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## Ocellar atavism in Coleoptera: plesiomorphy or apomorphy?

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### Abstract

Ocelli and ocellus-like structures on the vertex of the adult head were examined in different representatives of Coleoptera and the presence of these was confirmed for the suborder Polyphaga. The presence of structures, which are likely homologous with ocelli of other insects were confirmed by semi-thin sectioning in Hydraenidae, Staphylinidae, Derodontidae and Dermestidae. The presence of ocelli is newly recorded for a representative of Scydmaenidae (*Nesuthia fiji* Franz). The weakly pigmented areas on the vertex of *Neopeltops* (Leiodidae) lack a lens and associated nervous tissue and are referred to as pseudocelli, which may be present in other groups. The internal structure of Coleopteran ocelli is strongly simplified compared with other groups of Insecta where longitudinal retinula cells are arranged at a right angle to the cuticular surface and enclosed by a sheath of pigment cells. Such a regular arrangement is absent from all beetles examined histologically. A flattened group of cells without a rhabdom and without an enclosing layer of pigment cells is present underneath the cuticular lens. While, the infrastructure of the ocelli is more or less reduced in Coleoptera, the presence of these features in the ground-plan of Coleoptera is dependent on the confirmation of the presence of ocelli in Archostemata (Jurodidae?) and a robust phylogenetic hypothesis for the order.

**Key words:** Coleoptera – phylogeny – ocelli – vision – histology

### Introduction

Coleoptera are the largest group of insects at the ordinal level and explaining their numerical success based on any one set of characters has been elusive. Beetles have numerous synapomorphies that mark them as a monophyletic group (Lawrence and Britton 1991; Beutel and Haas 2000), but also have lost many features that seem typical for insects like the dorsal ocelli. This optic structure is used for orientation in most insects (Goodman 1981), is an important feature that is often cited in textbooks and in keys, and is usually absent from the vertex of the head in adult beetles. The presence of three ocelli on the vertex of the head in the adults and immature stages of insects is almost certainly a ground-plan feature of Insecta, although they are absent from some or all representatives of several orders (e.g. Grylloblattodea, Dermaptera, Embioptera, some Zygentoma and some Isoptera, Beutel and Gorb 2001) and from all larvae of Endopterygota. In hemimetabolous insects, ocelli are usually also present in the nymphs (e.g. Ephemeroptera, Odonata and Plecoptera) and generally absent from larvae of paraneopteran and endopterygotous insects with the exception of Mecoptera where one anteromedian ocellus is present in Bittacidae and Choristidae (Byers 1991). A single median structure resembling an ocellus is present on the frons of larvae of *Dissochaetus* (Gnaspini 1993), however, the internal structure of this feature is unknown.

Ocelli are absent from adults of most major extant groups of beetles and are usually never present in a triad apart from the jurodid *Sikhotealinea zhiltzovae* (Lafer 1996) and teratological specimens of Staphylinidae (Newton and Thayer 1995). A pair is present in Hydraenidae (most Ochthebiinae; Hansen 1991), Agyrtidae (*Pteroloma*; Newton 1997), Leiodidae (*Neopeltops* and *Ragydotis*; Newton 1998), many Staphylinidae (Newton and Thayer 1995) and Derodontidae (Lawrence and Hlavac 1979; Fig. 1b). A single ocellus is present in most Dermestidae (Fig. 1a) and *Metopsia* (Staphylinidae, Proteininae; Newton and Thayer 1995). Among the Staphylinidae, ocelli are present in the omaliine group (Lawrence and Newton 1995), more precisely in many Omaliinae tribes, some

Proteininae and members of Glypholomatinae, Microsilphiinae, and Neophoninae (Newton and Thayer 1995). The single ocellus in dermestids is present in five of eight of the subfamilies where its absence may be a synapomorphy for Dermestinae, Marioutinae, and Thorictinae (Lawrence and Newton 1995). The rare occurrence of and presence (mainly) in reduced number of dorsal ocelli in adult Coleoptera poses fundamental questions about the evolution and homology of this character which we address in this study: Are the dorsal ocelli in beetles homologous to those present in other insects and were they in the coleopteran ground-plan?

