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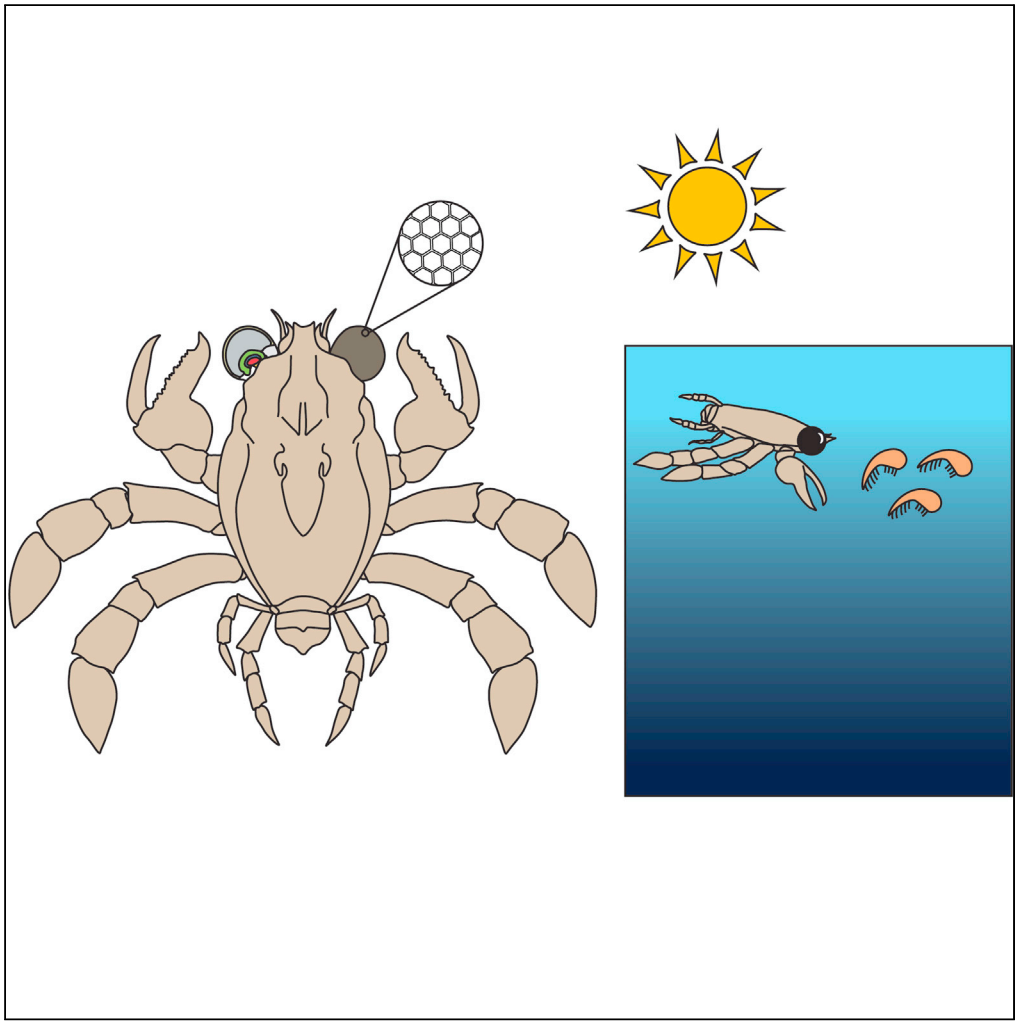

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Highlights

We report optical details of the Cretaceous brachyuran crab *Callichimaera perplexa*

It preserves both internal optic neuropils and external corneal elements

Callichimaera has a faster optical growth rate than a series of extant crabs

Callichimaera was a highly visual predator inhabiting well-lit environments

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The remarkable visual system of a Cretaceous crab

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SUMMARY

True crabs (Brachyura) are one of the few groups of arthropods to evolve several types of compound eye, the origins and early evolution of which are obscure. Here, we describe details of the eyes of the Cretaceous brachyuran *Callichimaera perplexa*, which possessed remarkably large eyes and a highly disparate body form among brachyurans. The eyes of *C. perplexa* preserve internal optic neuropils and external corneal elements, and it is the first known post-Paleozoic arthropod to preserve both. Additionally, a series of specimens of *C. perplexa* preserve both the eyes and carapace, allowing for the calculation of the optical growth rate. *C. perplexa* shows the fastest optical growth rate compared with a sample of 14 species of extant brachyurans. The growth series of *C. perplexa*, in combination with the calculation of the interommatidial angle and eye parameter, demonstrates that it was a highly visual predator that inhabited well-lit environments.

INTRODUCTION

True crabs (Brachyura) are among the few arthropod groups that have evolved several types of compound eye, reflecting their broad range of lifestyles (Gaten, 1998; Luque et al., 2019a). However, the origins and evolution of their visual systems remain poorly constrained, the eyes of most extant families of crabs are understudied, and fossil crabs rarely preserve compound eyes and internal soft tissues (Luque et al., 2019a, 2021). Here we present anatomical and ontogenetic details of the visual system of *Callichimaera perplexa* (Luque et al., 2019b), an exceptionally preserved crab from a recently discovered Cretaceous (95–90 mya) Lagerstätte of Colombia, northern South America. Compound eyes may reflect habitat (e.g., well-lit versus dimly light environment), activity patterns (e.g., diurnal versus nocturnal), and lifestyle (e.g., predator versus prey) (Bauer et al., 1998; Cronin, 2005). The detailed preservation of large compound eyes and soft tissues such as the optic lobe of *C. perplexa*, together with information on eye morphology and growth rates, permits a comparison with data on a diversity of extant crabs and shows that it was an active visual swimmer, likely a predator in well-lit marine environments.

