ACTA ENTOMOLOGICA MUSEI NATIONALIS PRAGAE

Published 15.vii.2013 Volume 53(1), pp. 369–380 ISSN 0374-1036

The first case of gynandromorphism in *Enolmis* (Lepidoptera: Gelechioidea: Scythrididae)

Pietro PASSERIN D'ENTRÈVES[1)] & Angela ROGGERO[1,2)]

[1)] University of Torino, Department of Life Sciences and Systems Biology, Via Accademia Albertina 13,
I-10123 Torino, Italy; e-mails: pietro.passerin@unito.it, angela.roggero@unito.it

[2)] corresponding author

Abstract. Gynandromorphism (i.e., organisms with both male and female characteristics) is a rare and interesting phenomenon that has been recorded for several taxa within Insecta, Crustacea, and Aves since the early 20th century. Recently, interest in this phenomenon has been revived, due to its potential contribution to elucidation of developmental mechanisms. Within insects, gynandromorphism includes several examples in Lepidoptera (mainly in the Macrolepidoptera). Yet, it is rare in the far less strikingly sexually dimorphic Microlepidoptera, mainly because it is harder to use external features to recognize gynandromorphs in this taxon. Here, we describe the first known case of gynandromorphism in Scythrididae, belonging to the genus *Enolmis* Duponchel, 1845. *Enolmis* species have light coloured external features, asymmetrical male genitalia, and developed henia in females. The different parts of male and female genitalia present in the *Enolmis* gynandromorph individual are described here.

Key words. Lepidoptera, Scythrididae, *Enolmis*, developmental patterns, genitalia, gynandromorph, Spain

Introduction

While gynandromorphism is a rare phenomenon (Josephrajkumar et al. 1998, Bernardino et al. 2007, Craig & Crosby 2008), it has long been documented in animal taxa (Nihei & Carvalho 2002). This phenomenon was first recorded in birds and butterflies (Morgan & Bridges 1919), and the causes for its development have been investigated since the beginning of the 20th century (Morgan 1907). Strictly speaking, a gynandromorph is a chimeric individual that is genetically both male and female, resulting from the loss of a sex chromosome at the early stages of embryogenesis, as documented in *Drosophila* Fallén, 1823 (Diptera: Drosophilidae) (Morgan & Bridges 1919). Alternatively, it may arise from the double fertilization of a bi-nucleate egg, as documented in the female-heterogametic Lepidoptera (Cockayne 1935, Bernardino et al. 2007, Allen et al. 2011). Thus, the body of a true gynandromorph consists of genetically different tissues that have well-differentiated feminine and masculine parts. In general, all individuals that have both male and female tissues are referred to as gynandromorphs, despite the fact that some should be considered phenotypical intersexes that are genetically male or female, but not both at the same time.

Gynandromorphism is far more often observed in insects (GEMENO et al. 1998, JOSEPHRAJKUMAR et al. 1998, NARITA et al. 2007, CRAIG & CROSBY 2008, NARITA et al. 2010, SILVA DIAS et al. 2012) and crustaceans (NARITA et al. 2010) than in other invertebrate taxa. Gynandromorphic individuals often exhibit impressive external features of both sexes together; however, in some species, gynandromorphism is only visible in internal structures (typically, the genitalia), being perhaps less noticeable but no less important (COCKAYNE 1927, PURI 1933, NIHEI & CARVALHO 2002).

Three types of gynandromorphs have been described based on the observed characteristics (COCKAYNE 1916). However, most correspond to Cockayne's second type, and are defined by PURI (1933) as "halved gynandromorphs" (or, bilateral gynandromorphs). Cockayne's second type of gynandromorphism is characterized by masculinized females developing male tissue body parts due to loss of a sexual chromosome in some cells. The earlier this chromosome is lost, the more likely the male/female parts are symmetrical along the longitudinal midline of the adult (KAGEYAMA et al. 2012). Another type is defined as a "mixed gynandromorph" (or, non-bilateral gynandromorph). In this case, individuals express a mosaic of male-female phenotypic characteristics, but usually have a clearly determined sex. Non-bilateral gynandromorphs are rarer (HODGES & BROWN 2007), and are induced as a result of alterations in the organization of several developmental modules (BÉTHOUX 2010).