Homology has numerous definitions and we follow, mainly, a cladistic definition where homology is equivalent to synapomorphy (de Pinna 1991) where at the very core of this concept of homology is the accurate identification and precise definition of what is the particular state(s) in a series of character transformations. The presence of ocelli is assessed by external examination of their occurrence on the vertex of the head. While recording presence or absence conforms to a strict criterion of position (Remane 1959), an incorrect assessment of homology could be made if the structures are indeed different externally and internally. This is especially true for complex characters such as ocelli, and in fact Franz (1958) argued that the protuberances on the head of *Laricobius* (Derodontidae) are not true ocelli but simple 'chitinous lobes', without an assemblage of nervous cells below. The occurrence of nervous tissue below the ocelli will substantiate the presence of functional ocelli. Apart from the examination of infrastructure, phylogenetic pattern will arbitrate whether or not a character is homologous. In this study, we examine the external and internal microstructure of beetle ocelli to determine if coleopterists over the centuries have been correct in the naming of dorsal ocelli and if these have the same structure as the ocelli present in other insects, and among beetles themselves. If these structures in Coleoptera are *de novo* 'ocelli' then they may have different components than those present in the remaining insects, a morphological signature of homoplasy.

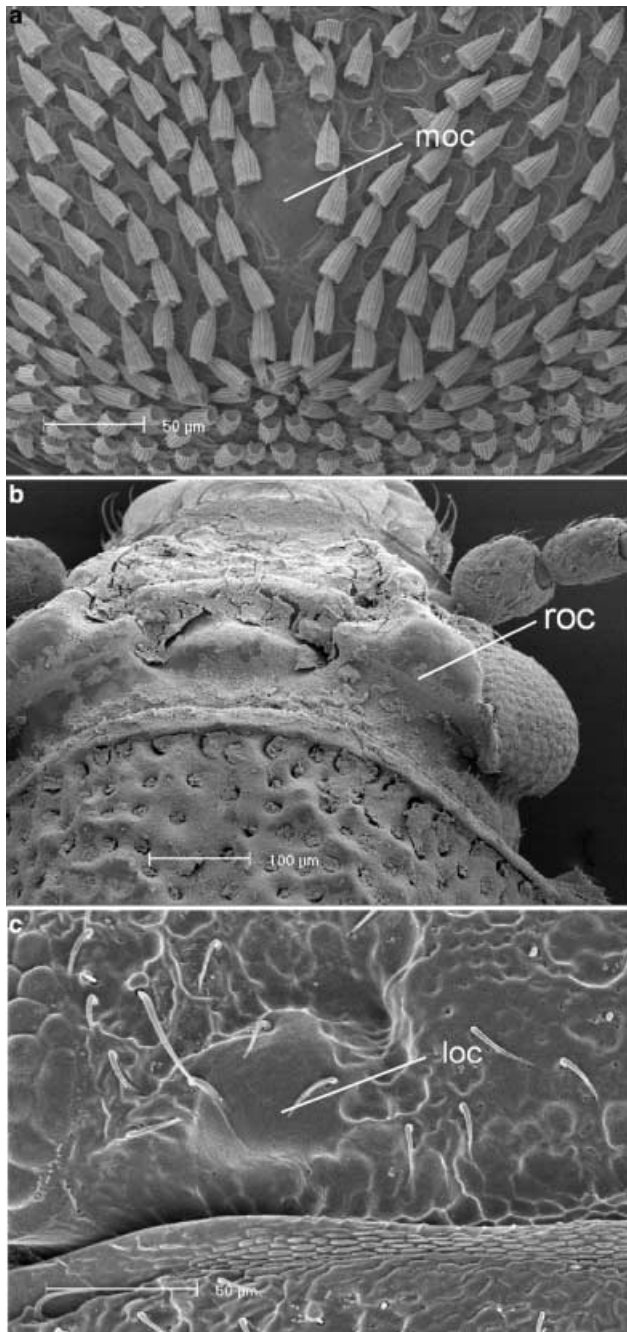


Fig. 1. Scanning electron micrographs, dorsal ocelli. (a) *Anthrenus* sp. (Dermestidae); (b) *Derodontus esotericus* (Derodontidae); (c) *Ochthebius exsculptus* (Hydraenidae). loc = left ocellus; moc = median ocellus, roc = right ocellus

