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The Eyes of *Isotelus* and *Nileus*

J. N. Rose [1]

Abstract. Facet counts and measurements indicate that growth in the holochroal eyes of *Isotelus iowensis* and *Nileus vigilans* is accomplished by addition of new facets at the base, probably during molting, and by increase in the size of the largest facets; the former is the dominant process. The rate of addition of facets appears to be nonuniform in many individuals.

The lateral eyes of trilobites are of two main types: the schizochroal (Clarke, 1889) or aggregate (Lindstrom, 1901), and the holochroal (Clarke, 1889) or compound (Lindstrom, 1901). The schizochroal eye is made up of relatively few (on the order of fifty to one hundred fifty), large biconvex lenses, each with its own corneal covering and separated from the other lenses by a sclera or by sclerotic walls which project down into the interior of the eyeball (Harrington, 1959). This type of eye is found exclusively in the Order Phacopida, particularly in the Phacopidae; well-known examples are *Phacops, Dalmanites* and *Acaste.*

The holochroal or compound eye contains many very small lenses, which are tightly packed together. All the lenses are covered by a single, thin, translucent cornea. The cornea is continuous with the cephalic shell. The eye facets, when visible, are the outlines of the lenses seen through the corneal covering; these presumably represent the outer portions of ommatidia, such as are found in the eyes of many modern athropods. The number of facets in the holochroal eye varies from several hundred to on the order of 15,000. (Harrington, 1959). The outlines of the lenses are generally hexagonal, but may also be rhombohedral or quadrate, or may vary within a single eye, according to position in the eye and the surface pattern of the facets. The shape of the outline of the facets is commonly complicated by variations in preservation, which, combined with close packing, gives the impression of roundness to the outline. In longitudinal section, the lenses may be prismatic and plano-convex, or thin and biconvex.

Isotelus iowensis Owen, 1852 and *Nileus vigilans* (=*Vogdesia vigilans*) (Meek & Worthen, 1875) are asaphid trilobites found in the Elgin Member of the Maquoketa Formation, of Upper Ordovician age. Both species have holochroal eyes, which appear to be similar. Material for this study was collected from the Elgin Member in a stream bed by a bridge on Fayette County Road Y, about one mile east of Clermont (near center of W. line, sec. 35, T. 95 N., R. 7 W., Fayette County). The bulk of the

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material was found in a single slab which measured about three feet by four feet by six inches. All specimens measured for this study are isolated fragments—the free cheek with the eye attached. Commonly, the fragile ends of the free cheeks are broken off, and many of the shell layers of the free check chipped away. Several hundred specimens were examined, but only a very few proved to be preserved in such a way that meaningful measurements could be made. In addition to the fragmentary material, a number of whole, enrolled specimens of *Nileus vigilans* from an unknown locality in Iowa were examined for comparison.

The purpose of the study was to determine the way in which increase in eye size was accomplished in the holochroal eye. Measurements of eye height and width, and size of facets, were made on a number of specimens of each species. These measurements were made both directly on the specimen, using either a micrometer eyepiece or calipers, and on photographs. Because of the extremely strong and variable curvature of the eye, the small size of the eye, and the large number of facets, it proved extremely difficult to make such measurements; they should therefore be regarded as approximate.

Descriptions and Measurements

Shape and Surface Pattern

Plate I, Figures a and b, are whole specimens of *Isotelus iowensis* and *Nileus vigilans* with the eyes attached. Plate I, Figures c and d show the detached free cheek and eye of each of these species. It can be seen that the eye approximates a truncated cone which extends upward from the free cheek and is open along the facial suture where it attaches to the glabella. The gentler slope of the eye surface is toward the anterior margin in both forms, although *Isotelus* eyes in general tend to be steeper than *Nileus* eyes, especially in the younger growth stages. Both are generally wider than they are high. Figure 1 shows a plot of eye height against eye width for both *Isotelus* and *Nileus;* there is very little difference in the two graphs. Measurements of the shape of the eye are complicated by the fact that the specimens, most of which probably represent molt fragments, are easily deformed without actual breakage.