RESULTS AND DISCUSSION

The pattern of optic neuropils differs from that in extant postlarval crabs

Pancrustaceans process visual information in the nested optic neuropils of the eyes (the lateral expression of the protocerebrum) before passing it to the central brain (Loesel et al., 2013). Those delicate neural tissues are rarely preserved in fossils, and even less in association with corneal lenses. Some examples of fossilized eyes and neural tissues are known from Cambrian species (Strausfeld et al., 2016a,b), e.g., the radiodont *Lyrarapax unguispinus* (Cong et al., 2014), apparently the bivalved arthropod *Odaraia* (Edgecombe et al., 2015; Ortega-Hernández, 2015), and the fuxianhuiid *Fuxianhuia protensa* (Ma et al., 2012), which has large hemispherical eyes with short to no eyestalks, reminiscent of those in *C. perplexa* (Figure 1). There are other Paleozoic arthropods, in addition to these Cambrian taxa, that preserve conspicuous external corneal elements (e.g., Paterson et al., 2011; Lee et al., 2011) or internal retinotopic and protocerebral neural tissues (Tanaka et al., 2013; Ortega-Hernández, 2015; Strausfeld et al., 2016a,b). Specimens of the Jurassic thylacocephalan *Dollocaris ingens* preserve spectacular details of facets and crystalline cones, and even retinular cells (Vannier et al., 2016), but optic neuropils or other lateral protocerebral tissues have not been reported.

Here we report the first example of preservation of external corneal lenses, corneagenous cells, and internal retinotopic neuropils in a post-Cambrian marine arthropod, *C. perplexa*, from the lowermost Upper Cretaceous of Colombia, South America (Figure 2). At least 11 of the >70 known specimens of

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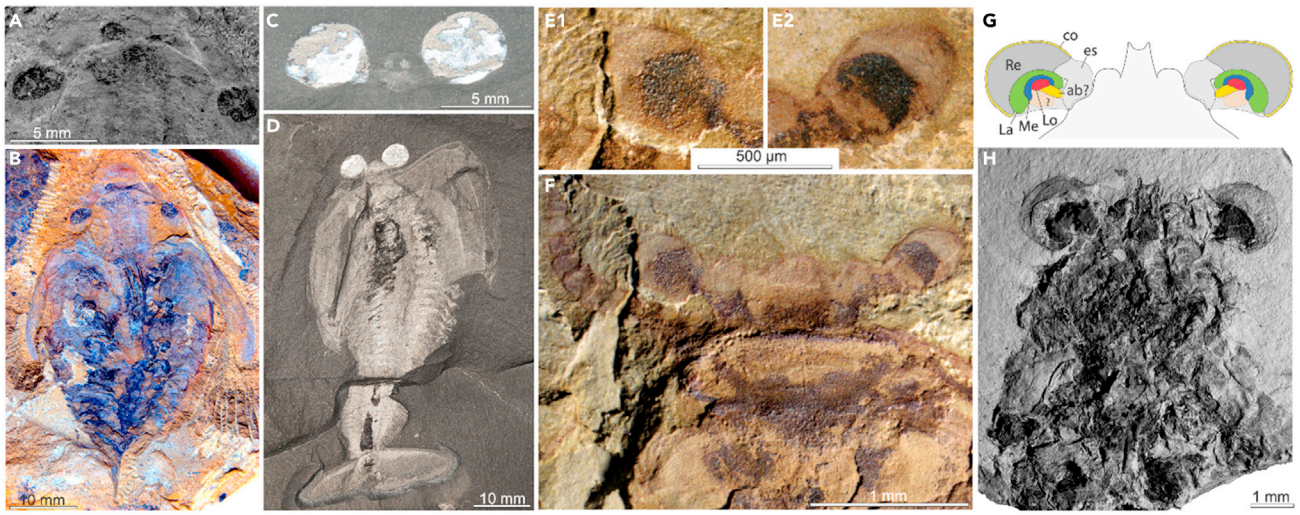

Figure 1. Selected fossil arthropods with large eyes and neural tissue preservation, including *Callichimaera perplexa*

(A and B) The radiodont *Lyrarapax unguispinus*, YKLP 13305, from the early Cambrian Chengjiang biota, China (images courtesy of Gregory Edgecombe, modified from Cong et al., 2014).

(C–D) The bivalved arthropod *Odaraia*, ROM 60746, from the early Cambrian of the Burgess Shale, Canada (images by Jean-Bernard Caron, courtesy of Javier Ortega-Hernández, modified from Ortega-Hernández, 2015).

(E and F) The fuxianhuiid *Fuxianhuia protensa*, YKLP 15006, from the early Cambrian Chengjiang biota, China (images courtesy of Gregory Edgecombe, modified from Ma et al., 2012).

(G and H) *Callichimaera perplexa*, from the Cretaceous of Colombia; (G) schematic reconstruction of anterior carapace and eyes with the optic lobe of H; (H) specimen IGM p881208 (images by Javier Luque, modified from Luque et al., 2019b). Abbreviations and colors in G: ab?, putative axon bundles (yellow); co, corneal eye; es, eyestalk (light gray); La, lamina (green); Lo, lobula (red); Me, medulla (blue); Re, retina (dark gray); ?, undetermined tissue (light orange).

C. perplexa (Luque et al., 2019b) preserve remains of the large hemispherical eyes. Specimens preserving the ommatidia show hexagonal facets packed in a hexagonal array, with the exception of one specimen that, in addition to well-developed hexagonal facets, preserves square-like facets in a rhomboidal packing in a region of the proximal cornea (Figures 2F, 2H–2I). Although a combination of hexagonal and square facets is known in a few decapods (Luque et al., 2019b), it is normally the result of packing toward the corneal edges rather than representing different underlying visual systems. This appears to be the case in *C. perplexa*, as square-like facets have not been observed in the other eye of the same specimen or in any other of the studied specimens.

