# Super black eyespots of the Eyed elater

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Scattering of light by surface structures leading to near complete structural absorption creates an appearance of "super black." Well known in the natural world from bird feathers and butterfly scales, super black has evolved independently from various anatomical structures. Due to an exceptional ability to harness and scatter light, these biological materials have garnered interest from optical industries. Here we describe the false eyespots of the Eyed elater click beetle, which attains near complete absorption of light by an array of vertically-aligned microtubules. These cone-shaped microtubules are modified hairs (setae) that are localized to eyespots on the dorsum of the beetle, and absorb 96.1% of incident light (at a 24.8° collection angle) in the spectrum between 300 – 700 nm.

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## Abstract

Scattering of light by surface structures leading to near complete structural absorption creates an appearance of "super black." Well known in the natural world from bird feathers and butterfly scales, super black has evolved independently from various anatomical structures. Due to an exceptional ability to harness and scatter light, these biological materials have garnered interest from optical industries. Here we describe the false eyespots of the Eyed elater click beetle, which attains near complete absorption of light by an array of vertically-aligned microtubules. These cone-shaped microtubules are modified hairs (setae) that are localized to eyespots on the dorsum of the beetle, and absorb 96.1% of incident light (at a 24.8° collection angle) in the spectrum between 300 – 700 nm.

## Introduction

Black in nature is often achieved by pigments (*e.g.* melanin) that absorb most visible light [1, 2]. In some cases, only ultraviolet light (320 – 400 nm) is reflected, such as in Asian whistling-thrushes [3]. Often, black pigment is overlaid by a glossy surface thereby imparting specular reflection increasing at angles normal to the illumination source, for example in many beetles [4]. Among insects, black pigmentation is typically achieved during the process of molting and tanning including sclerotization and melanization. In contrast, super black in butterflies, moths, birds, and snakes is usually achieved by structural absorption of nearly all light [5]. Three-dimensional structures, such as forest-like arrays of microtubules on butterfly wings and the highly ramified barbules on Bird of paradise feathers, act as a baffle to light [6, 7]. (But, there are instances of "pseudo"-black achieved through additive mixing of structural green and magenta iridescence [4]). In some of these instances, super black structures evolved to impart varying degrees of reflection (blackness) dependent upon angle [7]. In others, structural absorption is assisted by melanin, and in Jumping spiders, brush-like 3D scales absorb light and stray light is recaptured by an underlying melanin-containing microlens array [8]. Functional explanations of the evolutionary origins of super black include sexual selection [7], predator defense [9], hydrophobicity [10], and for scotopic vision [11]. In nearly all of these examples of structural black, there is an array of protuberances on the surface of the animal that are perpendicularly oriented. These protuberances, which vary in composition from setae, microtrichia, barbules, and scales, have evolved repeatedly across the Tree of Life. Super black surface structures from nature have been applied to human industry since

**Figure 1** Eyed elater click beetle, *Alaus oculatus*, (A) dorsal habitus view, (B) right lateral view (scale bar = 2.0 mm); Eyed elater false eyespots, (C) left dorsal view, (D) right oblique view (scale bar = 0.5 mm).

