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メタデータ	言語: eng 出版者: 公開日: 2021-04-15 キーワード (Ja): キーワード (En): 作成者: メールアドレス: 所属:
URL	https://doi.org/10.24517/00061634

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Source: Zoological Science, 26(12) : 846-850

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.26.846>

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Three-Dimensionally Preserved Decapod Larval Compound Eyes from the Cretaceous Santana Formation of Brazil

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Compound eyes are common in decapod crustaceans. Decapods have an abundant post-Palaeozoic fossil record, but hitherto morphological information about their eyes has been mainly restricted to Recent material. Here we report the discovery of compound eyes recovered from acetic acid residues of two fish-bearing nodules from the Cretaceous Santana Formation of Brazil; they include what are identified as decapod larval compound eyes. The fossil eyes are comparable to phyllosoma larval eyes because of the following characters: the hemispherical visual surface on a stalked eye; the relatively small-size of the visual surface of the eye; rounded facets are arranged in square arrays in the anterior region; the fact that the neighboring ommatidia are bounded by ridges and/or grooves; and the more convex inner surface of the cornea lens. This report represents the first description of a three-dimensionally preserved fossil decapod eye. We conclude that the eyes probably represent palinuroid phyllosoma larval eyes and were an adaptation to a planktonic lifestyle.

Key words: compound eye, Cretaceous, phyllosoma larva, Santana Formation, three-dimensional preservation

INTRODUCTION

Compound eyes are the most common device used for imaging by animals and evolved and became abundant in arthropods (Land, 1981). Arthropods have a fossil record from the Early Cambrian and have adapted to a range of dull to well lit environments. Evidence from fossils suggests that arthropods were already equipped with well-developed compound eyes in the Early Cambrian (Land and Nilsson, 2002; Parker, 1998, 2003). However, except for sessile compound eyes such as in trilobites (e.g., Clarkson, 1966; Clarkson and Levi-Setti, 1975; McCormick and Fortey, 1998; Gál et al., 2000), chelicerates (e.g., Størmer, 1992), isopod crustaceans (e.g., Polz, 1998, 2005; Gaillard et al., 2005), thylacocephalan arthropods (Vannier et al., 2006), and many hexapods in amber (e.g., Weitschat and Wichard, 2002), three-dimensionally preserved fossil stalked compound eyes have been rarely reported. Stalked compound eyes that are freely movable and focus clearly on objects are common in Malacostraca, and there are also sessile eyes in Isopoda and Amphipoda within this taxon. Perrier et al. (2006) reported on Carboniferous syncarids (Malacostraca) with three-dimensionally preserved eyestalks, although the ommatidia were not documented because the visual surface was covered by cuticle. Vannier et al. (2007) reported on two-dimensionally preserved compound eyes with eyestalks

from the arthropod *Tuzoia* from the Middle Cambrian Burgess Shale of British Columbia, Canada. Recently, Vannier et al. (2009) also mentioned a two-dimensionally preserved compound eye with eyestalks in the arthropod *Isoxys* from the Lower Cambrian Maotianshan Shale of Yunnan Province, China and from the Burgess Shale. Siveter et al. (2003, 2007) described lateral, presumed compound eyes from two myodocope genera, *Colymbosatton* and *Nymphatolina*, from the Silurian of Herefordshire, U.K. In Recent Malacostraca, stalked eyes are ubiquitous among decapods, and their morphology and function have been well studied (e.g., Land, 1981; Nilsson, 1989; Warrant and McIntyre, 1992; Meyer-Rochow, 2001). Fossil decapods have been reported throughout the post-Palaeozoic (Schram, 1982), but morphological information on their eyes is limited to two-dimensionally preserved impressions of the outlines of the eyes (e.g., Polz, 1996; Etter and Tang, 2002).

