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# Advanced stereopsis and predatory adaptation in a Cretaceous mantis

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Visual systems have been crucial for animals to detect light signals. Binocular stereopsis has affected prey-predator relationships throughout animal evolution by providing depth perception, among others. However, it has been difficult to reconstruct extinct binocular functions due to a lack of suitable fossil material. Here, we show, based on morphological analysis of well-preserved eyes, that an extinct mantis (*Ambermantis wozniaki* Grimaldi, 2003) in the Cretaceous New Jersey amber developed an advanced visual system as a predator. We found that *A. wozniaki* possesses large compound eyes with numerous, ca. 12 000 ommatidia. The interocular distance is narrower than the eyes, and the estimated binocular visual field is broader than in the typical extant basal and derived taxa. The large number of ommatidia indicates that the compound eyes of *A. wozniaki* achieved high spatial resolution to capture objects visually. The broad binocular field supports that *A. wozniaki* increased the stereoscopic area and developed an advanced prey-recognition system. These findings suggest that the Cretaceous basal mantises were highly adaptive visual predators, implying the ecological domination of mantises as visual specialists for 90 million years.

**Key words:** Insecta, Mantodea, palaeobiology, predatory behaviour, visual system, binocular vision, New Jersey amber.

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## Introduction

The eyes of animals detect light stimulation, and they are essential primary sensory organs responsible for simply perceiving environmental brightness to communicating complex social information (Land and Fernald 1992; Emery 2000; White et al. 2015). Although even one eye can achieve a broad visual field (e.g., nearly 180° in some vertebrates and insects) (Stevens 2006; Borst 2009; Bergman et al. 2021), most animals have two eyes and see objects “binocularly”. Stereopsis is a binocular visual function that extracts depth information based on different images recognised by the right and left eyes (binocular disparity) (Parker 2007; Read 2021). Depth perception by binocular stereopsis is crucial, especially for predatory animals, since it is advantageous for successful visual hunting, such as judging the distance to prey and breaking camouflage (Nityananda and Read 2017; Adams et al. 2019). Therefore, the evolution of

stereopsis can be regarded as a critical adaptation that has strongly affected prey-predator relationships in the deep-time evolution of animals. Although some previous studies reconstructed the binocular visual function of extinct vertebrates, they lack robust bases such as soft tissue: the eyes themselves (Stevens 2006; Marinho et al. 2013; Konishi et al. 2016). Extinct binocular systems have remained hard to access using direct fossil evidence despite their evolutionary significance.

Praying mantises (order Mantodea) include about 2500 extant species, all predatory with spiny raptorial forelegs (Izquierdo-López et al. 2024). Mantises were the first invertebrates proven to possess stereopsis based on neurobiological analysis, and they have been traditional models of binocular visual studies (Rossel 1983; Kral and Poteser 2009; Rosner et al. 2020). When prey-capturing, mantises need to recognise an appropriate distance to prey and judge whether to strike based on their stereoscopic ability with a

large binocular visual field and complex information process. Their visual ability has been investigated by combining behavioural experiments and neurophysiological and morphological analyses (Rossel 1979; Yamawaki and Toh 2003; Rosner et al. 2019). Since compound eyes of arthropods have chitinous exoskeletons, their morphological characteristics, such as micron-scale ommatidia, are potentially preserved as fossils (Lee et al. 2011; Lindgren et al. 2019). In some cases of insect eyes fossilised in amber, their three-dimensional structures are exceptionally preserved with almost their original morphology (Lin et al. 2019; Kundera et al. 2020; Vršanský et al. 2021b), although some taphonomic biases need to be noted (Koubová and Mlynský 2020). Fossilised mantises in amber can be therefore examined using the same morphological analysis as their extant counterparts. Fossil records of mantodeans are relatively rare: 38 species have been described, 25 from the Mesozoic and 13 from the Cenozoic (Delclòs et al. 2016; Li and Huang 2018; Terríquez-Beltrán et al. 2023; Vršanský 2024; Vršanský et al. 2025). All Mesozoic taxa, mostly from the Cretaceous and a few from the Late Jurassic, show plesiomorphic characters represented by short prothoraxes and forelegs (Vršanský 2002, 2024; Grimaldi 2003; Wieland 2013), and thus, the binocular vision of such basal taxa potentially can reveal the early evolution and ecology of the visual system of mantises.