There is a broad scientific interest in gynandromorphs, partly because of their rarity, but also because of their usefulness in gaining information about developmental pattern of the body parts, particularly the genitalia. In addition, this phenomenon is useful for the assessment of left-right asymmetry, particularly during development, as mechanisms of the process remain unclear (AW & LEVIN 2008, OKUMURA et al. 2008, NARITA et al. 2010, YANG & ABOUHEIF 2011). Non-bilateral gynandromorphs are particularly useful for studying developmental mechanisms that lie beneath the organization of different parts of the genitalia in both sexes (NARITA et al. 2010). Besides, during the development the main changes affect essentially the pupal stage, when the larval genital disc develops into a genital papilla that is well-differentiated in males and females (POSADA et al. 2011). Although the mechanisms of sex determination have not yet been completely clarified for all insects, it is hypothesized that all these mechanisms are variations of the same model (NARITA et al. 2010).

Through elucidation of such processes, an understanding of some peculiar phenomena, such as antisymmetry (i.e. chirality), may be obtained. Antisymmetry has been recently recorded in the male genitalia of *Scythris antisymmetrica* Nupponen, 2009 (Scythrididae), which is the first instance of this phenomenon in Lepidoptera (NUPPONEN 2009). While antisymmetrical valvae have not been previously recorded, cases of asymmetrical male genitalia are relatively common in this family (BENGTSSON 1997). For instance, a more or less pronounced asymmetry has independently appeared several times during evolution in this family, affecting different parts of male genitalia in different taxa. In fact, the emergence of "genital asymmetry" may involve various anatomical parts, separately or combined. Examples include the valvae in the species of *Enolmis* Duponchel, 1845 and some *Episcythris* Amsel, 1939 (Passerin d'Entrèves 1991, Bengtsson 1997), the gnathos in the species of *Bactrianoscythris* Passerin d'Entrèves & Roggero, 2009 (Passerin d'Entrèves & Roggero 2009), and in the *Scythris limbella* species-group (Bengtsson 1997), the sternite 8 (S8) in some species of the *Scythris sinensis* species-group (Zhang & Li 2010), or the tergite 8 (T8) in the *S. caramani* species-group (Passerin d'Entrèves & Roggero 2012).

The current study presents a detailed examination of the anatomical structure of the first gynandromorph recorded in the genus *Enolmis*, which represents one of the few known microlepidopteran gynandromorphic taxa (Narita et al. 2010). The objectives of this study are: i) to compare the differences and similarities of the *Enolmis* gynandromorph genitalia with regular *Enolmis* male and female genitalia; and ii) to improve our understanding of the developmental patterns of the Scythrididae genitalia anatomical structure through a detailed discussion of the genital characteristics of gynandromorphs.

Material and methods

A gynandromorph individual with genital structures of both sexes was found among some scythridids collected from various localities of the Sierra Nevada area (Granada, Spain). The specimen belongs to the material collected during a field survey in 1983 by G. Baldizzone and P. Triberti, who loaned the specimens to our research group for study. While the gynandromorph appeared to belong to the genus *Enolmis* based on its external appearance, we could not confirm this due to the heavy modification and reduction of the genitalia. This problem in identification was further exacerbated by accidental loss of the specimen after the slide preparation.

At present, 17 species are included in the genus *Enolmis*. This genus is characterized by a Western Palaearctic distribution (Bengtsson 2002, Passerin d'Entrèves & Roggero 2007); however, these species are primarily found in the circum-Mediterranean area (Bengtsson 1997).

