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A quadriocellar scoliid wasp (Hymenoptera, Scoliidae) from Mallorca, with a brief account of supernumerary ocelli in insects

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Abstract

A remarkable teratological female of *Megascolia* (*Regiscolia*) *maculata flavifrons* (Fabricius, 1775) (Scoliidae: Scoliinae: Scoliini) with a supernumerary median ocellus is described and illustrated. While supernumerary ocelli have been reported before from Diptera, Orthoptera, and Hymenoptera, this is the first record of such a malformation from a scoliid wasp. Four other teratological scoliid wasps have been reported in the literature but all were gynandromorphs. A brief summary of known records of supernumerary ocelli among insects is provided.

Key Words

Median ocellus
twin ocellus
binary anterior ocelli
para-median ocelli
teratology
aberration
malformation
morphology

Introduction

According to Nichols (1989) teratology is the "study of structural abnormalities, especially monstrosities and malformations." Most accounts of teratology in the literature derive from experimental manipulation of the developmental process, while naturally occurring malformations are less frequently reported. In the past, many of these malformations were often neglected or mentioned merely as footnotes. This is perhaps not surprising as most authors surely must have thought that no significant conclusions could be drawn from isolated aberrant individuals. Indeed, it is challenging to infer much from isolated cases (e.g., Glasgow 1925), but when teratologies are made known and eventually summed up with others, there exists a great potential for patterns to emerge and broader conclusions to be drawn. The description of individual cases serves to build up a larger data set from which explanatory hypotheses can be formulated, highlighting the great value of descriptive science (e.g., Grimaldi and Engel 2007). A great example is the occurrence of gynandromorphs among aculeates, where the gradual accumulation of often-isolated, published accounts over the last 125 years has amassed into a body of data sufficient for the exploration of generalized patterns (e.g., Wcislo et al. 2004, Michez et al. 2009, Hinojosa-Díaz et al. 2012), and has aided attempts to homologize traits across sexes (e.g., Michener 1944, Engel 2007). It is therefore worthwhile to contribute to the accumulation of data on teratologies in the hopes that someday sufficient numbers will exist to permit more critical study.

There exists a relative abundance of reports concerning insects with partially fused antennomeres (e.g., Asiain and Márquez 2009, Popovici et al. 2014), or gynandromorphs (e.g., Hinojosa-Díaz et al. 2012), particularly as these relate to understanding more standard morphologies, such as whether a reduction in total antennomere count results from fusion or loss. Less often are other structural anomalies reported, such as supernumerary appendages or organs like legs (e.g., Cockayne 1937), antennae (e.g., Cockayne 1938), ocelli (e.g., Engel et al. 2014), or even compound eyes (e.g., Banerjee and Kevan 1959).

The first major review of teratologies among Hymenoptera was by Dalla Torre and Friese (1899) who focused their attention on gynandromorphs. Balazuc (1958), however, was the first to provide a comprehensive account of teratological Hymenoptera, including all kinds of malformations. Among the aculeate Hymenoptera, malformed specimens are exceptionally well reported for bees (Anthophila), with gynandromorphs alone reported for more than 110 species in 29 genera (Hinojosa-Díaz et al. 2012). With respect to Scoliidae, however, the number of peculiar malformed specimens reported in the literature is limited to four records of gynandromorphs (De Romand 1835, Krombein 1949, Wolf 1989, Osten 1993). In the course of sorting several boxes of unidentified scoliid wasps VL recognized a female of *Megascolia* (*Regiscolia*) *maculata flavifrons* (Fabricius 1775) with four ocelli (Figs 1, 2). The aim of the present contribution is to describe and illustrate this specimen and to provide a short account on supernumerary ocelli in pterygote insects.

Materials and methods

Measurements were taken using a Keyence VHX 5000 Digital Microscope. The morphological terminology for the description of the specimen is adopted from Betrem (1971). 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 identification of the specimen, which is deposited in the entomological collection of the Übersee-Museum Bremen (UMB), is based on the key provided by Osten (2000).

