Superfamily Homolodromioidea † Alcock, 1900
Homolodromiidae † Alcock, 1900
Homolodromia † A. Milne-Edwards, 1880 [*H. robertsi* Garth, 1973; *H. paradoxa* A. Milne Edwards, 1880]
Dicranodromia A. Milne-Edwards, 1880 [*D. doederleini* Ortmann, 1892]
Goniodromitidae †† Beurlen, 1932
Eodromites †† Patruilius, 1959 [*E. grande* (von Meyer, 1857)]
Goniodromites †† Reuss, 1858 [imprint 1857] [*G. bidentatus* Reuss, 1858 [imprint 1857]; *G. hirotai* Karasawa and Kato, 2007; *G. polyodon* Reuss, 1858 [imprint 1857]; *G. serratus* Beurlen, 1929]
Pithonoton †† von Meyer, 1842 [*P. marginatum* von Meyer, 1842; *P. cardwelli* Armstrong et al., 2009]
Sabellidromites †† Schweitzer and Feldmann, 2008 [imprint 2007] [*S. inflata* (Collins and Karasawa, 1993); *S. scarabaea* (Wright and Wright, 1950)]
Prosopidae †† von Meyer, 1860
Prosopon †† von Meyer, 1835 [*P. mammillatum* Woodward, 1868]
Tanidromitidae †† Schweitzer and Feldmann, 2008 [imprint 2007]
Tanidromites spp.
- Superfamily Glaessneropsoidea †† Patruilius, 1959
Glaessneropsidae †† Patruilius, 1959
Glaessneropsis †† Patruilius, 1959 [*G. heraldica* (Moericke, 1889); *G. myrmekia* Schweitzer and Feldmann, 2009a]
Konidromitidae †† Schweitzer and Feldmann, 2010b
Konidromites †† Schweitzer and Feldmann, 2010b [*K. schneideri* (Stolley, 1924); *K. gibbus* (Reuss, 1858 [imprint 1857])]
- Superfamily Dromioidea de Haan, 1833
Basinotopidae †† Karasawa, Schweitzer and Feldmann, 2011
Basinotopus †† M'Coy, 1849 [*B. lamarckii* (Desmarest, 1822); *B. tricornis* Collins and Jakobsen, 2003]

Dromiidae de Haan, 1833

Conchoecetes Stimpson, 1858a [*C. artificiosus* (Fabricius, 1798)]

Dromia Weber, 1795 [*D. personata* (Linnaeus, 1758); *D. erythropus* (George Edwards, 1771)]

Epigodromia McLay, 1993 [*E. areolata* (Ihle, 1913)]

Epipedodromia André, 1932 [*E. thomsoni* (Fulton and Grant, 1902)]

Lauridromia McLay, 1993 [*L. dehaani* (Rathbun, 1923a)]

Sphaerodromiidae Guinot and Tavares, 2003

Sphaerodromia Alcock, 1899 [*S. lamellata* Crosnier, 1994]

Dromilites †† H. Milne Edwards, 1837 [*D. bucklandi* H. Milne Edwards, 1837 (in 1834-1840); *D. simplex* Quayle and Collins, 1981]

Dynomenidae Ortmann, 1892

Dynomene Desmarest, 1822 [*D. hispida* Guérin-Méneville, 1832; *D. pilumnoides* Alcock, 1900; *D. praedator* A. Milne-Edwards, 1878]

Diaulacidae †† Wright and Collins, 1972

Diaulax †† Bell, 1863 [*D. oweni* (Bell, 1850); *D. feliceps* Wright and Collins, 1972; *D. yokoi* Collins et al., 1993]

Xandarocarcinidae †† Karasawa, Schweitzer and Feldmann, 2011

Xandaros †† Bishop, 1988c [*X. sternbergi* (Rathbun, 1926)]

Section Homoloida Karasawa et al., 2011

Superfamily Homoloidea de Haan, 1839

Homolidae de Haan, 1839

Homola Leach, 1816 [imprint 1815] [*H. ranunculus* Guinot and Richer de Forges, 1995; *H. orientalis* Henderson, 1888]

Latreillopsis Henderson, 1888 [*L. bispinosa* Henderson, 1888]

Homolomania Ihle, 1912 [*H. sibogae* Ihle, 1912]

Paromola Wood-Mason in Wood-Mason and Alcock, 1891 [*P. macrocheira* Sakai, 1961]

Yaldwynopsis Guinot and Richer de Forges, 1995 [*Y. spinimanus* (Griffin, 1965)]

Latreilliidae Stimpson, 1858a

Latreillia Roux, 1830 [*L. valida* de Haan, 1839]

Mithracitidae †† Števcíć, 2005

Mithracites †† Gould, 1859 [*M. vectensis* Gould, 1859]

Poupiniidae Guinot, 1991

Poupinia Guinot, 1991 [*P. hirsuta* Guinot, 1991]

Section Callichimaeroida †† n. section

Superfamily Callichimaeroidea †† n. superfam.

Callichimaeridae †† n. fam.

Callichimaera †† n. gen. [*C. macrophthalma* n. sp.]