Here we describe three-dimensionally preserved compound eyes of juveniles of a decapod species from the lower Cretaceous Romauldo Member, Santana Formation of Brazil. Fish are the most common vertebrates in the Romauldo Member; pterosaurs, turtles, and occasional dinosaur bones have also been recorded (Martill, 1993). Invertebrates, in particular ostracods (Bate, 1971, 1972, 1973; Smith, 2000) and also decapods (Maisey and De Carvalho, 1995) and parasitic copepods (Cressey and Boxshall, 1989), are found in association with the fish. Decapods, unlike other invertebrates, are commonly found disarticulated within the stomach of a fish (Wilby and Martill, 1992), and are only occasionally found intact in the surrounding matrix. Due to the

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doi:10.2108/zsj.26.846

favorable preservation conditions that existed in the stomach of the fish, muscle and parts of the exoskeleton of shrimps are preserved in fine detail (Wilby and Martill, 1992; Briggs et al., 1993). Maisey and De Carvalho (1995) documented a sergestid shrimp, a brachyuran crab larva, and possible palaemonid decapods from the Santana Formation, but they did not record details on their compound eyes. The principal aim of the present paper is to describe the exceptionally preserved compound eyes of a Mesozoic decapod crustacean.

MATERIALS AND METHODS

Fish concretions from the Santana Formation, known to contain large amounts of preserved soft tissue, were targeted for study, as these specimens were more likely to produce well-preserved material. The fish nodules were washed and then dissolved in 5% acetic acid buffered with calcium carbonate. The residue was recovered, thoroughly washed, and picked for fossil remains. The compound eyes were examined with a Hitachi 3600 scanning electron microscope (SEM). All recovered specimens were deposited in the Department of Palaeontology, Natural History Museum, London (NHM IC.313–317).

Determination of the facet distribution in Recent arthropods has been undertaken using a goniometer to read the coordinates of the luminous pseudopupil (the eye glow of the ommatidium aligned with the direction of observer) where it exists (Stavenga, 1979). This method could not be used for the fossil eye because the inner structure is lost, and so other methods were considered. In order to establish the distribution of facets in the compound eye of the Santana fossil species, two well-preserved specimens (NHM IC.313, 316) with the largest number of ommatidia were studied biometrically. Stereo-pair images (using a 7° tilt angle) of various views of the fossil eye were captured as BMP files. The images were stored as JPG files, and measurements of the x and y coordinates of each ommatidium were made on the image using a computer program. The coordinate data sets were preserved as CSV files on a Microsoft Excel sheet. Based on the triangulation method (Ubukata, 2004), the z coordinate of each point was calculated from the x and y coordinates of the stereo-pair images. To determine the direction of the optical axis of each ommatidium, we first calculated the normal vector of each facet based on the ommatidial plane that was defined by the three coordininal points. The starting point of the normal vector was then placed on the center of the ommatidium, determined by the intersection point of the long and the short axes of the facet. Finally, we set the center of the compound eye on the center of the spherical coordinate system by using a coordinate transformation, and the coordinates of the optical axis were projected onto the surface of the sphere. We also measured the maximum diameter of each ommatidium from the two-point distance of the three-dimensional coordinates.

MORPHOLOGY OF THE FOSSIL COMPOUND EYES

We obtained five compound eye specimens (NHMIC. 313–317). However, two specimens (NHMIC. 314, 315) were not well enough preserved to be investigated by SEM. Thus, herein we detail three specimens (NHMIC. 313, 316, 317). We lack information on the entire body parts of the Santana Formation species, and therefore the possible orientation of the eye was tentatively determined on the basis of the morphology of Recent decapod eyes. In general, as crustacean larvae molt and grow, facets are added along the anterior edge of the compound eye (Harzsch and Walossek, 2000; Keskinen et al., 2002). Furthermore, some “squarish” facets are present along the anterior edge of the phyllosoma larval eye (Mishra et al., 2006). The fossil eyes possess a possible growing site of newly formed “squarish” ommatidia (‘sq’ in Fig. 1C) compara-