Scanning electron microscopy (SEM) revealed the outline of the two underlying corneagenous cells in facets of hexagonal and squarish outline (Figures 2J–2M), reflecting the ground plan in all insects and malacostracan crustaceans (Nilsson and Kelber, 2007). In crustaceans with compound eyes, each ommatidium has a pair of epithelial corneagenous cells underlying and secreting the corneal lens, and overlying four cone (Semper) cells and a tetrapartite crystalline cone, together forming the dioptric apparatus (Richter et al., 2010). The exceptional preservation of cellular details of the eye tissues in fossil arthropods is highly unusual (e.g., Vannier et al., 2016).

One specimen of *C. perplexa* (Figure 2A) preserves three discrete, tightly packed regions corresponding to the three retinotopic neuropils: lamina (Figures 2C and 2E, green), medulla (Figures 2C and 2E, blue), and lobula (Figures 2C and 2E, red). A columnar array (Figure 2E, yellow) extending proximally from the lobula corresponds in position to axon bundles and to fine pits in the lamina (Figures 2B and 2C), which may represent retinotopic processing units. The optic lobe neuropils are closely packed, separated only by narrow chiasmata (Figures 2D and 2E). This tight packing is largely within the eye, in contrast to the typical brachyuran crab ground pattern where some of the proximal neuropils are lodged in the eyestalk and separated from one another by wide chiasmata (Strausfeld, 2005). The tight packing is more reminiscent of that in some insects, e.g., flies, bees (Gowda and Gronenberg, 2019), and crab megalopae, e.g., *Carcinus maenas* (Harzsch and Dawirs, 1993; Spitzner et al., 2018), than in those adult crabs that have been studied (hermit, shore, and fiddler crabs: Wolff et al., 2012; Strausfeld and Olea-Rowe, 2021). The eyestalk is largely absent in insects, and the neuropils are enlarged and packed in a more organized fashion in the reduced

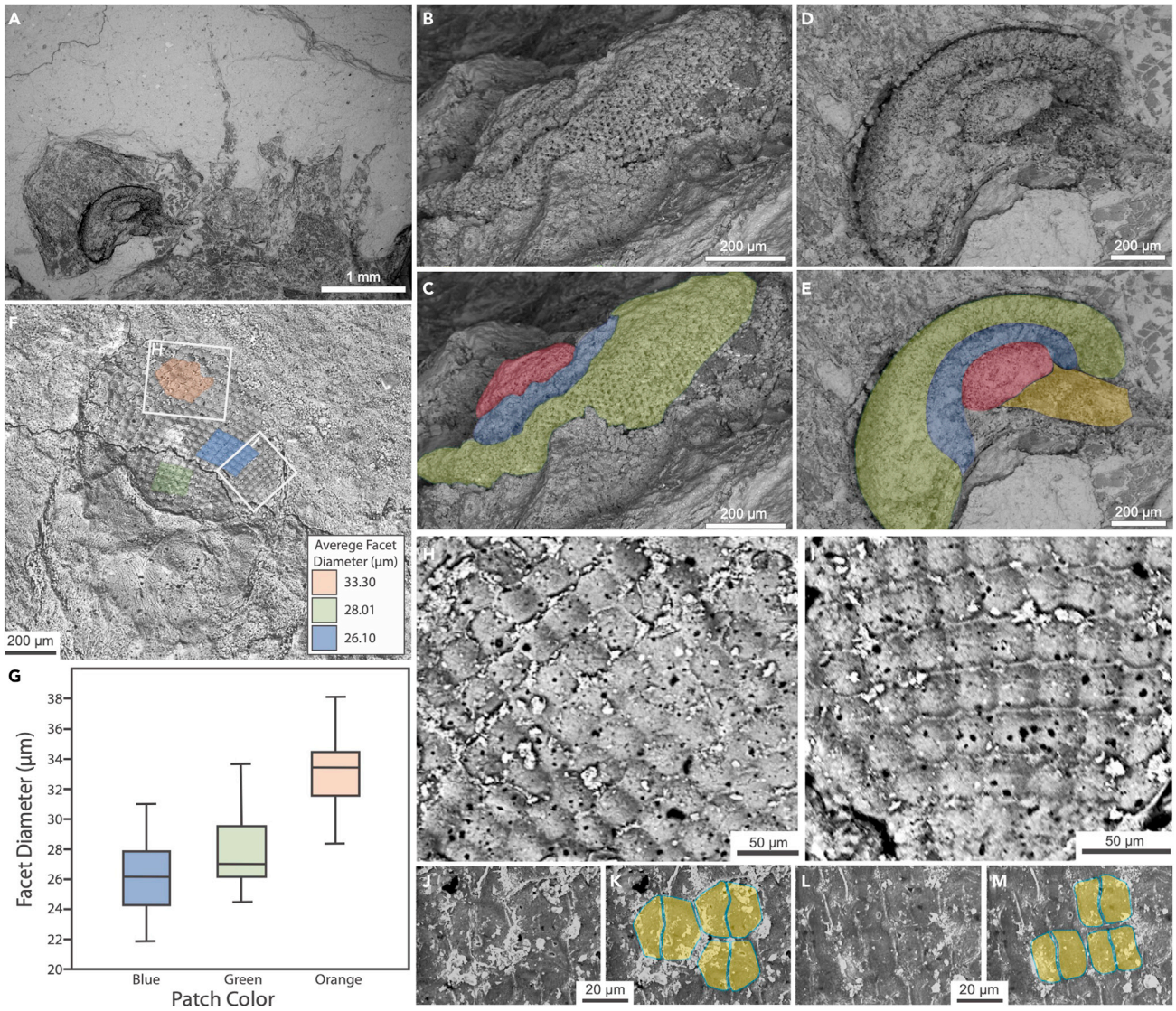

Figure 2. Exceptional preservation of eyes in the Cretaceous crab *Callichimaera perplexa*