64  they have application for solar technology, anti-reflective coatings for the military, and a coating
65  for the internal barrels of lenses in optical manufacturing [**8**, **12**].
66
67  Known colloquially as the Eyed elater or Eastern eyed click beetle, *Alaus oculatus* (Linneaus,
68  1758) (Fig. 1A, B) is a common beetle in the eastern U.S. with large and conspicuous eye-like
69  spots on its back [**13**]. False eyespots have evolved independently in several lineages of insects
70  including moths, cockroaches and mantises, butterflies, and beetles [**14**]. Two lineages of Click
71  beetles (family Elateridae) in the subfamily Agrypninae possess ostensibly false eyespots,
72  including some members of the genus *Alaus* and individuals of the tribe Pyrophorini [**15**]. The
73  latter possess bioluminescent eyespots atop the pronotum and include the Headlight elater
74  (*Pyrophorus noctilucus*), known colloquoially as the "cucuyo", and other pyrophorine genera
75  from the southern U.S. (*e.g. Deilelater*, *Ignelater*, *Vesperelater*). The bioluminescence of *P.
76  noctilucus* is so bright it can be seen from afar and, according to ship logs, was confused by
77  Spanish conquistadors with the smoldering matches of arquebusas held by indigenous
78  inhabitants, thereby discouraging attack [**16**]. Eyespots are often used to deter predators and
79  function to deflect attack to a non-vital body region or to startle predators [**17**]. These functions
80  are the false-head ("lose-little-to-save-much" ref. **18**) and deimatic strategies [**19**]; however, in
81  the case of the deimatic function it remains uncertain whether the eyespots deter attack because
82  they appear as eyes (often of a larger, more intimidating animal) or due to their conspicuousness
83  [**17**]. The false-head hypothesis for click beetles with eyespots atop their pronotum seems
84  unlikely since the thorax houses vital organs such as the dorsal vessel and thoracic ganglia.
85  Noting the similarity between the eyespots of the cucuyo and the Eyed elater, McDermott [**13**]
86  examined the latter to determine if the eyespots were "luminous, or at least have beneath its
87  chitin some structure indicating that the eyespots were a degradation of the photogenic organs of
88  the cucuyo". Although he found thicker cuticle underlying the eyespots, potentially due to
89  muscular attachments of the thoracic cavity, no structures consistent with the photogenic organs
90  of the cucuyo were found. McDermott [**13**] remarked that the false eyespots may be "an
91  extraordinary development of protective colouration."
92
93  As part of a study of structural coloration of insects in the Virginia Tech Insect Collection, we
94  found striking examples of iridescence, but while observing the eyespots of *A. oculatus* in the in
95  the collection and in the field in the Appalachian Mountains, we were struck by their profoundly
96  black appearance at all angles. By depositing a thin metal film on the eyespots to exclude
97  absorption by pigments, we tested if structural absorption provides the super black appearance.
98  We compared the microstructures inside the periphery of the eyespots versus elsewhere on the
99  exoskeleton of the beetle, and with the surface structural morphology of other instances of super
100  black in nature.
101
102
103  **Materials and methods**
104
105  We used material preserved in the Virginia Tech Insect Collection for this study (VTEC,
106  collection.ento.vt.edu). Three adult specimens of *A. oculatus* were selected for the analysis. The
107  individuals were pinned dried specimens collected from Fredericksburg, Virginia and College
108  Station, Texas (U.S.A.) with the following VTEC catalog numbers: VTEC000000784, 4961, and
109  4962. To visually examine gross morphology, the false eyespot of each specimen (right side) was

110 examined at 45° and 90° angles with a Leica M125 stereomicroscope illuminated by a LED fiber
111 optic light source. Setae composing the eyespot and the white ring encircling the eyespot (the
112 "eyeliner") were removed with a straight-edge razor and mounted in glycerin on a microscope
113 slide. Photographs of the setae were made with a Zeiss Axio Imager A2 microscope and
114 AxioCam ERc5s camera. The beetle specimen was photographed with a Canon EOS 6D digital
115 SLR camera illuminated with two Canon Speedlite 430EXII flashes diffused with a paper
116 cylinder.
117
118 To test the hypothesis that structural absorption contributes to the super black appearance,
119 eyespots were plasma coated with a thin layer of platinum (Pt) and palladium (Pd) metals to
120 control for absorption by pigments. From the middle of the right eyespot, including a piece of the
121 eyeliner and surrounding cuticle, a 4.25 X 2.3 mm$^2$ tile was removed with a straight-edge razor
122 and affixed on a 12.7 mm diameter aluminum scanning electron microscope (SEM) stub with
123 double-sided carbon tape. The stub was plasma coated under stable argon pressure with 20 nm of
124 Pt-Pd metals with a Leica EM ACE 600 high vacuum coater, and imaged on a FEI Quanta 600
125 FEG environmental SEM (5 kV, 3.5 spot size). A second round of 20-nm coating was carried out
126 to ensure that pigmentation was entirely concealed. The width, spacing, and density of setae on
127 the eyespots were calculated from the SEM images using the program ImageJ version 1.52k [20].
128
129 To measure reflectance, we used a spectrometer attached to a light source by a 400-µm diameter
130 fiber core reflectance probe with a 24.8° acceptance angle (Ocean Optics USB 4000
131 spectrometer, QR400-7-UV fiber, and DH-BAL 2000 deuterium-halogen light source). A disc of
132 PTFE was used as a reflectance standard to calibrate the measurements (Ocean Optics WS-1).
133 Reflectance measurements were made in a dark room with the probe oriented at a 45° and
134 normal incidence and at a detection distance of 3 mm. Units are in percent reflectance, and are
135 reflection factors, or empirical measurements of intensity normalized by the intensity of the
136 reflectance standard. Reflectance was measured between 300 – 700 nm, which encompasses the
137 visible range of most animals. The eyespot, eyeliner, and the exoskeleton were measured from
138 two individuals (VTEC000004961, 4962) three times. The R package pavo was used to analyze
139 and visualize the reflectance measurements [21]. To calculate overall percent reflectance
140 between 300 – 700 nm, area beneath the curve of the spectrum was summed with Riemann sums
141 and divided by the total area of 100% reflectance between 300 – 700 nm. Reflectance spectra
142 were averaged, standard error of the mean calculated, and plotted using the R package pavo.
143
144
145 **Results**
146