Here, we analysed the exceptionally well-preserved compound eyes of a fossilised mantis *Ambermantis woźniaki* in mid-Cretaceous amber and compared the morphological property to extant relatives. Based on the comparison, we reconstructed the binocular visual system and prey-recognition/capture ability of the primitive mantis.

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York, USA.

*Data availability.*—The fossil material is deposited in the American Museum of Natural History under the assigned number AMNH NJ1085. The original CT slice images of the studied specimen are available from the Figshare Data Repository: <https://doi.org/10.6084/m9.figshare.27916509>.

## Material and methods

The fossilised adult male mantis derived from the Raritan Formation (Turonian: 90–94 Ma) in central New Jersey (Gandolfo et al. 2018; Delclòs et al. 2023) and was described as *Ambermantis woźniaki* (Grimaldi 2003), deposited in the American Museum of Natural History (AMNH NJ1085). The specimen is three-dimensionally well preserved and shows nearly complete body remains except for some parts of the antennae and legs (Fig. 1).

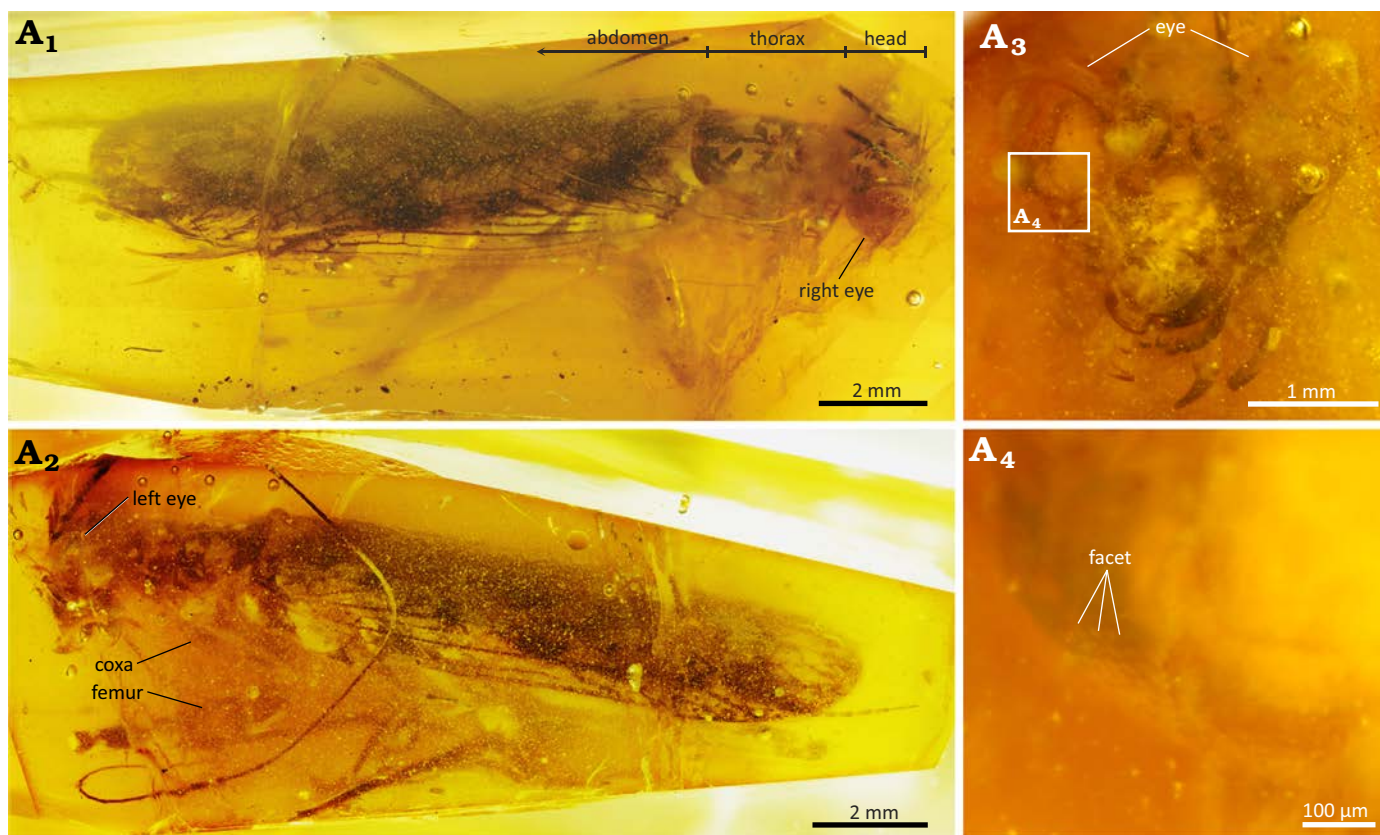


Fig. 1. Neomantodean mantis *Ambermantis woźniaki* Grimaldi, 2003 (AMNH NJ1085), New Jersey amber, Sayreville, Middlesex County (Raritan Formation, Turonian, 90–94 Ma); A<sub>1</sub>, specimen in dorsal view. The thorax is short, 1.8× the head in length; A<sub>2</sub>, specimen in left lateral view, showing the spiny raptorial foreleg; A<sub>3</sub>, head with large compound eyes; A<sub>4</sub>, enlarged image, showing many facets on the eye.



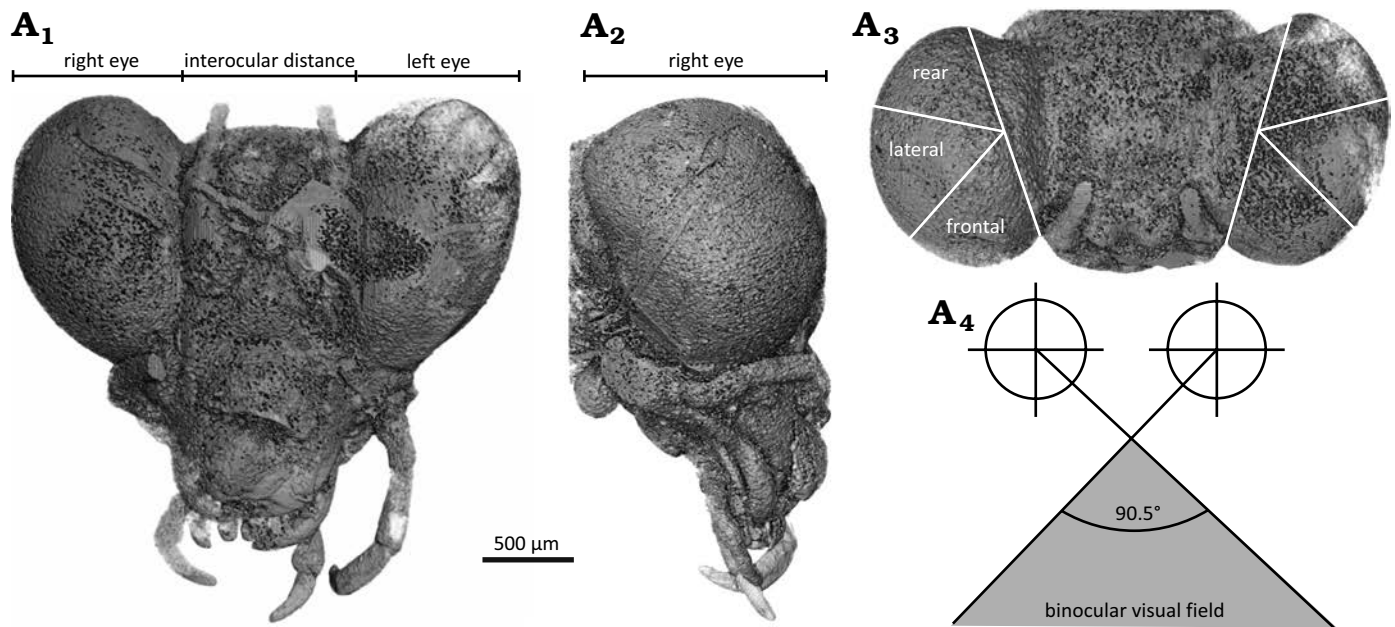


Fig. 2. Neomantodean mantis *Ambermantis wozniaki* Grimaldi, 2003 (AMNH NJ1085), New Jersey amber, Sayreville, Middlesex County (Raritan Formation, Turonian, 90–94 Ma). A three-dimensional model of the head from CT data ( $A_1$ – $A_3$ ) and estimated binocular visual field angle ( $A_4$ ) of *A. wozniaki*;  $A_1$ , in frontal view;  $A_2$ , in right lateral view;  $A_3$ , in dorsal view, showing three divided parts on the eyes;  $A_4$ , schematics of the binocular visual field reconstructed from the osculating circles of frontal parts on each eye.