(A–E) Adult individual (IGM p881209a); (A) SEM close-up of frontal region; (B, D) details of the layered optical lobe in left eye in oblique (B) and dorsal (D) views; (C–E) same views with colored optical lobe neuropils, i.e., lamina (green), medulla (blue), lobula (red), and putative axon bundles (yellow). (F, H–M) juvenile individual (IGM p881220) from which (G) regionalization, as well as inter-ommatidial angle, and eye parameter were calculated (Figure 5). (F) SEM image of the eye indicating the three regions where the average facet diameters were estimated (orange, green, and blue shading) in (G). White boxes indicate two different regions with facets of different shape and packing, i.e., hexagonal (H) and squarish (I); (J–M) Close-up SEM images of H and I, showing the outline of the two underlying corneagenous cells of hexagonal (K) and squarish (M) facets. Images A, D–E, and F modified after Luque et al. (2019b).

space between the basal membrane of the eye and the central part of the cerebrum (Wolff et al., 2017). A similar phenomenon may account for the nature and organization of the optic lobe neuropils in *C. perplexa* with its reduced eyestalks. This implies that image processing in *C. perplexa* occurred mainly in the eye itself and less so in the eyestalk, in contrast to most other postlarval brachyurans.

Callichimaera exhibits the fastest-growing eyes among true crabs

We examined the growth rate of the eye of *C. perplexa* and compared it with data we assembled on 14 species of extant brachyuran crabs belonging to 9 families, to determine the ecology and habits of this unusual Cretaceous crab. Previous work on crustaceans suggests that inferring depth from trends in the growth rates of the eyes is most accurate when sampling is restricted to members of the same family or genus (Hiller-Adams and Case, 1985). In general, the eyes of pelagic crustaceans are thought to grow faster

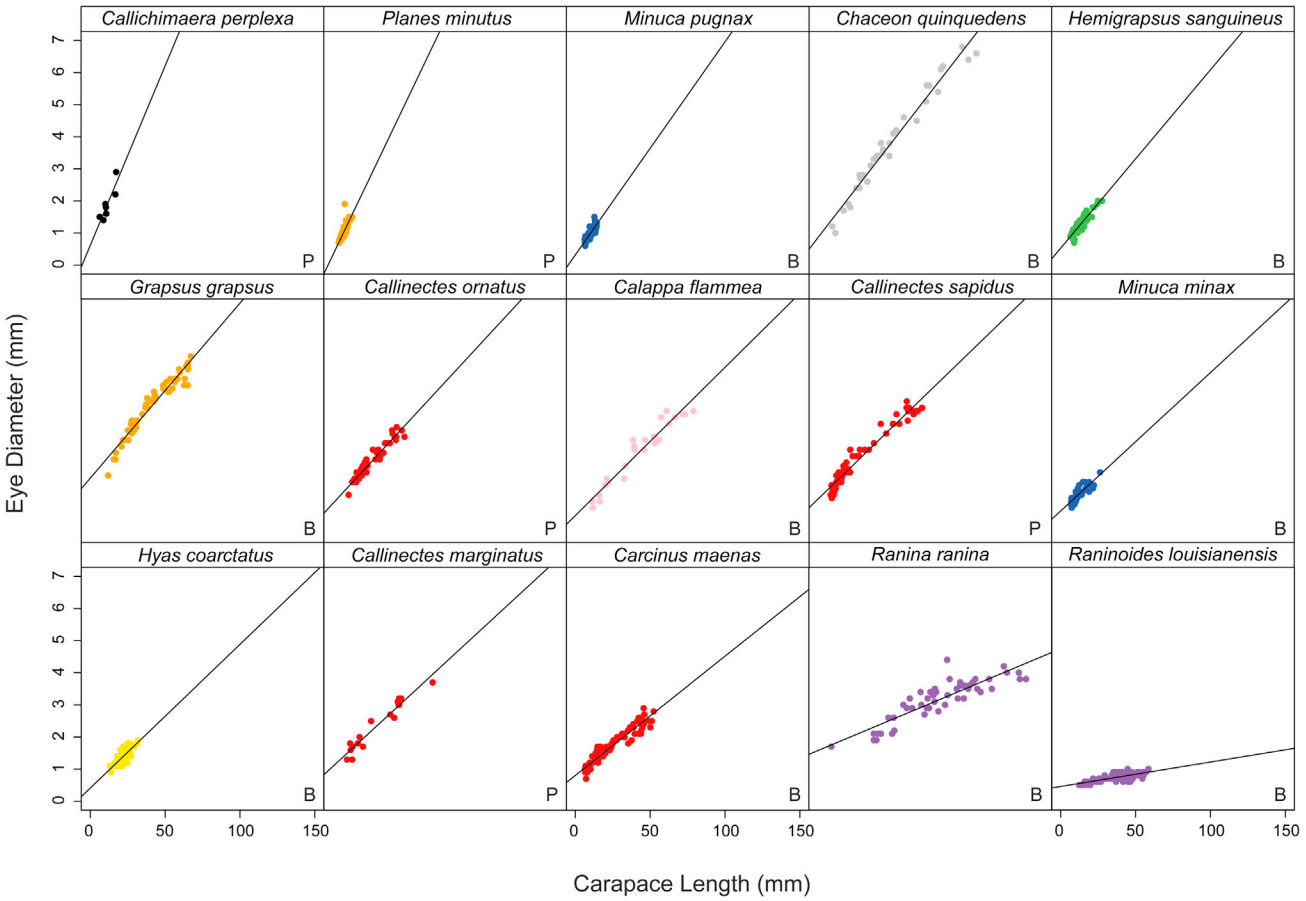

Figure 3. Growth rate of eyes in living brachyuran crabs relative to carapace length compared with that in *Callichimaera perplexa*

Panels are ordered by decreasing slope from top left to bottom right. Species of brachyuran crab are color coded by family as follows: Callichimaeridae, black; Grapsidae, orange; Ocypodidae, blue; Geryonidae, gray; Varunidae, green; Portunidae, red; Calappidae, pink; Oregoniidae, yellow; and Raninidae, purple. All measurements are recorded in millimeters. P, pelagic; B, benthic.