147 Based on visual examination
148 with the light microscope, *A.*
149 *oculatus* is generally black
150 with white irregularly-
151 shaped spots speckled across
152 the body. The beetle
153 possesses two large velvety
154 black spots on the pronotum
155 that are fringed in white
156 eyeliner (Fig. 1C – D). The
157 beetle is generally clothed
158 with V-shaped seta of
159 varying hue and texture, and
160 the irregularly-shaped spots,
161 white eyeliner, and false
162 eyespots are made up of this
163 seta. Outside of the false
164 eyespots, and generally
165 distributed across the cuticle
166 of the beetle, the setae are

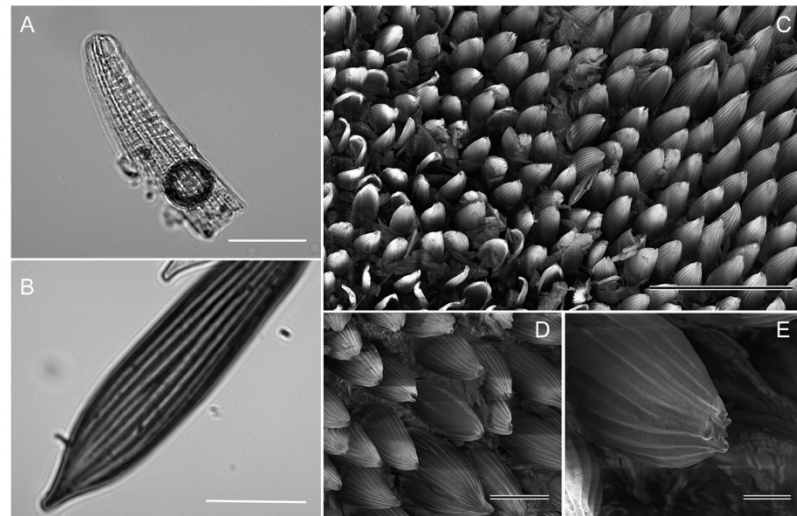



**Figure 2** Eyed elater click beetle, *Alaus oculatus*, setal morphology, (A) transmitted light photograph of eyeliner setae (scale bar = 30.0 μm), (B) transmitted light photograph of eyespot setae (scale bar = 40.0 μm), (C) scanning electron micrograph of the eyespot setae, magnified 326X—scale bar = 0.2 mm, (D) magnified 1247X—scale bar = 0.05 mm, (E) magnified 5033X—scale bar = 0.01 mm.

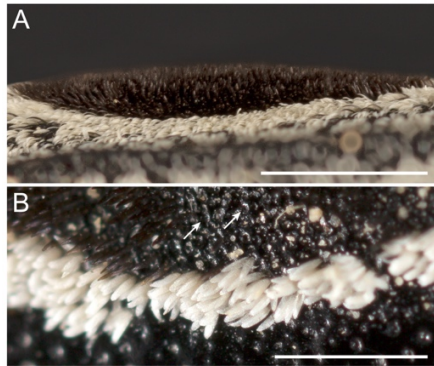
167 brick red and have a smooth surface. The cuticle outside of the eyespots is smooth and glossy
168 with lustrous specular reflection. The setae of the white eyeliner are translucent and lack pigment
169 (Fig. 2A). Eyeliner setae and those outside of the eyespots are decumbent. In contrast the setae
170 inside the periphery of the eyespots are erect, black with longitudinal grooves, and evenly spaced
171 (Figs 2B – E, 3A). The V-shaped setae in the eyespots are more canoe-shaped than the others,
172 with a flat slightly concave face opposite of the convex (hull) side (Fig. 2C, D). With the
173 grooves, these setae appear as caraway seeds cut in half longitudinally, striped with lines running
174 along its length (Fig. 2B – E). The cuticle underlying the eyespots is glossy and similar to the
175 cuticle outside of the eyespots; however, its surface is recessed and dimpled around setal sockets
176 (Fig. 3B). Some small pebbles and soil particles were trapped by the setae of the false eyespot.
177
178 When viewed at a 90° angle, even with the bright illumination of the microscope (illuminated at
179 ca. 45°), little surface structure was apparent and the eyespots appeared profoundly black,
180 appearing as voids in the body (Fig. 1C). When viewed at a 45° angle (and more acute angles),
181 surface structure was discernable and the setae appeared regularly spaced with the convex side
182 (hull) of the canoe-shaped hairs facing anteriorly (Fig. 3A). Along the periphery, the setae of the
183 eyespots are bent at a ca. 60° angle and gradually change in angle to 90° at the center of the
184 eyespot; in contrast, the setae at the posterior-facing margin remain upright and ca. 90° (Fig.
185 3A).
186