## Materials and Methods

Many taxa were examined externally, by dissection on permanent slide-mounts (+), and by semi-thin sectioning. Adults of the species marked by asterisks below were fixed in Formol-ethanol acetic acid or ethanol and imbedded in Historesin, cut at 3 µm in cross-sections with a Microm HM 360 rotation microtome (Walldorf, FRG) and stained with methylene-blue and acid fuchsin. Images of selected cross-sections were taken with the Analysis<sup>®</sup> (Münster, FRG) program. For scanning electron microscopy, specimens of *Ochthebius* sp., *Davidraena boukali* Jäch, *Derodontus esotericus* Lawrence and *Anthrenus* sp. were cleaned with ultrasound and gold-coated and examined with an XL 30

ESEM TMP (FEI Deutschland, Kussel, FRG). X-ray tomography of *Priacma serrata* was made with a Skyscan 1072 high-resolution Micro-CT (Aartselaar, Belgium) system after the specimen was critical point dried. Although we have examined internally the head of many Coleoptera, those listed below are those we selected specifically for this study.

## Species examined

Archostemata, **Cupedidae**: *Priacma serrata* LeConte; Jurodidae: *S. zhiltzovae* (Lafer) (externally). Adephaga, **Trachypachidae**: *Trachypachus holmbergi* Mannerheim\*. Myxophaga, **Hydroscaphidae**: *Hydroscapha natans* LeConte\*; Sphaeriidae: *Sphaerius* sp., Polyphaga, Staphylinidae. **Hydraenidae**: *Limnebius truncatellus* (Thunberg)\*, *Hydraena gracilis* Germar, *H. riparia* Kugelann, *H. isolinae* Jäch & Diaz\*, *Davidraena boukali* Jäch, *Meropathus aucklandicus* Ordish, *M. campbellensis* Brookes\*, *M. johnsi* Ordish, *Ochthebius exsculptus* Germar\*, *Ochthebius* sp., *Parhydraena pentatekta* Perkins. **Ptiliidae**: *Acrotichis* sp.\* **Agyrtidae**: *Pteroloma forstroomii* (Gyllenhal) +. **Leiodidae**: *Neopelatopeus edwardsi* Jeannel\* +, *Neopelatopeus* n.sp. 1–3 (Australia), *Ragytopeus ocellifera* Jeannel +. **Staphylinidae**, **Glypholomatinae**: *Glypholoma pustuliferum* Jeannel (fixed in ethanol)\*, *Glypholoma germaini* Thayer +. **Microsilphinae**: *Microsilpha littorea* Broun, *Microsilpha* spp. (four spp.) +. **Omalinae**: *Anthobium* sp., *Anthophagus* sp., *Brathinus nitida* LeConte, *Eusphalerum* sp., 'Elonium' *fractum* Fauvel, *Geodromicus* sp., *Lesteva punctata* Erichson, *Microedus* sp., *Olophrum* sp., *Orobanus* sp., *Phyllodrepa* sp. +, *Psephidonus brunneus* Say. **Proteininae**: *Metopsia clypeata* (Müller). **Neophoninae**: *Neophonus bruchi* Fauvel. **Scydmaenidae**: *Nesuthia fijii* Franz. Derodontidae, **Derodontidae**: *Derodontus esotericus* Lawrence, *D. macularis* (Fuss), *D. maculatus* Melsheimer +, *D. tuberosus* Hisamatsu & Sakai, *D. unidentatus* Lawrence, *Laricobius erichsoni* Rosenhauer +, *L. rubidus* LeConte, *Nothoderodontus gourleyi* Crowson +, *N. newtonorum* Lawrence, *N. watti* Lawrence, *Pelastasia tuberculata* Mannerheim +. Dermestidae, **Dermestidae**: *Anthrenus* sp.\* +, *Apsetus* sp., *Attagenus piceus* Olivier +, *Cryptorhopalum* sp. +, *Orphilus beali* Zhantiev, *Reesa* sp., *Thylodrias contractus* Motschulsky +, *Trogoderma signatum* Sharp +.