The genus *Enolmis* has been tentatively divided into three groups, according to the features of the male genitalia, but the division has never been formalized (Passerin d'Entrèves 1985). The three groups are: i) the *Enolmis acanthella* species-group; ii) the *E. desidella* species-group; and iii) the *E. delicatella* species-group (see Tab. 1 for the full list of species). The valvae are asymmetrical, with the right valva being reduced, thinly digitate and slightly bent in species belonging to the *E. acanthella* species-group. In comparison, both valvae are well developed but differently shaped in the *E. delicatella* species-group. Finally, the right valva is curved inward, elongate and subcylindrical in the *E. desidella* species-group. The well-defined features of the female genitalia correspond to those of the male (Bengtsson 1997), which further supports the division of the species into these three groups. Records of at least six *Enolmis* species – including *E. acanthella* (Godart, 1824), *E. delicatella* (Rebel, 1901), *E. nevadensis* Passerin d'Entrèves, 1997, *E. sierraenevadae* Passerin d'Entrèves 1997, *E. userai* (Agenjo, 1962), and *E. vivesi* Bengtsson & Passerin d'Entrèves, 1988 – exist from the slopes of the Sierra Nevada, which is a mountain range in Andalusia, with the highest peak of continental Spain.

Table 1. List of *Enolmis* species, with attribution to the three species-groups.

Species	***E. acanthella* group**	***E. desidella* group**	***E. delicatella* group**
E. abenhumeya (Agenjo, 1951)			x
E. acanthella (Godart, 1824)	x		
E. agenjoi Passerin d’Entrèves, 1988	x		
E. amseli Passerin d’Entrèves, 1997	x		
E. arabica Passerin d’Entrèves, 1987		x	
E. bimerdella (Staudinger, 1859)			x
E. delicatella (Rebel, 1901)			x
E. desidella (Lederer, 1855)		x	
E. gigantella (Lucas, 1942)	x		
E. nevadensis Passerin d’Entrèves, 1997			x
E. jemenensis Bengtsson, 2002		x	
E. saudita Passerin d’Entrèves, 1986		x	
E. seeboldiella (Agenjo, 1951)	x		
E. sierraenevadae Passerin d’Entrèves, 1997			x
E. tunisiae Bengtsson, 2002			x
E. userai (Agenjo, 1962)			x
E. vivesi Bengtsson & Passerin d’Entrèves, 1988	x		

Both live and dead specimens of gynandromorphs are usually easily distinguished by their external genital characteristics. For example, many Lepidoptera (Cockayne 1916, 1922; Josephrajkumar et al. 1998, Bernardino et al. 2007) are characterized by marked sexual dimorphism, with clear differences in wing size, shape and coloration (Allen et al. 2011). In contrast, the Scythrididae do not exhibit any external sexual dimorphism, with the exception of a few species (Bengtsson 1997). The main perceptible differences between sexes depend on the different mechanisms of the wing-coupling (i.e., a single, well-developed frenulum in male, and three shorter ones in female) and on the structure of the terminal portion of the abdomen (more or less enlarged and carrying a tuft of anal hair scales in males, while slender and tapering in females). Clearly, the second characteristic cannot be used here, as it is related to highly modified and often vestigial genitalia in gynandromorphs. Due to these manifest difficulties, such aberrations are only found by chance when examining the genitalia of long-preserved Scythrididae material.

Consequently, some of the analyses that are usually conducted on gynandromorphs, such as the tissue karyotype (Yang & Abouheif 2011), cannot be carried out on dry material, thus much useful information is not available for microlepidopteran gynandromorphs. Hence, we performed a morphological analysis of the genital traits and examined variation in the development of different parts of the external and internal genitalia.

The dissection and preparation of the genitalia followed the usual methods applied to Microlepidoptera, as presented in Robinson (1976) and Bengtsson (1997). The modified structures of the gynandromorph (Fig. 1A) were then compared to the male and female genital traits of the known *Enolmis* species (Fig. 1B–D), to ascertain how the different parts develop in both sexes. The terminology of genitalia follows Knots (1956) and Hodges (1998). The identified parts of the gynandromorph genitalia were marked in the photographs (Fig. 2).

The specimen slide has been deposited in the collection of Pietro Passerin d'Entrèves, housed at University of Torino (MIZT), Department of Life Sciences and Systems Biology (Torino, Italy).

Results

The abdomen of the gynandromorph individual is the same size as that of normal males and females; thus, major modifications in the developmental pattern of genitalia did not affect the size of various structures.