The fossil macrophotos were taken using a Canon EOS 5DS R (8688×5792 pixels) with a Canon MP-E 65 mm macro lens (F2.8, 1–5×) and a ZEISS LED Cold Light Source Dual Pipe Light System. We also used a Canon Extender EF 2× III for higher-magnified images. The amber was immersed in clove oil (Wako Pure Chemical Industries) to improve optical resolution by covering the surface cracks. The focus-stacked images of the specimen were obtained via Helicon Focus 8.2.3 (Helicon Soft). Facet diameters on the compound eyes were measured from these images, and the area of each facet was calculated by being regarded as a regular hexagon to estimate the ommatidium number explained below. The head was scanned with a microfocus X-ray CT system (60 kV, 3.5  $\mu\text{m}^3/\text{voxel}$ ; Bruker SKYSCAN 2214) at Tomakomai Industrial Technology Center (Hokkaido, Japan). The CT data were visualised as a 3D model, and its surface data were created with Amira 3D 2023.2 (Thermo Fisher Scientific) after being converted to 8-bit images. The surface data were imported into Blender 4.3.2 (Blender Foundation), and the surface area of the compound eyes was digitally measured on the software. The number of ommatidia was estimated by dividing this surface area by the facet area.

We measured the binocular visual field angle to estimate the stereoscopic and prey-recognition ability of *A. wozniaki* from the 3D model, following the methodology for extant mantis species (Prete et al. 2011; Fig. 2). Frontal, lateral and rear parts of the compound eye were determined in the dorsal view by drawing a line from the frontal-medial-most to rear-most edge and dividing the straight angle into three 60° parts. The curvature of the frontal part was represented by the osculating circle passing the edges, and the angle

between the two lines from the circle centres to the medial edges of each eye was regarded as the maximum binocular visual field angle. The drawing and measurement were performed on Serif Affinity Designer 2.5.5.

## Results

Many facets are visible on the compound eyes (Fig. 1A<sub>4</sub>). The diameter of each facet is  $\sim 30 \mu\text{m}$ , and its area was calculated as  $5.85 \times 10^{-4} \text{ mm}^2$ . The total surface area of both compound eyes was measured at  $7.26 \text{ mm}^2$  from the 3D model. The compound eyes were estimated to comprise 12 410 ommatidia from these data.

The compound eyes of *Ambermantis wozniaki* are well-developed and slightly protrude anteriorly (Figs. 1A<sub>3</sub>, 2A<sub>1</sub>–A<sub>3</sub>). They are distributed with an anterior tilt from the dorsal view and have an enlarged frontal area of the eyes. (Fig. 2A<sub>1</sub>, A<sub>3</sub>). The head width and interocular distance were 2.87 mm and 0.96 mm, respectively. The ratio of interocular distance to head width of *A. wozniaki* is 0.34; i.e., from the frontal view, the eyes of *A. wozniaki* occupy about two-thirds of the head in their width. By geometrical drawing of osculating circles on the frontal parts, the maximum binocular visual field angle of *A. wozniaki* is estimated at 90.5° (Fig. 2A<sub>4</sub>).

## Discussion

Insects recognise objects as images subdivided via ommatidia, and many ommatidia achieve a high spatial resolution

(Buschbeck and Friedrich 2008). The spatial resolution is also restricted by body size, limiting the number of ommatidia (Streinzer et al. 2016). The number of ommatidia in the specimen of *A. wozniaki* was estimated at ca. 12 000. The extant mantises generally used as a model for visual function, whose body lengths are 8–10 mm in early nymphs and 50–80 mm in adults, increase their ommatidia ontogenetically from 8000 to 18000 ommatidia (e.g., *Tenodora aridifolia*, *Mantis religiosa*, and *Polyspilota* sp.) (Kral 2012, 2014). Considering the small adult body length (13 mm), *A. wozniaki* was equipped with a large amount of ommatidia relative to the body size, indicating high visual resolution.