at shallower depths than species in the same family that live at greater depths (Hiller-Adams and Case, 1988). Conversely, the eyes of benthic crustaceans grow faster at greater depths (Hiller-Adams and Case, 1985). There are, however, some departures from these trends in our dataset (Figure 3, Table 1). Among pelagic Portunidae, there is no statistical difference in the growth rate of the eyes between the three species of *Callinectes*, even though they inhabit different maximum depths. Of the benthic Raninidae sampled here, *Raninoides louisianensis* lives at greater depths than *Ranina ranina,* but the eyes of *R. ranina* grow statistically faster. Thus, trends in eye metrics and habitat depth in Brachyura may vary more than in crustaceans in general or may be more strongly influenced by environmental or behavioral factors other than habitat depth.

C. perplexa shows the fastest growth rate of our sample (Figure 3, Table 1), although the values do not differ statistically from those for several living crabs that rely heavily on vision. These include two species from shallow depths and intertidal zones (i.e., *Minuca pugnax* and *Hemigrapsus sanguineus*), as well as *Planes minutus*, a pelagic crab that ranges from shallow water to deeper depths (Table 1). One deep-water crab, *Chaceon quinquedens*, also exhibits a high growth rate statistically similar to that of *C. perplexa*, despite inhabiting dim-lit environments. However, *C. quinquedens* engages in highly visual predatory behavior such as hunting mid-water fishes and squids (Steimle et al., 2001). In contrast to these visual predators, crabs that are less reliant on vision exhibit statistically slower growth rates, including the frog crabs *Ranina ranina* and *Raninoides louisianensis* (Raninidae), two species of fossorial crabs that spend most of their time concealed in the sediment and inhabit maximum depths that extend into the aphotic zone. Frog crabs also possess distinctly small eyes relative to their carapace size (Figure 4), which echoes

Table 1. Relationship between the eye diameter and carapace length from raw values

Taxon	Family	Sample size	Equation	r^2	Benthic or pelagic	Min depth (m)	Max depth (m)	Most records (m)
Calappa flammea	Calappidae	25	y = 4.0463x + 0.5475	0.94	Benthic	0	300	0–10
Callichimaera perplexa	Callichimaeridae	7	y = 0.1119x + 0.602	0.78	Pelagic	X	X	X
Chaceon quinquedens	Geryonidae	36	y = 0.0602x + 0.8553	0.97	Benthic	0	3,000	200–300
Planes minutus	Grapsidae	104	y = 0.096x + 0.3156	0.72	Pelagic	0	10,000	0–10
Grapsus grapsus	Grapsidae	56	y = 0.0544x + 1.7207	0.94	Benthic	0	10	0–10
Minuca pugnax	Ocypodidae	64	y = 0.0668x + 0.3187	0.73	Benthic	0	10	0–10
Minuca minax	Ocypodidae	36	y = 0.0435x + 0.6849	0.75	Benthic	0	10	0–10
Hyas coarctatus	Oregoniidae	54	y = 0.0432x + 0.4354	0.62	Benthic	0	600	40–50
Callinectes ornatus	Portunidae	63	y = 0.0494x + 0.9452	0.94	Pelagic	0	70	0–10
Callinectes sapidus	Portunidae	79	y = 0.0451x + 1.0606	0.96	Pelagic	0	140	0–10
Callinectes marginatus	Portunidae	17	y = 0.0426x + 1.0806	0.94	Pelagic	0	500	10–20
Carcinus maenas	Portunidae	85	y = 0.0368x + 0.8041	0.90	Benthic	0	140	0–10
Ranina ranina	Raninidae	52	y = 0.0196x + 1.5699	0.76	Benthic	0	400	50–70
Raninoides louisianensis	Raninidae	102	y = 0.0076x + 0.4498	0.59	Benthic	0	2,000	300–400
Hemigrapsus sanguineus	Varunidae	105	y = 0.055x + 0.5334	0.90	Benthic	0	10	0–10

All measurements were collected in millimeters. Depths are from obis.org. Raw measurements are stored on Mendeley (see Key Resources Table).

many deep-water crabs that have reduced or vestigial eyes (e.g., hydrothermal vent bythograeid crabs: Jinks et al., 2002). Although growth rates of the eyes do not show a direct correlation with habitat depth, high growth rates are common among crabs that engage in highly visual behaviors, such as active predation (as opposed to scavenging) or visual courtship.

Despite the similarity in growth rates of the eyes of *C. perplexa* and living highly visual crabs, it shows striking morphological differences from the other brachyurans sampled. The eyes of *C. perplexa* are the largest relative to carapace length (Figure 4). Its large compound eyes are unprotected and lack orbits, features consistent with retention of larval traits into adulthood via heterochronic development (pedomorphosis) (Luque et al., 2019b; Wolfe et al., 2021). However, these features are unusual in a swimming adult form. Relatively large eyes are known in other adult brachyurans (e.g., *Paragoneplax*; Castro, 2007), but they are usually borne on stalks that can be retracted into a protected orbit within the carapace (Gaten, 1998). Furthermore, extremely large eyes in crabs are typically associated with cryptic or dim-light environments to optimize capture of the minimal light available (Feldmann et al., 2008). Such eyes are unusual in pelagic crabs such as *C. perplexa* because they cause hydrodynamic drag and impose a buoyancy cost (Hiller-Adams and Case, 1985, 1988). Nevertheless, several extinct pelagic arthropods have large eyes in combination with other morphological adaptations indicative of predatory behavior in well-lit environments, including some trilobites (Fortey, 1985), thylacocephalans (Vannier et al., 2016), and the enigmatic *Isoxys* (Vannier et al., 2009). The fast growth rate of the eyes of *C. perplexa*, combined with other features of its morphology, suggests that it was a pelagic to nekto-benthic swimming crab engaged in highly visual behavior.