The arrangement of the facets in *Isotelus* and *Nileus* is in long diagonal intersecting rows. In *Isotelus*, vertical files are produced by the intersection of the diagonals in most cases; in *Nileus*, vertical files can only be traced for a few facets before the pattern is disrupted. Plate I, Figures e and f illustrate the differing facet patterns in the two forms, and also indicate a distinctive feature of *Nileus*: the presence of an area lacking in

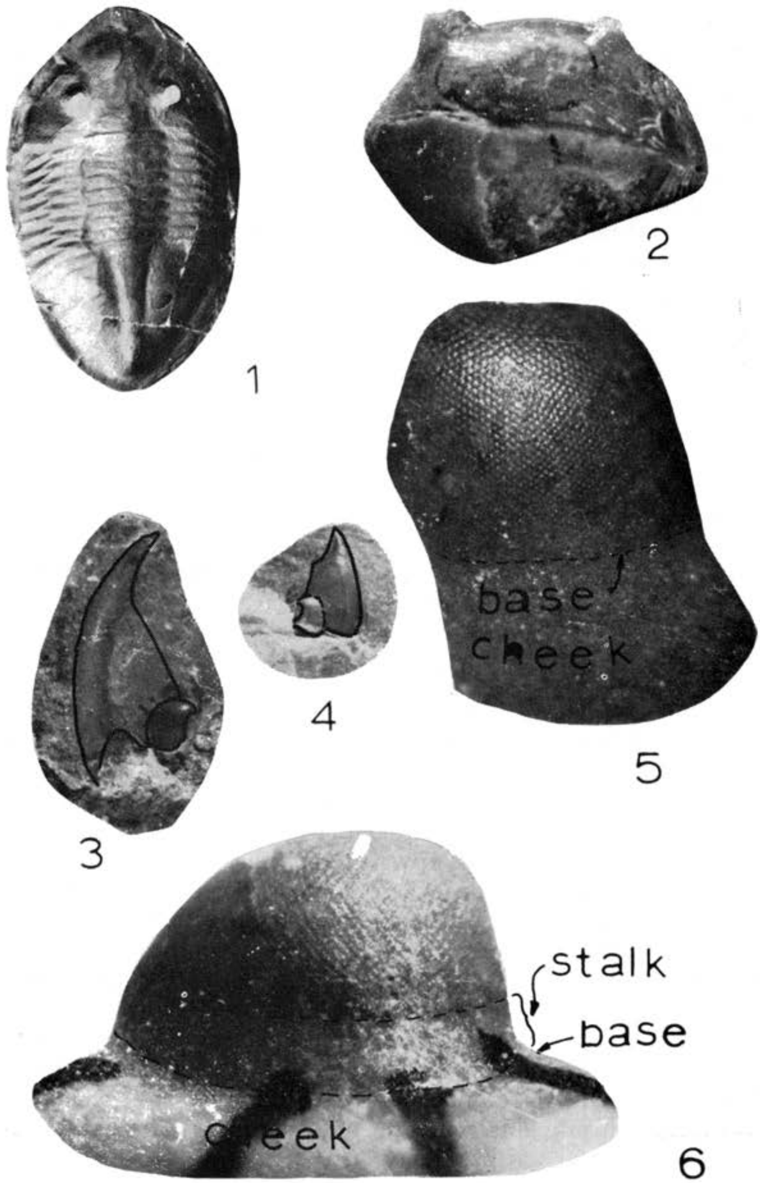

PLATE I

Figure 1. *Isotelus iowensis,* whole specimen, X1, SUI hypotype 9140. Note shape of facial suture and free cheek.

Figure 2. *Nileus vigilans,* whole enrolled specimen, X4 approx., SUI hypotype 32046. Note shape of facial suture and free cheek.

Figure 3. Free cheek and left eye of *Isotelus iowensis,* X 1⅓ approx., SUI hypotype 32029.

Figure 4. Free cheek and right eye of *Nileus vigilans,* X2, SUI hypotype 32047.

Figure 5. Close-up of eye of *Isotelus iowensis,* X 16 approx., SUI hypotype 32048. Note diagonal rows forming vertical files; facets extend to base.

Figure 6. Close-up of eye of *Nileus vigilans,* X 23.3 approx., SUI hyptotype 32038. Note stalk.

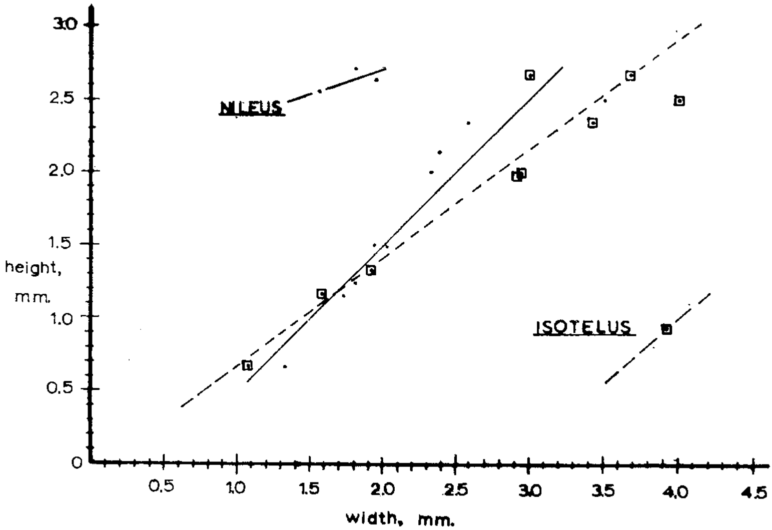

Figure 1. Graph of eye height against eye width for *Isotelus iowensis* and *Nileus vigilans*. *I. iowensis* specimens are SUI hypotypes 32028 through 32036; *N. vigilans* specimens are SUI hyptotypes 32037 to 32045.

surface facets, called the stalk, at the base of the eye. In *Isotelus*, the facets extend all the way to the base of the eye.