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**Figure 3** Eyed elater click beetle, *Alaus oculatus*, false eyespots, (A) lateral view (scale bar = 1.0 mm); (B) right dorsal view, dimples denoted by arrows (scale bar = 0.5 mm) [left side of A and B is anterior]

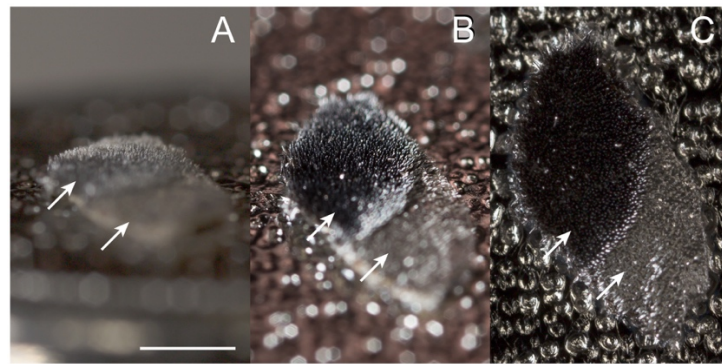
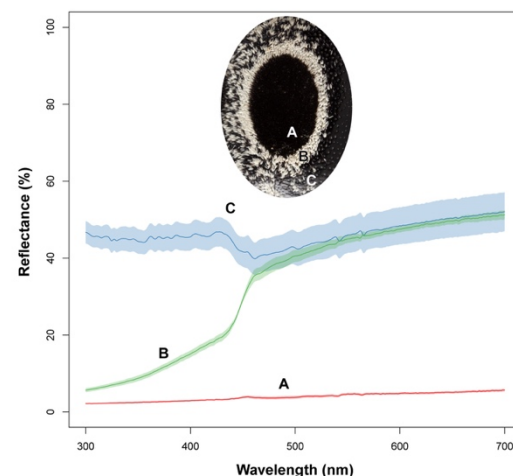



**Figure 4** Eyed elater click beetle, *Alaus oculatus*, false eyespot (top arrows) and eyeliner (bottom arrows) coated with a 40-nm layer of platinum and palladium, (A) 30° view, (B) 45° view, (C) 90° view.

188
189    As a result of plasma coating, the SEM stub possessed a
190  lustrous metallic surface, however the eyespot retained a deep black appearance at normal
191  incidence (Fig. 4, Supplemental Movie). Based on examination of the eyespots with the SEM
192  (between 326 – 5,033X magnification), the V-shaped seta are lined with about 14 longitudinal
193  ridges (mean = 13.97, standard deviation = 1.92, n
194  = 30) with a smooth somewhat concave opposing
195  surface (Fig. 2B – E). The apices of the setae are
196  dividing into two or occasionally three shallow
197  furcations (Fig. 2E). Setae are about 38.33 µm in
198  width (mean, standard deviation = 2.15, n = 30)
199  and spaced about 10.30 µm edge-to-edge from one
200  another (mean, standard deviation = 2.67, n = 30).
201  Within in a 726.68 µm² area of the eyespot there
202  are 250 setae, and 1,756 setae within the eyespot
203  area in total.
204
205  From the measurement of reflectance, the white
206  eyeliner, the glossy exoskeleton and the black
207  eyespot possessed spectra of different shapes (Fig.
208  5). The black eyespot spectrum was a flat profile,
209  indicating a general lack of reflectance across a
210  broad range of wavelengths. The white eyeliner

**Figure 5** Reflectance spectra of the Eyed elater eyespot, (A) red line = eyespot, (B) green = white eyeliner, (C) blue = glossy cuticle