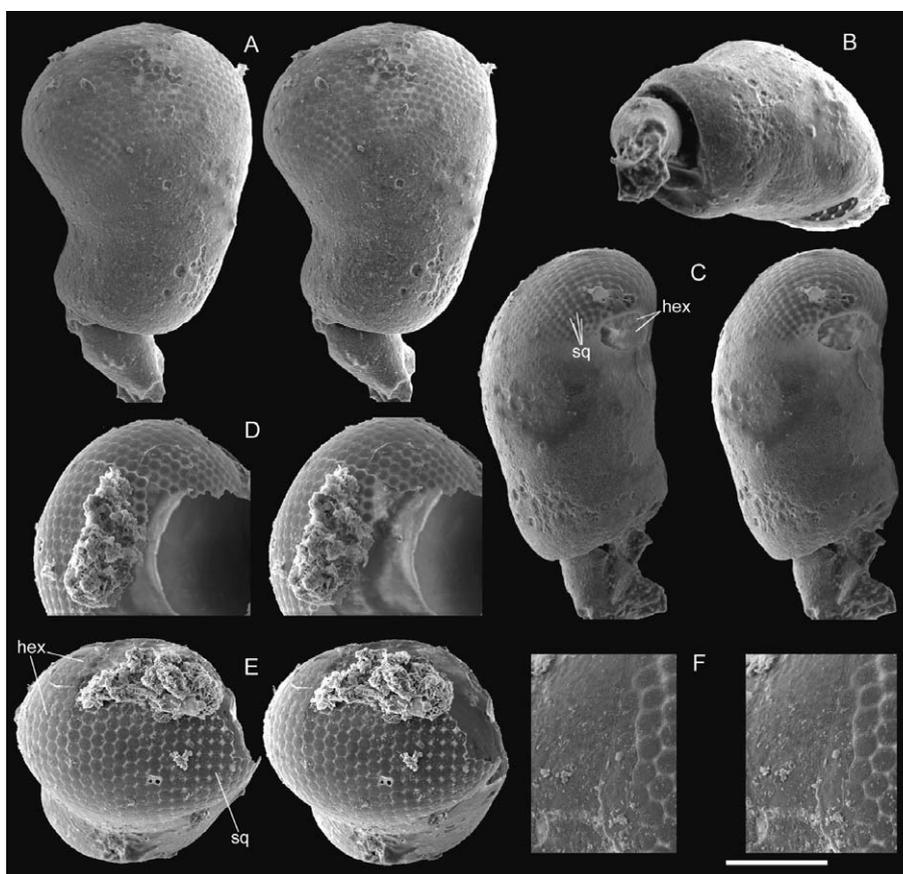


Fig. 1. Compound eyes from a decapod larva from the Romualdo Member, Santana Formation, Cretaceous of Brazil. Except for (B), all the scanning electron micrographs are stereo-pairs. **(A–C)** Left eye (NHM IC.316). **(A)** Dorsal view of the compound eye showing the entire visual surface and the eyestalk. **(B)** Oblique basal view of the eyestalk. Note the inclusion matter emerging from the ocular sinus. **(C)** Anterior view of the stalked eye showing small ommatidia arranged in a square pattern (sq). Note the inner surfaces of the large hexagonal facets (hex) seen through the large hole in the antero-ventral part of the eye. **(D–F)** Right eye (NHM IC.313). **(D)** Dorsal view of the compound eye showing a well preserved pattern of hexagonal facets. The diameter of the facets is smaller in the dorsal part than in the lateral part. **(E)** Lateral view of the visual surface area. The anterior region has round facets arranged in a square pattern (sq). Hexagonally packed ommatidia (hex) are evident between the lateral and posterior parts, and the neighboring facets are densely packed toward the posterior part (left side). **(F)** Boundary between the ommatidium-bearing part of the eye and the eyestalk, showing ommatidia of various sizes. Scale bar: 200 μ m (A–E), 25 μ m (F).

ble to that in Recent phyllosoma larva (Mishra et al., 2006). In Recent decapod larval eyes, the eye and eyestalk intersect at a narrower angle in the ventral area than in the dorsal area (e.g., Fig. 7 of Van Herp et al., 1979), and the visual surface tends to overhang the eyestalk on its ventral side (e.g., Fig. 1 of Suzuki et al., 2006). Such a recumbent position between the visual surface and the eyestalk is also discernible in the Santana fossil eyes (Figs. 1C, E; 2A, B).