The genital structures were partly recognizable, despite being greatly deformed, reduced and displaced with respect to the typical model of *Enolmis* genitalia. In this case, the separation of male and female genitalia apparently does not occur along the midline (i.e., the bilateral gynandromorph model, see Nekrutenko 1965), as it is often found in Lepidoptera Rhopalocera (Aw & Levin 2008). Therefore, it might be hypothesized that the phenomenon did not begin at the early stages of development in this individual, but occurred at a later phase of the developmental pattern. For instance, it may have occurred when the anatomical structure (possibly of the predominant sex) was already partly formed. This type of gynandromorph is highly rare, and hence particularly interesting and useful to this field of research (Hodges & Brown 2007).

Here, the identification of different parts of the genitalia was made easier when comparing structures with their hypothesized positions on the abdominal segments (Tab. 2) according to the literature (Mehta 1933, Dodson 1935, Sibatani et al. 1954, Okagaki et al. 1955, Mutuura 1972). In parallel, the known modifications of the abdominal segments for the adults of both sexes (Kristensen 2003) were confirmed by the observation of the gynandromorph. Although both male and female genitalia were present in the specimen, different development was recorded in each abdominal segment. For instance, the female structures were more easily identifiable in the proximal part (the segment VIII, see Fig. 2) while the male structures were more easily identifiable in the segments IX and X (Fig. 2), but were not fully developed.

In the distal part of abdomen, the uncus (Un) was identified in a structure consisting of two parts, rather than being fused in a single, narrow and elongate plate, as is typical in *Enolmis* (Fig. 1). However, this structure had thick and short setae that are characteristic of the uncus in this genus, corroborating the identification of this anatomical part. Furthermore, the uncus (Un, male structure) and the papillae anales (AP, female structure) are coincident here (Fig. 2), with parts from both sexes developing in the same abdominal segment (Tab. 2), even though the uncus is often considered a dorsal appendage of the segment X rather than being constituted by the segment itself (Ogata et al. 1957). The tegumen (Te, the dorsal part of segment IX) constitutes a complex with the unapparent vinculum (Vi, the ventral part of segment IX), and the valvae (Va). The valvae were barely visible and vestigial. Furthermore, the structure was asymmetrical, which is normal for the valvae of this genus, but cannot be attributed to any known *Enolmis* species. Thus, this structure could not be used to identify the specimen. In addition, a tuft of long setae (the clavus, according to Knots 1956), which is characteristic of