211  spectrum had a plateau shape, lacked near-ultraviolet reflectance, and with uniformly high
212  reflectance between 400 – 700 nm. The glossy exoskeleton spectrum was generally flat in profile
213  but with consistently high overall reflectance (including ultraviolet) indicating a high glare from
214  the lustrous cuticular surface. The overall reflectance of the black eyespot patch was 3.90%, the
215  white eyeliner was 32.92%, and glossy exoskeleton was 46.14%. The overall reflectance of the
216  black eyespot measured at a 45° specular orientation was three-fold less: 1.26%.
217
218
219  **Discussion**

220
221   We found that structural absorption gives a super black appearance to the eyespots of *A.*
222 *oculatus*. By depositing a thin metal film on the eyespots to conceal light absorption by
223 pigments, we demonstrated that pigmentation alone is not responsible for their deep black form.
224 Based on our examination of the black eyespots, we found that their surface morphology was
225 equivalent in shape, orientation, and general photonic properties of other super black structures
226 in nature. In particular, the eyespot composed an array of perpendicularly aligned linear
227 protuberances that absorb 96.1% of light and is analogous to the three-dimensional array of
228 microtubules on butterfly wings [6] and the ramified barbules on Bird of paradise feathers and
229 Jumping spiders [7, 8]. Other examples of structural super black in nature with similar
230 perpendicularly aligned protuberances include the nipple array of moth eyes [11], cuticular
231 papillae of stick insects [10], and leaf-like microstructures on viper and Peacock spider scales [8,
232 9]. These surface structures scatter light, causing structural absorption and leaving little light
233 available to reach the viewer's eye. While human-fabricated super black materials typically
234 absorb more than 95.5% of light, in nature, Bird of paradise feathers come close to this with
235 incident reflectance of about 0.5%. Butterflies and moths, snakes, stick insects, and click beetles
236 with super black patches reflect more (incident) light with between about 3 – 11%.
237
238 Melanin is a ubiquitous black pigment of insect exoskeletons, and is an expected component of
239 the setae of the Eyed elater's eyespots. Melanin, or another pigment, contributes to the super
240 black form of the eyespots by absorbing light in concert with structural absorption. The pigment
241 directly absorbs light and perhaps also recaptures light that strays from structural absorption. We
242 showed that the eyespot setae sit in a concavity (Fig. 3B), and the cuticle underlying the eyespots
243 has a dimpled topography. These concavities are smooth and have a black pigmentation. Other
244 arthropods possess similarly shaped concavities that scatter light and impart additive mixing (of
245 blue and yellow iridescence such as in the Emerald swallowtail [22]), or augment melanin
246 absorption thereby decreasing reflectance and producing super black (as in Peacock spiders [8]).
247 These lens like concavities of the Eyed elater's eyespots and the 14 longitudinal ribs on the setae
248 could be features that assist a super black. Additionally, scattering of light may be directional
249 (*e.g.* backwards) given the shape and orientation of the setae on the eyespots. Optical modeling
250 integrating these features would be fruitful to understand how this ensemble of features work in
251 concert to affect light.
252
253 The function of super black eyespots in the Eyed elater may be for predator deterrence including
254 aposematism, deimatism, or as a false head. A role as a false head is unlikely since the eyespots
255 are in close proximity to the real head and not posteriorly located as in other insects (*e.g.*
256 hairstreak butterflies). Since there are large dorsal intersegmental muscles directly beneath the
257 eyespots [23], thermoregulation or muscle-heating is another functional hypothesis. While the
258 startle function is the most likely, click beetles have a powerful clicking mechanism that is
259 noxious to birds [23, 24] and disentangling aposematic versus startle function would ideally be
260 tested using field experiments.
261
262 The study of super black structures in nature have uncovered a diversity of morphologies that
263 cause near complete absorption of light. Some of these structures collimate light for subsequent
264 excitation of photopigments of compound eyes (*e.g.* crepuscular moths, ref. 11) and others act as
265 a general baffle of light where light is scattered (*e.g.* crypsis in snakes, ref. 9). Since super black