## Results

Below we have summarized the results for each group that have ocelli, or ocellus-like structures, including fossil taxa (see Agyrtidae). There were no internal traces of nervous tissue in the dorsal portion of the head in Archostemata, Adephaga, Myxophaga and most Polyphaga (*Hydraena*, *Limnebius*, and *Acrotichis*) examined histologically. In those taxa marked with an asterisk (\*), the internal arrangement of ocellar tissue is simple and irregular, that is, the cells are not longitudinal and not arranged at right angles to the external cuticle. Special pigment cells and a rhabdom are absent and the morphology is similar to that present in some other insects like Zoraptera (Fig. 2a), which have also ocelli with a simplified internal structure.

## Jurodidae

### *Sikhotelealina*

Three ocelli present (one illustrated by Lafer 1996); not delimited; smooth and not highly convex; colour yellow.

## Hydraenidae

### *Meropathus*\*

Two ocelli present near the posterodorsal margin of the compound eyes; delimited; round and convex; colour yellow (Fig. 2e). The internal structure is similar to that of

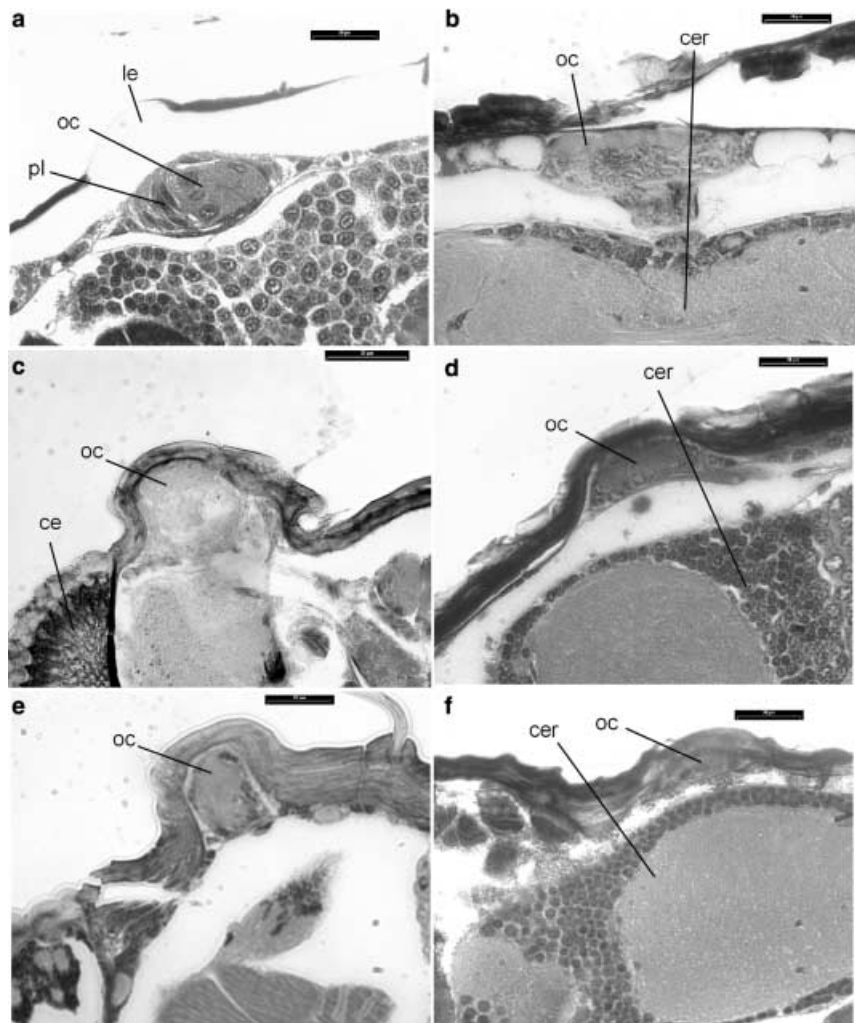


Fig. 2. Microtome sections; (a) *Zorotypus hubbardi*, alate specimen (Zoraptera); (b) *Anthrenus* sp. (Dermestidae); (c) *Derodontus esotericus* (Derodontidae); (d) *Glypholoma pustuliferum* (Staphylinidae); (e) *Meropathus campbellensis* (Hydraenidae); (f) *Ochthebius exsculptus* (Hydraenidae). cer = cerebrum; le = lens; oc = ocellus; pl = pigment layer. Scale bar = 20  $\mu$ m in a, b, d-f, 50  $\mu$ m in c.

*Ochthebius*, but the ocellus is distinctly larger and internally composed of a higher number of cells.

#### *Ochthebius*\*

Two ocelli [=interocular tuberculi, Perkins (1980)] present posterior to the frontal foveae; not distinctly delimited; round and not convex; colour matching that of vertex (Figs 1c and 2f).

#### *Parhydraena*

Two ocelli present between the compound eyes; delimited; round and convex; colour yellow.

#### Agyrtidae

##### *Mesecanus*

Two ocelli present between the compound eyes towards the back of the head (see figures in Ponomarenko 1977). Note that the Jurassic beetles of the genus *Mesecanus* Newton (= *Mes-agyrtes* Ponomorenko) are presently placed in Agyrtidae (Newton 1997; Perkovsky 1999, 2001), not in Leiodidae or Silphidae.