Visual acuity in *Callichimaera perplexa* indicates predatory behavior

The average interommatidial angle (IOA) in the eyes of *C. perplexa* is 0.57°, indicating a high degree of visual acuity comparable with that of modern predatory arthropods (Figure 5A, Table S2). This value is smaller, indicating more acute vision, than that in two species of highly visual extant crabs: the intertidal *Austruca annulipes* (IOA 1.33: Land, 1999) (Table S3), which conducts visual mating displays characteristic of fiddler crabs, and *Callinectes sapidus* (IOA 1.6: Baldwin and Johnsen, 2011), which is an active predator. Acute vision in predatory arthropods favors tracking, capturing, or ambushing prey (Wehner, 1981). IOA values are low in predatory arthropods regardless of whether they are an active predator or a sit-and-wait ambush predator—IOA values do not differentiate the two styles of prey capture (Anderson et al., 2014). However, the high visual acuity in *C. perplexa* (Figure 5A), coupled with its large oar-like swimming legs, indicates an active swimming predatory style, perhaps targeting pelagic comma shrimp (cumaceans)

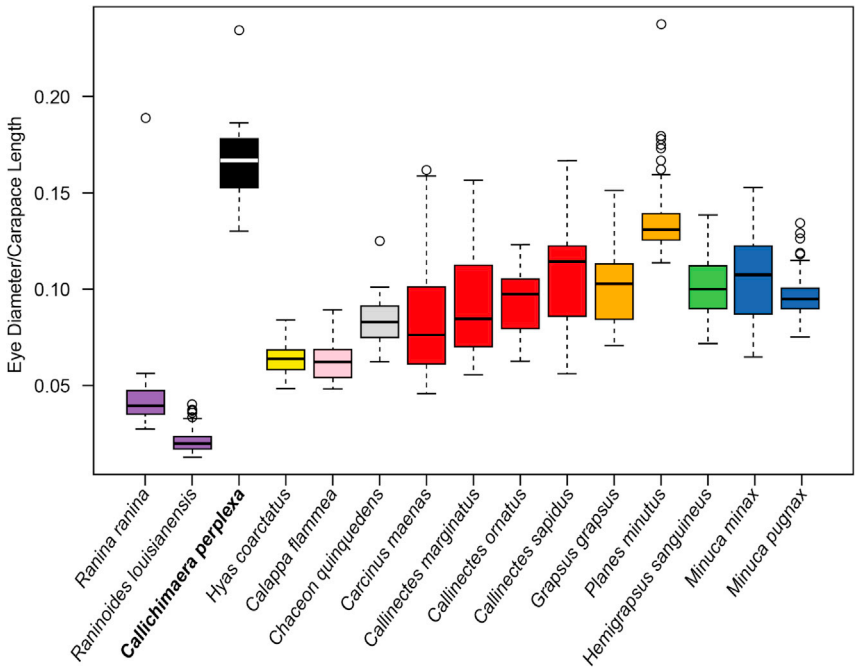

Figure 4. Boxplots of the mean and standard deviation of the ratio of eye diameter to carapace length in brachyuran crabs

Species of brachyuran crabs are color coded by family as follows: Callichimaeridae, black; Grapsidae, orange; Ocypodidae, blue; Geryonidae, gray; Varunidae, green; Portunidae, red; Calappidae, pink; Oregoniidae, yellow; and Raninidae, purple. Bold font indicates extinct taxa. Outliers indicated by open circles.

such as *Eobodotria muisca*, which is found in hundreds to thousands associated with *C. perplexa* (Figure 6) (Luque and Gerken, 2019).

Compound eyes often incorporate an "acute zone" of larger facets capable of increased resolution (Land, 1989). In shore and intertidal crabs, the acute zone appears as an equatorial band of ommatidia, suited for visualizing flat environments where resolution along the horizon is necessary (Zeil et al., 1989; Zeil and Al-Mutairi, 1996; De Astrada et al., 2012). Forward-pointing acute zones, which allow small prey to be detected at greater distances, are found in predatory arthropods such as praying mantises and in insects that engage in seeking behaviors and forward flight, e.g., bees, wasps, and butterflies (Land and Eckert, 1985; Warrant et al., 1999; Petrowitz et al., 2000). Similar patterns are present in the eyes of *C. perplexa*, where facets with larger average diameters are more prevalent in the center of the eye than closer to the accreting edge (Figures 2F and 2G). Overall, the facets of *C. perplexa* are relatively small (<34 μm), similar to those of arthropods active in bright environments, whereas the horseshoe crab *Limulus* (a chelicerate), at the opposite extreme, has facets up to 300 μm to facilitate night vision (Land, 1989). The average value of the eye parameter (*P*) of *C. perplexa* is relatively low (0.35), consistent with shallow well-lit environments (Figure 5B, Table S4), whereas nocturnal species or those inhabiting dark environments exhibit larger values (4+). This low value of *P* suggests that *C. perplexa* inhabited environments of the highest illumination, likely shallow water, and exhibited diurnal activity patterns (Hiller-Adams and Case, 1984).

Conclusions

Information on the optics and ontogeny of the eyes of *C. perplexa* indicates that it was a highly visual crab, active in well-lit, shallow marine environments. The size and rapid growth of its eyes, the arrangement and size of the hexagonal facets, and the confined space for the optic lobe neuropils between the basal membrane of the compound eye and the central brain, combined with the overall morphology of the crab, indicate a predatory lifestyle. The unusually large and unprotected nature of the eyes of *C. perplexa* is consistent with retention of larval morphology via pedomorphosis. *Callichimaera* is one of nine higher brachyuran branches (five extant) and one of the few groups to have colonized the pelagic/nektobenthic zone since the Cretaceous Crab Revolution.

