Extreme male leg polymorphic asymmetry in a new empidine dance fly (Diptera: Empididae)

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A new dance fly (Empididae: Empidinae) with hugely modified male fore tarsus, either on the right, left, both or neither sides, is described from Japan. Such massive polymorphic asymmetry occurring with so high an incidence in a population is previously unreported. In view of the courtship behaviour of other Empidinae, we hypothesize that the oversized tarsus is a secondary sexual character employed by males for attracting females. Alternative hypotheses are also discussed. We suggest that this extraordinary new species is a potential model for the study of mating biology in Empidinae and the evolution of mating systems in general.

Keywords: *Empis*; new species; polymorphic asymmetry; mating behaviour

1. INTRODUCTION

Deviations from bilateral symmetry are widespread in invertebrates. The terms fixed (directional asymmetry) and random asymmetry (antisymmetry) describe only the form of the frequency distribution of asymmetrical characters rather than providing causative explanations [1]. In contrast, sexual mosaicism (gynandromorphism and intersexuality) has better defined genetic or environmental causes expressed as often extreme asymmetric sexual characters [2]. Although symmetry is extremely important in courtship behaviour [3], asymmetric exaggerated male traits important in mate choice are also known, for example in fiddler crabs (*Uca* spp.) where males have one cheliped that is greatly enlarged [4].

Here we describe a new empidine dance fly in which males display a polymorphic extreme leg asymmetry. We hypothesize that this massive asymmetry is a secondary sexual character used by males for attracting

females. We also discuss alternative hypotheses including mosaicism, male contests and male choice.

2. MATERIAL AND METHODS

Specimens (preserved in alcohol) were collected between 17 August and 6 September 1999 in six Malaise traps operated between 1600 and 2000 m on Mount Fuji, Japan. Taxonomic description mainly follows Daugeron [5]. The postabdomen of 10 males (belonging to symmetrical males with unmodified tarsus and asymmetrical males) were dissected. Scanning electronic microscopy was performed at the Royal Belgian Institute of Natural Sciences, Brussels (RBINS) (environmental microscope Philips XL 30).

To evaluate potential causes of male polymorphism, we used geometric morphometrics estimates for testing leg and wing size differences between male morphs (symmetrically and asymmetrically modified and unmodified) (additional technical details are given in the electronic supplementary material). Only 11 males were measured owing to the large number of shrunken enlarged tarsi because of the preservation in alcohol.

3. RESULTS

(a) *Empis* (Coptophlebia) jасschhoforum

Daugeron sp. nov.

Insecta Linnaeus, Diptera Linnaeus, Empididae Latreille, Empidinae Rondani, *Empis* Linnaeus, *Coptophlebia* Bezzi (figure 1).

(b) *Etymology*

The species name commemorates the collectors, Catrin and Mathias Jaschhof.

(c) *Description*

Male (holotype): Holoptic. Occipital and ocellar setae black, postgenal setae yellowish. Stylus as long as postpedicel. Labrum about 2.5 times head height. Thorax brownish with all setae yellowish. Proepisternum and prosternum with a few fine short setae. Acrostichals absent. Dorsocentrals uniserial ending in two strong, long setae in prescutellar depression. Coxae with yellowish setae. Fore femur with yellowish ventral setae basally; fore tibia with fine, rather short ventral setae apically; fore tarsus unmodified (figure 1c,d). Mid-tibia enlarged apically with one strong, long anteroventral seta at 0.3 from base; strong antero- and posteroventral setae apically. Hind femur with a posteroventral group of strong, long subpennate golden yellow setae basally. Wing (4–4.5 mm) feebly tinted with brown; M₁ abbreviated. Haltere brownish at base, whitish knob. Abdomen brownish with yellowish fine setae. Pregenital segments and hypopygium (figure 1f) similar to *Empis* (C.) *hyalipennis* (additional details in the electronic supplementary material), but epandrial setae of the anterodorsal lobe stronger, phallus with a pointed ventral projection at 0.3 mm from base. Female (figure 1g) similar to male except for the following characters: dichoptic, scutum black, subshining. Fore femur with short anterodorsal pennation at middle; fore tibia with short dorsal pennation at middle. Hind femur with long anterodorsal and posteroventral pennation, very short posterodorsal and anteroventral pennation; hind tibia with long dorsal pennation, long ventral pennation except apically.

(d) *Type material*

Holotype: JAPAN, Honshu, Yamanashi Prefecture, Oyama Town, Mt Fuji; 17.VIII-06.IX.1999; Malaise trap; leg. Jaschhof (Muséum national d'Histoire

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Figure 1. *Empis* (*C.*) *jaschhoforum* sp. nov. (a) Symmetric male with both fore legs modified. (b) Asymmetric male with the left fore leg modified. (c) Symmetric male with both fore legs unmodified. (d) Unmodified fore leg in scanning electronic microscopy. (e) Modified fore leg in scanning electronic microscopy. (f) Male hypopygium, lateral view. (g) Female habitus, dorsal view. t1–t5 = fore tarsomeres 1–5. Scale bars, (d,e) = 500 μ m; (f) = 0.1 mm. Cerc, cercus; ej ap, ejaculatory apodeme; epn, epandrium; hyp, hypandrium; ph, phallus.

naturelle, Paris (MNHN)). Paratypes: 33 males, 97 females, same data (Fukuoka University; MNHN; National Museum of Wales, Cardiff; Personal Collection of Andreas Stark, Saale; Personal Collection of Toyohei Saigusa, Fukuoka) (additional details are given in the electronic supplementary material).

