

An anocellar polistine wasp (Hymenoptera, Vespidae, Polistinae) from Texas

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Abstract

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A remarkable teratological female of *Polistes (Fuscopolistes) dorsalis neotropicus* Bequaert, 1940 (Vespidae: Polistinae) is described and illustrated. The specimen lacks all three external dorsal ocelli but is normally developed in almost every other aspect. Additionally, similar findings in other Hymenoptera are briefly discussed, as are the consequences and the reasons that might cause the random loss of ocelli.

Key Words

teratology

aberration

malformation

morphology

Polistes dorsalis

social wasp

paper wasp

Introduction

In contrast to the multi-lensed compound eyes, the dorsal ocelli of insects are simple lens eyes forming the second visual system. Externally they consist of a single, usually round or oval aperture lens while internally hundreds of photoreceptors converge into a small suite of neurons targeted to neuropils (Berry et al. 2007, and citations therein). Many hypotheses have been proposed regarding the function of the ocelli, some of which suggest these simple eyes may play a direct or indirect role in a wide range of physiological processes, such as light response, flight stabilization, circadian rhythm, foraging, orientation, and navigation (e.g., Taylor 1981a, 1981b, Rence et

al. 1988, Schuppe and Hengstenberg 1993, Warrant 2006, Warrant et al. 2006, Schwarz et al. 2011a, 2011b, Viollet and Zeil 2013). Despite their obvious importance, ocelli have been reduced in number, size, and form in many groups of insects, e.g., Lepidoptera (if present, no more than two ocelli: Kristensen 2003), Coleoptera (most species lack ocelli, but if present, then never more than two: Gillott 2005), and Miridae (Hemiptera) (except for the basal Isometopinae, all members lack ocelli outright: Ferreira et al. 2015). Indeed, the loss of ocelli has occurred numerous times in various insect lineages, and in some there have been apparent secondary re-acquisitions of ocelli-like, photosensitive areas or lenses, but for which direct homology to true ocelli has not been conclusively

established (e.g., when present, the ‘ocelli’ or ‘ocelloids’ of worker termites: Engel et al. 2009).

As in most other insects, Hymenoptera usually have three slightly oval, convexly rounded dorsal ocelli: one median (anterior) and two lateral (posterior) (Huber and Sharkey 1993). But this general pattern has been modified multiple times within the order. For example, the number of ocelli has been reduced in several groups within Formicidae (most workers) or females of different mutillid subfamilies (Brothers 1975), while the ocelli have been morphologically modified in others, such as the hemispherical or gibbous forms of some Larrinae and Bembicini (apoid wasps) (Bohart and Menke 1976) or the greatly enlarged forms found in many nocturnal genera of bees and wasps e.g., *Megalopta* or *Apoica* (e.g., Kerfoot 1967, Warrant et al. 2006).

As with many anatomical structures, there are at times developmental aberrations or malformations that impact the ocellar system (e.g., Alfonsus 1931, Ohtani 1977). With respect to the dorsal ocelli there are a number of different malformations reported in the literature, e.g., supernumerary anterior or posterior ocelli (e.g., Tussac and Balazuc 1991, Engel et al. 2014, Lohrmann and Engel 2015); the duplication of a complete ocellar triangle (Tussac and Balazuc 1991); the reduction of one, two, or all three ocelli (e.g., Tussac and Balazuc 1991); or underdevelopment and misplacement of ocelli (e.g., Hopwood 2007, Gibbs 2010). Any of these developmental anomalies must certainly have dramatic consequences on the visual system of the individuals involved, and thereby on other aspects of the functional biology of the organism (e.g., impacts on flight, orientation, light sensitivity). Unfortunately, the study of such aberrations has been scarcely systematic and experimental manipulation of or functional investigation into these are virtually absent aside from earlier work in Orthoptera and Hymenoptera (e.g., Schremmer 1950, Schricker 1965, Taylor 1981a, 1981b, Schwarz et al. 2011a). Nonetheless, the documentation of these aberrant morphologies when they occur in sampled individuals that were seemingly undergoing typical lives is of interest and potential future value for understanding the use of ocelli and impacts of their loss or alteration.

In this context it is interesting to note that while recently discussing a malformed quadriocellar scoliid wasp (Lohrmann and Engel 2015), GCW mentioned the discovery of an anocellar female of a eusocial paper wasp (Vespidae: Polistinae: Polistini), which is described, illustrated, and discussed here.

Materials and methods

Measurements were taken using a Zeiss SteREO Discovery.V20 combined with an ocular micrometer. The photographs were captured with a Nikon D800 digital camera with a Nikon AF-S Micro-NIKKOR 60 mm 1:2.8G ED lens in combination with the software programs Helicon Remote, Adobe Lightroom und Helicon Focus Pro. The

illustrations have been cleaned with Adobe Photoshop. The specimen, which is deposited in the entomological collection of the Übersee-Museum Bremen (UMB), was collected and identified by GCW and the identification was confirmed by Matthias Buck (Edmonton).