266  materials have application for human industry (*e.g.* solar cells, anti-reflective coatings, etc.) the
267  structural morphology of these various materials in nature are an ideal domain as creativeness for
268  fabricating structures and as a means to understand the evolution of adaptive coloration and
269  natural selection.
270
271
272  **Acknowledgements**
273
274  Thanks to Drs. Ellen Brown and Barry Lee Bressler for support of the Virginia Tech Insect
275  Collection and a donation of beetle specimens, including the two Eyed elaters used in this study.
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278  Fabrication Laboratory at the Virginia Tech Institute for Critical Technology and Applied
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280  manuscript, and anonymous reviewers for suggestions and improvements.
281
282  **Data accessibility**
283
284  R script, uncompressed image files, and TXT text file spectral data are available to download
285  from VTechData [**25**], https://data.lib.vt.edu/collections/rf55z781b
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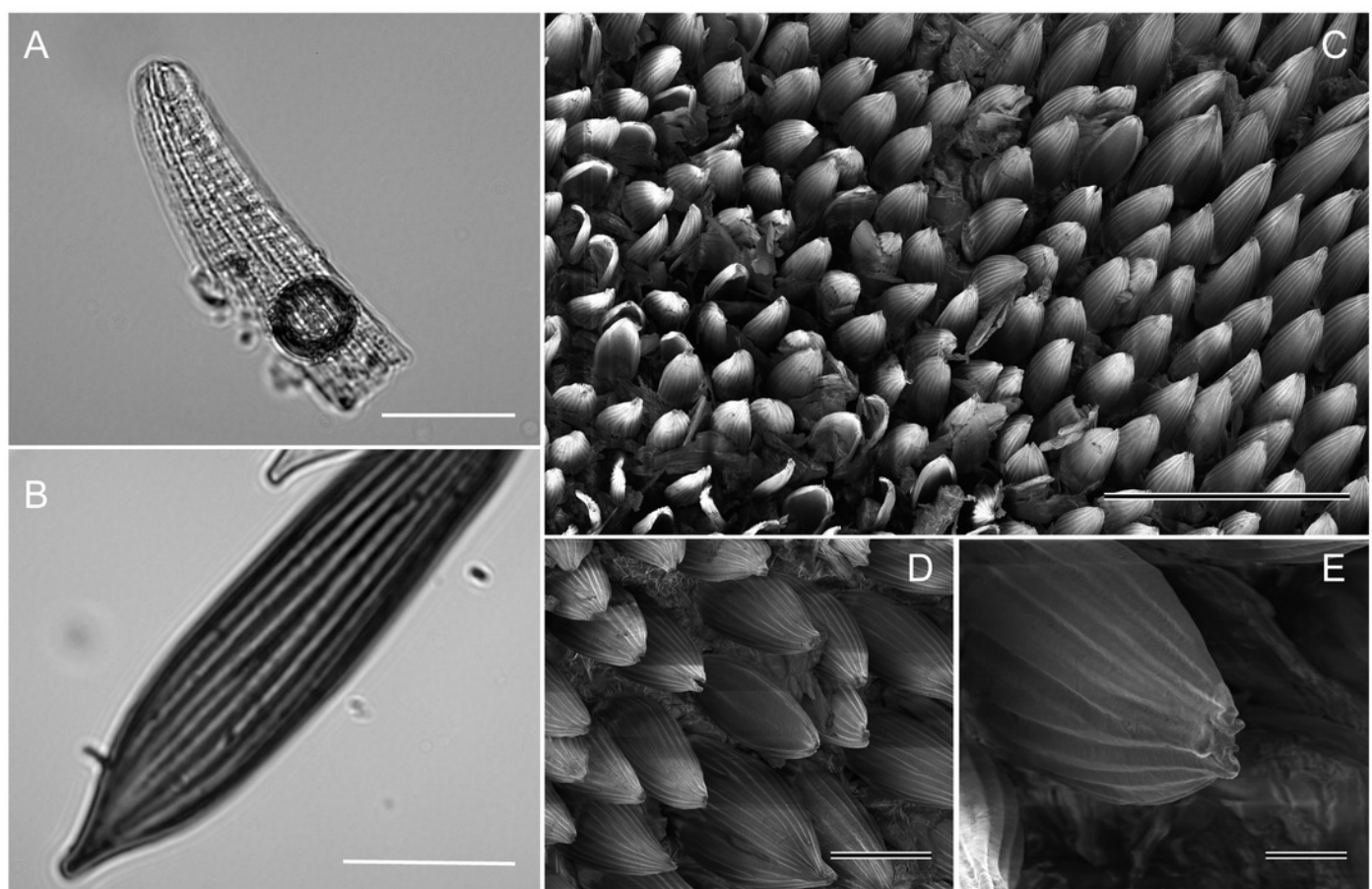
# Figure 1