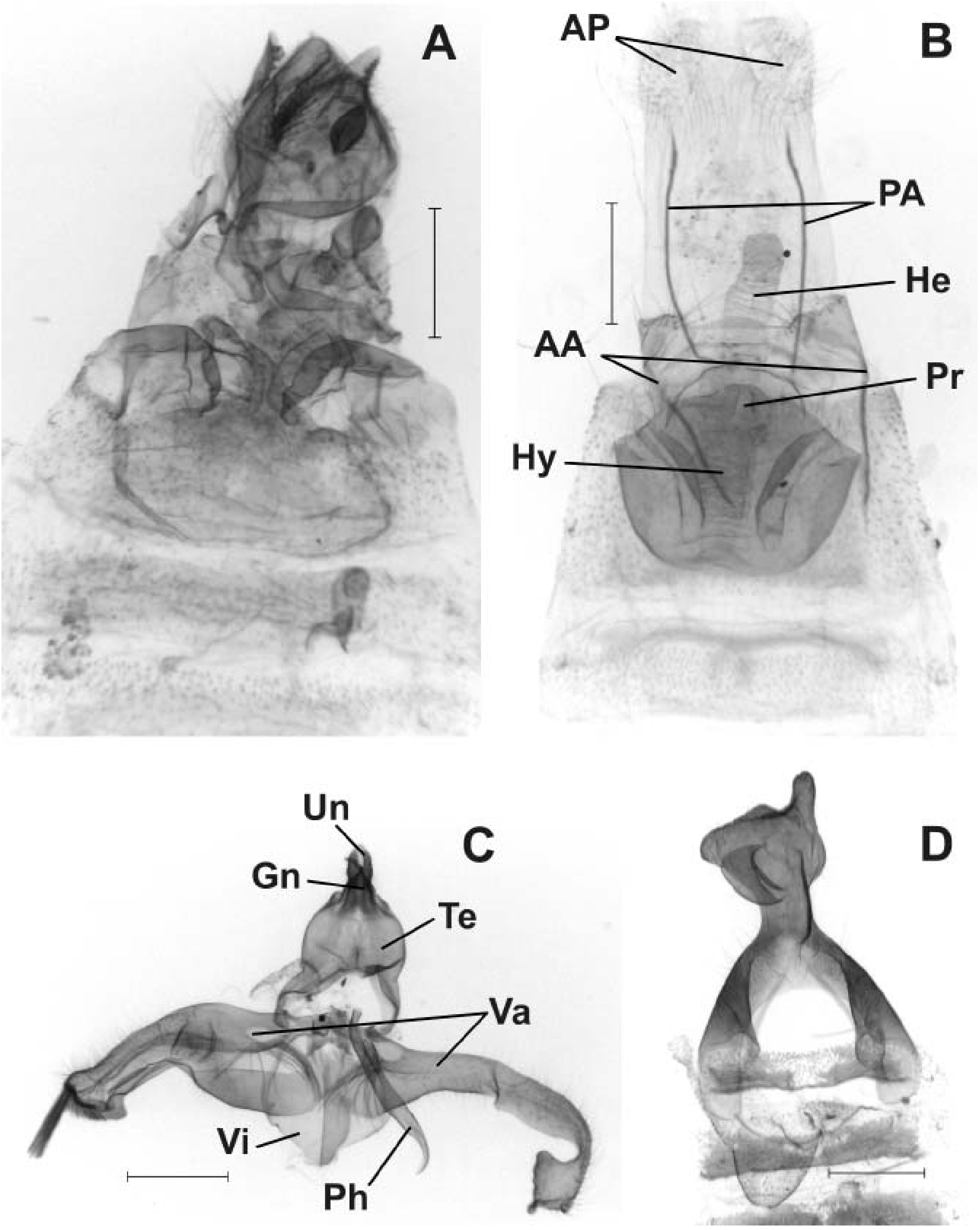

Fig. 1. A – *Enolmis* sp., gynandromorph abdomen; B – *Enolmis delicatella* species-group, female genitalia, with the various parts marked by acronyms: anterior apophyses (AA), caudal processes (Pr), henia (He), hypostema (Hy), papillae anales (AP), and posterior apophyses (PA). C–D – *Enolmis sierraenevadae* Passerin d'Entrèves, 1997: C – male genitalia, with the various parts marked by the acronyms: uncus (Un), gnathos (Gn), tegumen (Te), phallus (Ph), valvae (Va), vinculum (Vi), D – male VIII segment. Scale bar = 0.2 mm.