##### *Pteroloma*

Two ocelli present between the compound eyes; not delimited; round and slightly convex; colour yellow or unpigmented (see also Newton 1997).

#### Leiodidae

##### *Neopelatops*

Two 'ocelli' present between the compound eyes; not delimited; round and smooth; colour yellow or pale. The 'ocelli' were observed in three of the four species examined and internal nervous tissue is absent. A distinct lens is absent, and the area seen externally is the attachment area of the frontohypopharyngalis muscle that attaches to the hypopharynx.

##### *Ragytodes*

Two ocelli present between the compound eyes; delimited; round and smooth; colour yellow or pale. A distinct lens is present in slide preparation (see also Newton 1998).

#### Staphylinidae

##### *Glypholoma*\*

2 ocelli present posteromesad to the compound eyes; delimited; round and slightly convex; colour transparent (Fig. 2d).

##### *Microsilpha*

Two ocelli present between compound eyes; delimited (*M. littorea* Broun) or not; round and slightly to strongly convex (*M. littorea*); colour transparent or yellow.

*Omalinae\**

Two ocelli present between or slightly behind compound eyes; well to slightly delimited; round or oval and weakly to strongly convex; colour transparent, yellow or silver, or matching that of vertex.

*Metopsia*

One ocellus present between compound eyes; delimited; round and strongly convex; colour yellow.

*Neophonus*

Two ocelli present between compound eyes; not well delimited; oval and strongly convex; colour yellow (see also Thayer 1987).

**Scydmaenidae***Nesuthia*

Two ocelli present between compound eyes; delimited; round and strongly convex; colour same as vertex. This is the first record of ocelli in Scydmaenidae (Sean T. O'Keefe, personal communication). They were mistaken as fovea by Franz (1986). The genus is in the tribe Cephenniini and contains 22 species distributed mainly in the islands of the Pacific and Indian oceans and Australasia (Franz 1971, 1986; Newton and Franz 1998). Two specimens of *N. fiji* Franz deposited in the Queensland Museum, Brisbane, were examined with the following label data: Fiji: Kadavu, Lagalevu, 20 m, 2–5 July 1987, Monteith, Pyrethrum/logs and trees.