We calculated the ratio of interocular distance and head width of *A. wozniaki* at 0.34. This value is significantly smaller than for extant mantises; basal and small species: 0.44 in *Chaeteessa valida*, 0.38 in *Metallyticus splendidus*, 0.45 in *Mantoida maya*, 0.44 in *Amorphoscelis hamata*; derived and large species: 0.35 in *Tenodora aridifolia*, 0.41 in *Mantis religiosa*, 0.52 in *Clinia humeralis* (Roy and Stiewe 2009; Prete et al. 2011; Wieland 2013) and for other Cretaceous mantises recorded an adult with the complete and clearly observable heads/eyes; 0.41 in *Burmantis hexispinea*, 0.42 in *Santanmantis axelrodi* (Hörnig et al. 2017; Li and Huang 2018). The short interocular distance to head width indicates that compound eyes occupy a large proportion of the head. *A. wozniaki* possessed relatively large eyes, even compared to modern eumantodeans. The interocular distance to head value 0.34 of *A. wozniaki* is also smaller than for extinct Cretaceous cockroaches, closely related to mantodeans in phylogeny and ecology: 0.53 in *Stavba babkaeva* (Liberiblattindiae), 0.56 in *Pseudomantina occisor* (Blattulidae), 0.48 in *Manipulatoides obscura* (Manipulatoridae), 0.52 in *Caputoraptor elegans* (Alienopteridae) (Vršanský et al. 2019, 2021a; Wipfler et al. 2019; Li and Huang 2022; Luo et al. 2022; Sendi et al. 2023; Vršanský 2024). These comparisons imply that *A. wozniaki* evolved the broad frontal visual field after splitting from the cockroach-like ancestral stage.

Mantises utilise their stereoscopic ability to perceive the distance to prey and strike them at a critical distance (Nityananda et al. 2016; Read 2023). They detect the kinetic disparity of images between right and left compound eyes for the stereopsis (Nityananda et al. 2018; Read 2021); thus, large binocular visual field angles enlarge the range of depth perception. The potential binocular visual field angle of *Ambermantis* is 90.5°, considerably broader than extant derived species (ca. 70° in *Tenodora australasiae*, *Tenodora aridifolia*, *Mantis religiosa* and 44.0° in *Clinia humeralis*) (Rossel 1983; Prete et al. 2011) (Fig. 2A<sub>4</sub>). This suggests that *A. wozniaki* increased the area where distance can be measured through binocular stereopsis and search their prey in a broad range. Behavioural experiments with extant species have shown that mantises cannot define the target as prey if it is too large to capture enough within the binocular visual field (Prete and McLean 1996; Prete et al.

2011, 2012). In other words, the broader the binocular field, the greater the opportunity to recognise prey. *A. wozniaki* likely developed a broad binocular visual field and effectively captured their prey.

The extant derived mantises (most species are larger than 50 mm) are top predators among terrestrial invertebrates, and their predators are often also vertebrates (Yamawaki 2017). In contrast, *A. wozniaki* is very small (13 mm in body length), meaning the genus occupied middle-rank predatory status. They were likely preyed on by various higher predators, including insects or other arthropods. The large and high-resolution eyes of *A. wozniaki* may have also helped detect predators and escape from them, considering that extant species rely on visual stimulation in their defensive behaviour (Yamawaki 2011, 2017). Our lines of evidence suggest that *A. wozniaki* was a highly adaptive visual animal, enhancing the ability to search and recognise prey by equipping numerous ommatidia into the compound eyes and broadening its binocular stereoscopic visual field. The ancient tiny mantis from the Cretaceous period may have occupied the ecological niche as an adaptive predator comparable to modern derived relatives. The advanced visual ability of praying mantises seems to have supported their role as principal predators for 90 million years.

## Conclusions

In this study, the compound eyes of a fossilised mantis, *Ambermantis wozniaki*, were analysed morphologically and compared to extant species. The *A. wozniaki* specimen showed exceptionally preserved eyes in 3D, and we could directly apply the analytical method established in extant mantises. Our results revealed that the compound eyes were composed of ca. 12 000 ommatidia, the ratio of interocular distance to head width was 0.34, and the binocular visual field angle was 90.5° in *A. wozniaki*. These data indicate that *Ambermantis* had advanced visual abilities supported by large, high-resolution eyes and broad binocular stereoscopic field comparable to extant relatives. Although it is considerably small and has a basal position in the mantodean phylogeny, *Ambermantis* likely occupied an adaptive predatory niche with a superior visual system, suggesting a long evolutionary history and ecological success of mantis hunting style relying on their vision on a geological time scale.

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## Authors' contributions

Conceptualisation: RT; Methodology: RT and YF; Investigation: RT, YF and KS; Visualisation: RT and KS; Funding acquisition: RT and YI; Supervision: YI; Writing—original draft: RT; Writing—review and editing: All authors.

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