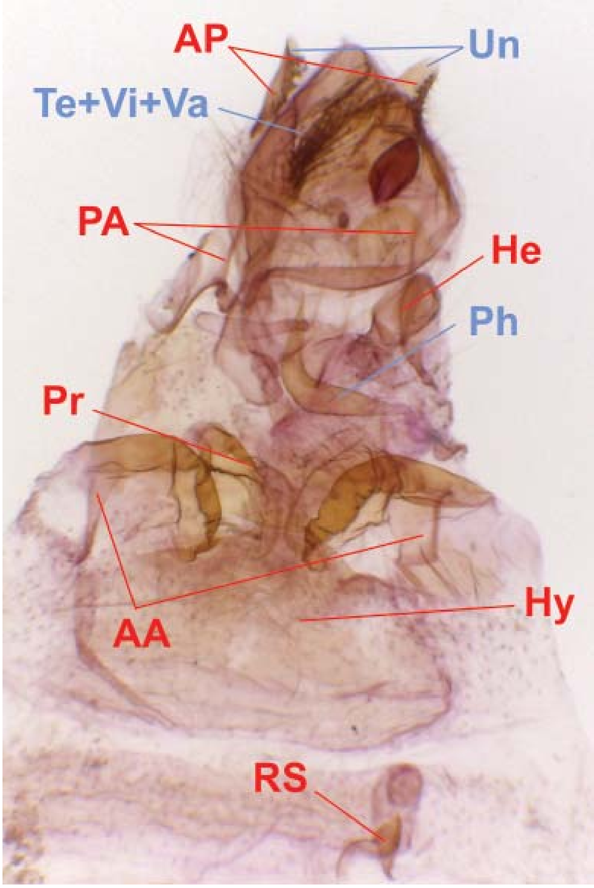

Fig. 2. The gynandromorph specimen (male parts marked in blue, female parts marked in red). Male structures: phallus (Ph), tegumen (Te), uncus (Un), valvae (Va), vinculum (Vi); females structures: anterior apophyses (AA), caudal processes (Pr), henia (He), hypostema (Hy), papillae anales (AP), posterior apophyses (PA), receptaculum seminis (RS).

the *Enolmis* species, was visible in relation to the basal ventral part of the valva. The phallus (Ph), a new structure of ectodermal origin, was clearly discernible, despite being rudimentary. The juxta (Ju) was not identified with certainty. The tergite 8 (T8) and sternite 8 (S8) did not exhibit masculine characteristics. Furthermore, only the female structures could be identified in segment VIII, leading to a hypothesis that the male parts were not identifiable because they were either extremely reduced or coincided with the female ones.

The gnathos (Gn) could not be identified, since the ventral part of the abdominal segment X was not constructed as in a typical *Enolmis* (Fig. 1). The structure was possibly reduced into a rounded, poorly differentiated plate. The female parts were mainly distinguishable on the abdominal segment VIII, with the hypostema (Hy) and its caudal processes (Pr) which were sufficiently developed. Based on the complicated shape of sternite 8 (S8), the specimen should be placed in the *E. delicatella* species-group which has a similar structure. The henia (He), while less evident, was shaped as is typical for *Enolmis*. The anterior apophyses

Table 2. Origin of different parts of male and female genitalia.

	Male	**Female**
Segment X	uncus gnathos tegumen valvae	papillae anales
Segment IX	valvae tegumen vinculum	posterior apophyses
Segment VIII	sternite 8 tergite 8	anterior apophyses henia hypostema receptaculum seminis ostium bursae ductus bursae bursa copulatrix
Segment VII		sclerotization

(AA) were present and easily identified, with the right one not being completely developed. In addition, the receptaculum seminis (RS), which was at an early stage of invagination on the membrane of the segment VIII (ectodermal origin), was identified. With respect to the structures on the segment IX (Tab. 2), the posterior apophyses (PA) were present and both were fully developed, coexisting with the predominant male parts (see above).

Some parts could not be identified, possibly because the genital parts were not completely differentiated due to male and female developmental mechanisms simultaneously operating on the same anatomical structures.

Discussion

To the best of our knowledge, this is the first known case of a gynandromorph being recorded in Gelechioidea to date. However, various authors have documented some gynandromorph specimens in Microlepidoptera. For instance, a bilateral gynandromorph specimen of *Harmaclona tephrantha* (Meyrick, 1916) belonging to the Tineidae was reported by DAVIS (1994, 1998) from Indonesia. That specimen was characterized externally by an equal division with a male right side and a female left side, while the genitalia displayed a predominance of male characteristics, as is often found in bilateral gynandromorphs (KUZNETSOV 1916). HODGES & BROWN (2007) described a gynandromorphic *Acleris celiana* Robinson, 1869) (Tortricidae), in which both male and female genitalia were well developed, and probably functional. In fact, gynandromorphic individuals are often able to mate, but cannot usually reproduce. In some cases, gynandromorphs are able to lay fertilized eggs after the mating, with the female part being fully functional (GEMENO et al. 1998).