**Derodontidae***Derodontus\**

Two relatively large ocelli present as forming large protuberances and more or less part of a ridge system dorsal and proximal to the compound eyes, separated by a median fovea and a pore-canal system (Lawrence and Hlavac 1979), resting against the anterior margin of the pronotum while the head is in repose; not delimited; shape variable but more or less oval to round and convex; colour yellow (Figs 1b and 2c). The presence of nervous tissue in *Derodontus* is in contrast to the findings of Franz (1958) for *Laricobius*.

*Laricobius*

Two ocelli present beside the hind margin of compound eye, separated by a broad impression on the vertex; not well delimited; round and convex; colour dark yellow or pale (same as the vertex in some specimens).

*Peltastica*

Two ocelli present, resting against the mid-dorsal margin of the eye; well delimited; round and convex; colour yellow.

*Nothoderodontus*

Two ocelli present, resting against the outer margin of the eye; not well delimited; round and convex; colour yellow or pale.

**Dermestidae***Anthrenus\**

One ocellus present between the compound eyes on the posteromedian frontal area; delimited; round and convex; colour dark brown. Internally simple; pigment absent; rhabdom and retinula cells not apparent. In cross-section the lens

consists of transparent cuticle with a moderately flattened complex of nervous tissue beneath (Figs 1a and 2b). The ocellus is dorsomedially connected with the protocerum by a thick and short ocellar nerve.

*Other Dermestidae*

One ocellus present between the compound eyes; delimited or not (*Apsectus*); round and convex or smooth (*Apsectus*); colour dark brown, yellow, or the same as vertex (*Cryptorhopalum*). Crowson (1981) mentioned that the single ocellus in this group has 'indications' of a paired origin, but we have no available evidence for this.

**Discussion**

A comparative study of the microstructure of beetle ocelli has not been carried out, although these structures have been mentioned in broader studies of the ommatidia (Paulus 1979) or in general textbooks on insect morphology (Chapman 1982). For this study, we record the presence of true ocelli by gross examination, and not through detailed study of ultrastructure for all of the species examined. A typical dorsal ocellus consists of a thickened cuticular lens or simple transparent area that can be seen in externally (Fig. 1). The lens is much larger than the single ommatidia that make up the compound eye (compare the ocellus with the eye in Fig. 2c). Often times underlying pigment or pigment cells may be present and seen in live specimens, but pigments are best observed in semi-thin sections (Fig. 2b). A reflecting tapetum may also be present in some insects, and in pinned beetles this may be the structure that produces a silvery colour to the ocellus, but this must be studied further. In insects with a well developed ocellus, there are retinula cells subtending the lens and connecting to the basement membrane of the ocellus and are then connected to the protocerebrum through the ocellar nerve (Goodman 1981; Chapman 1982): these are absent in Coleoptera.

Based on gross morphology, the presence of ocelli in Coleoptera is restricted to eight families and confirmed for most groups apart from *Neopelatops* that has no traces of internal ocellar tissue subtending the yellow areas on the vertex of the head. Other taxa with similar looking structures to *Neopelatops* (like *Pteroloma* and other species of staphylinids in the omaline group) would have to be studied histologically to confirm the presence of optic tissue. The infrastructure of the ocellus is different among the groups studied. For example, externally, the ocellus may be flush with the vertex of the head or convex with high topography. The ocellar lens may also be rather weakly or strongly delimited around its border. Meanwhile, the external colour in pinned specimens also varies from transparent to yellow or silver and may be attributable to preservation method. For example, in one series of *L. rubicus* the ocelli are the same colour as the vertex, while in another series it is yellow. However, in most taxa the ocelli are yellow and rarely silver, and may reflect variation of the type of nervous tissue within the ocellus as well as the presence of a tapetum. Moreover, the relative amount of dense yellow optic tissue varies, and in *Derodontus* (Fig. 2c), the tissue is rather massive and visible through the rather impressive protuberances (Fig. 1b). Gross internal structure of the ocellus is similar among the groups, although shape of the tissue varies and may be related to the form of the lens. For example, the optic tissue is more strongly flattened in Dermestidae compared with the other groups studied. The ocelli may be considered as vestigial

as they lack regularly arranged retinula cells, a rhabdom and also pigment cells; although, pigment layers are clearly seen in some taxa.