The visual surface of the specimen of the left eye (NHM IC.316; Fig. 1A–C) is hemispherical in shape and 440 μm across the maximum long axis, which is located approximately halfway down the eye surface from the apex of the lateral side (Fig. 1A). Below the faceted area, the eyestalk tapers towards a constricted basal part (Fig. 1A–C). In anterior view the eye has a logarithmic spiral outline (Fig. 1C). The round facets are close packed hexagonally in almost all regions but are nearly squarely packed in the anterior area (Fig. 1A, C). In the dorsal plane, the visual surface of the ommatidia are distributed through approximately 110° , from the lateral apex to about 20° below (Fig. 3A). The facets of the eye cover approximately 180° of the eyestalk in the horizontal plane (from anterior to posterior). The median diameter of the ommatidia is 25 μm ($n=290$). However, we could not measure the facets in the ventral area of the left eye (Fig. 1A–C) because the specimen was attached to the SEM stub in that region.

In the specimen of the right eye (NHM IC.313) (Figs. 1D–F; 2A, C, D), where only about half the visual surface has been preserved, hexagonally packed facets are widely distributed, although some squarish facets are present in the anterior area. The median diameter of the ommatidia is 28 μm ($n=291$). Small facets (19–22 μm) are distributed at the ventral margin and in the anterior area (Figs. 2A, 3B). The ommatidia cover approximately 180° of the eyestalk in the horizontal plane and 60° – 90° in the vertical plane (Fig. 3B). The corneal lenses of the ‘square’ facets are relatively thin (6 μm in their thickest region) and plano-convex in shape (Fig. 2C, D). Taking into account any missing parts of the visual surface, the total number of ommatidia of a compound eye is probably about 500–550 in both the left (NHM IC. 316) and the right eye (NHM IC. 313).

The surface of the eye in specimen NHM IC.317 is generally well preserved, with well-defined ridges between the facets in some regions (Fig. 2E, F). The ridges are probably the result of the buckling up of this surface. Other specimens (NHM IC. 313, 316) have grooves between the facets

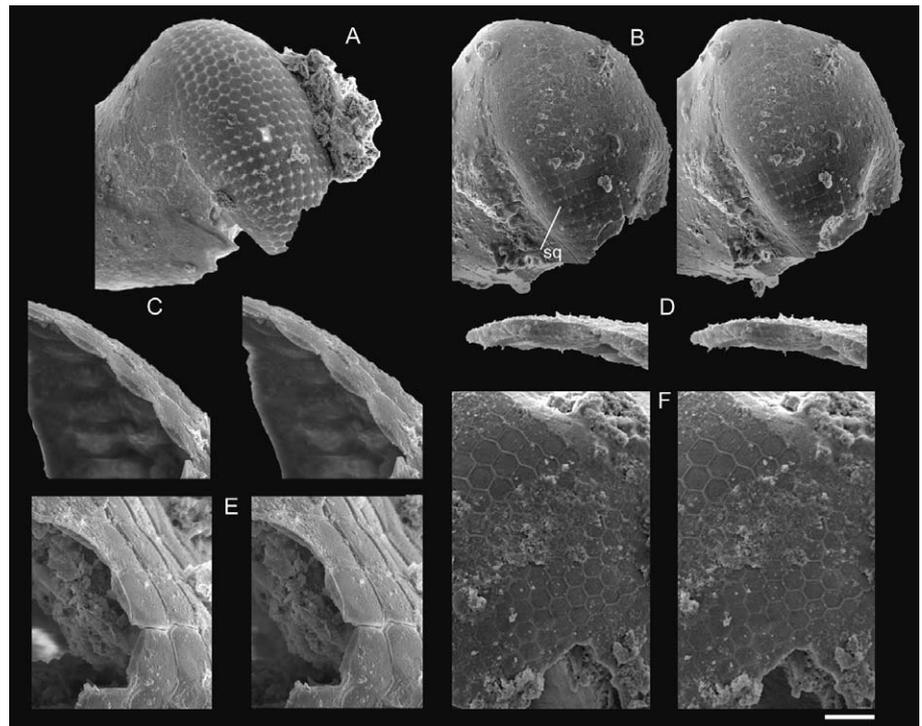


Fig. 2. Right eyes of decapod larvae from the Romualdo Member, Santana Formation, Cretaceous of Brazil. Except for (A), all the scanning electron micrographs are stereo-pairs. (A) Ventral view of a compound eye. (B) Ventral view of a compound eye showing square facets (sq) in the antero-ventral area; the anterior and posterior areas are lacking and/or crushed. (C) Broken section of square facets. Each ommatidium is biconvex and connects with a thin corneal boundary. (D) Detail of a section of one ‘squarish’ facet. Compared with the area depicted in the eye in (A), the boundaries of neighboring ommatidia are much clearer. (E) Detail of a section of both hexagonal and squarely packed ommatidia. (F) Dorso-lateral surface of the eye showing small diameter facets in the dorsal part (lower right side). A, C, and D are from NHM IC.313; B, E, and F are from NHM IC.317. Scale bar: 100 μm (A, B), 50 μm (F), 20 μm (C, E), 10 μm (D).