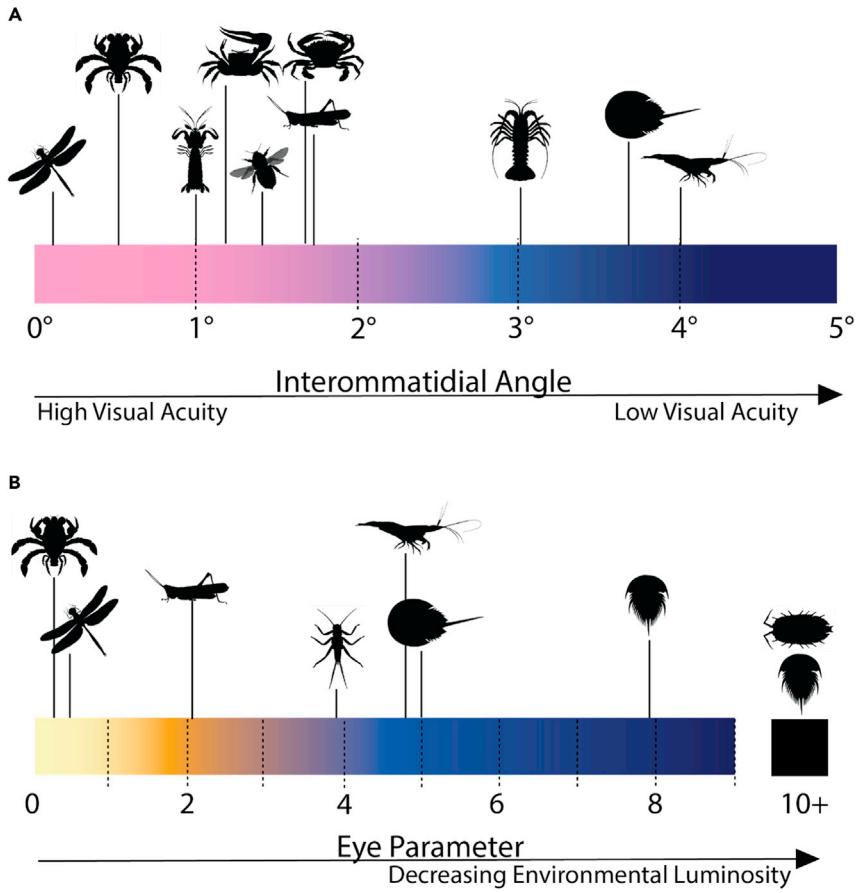

Figure 5. Visual acuity and eye parameter of *Callichimaera*

(A) Interommatidial angles $\Delta\varphi$ of *C. perplexa* and marine and terrestrial arthropods reflecting visual acuity.

(B) Eye parameter (*P*) values in *C. perplexa* and marine and terrestrial arthropods that correspond to decreasing environmental luminosity. Raw values and PhyloPic attributions are provided in the supplement (Tables S3 and S4).

C. perplexa had a remarkable visual system compared with other extinct and extant crabs, and the exceptional preservation of retinotopic neuropils, together with delicate features of the corneal eye lenses, is the first of its kind found in a post-Cambrian marine arthropod.

Limitations of the study

Although the ocular anatomy is preserved in exquisite detail in several specimens of *C. perplexa* and demonstrates the unique visual system in this crab, it does not reveal the origin and evolution of the many types of compound eyes found in extant crabs. Phylogenetically, *C. perplexa* is the basalmost brachyuran crab to possess hexagonal facets, constraining the loss of reflecting superposition (mirror) eyes, which have square facets (Luque et al., 2019a). However, three different types of compound eyes possess hexagonal facets (apposition, parabolic, and refracting superposition eyes), all of which are present in extant brachyurans. In the absence of more information about the underlying visual system, determining the specific type of compound eye in *C. perplexa* and other fossil crabs is not possible beyond confirming the absence of reflecting superposition (mirror) eyes, which is the plesiomorphic condition for decapods in general and brachyuran crabs in particular (Land, 2000). As such, the origins and diversification of these types of compound eyes within Brachyura remain enigmatic. Furthermore, calculations of IOA and *P* are based on one specimen because it was the only specimen to preserve facets near the accreting edge without significant wrinkling or other deformation. Compaction may impact facet dimensions in fossils, but we have used a methodology designed to minimize this effect (Anderson et al., 2014). IOA and *P* typically vary across the surface of compound eyes, as reflected in the transects measured for the calculations of these values.

Figure 6. Reconstruction of the extinct *Callichimaera perplexa*

Rendition depicting *C. perplexa* swimming after a male comma shrimp *Eobodotria muisca* (Cumacea), courtesy of Masato Hattori.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2021.103579.