Systematics

Megascolia (*Regiscolia*) *maculata flavifrons* (Fabricius, 1775)

'Quadriocellar Deformity'
Figs 1–4

Material. ♀; E [Spain], Mallorca, Finca bei Polença, 09. 06. 2010, leg. D. Pawelek (UMB).

Measurements. Total body length: 38.0 mm; head width: 7.0 mm; forewing length: 32.5 mm; hind wing length: 16.0 mm; mesoscutal width: 5.8 mm.

Descriptive notes. The female specimen, which seems to be normal in every other respect, has four ocelli instead of the three which is the common state in the family and generally so across Aculeata. In this specimen the posterior ocelli are normal in position, form, and size whereas the anterior ocellus is represented by two, perfectly-formed ocelli that are disposed symmetrically, one on each side of the fissura frontalis by which they are separated (Figs 3, 4). The two aberrant anterior ocelli, which are located together in a single ocellar depression, are of the same size (maximum diameter) as the posterior ocelli whereas the anterior ocellus is about 1.1 times larger than the posterior ocelli in normal individuals (Figs 5, 6). This specimen shows no other malformations nor any traces of stylopisation.

Comments. This particular subspecies is represented in the collection of the UMB by an additional 10 males and 17 females from Italy (Liguria, South Tyrol, Apulia, and Sardinia), Spain (Catalonia and Ibiza), and France (Corsica). None of them has been collected at the same locality as the above female, nor does any show a similar malformation. Scoliids are moderately diverse, with approximately 560 species in 143 genera (Aguiar et al. 2013), and are often robust and large insects such that if teratologies are discovered they should be readily spotted.

Discussion

Among the recorded wild forms of pterygote insects with supernumerary ocelli, two different kinds of teratology are known – those resulting from duplication of the anterior ocellus, such as reported here, or of the lateral ocelli (Table 1). Whereas most records report a supernumerary anterior ocellus, Engel et al. (2014) reported an augochlorine bee with five ocelli – a single median ocellus and two sets of posterior paired ocelli. The only other account of malformed posterior ocelli is that of Ashmead (1880) who described a new species of the aphelinid genus *Aphytis* Howard with the type specimens having "three ocelli triangularly arranged, with two smaller red ones back of these". However, according to Rosen and DeBach (1979), "Ashmead apparently mistook the pigment spots, commonly seen in dry or slide-mounted specimens of small Chalcidoidea, for supernumerary ocelli." While their assessment is likely accurate, it remains unclear whether Ashmead might have found a true malformation given that his type material for the species in question has been lost (Rosen and DeBach 1979; and sources cited therein). These two records aside, all other accounts pertain to modifications of the anterior ocellus and result either from an apparent division of the structure or for its reappearance.

Figures 1–6. *Megascolia* (*Regiscolia*) *maculata flavifrons* (Fabricius). **1–4.** Quadriocellar female from Mallorca. **1.** Habitus in lateral view. **2.** Habitus in dorsal view. **3.** Head in dorsal view. **4.** Ocellar area. **5–6.** Normal female from Ibiza. **5.** Head in dorsal view. **6.** Ocellar area. Photos: Matthias Haase.

Supernumerary ocelli have been reported from Diptera, Orthoptera, and Hymenoptera (Table 1), but since these particular deformations are not as abundant as gynandromorphs a proper name has never been established for them. Thus they appear under quite different 'labels' in the literature. It was perhaps the naturalist explorer Henry Walter Bates (1825–1892) who first recorded an observation of supernumerary ocelli, which he dubbed a "twin ocellus" (Bates 1863; the same term was used later by Brent 1886). Other authors described this unusu-

Table 1. List of recorded aberrant insect specimens with supernumerary ocelli from nature. Records are for each kind of aberration within a sex for a given species or subspecies. Thus, records of multiple or additional individuals with an identical teratology for a given sex and species are combined (citations for the individual accounts provided), while different teratologies for a species are listed individually. The numbering system for ocellar counts is formatted as: total # of ocelli (# of anterior ocelli + # of lateral ocelli) typical # of ocelli. All formicid records were for the worker caste (note that for some of the myrmecines listed the worker may have a normally reduced number of ocelli when compared with the gyne and so the total number listed is for the caste reported, and even major and minor workers may differ in their total number of ocelli). Generic and specific names have been updated to their current classification.

