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Eye Structure and the Classification of Stomatopod Crustacea

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The cornea in most stomatopods is divided into two halves by a band of specialized ommatidia, the middle band. This band is absent in the Bathysquilloidea, but present in the three other superfamilies. It is two facets wide in the Squilloidea and six facets wide in the Lysiosquilloidea and Gonodactyloidea. This differentiation must have occurred very early in the evolutionary history of the group.

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Introduction

Stomatopod crustaceans exhibit a wide range of eye shapes, from the minute bilobed corneas of *Clorida*, dwarfed by the stalk in some species, to the enlarged, T-shaped eyes of *Harpiosquilla* or the ovoid or almost spherical eyes of *Hemisquilla* and *Odontodactylus* [see figures in Serène (1962) and Manning (1978), for some examples of the range of eye shapes in stomatopods].

Stomatopods are visual predators (Caldwell & Dingle 1975). All live in burrows which serve as refuges (Reaka 1980). Among the unique features of stomatopods are their enlarged second maxillipeds, the raptorial claws, which are used to stab or smash prey, repel predators and for inter- and intraspecific fights. Some stomatopods, especially gonodactyloids, are brightly colored and many species also have a brightly colored spot on the inner, dorsal surface of the merus of the raptorial claw (Hazlett 1979), which, in *Gonodactylus*, is species-specific (Caldwell & Dingle 1975). These spots are displayed in agonistic encounters, during which substantial amounts of information are also transmitted by visual signals (Dingle 1969). Trevino & Larimer (1969) suggest that the visual system of *Squilla* makes it incapable of color vision, but the work of Schiff (1963) suggests that color vision exists in members of this genus. It seems highly likely that color vision has developed in other stomatopod stocks, especially in species of *Gonodactylus* but color vision has not been studied in other genera.

Here we present some preliminary results of our studies on the structure and function of stomatopod eyes, with the primary purpose of emphasizing the unexpected relationship of eye structure, specifically the condition of the middle band, to the classification of the Stomatopoda.

Materials and methods

We have examined the eyes of representatives of each of the four Recent superfamilies of Stomatopoda: Bathysquilloidea, Gonodactyloidea, Lysiosquilloidea and Squilloidea [see Manning (1980) for accounts of these taxa]. Observations on the corneas and the condition of the middle band were made on living specimens as well as on preserved material. Photographs of the eye surface of representatives of three superfamilies in which the middle band is developed are given in Figs. 1–8 to show the differences in the band and the ommatidia making up the band.

Here we limit our observations to members of only four species, *Squilla mantis* (L.) (Squilloidea), *Odontodactylus scyllarus* (L.) (Gonodactyloidea), *Coronis excavatrix* Brooks and *Lysiosquilla scabricauda* (Lamarck) (both Lysiosquilloidea). However, our conclusions are based on examination of the following species as well as these:

Bathysquilloidea:
 Bathysquillidae: *Bathysquilla crassispinosa* (Fukuda) and *B. microps* (Manning).

Gonodactyloidea:
 Hemisquillidae: *Hemisquilla ensigera* (Owen). Pseudosquillidae: *Pseudosquilla ciliata* (Fabricius). Gonodactylidae: *Gonodactylus bredini* Manning and six other species of *Gonodactylus*. Protosquillidae: *Protosquilla guerinii* (White).

Squilloidea:
 Harpiosquillidae: *Harpiosquilla* sp. Squillidae: *Meiosquilla oculinova* (Glassell).

The structure of the cornea in all of these species follows the pattern we describe here.

Eye structure in Stomatopoda

Although eye shape in stomatopods has been used as a character at the specific, generic and familial levels (Manning 1968, 1980), the structure of the eye largely has been overlooked in the classification of stomatopods. Fincham (1980) has pointed out the potential use of eyes and optical mechanisms in the classification of other malacostracan crustaceans, including the decapods. he noted that most brachyuran crabs use apposition optics, with hexagonal facets in the eyes, whereas other mala-