Systematics

Polistes (Fuscopolistes) dorsalis neotropicus Bequaert, 1940

‘Anocellar Deformity’

Figs 1–4

Material. ♀; USA, TX, Randall Co., Palo Duro Canyon, (34°56’37” N, 101°39’39” W), 21.viii.2008, F. Cliff Camp, G.C. Waldren (UMB).

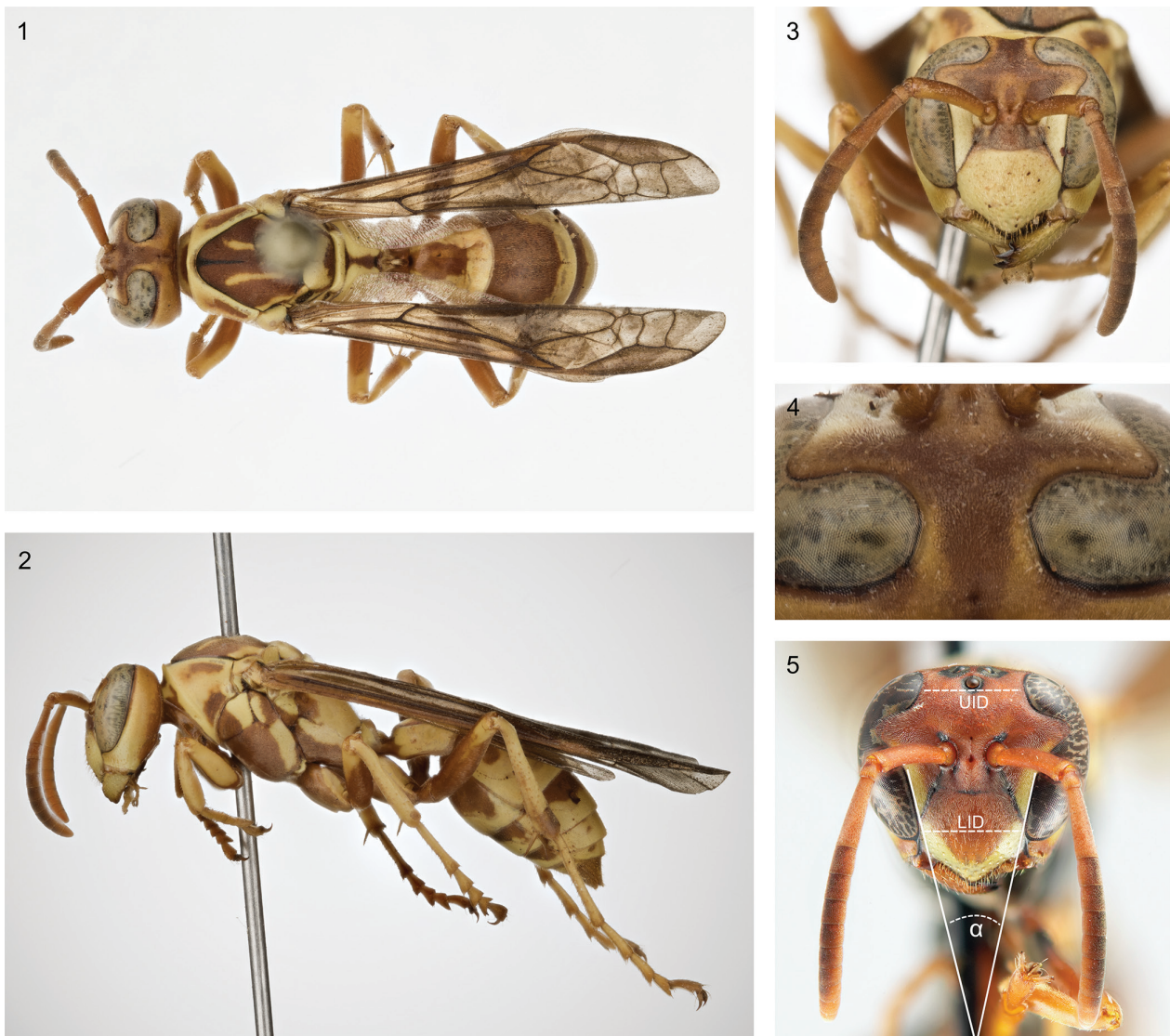
Measurements. Total body length: 14.0 mm; head width: 3.2 mm; forewing length: 11.5 mm; hind wing length: 8.7 mm; mesoscutal width: 2.4 mm.

Descriptive notes. The female specimen, which seems to be normal in almost every other respect, shows a remarkably deformed head (Figs 3, 4). Most notably it completely lacks all three external dorsal ocelli. Additionally, the vertex shows a longitudinal median impression, giving the head a heart-like shape when seen from the front. The deepest point of the ocular sinus is shifted upwards and the upper end of the compound eye is slightly elongate mesally. As a result, the upper interorbital distance is much shorter than in normally developed specimens (UID : LID = 0.43 vs. 0.94; compare Figs 3 and 5). Finally, the lower inner orbits are rather moderately converging ventrally ($\alpha = 11^\circ$ vs. 25°), and the median keeled groove on the frons is lacking. However, this specimen is perfectly bilaterally symmetrical and shows no other malformations, nor any traces of stylopisation or other parasitic infestation.