Despite the highly reduced condition of beetle ocelli, it is more plausible to assume that they are homologous with median eyes of other hexapods, than to assume that they have evolved *de novo*. If this assumption is correct, it suggests that presence of ocelli is a ground-plan character state of Coleoptera. However, to confirm (or refute) this hypothesis, it is necessary to examine the distribution of ocelli in the context of known phylogenies for Coleoptera. We note, however, that this task is not easy to perform because the distribution of ocelli is wide and sporadic among beetle lineages, there is a general paucity of complete phylogenetic hypotheses for most groups, the monophyly of the suborders (i.e. Archostemata with the inclusion of Jurodidae; see also Lawrence 1999) may be problematic, and the genetics of ocellar expression is not known for Coleoptera. For example, the various levels of inquiry manifests itself in the assertion by Newton and Thayer (1995) that the presence of ocelli in the omaliine group was an apomorphic 'reactivation of a suppressed genetic capability' rather than a plesiomorphy with numerous losses. In other words, the genes coding for ocelli may be present throughout the group, with the expression of ocelli treated as a homoplasy. We focus on the presence of ocelli as a potential homology, and not on genetics (see Rieppel 1994 for further discussion).

The occurrence of true ocelli in a possible member of Archostemata (*S. zhiltzovae*) could not be completely confirmed in this study. These structures are absent from representatives of the remaining families of the suborder, both living and extinct, as well as members of Adephaga and Myxophaga. Within Polyphaga, paired ocelli occur in three families of Staphylinoidea and in Derodontidae, and an unpaired ocellus is present in Dermestidae. The polyphagan families having ocelli are not entirely related to each other, although Derodontidae may be a primitive member of the suborder (e.g. Caterino et al. 2002) and within staphylinoids, ocelli are present in the relatively primitive taxa Hydraenidae, Agyrtidae, Leiodidae, and omaliine group (Staphylinidae). For the following discussion, we assume that the suborders are monophyletic and that the presence of ocelli is a ground-plan feature of Archostemata and Polyphaga.

The relationships of the suborders is contentious, as there are four hypotheses to choose from, with a sister relationship to Neuropterida (Beutel and Haas 2000), which has the ocelli present. The most robust hypothesis is that elucidated by Beutel and Haas (2000), based on a large number of morphological features and a wide array of terminal taxa while the most recent is that of Caterino et al. (2002) based on molecules. The available hypotheses are as follows with the clades with ocelli marked by an asterisk (\*):

Hypothesis A: Archostemata\* [Adephaga (Myxophaga + Polyphaga\*)] – Klausnitzer (1975), Crowson (1981), Beutel (1997), Beutel and Haas (2000).

Hypothesis B: (Archostemata\* + Adephaga) (Myxophaga + Polyphaga\*) – Baehr (1979).

Hypothesis C: Polyphaga\* [Archostemata\* (Myxophaga + Adephaga)] – Kukulová-Peck and Lawrence (1993).

Hypothesis D: Archostemata\* [Myxophaga (Adephaga + Polyphaga\*)] – Caterino et al. (2002).

Assuming that Archostemata had ocelli (assumption 1, see Table 1), then these structures were in the ground-plan of

Table 1. Character distributions among hypotheses for the Coleoptera suborders

H	Assumption 1 <sup>1</sup>			Assumption 2 <sup>2</sup>		
	GP	Losses	Gains	GP	Losses	Gains
A	Y	2 <sup>D</sup> /1 <sup>A</sup>	1 <sup>A</sup>	N	–	1
B	Y	2	–	Y <sup>D</sup> /N <sup>A</sup>	2 <sup>D</sup>	1 <sup>A</sup>
C	Y	1	–	Y	1	–
D	Y	2 <sup>D</sup> /1 <sup>A</sup>	1 <sup>A</sup>	N	–	1

<sup>1</sup>Archostemata had ocelli in their ground-plan.