As can be seen from Plate I, Figures e and f, in both species the facets at the base of the eye are smaller than those at the top. A similar, but inverse, pattern is seen in the eye of the lobster, *Homarus americanus* where the zone of smaller facets is found around the proximal margins of the eye, rather than the distal margins.

Addition of Facets

Regardless of the difficulties involved with measurement and counting of facets, it certainly can be seen in both species that the number of facets increases with increasing size of the eye. Numerical estimates of facet number for three specimens of different sizes of each species are shown in Table 1.

In addition to the increase in the number of facets with size, an increase in the size of the largest facets with increasing eye size is found, particularly in *Isotelus* (see Table I). A similar situation was found in *Nileus,* as interpreted from facet densities at various points from the base to the top of the specimen (Fig. 2).

Facets are, then, apparently added at the base of the eye; thus, the size of the smallest facets remains about the same, regardless of the size of the individual (Fig. 2). What are presumed to be developing facets are seen in the stalk region of *Nileus* and near the base of *Isotelus.* This is plainest in vertical sections through

Table 1. Eye Height, Maximum Facet Size or Facet Density and Number of Facets for Selected Specimens of *Isotelus iowensis* and *Nileus vigilans*

	Isotelus iowensis		
Specimen No.	Total Height of eye	Number of Facets	Size of Largest Facet
SUI 32030	0.67 mm.	300-400	0.05 mm.
SUI 32031	1.97 mm.	2750-2850	0.06 mm.
SUI 32032	2.50 mm.	4700-4900	0.07 mm.
	Nileus vigilans		
Specimen No.	Total Height of eye	Number of Facets	Facet Density at Top of Eye
SUI 32041	1.16 mm.	900-1000	not measured
SUI 32038	1.49 mm.	1200-1300	12/0.036 mm.^{2}
SUI 32040	1.50 mm.	not estimated	14/0.036 mm.^{2}
SUI 32042	2.12 mm.	1900-2000	10/0.036 mm.^{2}

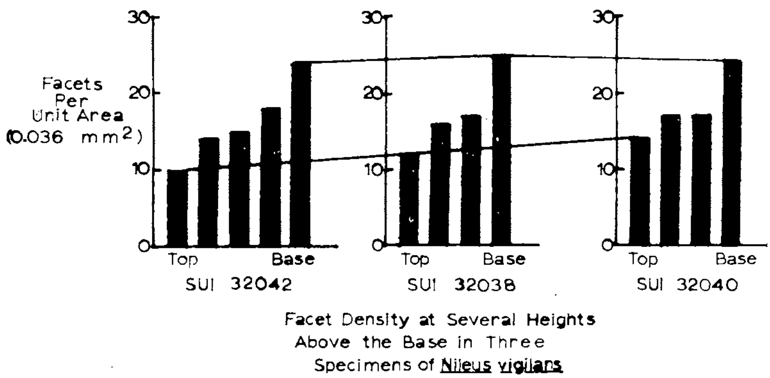

Figure 2. Facet densities for several specimens of *Nileus vigilans;* largest specimen is on the left.

the eye (see Lindstrom, 1901), but in some types of preservation it is possible to see this through the outer, non-facetted layers. Actual addition of and growth of the facets presumably takes place during molt stages, as is the case with growth in general among arthropods. In modern arthropods, cell division and development of new structures is accomplished before the shell is actually shed; but the newly formed cells and structures are small. While the newly-developing shell is still very soft, water is taken into the cells, which therefore increase in size. Some similar mechanism probably operated among the trilobites.