Comments. *Polistes dorsalis* (Fabricius, 1775) is currently classified into five subspecies and occurs throughout the southern half of the US to Costa Rica (Buck et al. 2008). Similar specimens from the South Central US, the great majority of which without or with less well-defined mesoscutal stripes, are usually assigned to *P. dorsalis neotropicus* Bequaert, 1940 – a subspecies first described from Honduras. The present specimen belongs to this subspecies as it is currently circumscribed, although it remains to be determined by future work whether *P. d. neotropicus* should be further restricted, perhaps excluding Nearctic occurrences (Matthias Buck pers. comm.).

Discussion

There are a number of similar findings of malformed Hymenoptera reported in the literature, among bees in par-



Figures 1–6. *Polistes (Fuscopolistes) dorsalis neotropicus* Bequaert, 1940. **1–4.** Anocellar female from Texas. **1.** Habitus in dorsal view. **2.** Habitus in lateral view. **3.** Head in anterior view. **4.** Ocellar area in dorsal view. **5.** Normal female from South Carolina; head in anterior view. Abbreviations: **LID** = Lower interorbital distance; **UID** = Upper interorbital distance. Photos: **1–4.** Matthias Haase. **5.** Used with permission from Buck et al. (2008), Illustration C75.4.

ticular. The most similar aberration has been reported by Tussac and Balazuc (1991, p. 51) who describe and figure a female specimen of *Epyris niger* Westwood, 1832 (Bethyridae) that lacks the dorsal ocelli and which has the dorsal aspects of the compound eyes more closely together but not fused. Like this specimen, most anocellar specimens show additional malformations of the head and it seems that the loss of ocelli often occurs in cyclopic (holoptic) individuals or “half-way” cyclops (specimens with completely or nearly fused compound eyes) (e.g., Alfonsus 1931, Miller 1936, Haydak 1948, Ohtani 1977). However, the absence of “external ocelli” does not necessarily mean that the ocelli are completely lost. Miller (1936) observed that the ocelli of cyclopic bees were well developed except for the external lenses, but are misplaced and concealed by a prominent lobe above the bases of the antennae. Thus, the individual of

Polistes reported herein may still have a well-developed set of ‘internal ocelli’, and almost assuredly retains the complete neural architecture for ocelli, despite the lack of externally functional components. However, since the specimen was dry-mounted the impact of dried preservation (e.g., desiccation and shrinking of tissues, etc.) does not allow a closer examination of the innervation through micro computed tomography (micro CT) or histological methods like semi-thin sections.

Whether ‘internal’ ocelli retain some minimal light-detecting function remains unclear. Indeed, the overall impact of such developmental malformations are challenging to predict given that the function of ocelli seem to differ between walking and flying insects (Schwarz et al. 2011a), made worse by the lack of a comprehensive understanding of ocellar function (Berry et al. 2007, Krapp 2009). It has been shown for

other social Hymenoptera that individuals with experimentally blinded ocelli might carry on relative normal lives. Most recently, Schwarz et al. (2011a) demonstrated that the red honey ant (*Melophorus bagoti* Lubbock, 1883) with blinded ocelli could readily orient towards the nest, and despite simultaneously showing that the ocelli contribute to the encoding of the celestial compass used in orientation. Similarly, it has been shown that blinding of one, two, or all three ocelli of honey bee workers (*Apis mellifera* Linnaeus, 1758) resulted in a narrower foraging period rather than in a termination of foraging behavior (Schricker 1965; but see Renner and Heinzler (1979) for a counter argument), whereas Schremmer (1950) reported that bumble bees (*Bombus lucorum* (Linnaeus, 1761) and *B. hortorum* (Linnaeus, 1761)) with blinded ocelli rarely flew spontaneously. Thus, the impact of blinding the ocelli seems to have diverse, at times seemingly contrary, impacts on the behavior of the individuals involved, with no consistent pattern of diminished function. The *Polistes* reported herein did not show any kind of unnatural behavior before or while getting caught, nor does it seem that it had to deal with dramatically negative consequences caused by the loss of the ocelli.

Brachyptery or aptery is often associated with the reduction or loss of ocelli (e.g., Brothers 1975) — but what may cause the random loss of ocelli in exceptionally good flying insects, such as most Hymenoptera? Experimental studies with *Drosophila* have shown that mutations in the “eyes absent” (*eya*) gene (Bonini et al. 1998), mutations that reduce or abolish “orthodenticle” (*otd*) gene expression in the vertex primordium (Yorimitsu et al. 2011), elimination of the “hedgehog” (*Hh*) function during the third instar development (Amin et al. 1999), and clones of the “shaggy” (*sgg*) gene elsewhere in the head other than the eye field (Heslip et al. 1997), result in the loss of ocelli. Furthermore, flies homozygous for one of the “*Drosophila sine oculis*” (*so*) alleles *so*¹, *so*², or *so*⁵ also result in the loss ocelli (Kawakami et al. 2000). However, since all of these experiments have been conducted only with flies it remains unclear the degree to which this can be translated to Hymenoptera and as potential mechanistic explanations for the malformation reported herein.

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