(e) Variation

(i) Male morphs and choice of holotype

The sample comprises 18 symmetrical males with unmodified tarsus on both fore legs (figure 1c,d), 14 asymmetrical males with modified tarsus on left or right fore leg (first tarsomere swollen basally, with numerous strong, long ventral setae basally; second

tarsomere elongated, about as long as tibia; third and fourth tarsomeres considerably enlarged, inflated, balloon-like, dorsally covered with numerous strong very long setae) (figure 1b,e), and one symmetrical male with tarsus modified on both fore legs (figure 1a). The incidence of asymmetric hypertrophy in males is therefore particularly high, reaching 0.438 ($n = 14$, binomial CI ($\alpha = 0.95$): 0.254–0.623). The holotype was selected from males with unmodified tarsus on both legs.

(ii) Leg and wing size differences

Figure 2, comparing overall leg size with wing centroid size (WCS), indicates a large size difference between

Table 1. ANCOVA of leg size over wing centroid size (WCS) and male morphs.

	d.f.	sum Sq	mean Sq	F-value	Pr ($>F$)
WCS	1	0.071709	0.071709	43.8244	0.0005723
morphs	2	0.288897	0.144449	88.2786	3.55e – 05
WCS: morphs	1	0.000973	0.000973	0.5949	0.4697980
residuals	6	0.009818	0.001636

Figure 2. Patterns of variability of leg and wing size between male morphs: unmodified legs of symmetric males (filled triangles), unmodified (filled squares) and modified (filled circles) legs of asymmetric males and modified legs of a single symmetric male (filled diamonds).

modified and unmodified legs. An ANCOVA controlling for WCS confirms that leg size differences are highly significant (table 1) while WCS differences appear not to be significant (ANOVA, $F = 0.644$, d.f. = 2/8, $p = 0.55$), a result that nevertheless calls for further analyses with larger sample sizes.

4. DISCUSSION

Deviation from bilateral symmetry arises from a variety of intrinsic (genetic) and extrinsic (environmental) factors. For example, while marked sexual mosaicism is poorly understood in Diptera, mermithid nematodes can feminize structure and behaviour in some Nematocera [6], and might explain similar phenomena in *Empis jaschhoforum*, but we did not find nematodes in dissected males (although in some cases nematodes leave the pupa before the adult emerges).

No differences in the genitalia and no female characteristics or additional asymmetries in sexually dimorphic characters (e.g. dichoptic eyes, pennate setae on legs or shorter thoracic or abdominal chaetotaxy) were found in the different male morphs. Furthermore, mosaicism usually occurs with a very low incidence in a population [6,7], yet we found a similar proportion of asymmetric and symmetrically unmodified males, suggesting that another explanation is required.

For these reasons and also because enlargement and sometimes extreme ornamentation of the legs are

prominent in the epigamic displays of many Empidinae [3], it is more likely that the oversized tarsus is a secondary sexual character used by males for attracting females.

Most Empidinae form mating swarms in which nuptial gifts are exchanged between the sexes prior to mating. In the genus *Hilara*, nuptial gifts usually consist of a prey item wrapped in silk produced from silk glands situated in the enlarged male first fore tarsomere [8].

The nutritional value of gifts may be important in some Empidinae, but there is little or no nutritional benefit for the female in many others [9], and males may successfully ‘cheat’ the female with inanimate objects such as a willow seed or an empty silk ‘balloon’ [10,11]. Sometimes successful mating can even occur without transfer of a nuptial gift, or the gift has been entirely replaced by the enlarged male tarsal segments acting as ‘releasers’ important in female choice during epigamic activity [10].

Consequently, the size and the ornamentation of the modified fore tarsus of males of *E. jaschhoforum* could play an important role in mate selection of this species.

Nevertheless, the presence of males lacking tarsal enlargement remains difficult to explain. The difference in leg size between males with modified and unmodified tarsi (figure 2) is highly significant even when controlling for wing size (usually used as an indicator of the body size). This argues against simple conditional expression (polyphenism), which is usually characterized by a strong correlation between body size and ornament size [12]. Alternative explanations for persistence of polymorphism involve frequency-dependent selection, with some sort of selective benefit to unmodified males. Sadowski [13] showed that in *Empis snoddyi* (Diptera: Empididae), the largest males with intermediate-sized silk balloons were the most successful in obtaining matings; these results were explained by a trade-off between long-range attraction of females using large balloons and close-range attraction of females using improved flying efficiency associated with smaller balloons.

In *E. jaschhoforum*, flying speed and/or flying ability, and thus the duration of swarming, could be enhanced in symmetric males with unmodified legs, increasing the probability of obtaining a mate, while the presence of a balloon-like male fore tarsus would allow a more efficient visual stimulus for long-range attraction of females. Selection would act in promoting asymmetric males (14 of 33 studied males) and symmetric males with unmodified tarsi (18 in 33). Constraints of body size [14], load-lifting [15] or the impact of predators [16,17] could mean that symmetric males with modified tarsus on both sides are considerably disadvantaged (only 1 in 33 (3%)).

Male contests could be an alternative to the female choice hypothesis. Some morphological traits may be selected to improve success in male–male fights (large size, strength, weaponry, agility, threat signals) [18]; the oversized tarsus of the asymmetric males of *E. jaschhoforum* could have evolved in a similar way.

The presence of pennate setae on female legs suggests some degree of male choice in the mating system of *E. jaschhoforum*, as already known for several other empidine species [9]. Even if we cannot explain how a large fore tarsus could help to evaluate females, we cannot completely rule out the possibility that this trait allows male choice among females.

The remarkable courtship behaviour of empidine dance flies has stimulated a renewal of interest in using them as models in the study of the evolution of mating systems (e.g. see [16,17,19–21]). We suggest that *E. jaschhoforum* could be a new relevant model.

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