Eyed elater click beetle, *Alaus oculatus*, dorsal habitus and false eyespots

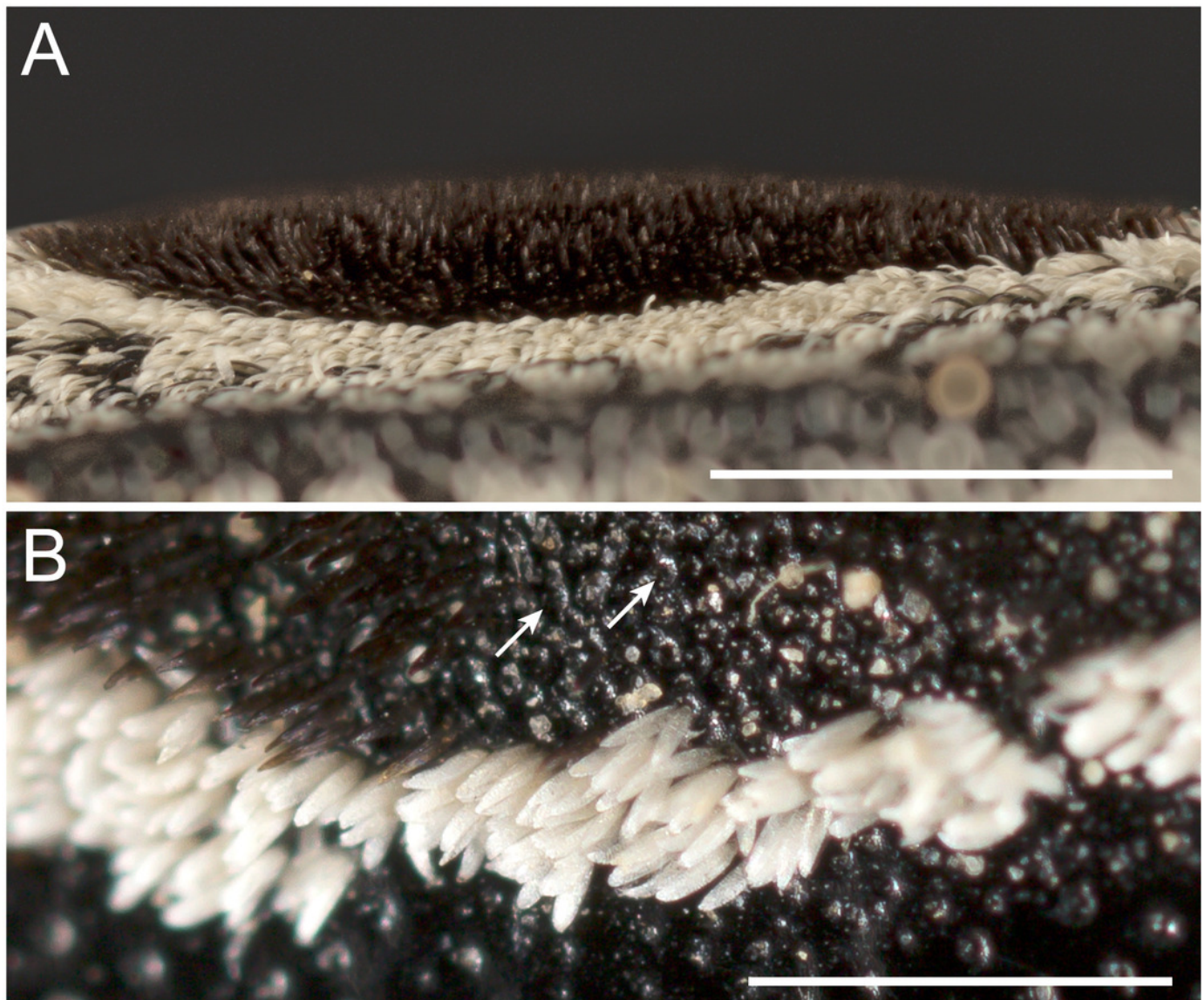
**Figure 1** Eyed elater click beetle, *Alaus oculatus*, (A) dorsal habitus view, (B) right lateral view (scale bar = 2.0 mm); Eyed elater false eyespots, (C) left dorsal view, (D) right oblique view (scale bar = 0.5 mm)