Order	Family	Species/subspecies	# of ocelli	Sex	References
Hymenoptera	Aphelinidae	*Aphytis flavus* (Ashmead) ‡	5 (1+2/2) 3	♀	Ashmead 1880
	Formicidae	*Acromyrmex coronatus* (Fab.)	2 (2+0) 0	♀	Weber 1947
		Atta cephalotes (L.) §	2 (2+0) 3	♀	Bates 1863, Wheeler 1936, Weber 1947
			3 (2+1) 3	♀	Wheeler 1936
			4 (2+2) 3	♀	Wheeler 1936, Weber 1947
		Atta laevigata (Smith)	4 (2+2) 3	♀	Weber 1947
		Atta sp.	2 (2+0) ?	♀	Brent 1886
		Cephalotes atratus (L.)	4 (2+2) 3	♀	Wheeler 1936
		Carebara diversus laotinus (Santschi)	2 (2+0) 1	♀	Wheeler 1936
	Halictidae	*Caenaugochlora inermis* (Vachal) |	5 (1+2/2) 3	♀	Engel et al. 2014
	Scoliidae	*Megascolia maculata flavifrons* (Fab.)	4 (2+2) 3	♀	Herein
	Tenthredinidae	*Tenthredo semirubra* (Norton)	4 (2+2) 3	♂	Smulyan 1923
		Hemichroa crocea (Geoffrey)	4 (2+2) 3	♀	Moller 1975
Orthoptera	Acrididae	*Melanoplus differentialis* (Thomas)	4 (2+2) 3	–	Glasgow 1925
		Melanoplus d. differentialis (Thomas)	4 (2+2) 3	♂	Slifer 1960
		Melanoplus d. nigricans Cockerell	4 (2+2) 3	♀/♂	King and Slifer 1965
		Melanoplus femurrubrum (DeGeer)	4 (2+2) 3	–	Blackman 1912
Diptera	Calliphoridae	*Calliphora grahami* Aldrich	4 (2+2) 3	♂	Hori et al. 1967
	Drosophilidae †	*Drosophila melanogaster* Meigen	4 (2+2) 3	–	Waddington et al. 1942, Baker et al. 1985

† The records of supernumerary ocelli in specimens of *Drosophila* Fallén are based on laboratory manipulations and not wild forms. Thus, we made no attempts for an exhaustive literature search for this genus and only report a couple here as examples.

‡ As discussed in the text, the supernumerary ocelli described by Ashmead (1880) are likely misinterpreted pigment spots (Rosen and DeBach 1979).

§ Weber (1947, footnote) discussed the taxonomic affinities of the specimens reported in Bates (1863). The following subspecies of *Atta* reported by Wheeler (1936) and Weber (1947), *Atta cephalotes integrior*, *A. c. isthmicola*, and *A. c. opaca*, are synonyms of *Atta cephalotes* (Borgmeier 1959). However, the subspecies "*Atta cephalotes gorgo*" (in Wheeler 1936), seems to be unavailable as the paper Wheeler alludes to for its formal description never appeared and the name was not treated by Borgmeier (1959) (Wheeler died in 1937 of a sudden heart attack and likely never had the opportunity to complete his work).

| This is the only validated record of a wild form where the lateral ocelli are affected, in all other listed records it is the median ocellus.

al development as either "supernumerary median ocelli" (Blackman 1912), "four [dorsal] ocelli" (Smulyan 1923, Glasgow 1925, Hori et al. 1967), "para-median ocelli" (Glasgow 1925), "binary anterior ocelli" (Wheeler 1936, Weber 1947), "two median ocelli" (Blackman 1912, Slifer 1960, King and Slifer 1965, Hori et al. 1967), or "abnormal median ocelli" (King and Slifer 1965). The term 'supernumerary ocelli' seems appropriate for the general class of teratologies involving the duplication of ocelli, with individual malformations dubbed by the number involved (e.g., quadriocellar, quintocellar). Once a more sizeable number of these deformations are documented a more systematic classification can be established.