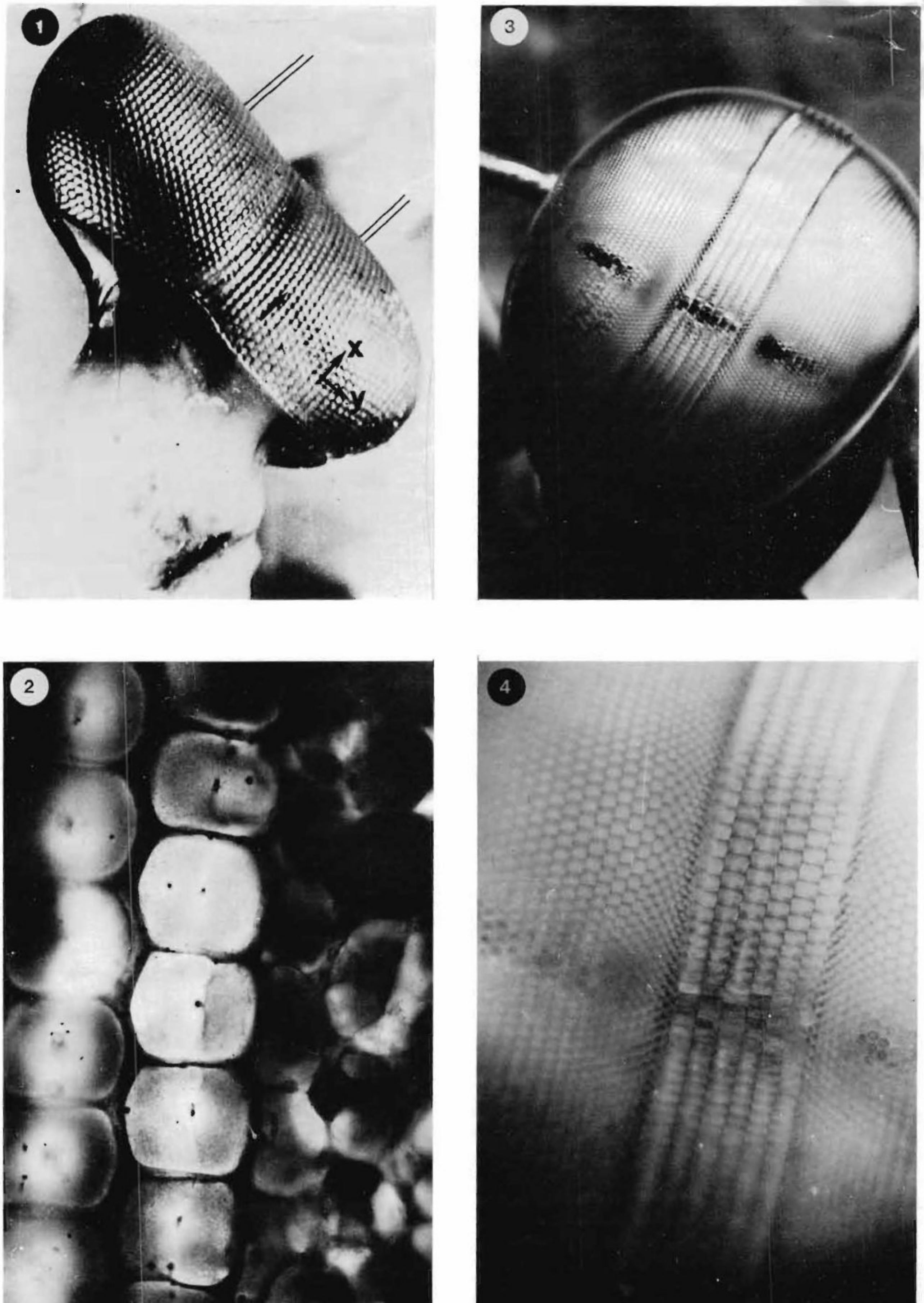
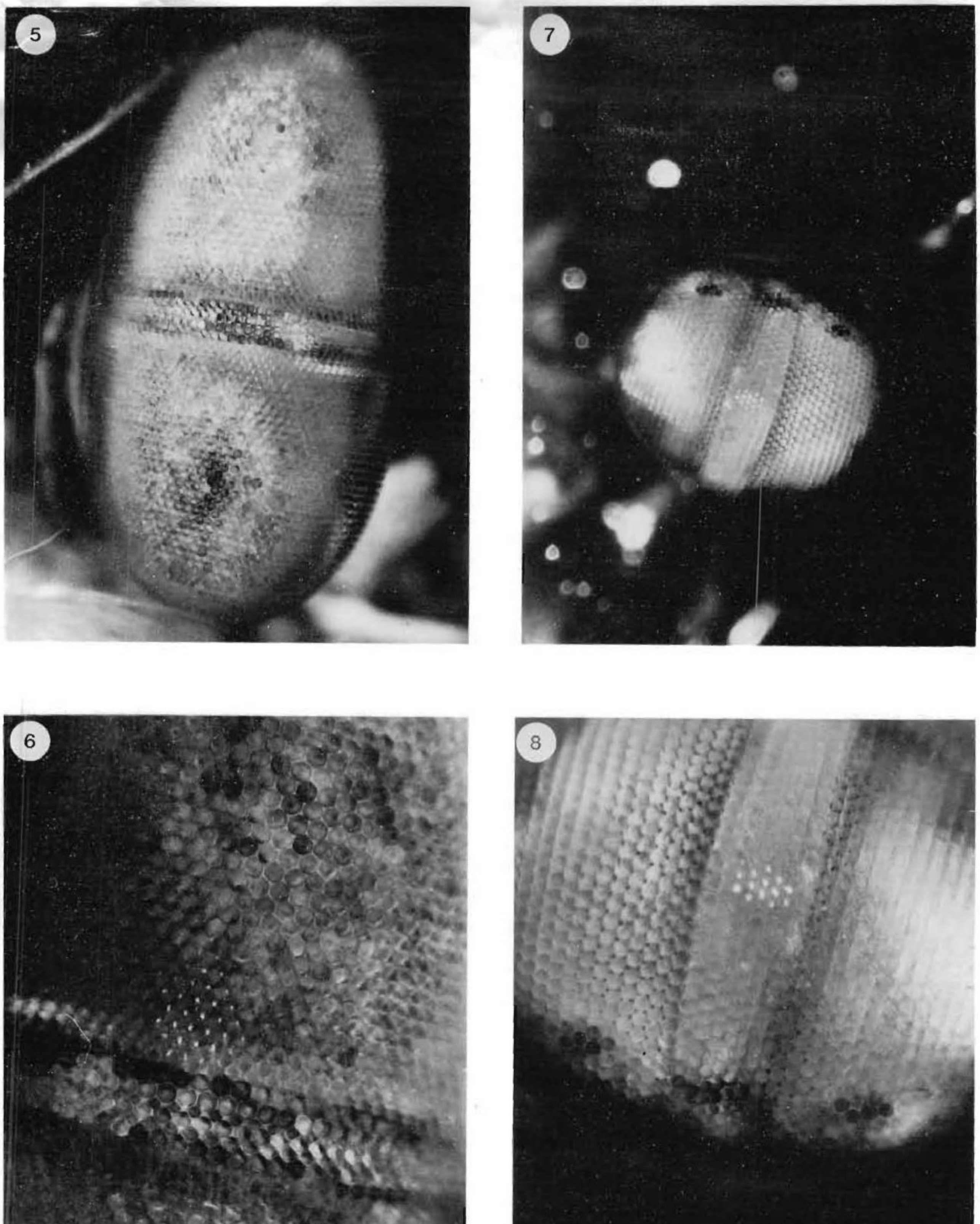