<sup>2</sup>Archostemata did not have ocelli in their ground-plan.

Superscripts refer to optimizations of characters using ACCTRAN (A) and DELTRAN (D) (Maddison et al. 1984).

H = hypothesis; GP = ground-plan.

Coleoptera and lost at least once or twice; otherwise, ocelli were not in the ground-plan in Coleoptera or were lost once and regained (hypotheses A and D), and lost twice (hypothesis B). Assuming that only Polyphaga had ocelli (assumption 2), only in hypotheses B and C is there possible evidence that ocelli were in the ground-plan of Coleoptera, with other hypotheses favouring ocelli as a new acquisition in the Order. Of course, these hypotheses do not consider the patterns of evolution within Polyphaga, where the evolutionary pattern is complex due rampant losses and gains. To assume that Archostemata had ocelli in their ground-plan may be far-fetched because fossil Archostemata have not been reported to have these structures. Moreover, the assignment of Jurodidae (*Sikhotealinia*) to Archostemata (Kirejtshuk 1999) is problematic and is not based on clearly defined apomorphies (if their position within Archostemata is doubtful, the case of ocelli as ground-plan feature of Archostemata is weakened) and critical study of this genus is imperative for determining the presence of ocelli in the ground-plan of Archostemata. By contrast, Polyphaga apparently had ocelli in the fossil record, being reported in the genus *Mesecanus* that was thought to be allied to Derodontidae (Crowson 1981).

To summarize, the presence of ocelli in the ground-plan of Coleoptera depends on the resolution of two issues. First, it must be determined if *Sikhotealinia* is a member of Archostemata and whether or not this taxon has true ocelli. Secondly, a robust phylogeny for the Coleoptera produced by combining all of the morphological and molecular characters is necessary. Once we understand the homology of ocelli, we can then begin addressing questions about the function of ocelli in beetles, their patterns of distributions in other groups (such as staphylinids, Newton and Thayer 1995), and why ocelli have such a mysterious taxonomic distribution.

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## Zusammenfassung

*Ocellen als Atavismus bei Coleopteren: Plesiomorphie oder Apomorphie?*

Ocellen und an Ocellen erinnernde Strukturen auf dem Vertex von Imagines von verschiedenen Teilgruppen der Coleoptera wurden untersucht und das Vorhandensein wurde für verschiedene Vertreter der Polyphaga bestätigt. Die Homologie mit echten Ocellen wird durch die Ergebnisse von histologischen Untersuchungen (Semidünnschnitte) für folgende Gruppen nahegelegt: Hydraenidae, Staphylinidae, Derodontidae, und Dermestidae. Das Vorhandensein bei einer Art der Scydmaenidae (*N. fijii* Franz) wurde erstmals festgestellt. Den schwach pigmentierten paarigen Regionen auf dem Vertex von *Neopelatops* (Leiodidae) fehlt eine Linse und darunter gelegene nervöse Strukturen. Sie werden deshalb als Pseudocelli bezeichnet, die möglicherweise auch bei anderen Gruppen vorhanden sind. Die mit den Ocellen assoziierten inneren Strukturen sind bei den Coleopteren stark vereinfacht im Vergleich zu anderen Insektengruppen, bei denen Retinulazellen parallel und senkrecht zur Oberfläche angeordnet und von Pigmentzellen umgeben sind. Vergleichbar organisierte Ocellen fehlen bei allen histologisch untersuchten Käfern. Unter der Linse ist lediglich eine abgeflachte Gruppierung von Nervenzellen vorhanden, ohne die Ausbildung eines Rhabdoms und ohne eine Schicht von Pigmentzellen. Ob vereinfachte Ocellen zum Grundplan der Coleoptera gehören oder sekundär entstanden sind hängt davon ab, ob sie innerhalb der Archostemata auftreten (Jurodidae?) und von einer soliden Rekonstruktion der Verwandtschaftsbeziehungen der Unterordnungen.

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