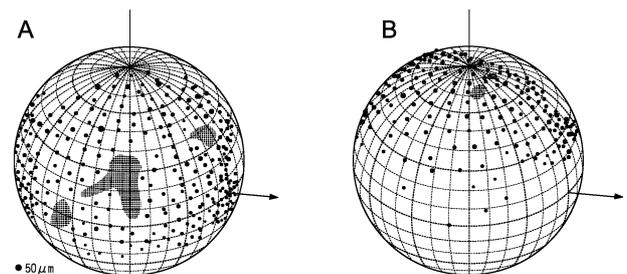


Fig. 3. Stereographic projection charts of the optical axis and the diameter of two of the fossil compound eyes. (A) Antero-dorsal view of the left eye (NHM IC.316). (B) Antero-ventral view of the right eye (NHM IC.313). The axis of the arrow indicates the anterior direction, and the polar axis is lateral. Shaded regions indicate areas where facets are missing. The scale (circle) indicates a diameter of 50 μm .

(Figs. 1F, 2C). The corneas of the square and hexagonally packed facets are relatively thin (6 μm in their thickest region) and plano-convex in shape (Fig. 2E).

VISUAL CAPABILITIES OF THE DECAPOD & CONCLUSIONS

We identified the fossil eyes from the Cretaceous

Romauldo Member as the early stage of a phyllosoma larval eye of a palinuroid decapod (e.g., Mishra et al., 2006) on the basis of the following characters: (1) hemispherical visual surface on a eyestalk; (2) relatively small eye size; (3) the round facets are closely packed hexagonally in almost all regions but are squarely packed in the anterior area; (4) the neighboring ommatidia are bounded by ridges and/or grooves; and (5) the inner surface of the cornea lens is more convex than the outer surface. However, the fossil compound eyes were equipped with small (25–28 μm in median diameter) and many (500–550 facets) ommatidia compared with the same size of the phyllosoma larval eye of the Recent rock lobster *Jasus edwardsii* (40.7 μm in diameter and 220 facets; Mishra et al., 2006). *Jasus edwardsii* has hexagonal facets and an ineffective clear zone in phyllosoma larvae, and square facets and a large effective clear zone in adults (Mishra et al., 2006). The eye of the adult stage is known to be of the superposition type, in which light entering the eye through a large patch involving many neighboring facets is focused on one more or less small spot on the retina deep in the eye. The superposition eye ensures that a considerable degree of resolving power is maintained, while at the same time sensitivity is vastly improved (Warrant, 1999). Thus, the adult eye of the rock lobster is an adaptation for dimly lit environments such as the bottom of the deep sea. On the other hand, the phyllosoma larva of the rock lobster has an apposition eye, in which the sensitivity is not improved compared with the superposition eye. The larvae spend a great deal of their life in the well-illuminated upper zone of the ocean, where adaptation to see in dim or dark conditions is of limited use. The fossil palinuroid phyllosoma larval eye must be of the apposition type, and the larva probably had a planktonic lifestyle in the well-illuminated upper zone of the Mesozoic ocean.

ACKNOWLEDGMENTS

We are grateful to Dr. H. Karasawa (Mizunami Fossil Museum) and an anonymous reviewer for helpful comments that improved the paper. We thank Professor V. B. Meyer-Rochow for suggestions on the morphology of the fossil eyes and for drawing our attention to several pertinent references. JSPS funded G. T's study year at the University of Leicester. We also thank the University of Leicester for facilities and R. Branson for technical assistance. Funding for this work was also provided in part by a Grant-in-Aid for Scientific Research (No. 21740370) from the Ministry of Education, Culture, Sports, Science and Technology, Government of Japan.

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(Received June 13, 2009 / Accepted September 8, 2009)