Fig. 1–4.—1. Eye of *Squilla mantis* (L.) (cornea width = 7 mm). Rows of ommatidia are defined by "x", columns of ommatidia by "y".—*2.* Middle band of cornea of *S. mantis*, ×237.—*3.* Eye of *Odontodactylus scyllarus* (L.), ×17.—*4.* Middle band of cornea of *O. scyllarus*, ×33.



Figs. 5–8.—*5.* Eye of *Lysiosquilla scabricauda* (Lamarck), ×28.—*6.* Middle band of cornea of *L. scabricauda*, ×61.—*7.* Eye of *Coronis excavatrix* Brooks, ×61.—*8.* Middle band of cornea of *C. excavatrix*, ×28.

costracans have refracting, superposition eyes with hexagonal facets or reflecting, superposition eyes with square facets.

Our preliminary investigations of eye structure in stomatopods reveals that four distinct kinds of eyes have evolved within the group, one characteristic of each of the four recognized superfamilies. Most stomatopods have the cornea divided into two halves by a band of specialized ommatidia, the middle band. This band is absent in members of the genus *Bathysquilla*, superfamily Bathysquilloidea, but present in members of the other three superfamilies. It is two facets wide in species of *Squilla*, *Meiosquilla* and *Harpiosquilla* (Figs. 1–2), members of two families in the superfamily Squilloidea, six facets wide in *Gonodactylus*, *Pseudosquilla*, *Hemisquilla* and *Odontodactylus* (Figs. 3–4), each from a different family of the Gonodactyloidea, and also six facets wide in *Lysiosquilla* (Figs. 5–6) and *Coronis* (Figs. 7–8), representing two different families of the Lysiosquilloidea. The shapes and sizes of the facets in the middle band are different in members of the gonodactyloids and lysiosquilloids. Whereas the facets are rectangular in the gonodactyloids, they are hexagonal or nearly spherical in the lysiosquilloids. Furthermore, in the gonodactyloids the largest facets are in the middle band, but in lysiosquilloids all facets are approximately the same size, except for two rows in the middle band of *Lysiosquilla* which have smaller, rhombic facets.

Conclusions

The function of the middle band in stomatopods is not known, but it may be related to monocular and binocular distance vision and the strike of the second maxilliped, ambient light in the habitat and, together with the organization of the two halves of the cornea, to the recognition of bright colors and/or highly developed agonistic displays in some members of the group.

That four distinct kinds of eyes, corresponding to recognized superfamilies, have developed in the group supports the recognition of these taxa and suggests that these different kinds of eyes must have been developed early in the evolutionary history of these animals. Moreover, three of the superfamilies contain species that live in bright as well as dim habitats and maintain the distinct structure of the ommatidia in the middle band in spite of other functional and structural evolutionary adaptations to their habitats.

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