A series of measurements was made on a large and a small specimen of the eyes of *Isotelus iowensis* (SUI hypotypes 32029 and 32030 respectively), along a vertical file from the base to the top of the eye (Fig. 3). In the smaller specimen (SUI 32030), it can be seen that there is a fairly steady increase in

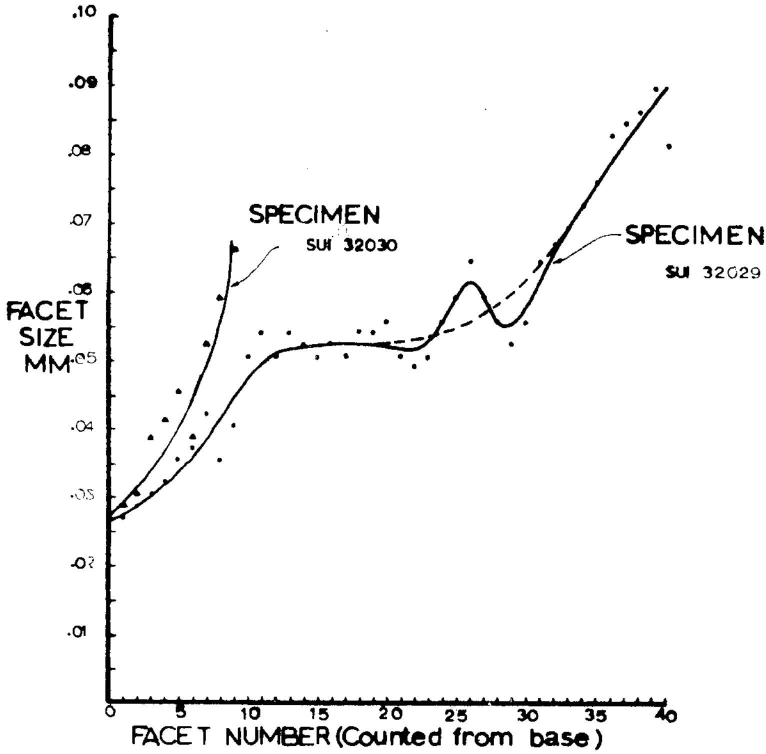

Figure 3. Size of facets from base of eye to top of eye for a large and a small specimen of *Isotelus iowensis*, SUI hyptotypes 32029 and 32030 respectively.

facet size from base to top, suggesting addition of perhaps one horizontal row at a time, each horizontal row growing somewhat during succeeding molts. In specimen SUI 32029, however, there is a "flat" place on the curve, suggesting some non-uniformity in the growth. This could be interpreted as indicating a slow initial rate of facet addition, followed by a sudden spurt during which many rows of facets were added, either during a single molt stage or in a series of rapid molts (depending on the interpretation of a possible extra "hump" in the "flat" of the curve); and a return to a relatively regular growth rate.

Facet densities determined on three different-sized specimens of *Nileus* at various levels in the eye show a similar pattern (Fig. 2). The density at the base is nearly the same for all three specimens, but facet density at the top decreases with increasing eye height (although not as regularly as in *Isotelus*, among the specimens measured—see Table I), indicating that the facets at the top are larger on the larger individuals. A "flat" in the density graphs for *Nileus* suggests a difference in growth rate during ontogeny for this species as well as for *Isotelus iowensis.*

Relief

One of the factors contributing to the difficulty of measurement in *Nileus* in particular, and indeed to all the large specimens, is the lack of relief of the facets in the larger individuals. Small specimens of both forms generally have moderately prominent facets, although the whole, enrolled specimens of *Nileus* display little relief even on the smallest eyes. Presumably, the thickness of the corneal layer increases with the age of the individual, and this trait is more pronounced in *Nileus* than in *Isotelus.* Lindstrom (1901) commented on the "exceedingly thick exterior integument above the lenses" found in *Nileus armadillo.* In some asaphid genera, the corneal layer was so thick that he doubted that the animal was able to see. It has been suggested that apparently opaque material in modern arthropod eyes likewise prevents the animals from seeing. However, the ommatidia are capable of conducting impulses in such forms as *Limulus,* the horseshoe crab (Smith *et al.,* 1965), which sometimes has an opaque, milky-appearing material in the facets.

Summary And Conclusions

Isotelus iowensis and *Nileus vigilans* have similar, holochroal eyes which show similar, although not identical, patterns of growth. Two major growth patterns are involved: addition of more facets with increasing eye size, and increase in the size of the largest facets. The increase in number is dominant. This is in contrast to the situation in schizochroal eyes, where the total number of vertical files is established early in ontogeny (Clarkson, 1966), and where even the number per vertical file changes only a relatively small amount thereafter, much of the increase with increasing eye size being in the diameter of the facets.

Holochroal eyes in this respect appear similar to the typical lateral compound eyes of decapod crustaceans, although the facets are added distally in trilobites and proximally in, for example, the lobster.

Growth appears to be non-uniform, although it is not known exactly how many facets or rows of facets are added at each molt stage. In this regard, it would be interesting to examine successive molt-skins of modern arthropods in order to determine the number of facets added per molt.

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