A casual perusal of the list of occurrences of supernumerary ocelli (Table 1) would give the impression that some groups are more prone than others toward developing such teratologies. All records of ants with supernumerary ocelli are from the subfamily Myrmicinae, and particularly the leaf-cutting ants (Attini), whereas all recorded Orthoptera are from a single genus (*Melanoplus* Stål). While on the surface this is interesting, it perhaps reflects more the interest of those working on such groups. For example, species of *Melanoplus* are some of the most intensely studied of agricultural pests, and Weber was particularly interested in attines during the course of his myrmecological career, perhaps accounting for the fact that all of his records stem from that one tribe (Weber 1947). Indeed, even Wheeler's records stemmed largely from taxonomic work he was undertaking on the genus *Atta* Fabricius (Wheeler 1936, p. 188). Until more extensive studies into the occurrence of such teratologies are completed, it is impossible to say whether particular clades are more susceptible or not. In order to get an idea of the relative abundance of such malformed specimens we contacted several colleagues and asked for similar observations in their respective groups of Hymenoptera: Stephan Blank, Symphyta; Andrew Polaszek, Platygastroidea and Chalcidoidea; Heinrich Wolf, general Aculeata; Celso O. Azevedo, Bethylidae; Denis J. Brothers, Mutillidae, Bradynobaenidae, Plumariidae, and Scolebythidae; James M. Carpenter, Vespidae; James P. Pitts, Mutillidae and Pompilidae; Lynn S. Kimsey, Tiphiidae, Chrysididae, and apoid wasps; Michael Ohl, apoid wasps; Fritz Gusenleitner, Andrenidae. Since none had come across a similar malformation, we assume that the low number of published records generally reflects the rarity of this kind of teratology in Hymenoptera.

The presence of supernumerary ocelli is almost certainly not the result of mutation, and therefore not present in the genetic makeup of the individual or heritable, instead resulting from errors in the developmental process and formation of adult tissues. That said, for at least one report in *Melanoplus*, King and Slifer (1965) found that their quadriocellar individuals successfully reproduced and that a "large proportion" of the offspring were similarly quadriocellar in condition. This suggests that for some cases there might be a genetic component, although the general rarity of supernumerary ocelli in other groups tends to suggest that such apparent heritability is far from the norm. What is remarkable is that these aberrant individuals are often captured while carrying on otherwise seemingly normal lives, a particularly remarkable fact given that ocelli are implicated in light responses and orientation (e.g., Taylor 1981a, 1981b, Schuppe and Hengstenberg 1993, Warrant 2006, Berry et al. 2006, Viollet and Zeil 2013). The scoliid wasp reported herein was perfectly developed in all other respects, and it does not seem that it had to deal with negative effects caused by the supernumerary ocellus. The consequences of malformations such as this are hardly predictable given that a complete understanding of ocellar function remains elusive (e.g., Wilson 1978, Goodman 1981, Stange et al. 2002).

Investigating the supernumerary median ocelli one is tempted to interpret such a malformation as an individual evolutionary throwback considering the hypothesis on the evolution of the median ocellus in insects. Snodgrass (1935) surmised that the median ocellus was formed by the fusion of two primitive anterior ocelli, and according to Paulus (1979) the anterior ocellus is homologous to the anterior pair of *Nauplius* eyes in Crustacea and the pair of median ocelli in *Limulus*. Indeed, the fusion hypothesis of Snodgrass has considerable support (Mizunami 1994), and in various groups the paired origin remains visible during ontogeny (e.g., Patten 1887, Viallanes 1887, Mobbs 1979). Even in adults the median ocellus retains its paired innervation, while the lateral ocelli are singly innervated (e.g., Leydig 1864, Hesse 1901, Imms 1948). It seems plausible that due to some unknown disruption during development the fusion has failed in those individuals with two anterior ocelli. However, it is quite obvious that significantly more information is needed, including extensive documentation of further occurrences of supernumerary ocelli. It is hoped that this account will spur entomologists to pay greater attention to the occurrence of such teratologies and to put them on record. The scarcity of literature reports of aberrant insect specimens assuredly does not reflect their immense diversity nor their abundance in natural history collections.

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