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AUTHOR CONTRIBUTIONS

Conceptualization, all authors; data collection: K.M.J. and J.L.; data curation and analysis, K.M.J.; funding acquisition, all authors; investigation, all authors; methodology, K.M.J.; visualization, K.M.J. and J.L.; writing – original draft, K.M.J. and J.L.; writing – review and editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Callichimaera perplexa (fossil specimens)	Palaeontological Collections, Colombian Geological Survey, Bogotá, Colombia; Mapuka Museum of Universidad del Norte, Barranquilla, Colombia	IGM p881207, IGM p881210, IGM p881211, MUN STRI 27044-02a, MUN STRI 27045-09
Lyrarapax unguispinus (fossil specimen)	Yunnan Key Laboratory, Kunming, Yunnan Province, China	YKLP13305
Fuxianhuia protensa, (fossil specimen)	Yunnan Key Laboratory, Kunming, Yunnan Province, China	YKLP 15006
Odaraia (fossil specimen)	Royal Ontario Museum, Toronto, Canada	ROM 60746
Calappa flammea	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 890, 988, 1503, 1744, 2111, 3625, 3907, 3997, 6225, 6407, 37061, 37090, 38030, 38031, 41455, 41467-41468, 41842, 43379
Callinectes marginatus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 1427, 1736, 3643, 3646, 3630, 3679, 41865-41866, 41869-41871, 42859
Callinectes ornatus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 3658, 3678, 3693,6395, 6397, 6389, 21234, 22621
Callinectes sapidus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 1034, 1207-1208, 3635, 28005, 30689, 41903, 48005, 55484, 103740
Carcinus maenas	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 5773, 30731, 41912-41913, 41915, 42927, 44294, 67205, 69150
Chaceon quienquedens	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 2546, 3882, 8139, 37192, 41814-41827, 41832, 43364
Grapsus grapsus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 1731, 3046, 3049, 3972, 4021, 5674, 5838, 5895-5896, 23349, 24519, 27784, 42515-42516, 42518, 42520, 42522, 42701, 42938, 43301, 43346-43349
Hemigrapsus sanguineus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 23805, 67838-67870, 67873-67888, 67890-67891, 67893, 67895-67897, 67899-67905, 67907, 67909-67911, 67913-67924, 67927-67933, 67936, 67938, 67943-67950, 67953-67957, 67959-67967, 67969, 78539
Hyas coarctatus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 41588
Planes minutus	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 30824, 36956
Ranina ranina	Muséum national d'Histoire naturelle, Paris, France; Queensland Museum, Brisbane, Australia; United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA	MNHN-IU-2000-220, -2000-223, -2000-228, -2016-2011, -2016-2019; QMW uncatalogued, QMW 686, 698, 706, 908, 1687, 1805, 1972, 2019, 5230, 12264, 14879, 15725, 21523; USNM 2044, 26286, 41502-41503, 64628, 66640, 106160, 1132860, 1277456-1277457, 128588, 239219-239220, 265062, 268504, 268506
Raninoides louisianensis	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 21048, 21072, 21116-21117, 21150, 21179, 21187, 36865, 36867, 36877, 36882

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Uca minax	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 3690, 5869, 30831, 37130, 37147, 42466-42467
Uca pugnax	Yale Peabody Museum of Natural History, New Haven, Connecticut	YPM IZ 3699, 3721, 5877, 30840, 42474-42476
Deposited data		
Raw data used for the calculation of optical growth rate	This study	https://doi.org/10.17632/tbdhjvrf6w.1
Software and algorithms		
R version 4.0.3	Venables and Smith (2003)	https://www.r-project.org/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Kelsey M. Jenkins (Kelsey.jenkins@yale.edu).

Materials availability

All specimens are deposited in museum collections as listed in the key resources table.

Data and code availability

- The raw measurements used for the calculation of the optical growth rate have been deposited at Mendeley and are publicly available as of the date of publication (https://doi.org/10.17632/tbdhjvrf6w.1).
- This paper does not report original code.

METHOD DETAILS

Visual acuity and ontogeny

Measurements of compound eyes (e.g., facet diameter) can be used to quantify visual acuity and predict the luminosity of the environment inhabited in both living (Horridge, 1977, 1978; Snyder, 1977; Snyder et al., 1977; Land, 1981) and fossil eyes (Fordyce and Cronin, 1989, 1993; McCormick and Fortey, 1998), including fossil eyes that have been subjected to compression (Paterson et al., 2011; Anderson et al., 2014). We estimated visual acuity in *Callichimaera perplexa* (specimen IGM p 881,220) by calculating the inter-ommatidial angle $\Delta\varphi$ (IOA), which is the angle between the optical axes of adjacent lenses, and eye parameter (*P*), which indicates the luminosity of the environment an arthropod inhabits, using methods previously applied to compressed, fossil arthropod eyes (Figure 5) (Anderson et al., 2014). This method allows the total angle subtended by the eye to be reconstructed, as opposed to an upper estimate that the method developed by Paterson et al. (2011) provides for IOA (we report our variables in the manner of Anderson et al., 2014). All measurements were collected using ImageJ. IOA was estimated by reconstructing the angle subtended by three transects measured across the eye (Figure S1, Table S2). The average IOA was calculated using the average of those three transects. Eye parameter *P*, which reflects the relative luminosity of an arthropod's environment, was also calculated for each transect and averaged. *P* was calculated as the product of the average lens diameter x average IOA x ($\sqrt{3}/2$). To further assess visual acuity and regionalization in *C. perplexa*, we calculated the average facet diameter of three areas within the eye of IGM p881220 (Figure 2F and 2G). Further details are included in the supplement.

Eye growth rates and proportions

We investigated the growth rate of the eye in 15 brachyuran species representing the families Callichimaeridae (extinct), and Grapsidae, Ocypodidae, Geryonidae, Varunidae, Portunidae, Calappidae, Oregoniidae, and Raninidae (extant) (Table 1). Our approach is similar to that used in previous work investigating the relationships between eye growth and habitat (Klompmaker et al., 2016), although that work only used orbit size as a proxy for eye size and lacked a growth series for the fossil crab studied. Here we include benthic and pelagic examples ranging from shore and intertidal environments to deep water. Depths are reported

from the Ocean Biodiversity Information System (obis.org) (Fornwall, 2000) and were confirmed from collection data, where available. We measured the maximum corneal eye diameter, and carapace length along the midline, of each individual to the nearest 0.01 mm with Mitutoyo digital calipers (see Supplemental information). We did not differentiate between sexes in these analyses.

QUANTIFICATION AND STATISTICAL ANALYSIS

We performed an analysis of covariance (ANCOVA) to compare eye diameter versus carapace length (i.e., relative growth rate) among species. Following that, a post hoc pairwise comparison was conducted to assess individual differences in growth rates between species (Table S1). To assess the relative size of the eyes, we divided the eye diameter by the carapace length for all specimens and conducted an analysis of variance (ANOVA) on the resulting ratio. Tukey's Honest Significant Difference method was used for post hoc pairwise comparison. All statistical computations were conducted in R version 4.0.3 (Venables and Smith, 2003)