Section Tornyommoida †† Karasawa et al., 2011

Superfamily Tornyommoidea †† Glaessner, 1980

Tornyommidae †† Glaessner, 1980

Tornyomma †† Woods, 1953 [*T. dentatum* Glaessner, 1980; *T. flemingi* Glaessner, 1980; *T. quadrata* Woods, 1953]

Section Etyoidea †† Karasawa et al., 2011

Superfamily Etyoidea †† Guinot and Tavares, 2001

Etyidae †† Guinot and Tavares, 2001

Etyus †† Mantell, 1822 [*E. martini* Mantell, 1822]

Etyxanthosia †† Fraaije, van Bakel, Jagt, and Artal, 2008 [*E. aspera* (Rathbun, 1935); *E. pawpawensis* (Schweitzer, Salva, and Feldmann, 1999)]

Xanthosia †† Bell, 1863 [*X. buchii* (Reuss, 1845); *X. gibbosa* Bell, 1863; *X. granulosa* (M'Coy, 1854); *X. sakoi* Karasawa, Ohara, and Kato, 2008; *X. similis* (Bell, 1863)]

Feldmanniidae †† Schweitzer, Feldmann, Frantescu, and Klompaker, 2012

Feldmannia †† Guinot and Tavares, 2001 [*F. wintoni* (Rathbun, 1935)]
Caloxanthus †† A. Milne Edwards, 1864 [*C. americanus* Rathbun, 1935]

Section Raninoidea † Ahyong et al., 2007

Superfamily Necrocarinoidea †† Förster, 1968

Camarocarcinidae †† Feldmann, Li, and Schweitzer, 2007

Camarocarcinus †† Holland and Cvancara, 1958 [*C. arnesoni* Holland and Cvancara, 1958; *C. quinquetuberculatus* Collins and Rasmussen, 1992]

Cretacocarcinus †† Feldmann, Li, and Schweitzer, 2007 [*C. smithi* Feldmann et al., 2007]

Cenomanoarcinidae †† Guinot, Vega, and van Bakel, 2008

Campylostoma †† Bell, 1858 [*C. matutiforme* Bell, 1858]

Cenomanoarcinus †† Van Straelen, 1936 [*C. vanstraeleni* Stenzel, 1945]

Necrocarinidae †† Förster, 1968

Necrocarcinus †† Bell, 1863

Orithopsidae †† Schweitzer et al., 2003

Orithopsis †† Carter, 1872

Planocarcinus Luque et al., 2012 [*P. olssoni* (Rathbun, 1937)]

Superfamily Palaeocorystoidea †† Lörenthey in Lörenthey and Beurlen, 1929

Palaeocorystidae †† Lörenthey in Lörenthey and Beurlen, 1929

Ferroranina †† van Bakel et al., 2012 [*F. dichrous* (Stenzel, 1945)]

Joeranina †† van Bakel et al., 2012 [*J. kerri* (Luque et al., 2012)]

Eucorystes †† Bell, 1863 [*E. broderipi* (Mantell, 1844); *E. carteri* M'Coy, 1854]

Notopocorystes †† M'Coy, 1849 [*N. japonicus* (Jimbô, 1894); *N. stokesii* (Mantell, 1844)]

Superfamily Raninoidea † de Haan, 1839

Lyreididae † Guinot, 1993

Lyreidus † de Haan, 1841 [*L. tridentatus* de Haan, 1841]

Raninidae de Haan, 1839

Ranina † Lamarck, 1801 [*R. ranina* (Linnaeus, 1758)]

Symethis Weber, 1795 [*S. variolosa* (Fabricius, 1787)]

Section Dakoticancroidea Karasawa et al., 2011

Superfamily Dakoticancroidea †† Rathbun, 1917

Dakoticancridae †† Rathbun, 1917

Avitelmessus †† Rathbun, 1923b [*A. grapsoides* Rathbun, 1923b]

Dakoticancer †† Rathbun, 1917 [*D. australis* Rathbun, 1935; *D. overanus* Rathbun, 1917]

Tetracarcinus †† Weller, 1905 [*T. subquadratus* Weller, 1905]

Ibericancridae †† Artal et al., 2008

Ibericancer †† Artal et al., 2008 [*I. sanchoi* Artal et al., 2008]

Section Cyclodorippoidea Ahyong et al., 2007

Superfamily Cyclodorippoidea Ortmann, 1892

Cyclodorippidae Ortmann, 1892

Tymolus † Stimpson, 1858b [*T. japonicus* Stimpson, 1858b; *T. uncifer* (Ortmann, 1892)]

Xeinostoma † Stebbing, 1920 [*X. eucheir* Stebbing, 1920]

Cymonomidae † Bouvier, 1897

Cymonomus † A. Milne-Edwards, 1880 [*Cymonomus* sp.]

Cymonomoides Tavares, 1993 [*C. guinotae* (Tavares, 1991)]

Phyllotymolinidae Tavares, 1998

Genkaia Miyake and Takeda, 1970 [*G. gordonae* Miyake and Takeda, 1970]

Phyllotymolinum Tavares, 1993 [*P. crosnieri* Tavares, 1993]

Section Eubrachyura de Saint Laurent, 1980

Heterotreme grade

Superfamily Componocancroidea †† Feldmann et al., 2008

Componocancridae †† Feldmann et al., 2008

Componocancer †† Feldmann et al., 2008 [*C. roberti* †† Feldmann et al., 2008]

Superfamily Corystoidea † Samouelle, 1819

Corystidae † Samouelle, 1819

Corystes † Bosc, 1802 [*C. cassivelaunus* (Pennant, 1777)]
Superfamily Dorippoidea MacLeay, 1838
Goniochelidae †† Schweitzer and Feldmann, 2011b
Goniochele †† Bell, 1858 [*G. angulata* Bell, 1858; *G. madseni* Collins and Jakobsen,
2003]
Superfamily Portunoidea Rafinesque, 1815
Carcinidae † MacLeay, 1838
Carcinus † Leach, 1814 [*C. maenas* (Linnaeus, 1758)]
Subsection Thoracotremata Guinot, 1977
Superfamily Grapsoidea MacLeay, 1838
Varunidae † H. Milne Edwards, 1853
Helice De Haan, 1833 [*H. tridens* (De Haan, 1835)]