# Figure 2

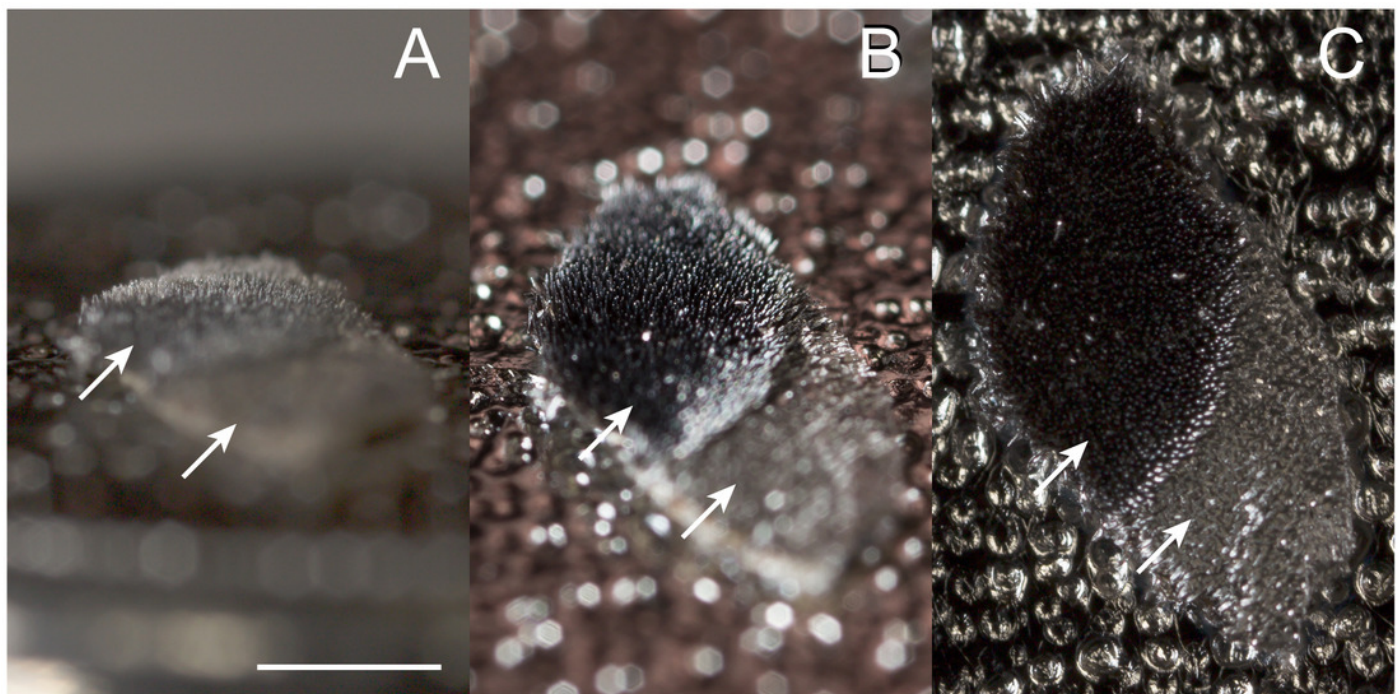
Eyed elater click beetle, *Alaus oculatus*, setal morphology of false eyespot and eyeliner, photographed with transmitted light.

**Figure 2** Eyed elater click beetle, *Alaus oculatus*, setal morphology, (A) transmitted light photograph of eyeliner setae (scale bar = 30.0 μm), (B) transmitted light photograph of eyespot setae (scale bar = 40.0 μm), (C) scanning electron micrograph of the eyespot setae, magnified 326X—scale bar = 0.2 mm, (D) magnified 1247X—scale bar = 0.05 mm, (E) magnified 5033X—scale bar = 0.01 mm.

# Figure 3

Eyed elater click beetle, *Alaus oculatus*, false eyespots, lateral view and exoskeletal dimples of eyespot setae

**Figure 3** Eyed elater click beetle, *Alaus oculatus*, false eyespots, (A) lateral view (scale bar = 1.0 mm); (B) right dorsal view, dimples denoted by arrows (scale bar = 0.5 mm) [left side of A and B is anterior]

# Figure 4

Eyed elater click beetle false eyespot and eyeliner coated with a 40-nm layer of platinum and palladium

**Figure 4** Eyed elater click beetle, *Alaus oculatus*, false eyespot (top arrows) and eyeliner (bottom arrows) coated with a 40-nm layer of platinum and palladium, (A) 30° view, (B) 45° view, (C) 90° view.

# Figure 5

Reflectance spectra of the Eyed elater eyespot, white eyeliner, and glossy cuticle.

**Figure 5** Reflectance spectra of the Eyed elater eyespot, (A) red line = eyespot, (B) green = white eyeliner, (C) blue = glossy cuticle