KUIJTEN (1973) recorded the first bilateral gynandromorphic *Yponomeuta cagnagellus* (Hübner, 1813) (Yponomeutidae), in which the right side was completely masculine, while the left side showed a clear reduction of the male component and presence of female structures, such as anal papillae and apophyses. Externally, the specimen exhibited no notable differences between the left and right halves, except for the frenulum, which was female on the left and male on the right side (Kuijten 1973). Furthermore, the halved gynandromorphs can be easily identified by the wing structure in other Lepidopteran taxa, such as Noctuidae that exhibit a relatively large number of gynandromorphs (Hellberg & Torstenius 1974, Gemeno et al. 1998, Josephrajkumar et al. 1998, Narita et al. 2010). Accidental loss of the specimen in the current study resulted in our being unable to evaluate any differences on the two sides of the body through the examination of external features.

A number of examples of gynandromorphism, exhibiting highly diverse genitalia structure, are present in Lepidoptera (Narita et al. 2010). However, interest in gynandromorphs' variation mainly focuses on the missing parts of the genitalia, and the relevance of this loss. These aberrations are related to processes that operate on the preimaginal, undifferentiated tissues leading to the development of male and female genitalia at the same time. The absence of different parts in various gynandromorphs would mean that the tissues are affected by these processes at different times. In fact, the genitalia of larvae are constituted of undifferentiated genital disc cells that generate the internal reproductive organs, while the abdominal segment does not show any type of variation. During later development, the genitalia appear barely perceptible in the pupa as rudimental structures, but are fully developed in the adult (Dodson 1935, Sendi et al. 1993).

The rare gynandromorph scythridid that was identified in this study was characterized by merged male and female genitalia, as opposed to the more common bilateral form. It is highly unlikely that this specimen was able to mate because the male/female genitalia structures were located too close to each other, based on the knowledge of the coupling mechanisms of Lepidoptera which have been studied for various taxa (see Miller 1988 for a detailed review).

Spencer (1927) observed that a *Drosophila funebris* (Fabricius, 1787) gynandromorph with the male genitalia positioned posterior and dorsal to the female ones was unable to copulate; hence, it is extremely unlikely that the *Enolmis* individual could copulate as a male. The main difference between the two cases is that Spencer's *Drosophila* carried a full set of male and female external genitalia (despite being almost surely sterile), while the genitalia of the *Enolmis* gynandromorph were vestigial for both sexes, and hence were not operational.

Gynandromorphs do not usually reproduce, but may sometimes behave as normal female, normal male or both in response to sex pherormones causing them to exhibit courtship and mating display behaviour (Gemeno et al. 1998). Furthermore, cases of gynandromorphs mating or laying eggs have been recorded, even though the eggs do not hatch (Gemeno et al. 1998). These individuals usually exhibit the gynandromorphic characteristic on limited areas of the body that are not involved in mating, such as the head and thorax. The gynandromorphic characteristics exhibited by the *Enolmis* in the current study precluded it from both egg laying and almost certainly mating. Following the definition of Josephrajkumar et al. (1998), and based on existing knowledge, this *Enolmis* specimen could be considered both an antero-posterior gynandromorph and a mosaic gynandromorph due to the presence of male/female genitalia and the reciprocal positioning of these structures.

Acknowledgements

We would like to thank G. Baldizzone (Asti, Italy) for the loan of the material. We are very grateful to J. W. Brown for useful information about the gynandromorphic Tortricidae. The research was supported by grants of the MIUR (Italian Ministry of Education, University and Research).

References

ALLEN C. E., ZWAAN B. J. & BRAKEFIELD P. M. 2011: Evolution of sexual dimorphism in the Lepidoptera. *Annual Review of Entomology* **56**: 445–464.

AW S. & LEVIN M. 2008: What's left in asymmetry? *Developmental Dynamics* **237**: 3453–3463.

BENGTSSON B. Å. 1997: *Microlepidoptera of Europe. Scythrididae. 2.* Apollo Books, Sternstrup, 301 pp.

BENGTSSON B. Å. 2002: Scythridids of the Arabian Peninsula, II: Yemen (Lepidoptera: Scythrididae). *Esperiana* **9**: 61–127.

BERNARDINO A. S., ZANUNCIO T. V., ZANUNCIO J. C., LIMA E. R. & SERRÃO J. E. 2007: Note on gynandromorphism in the eucalyptus defoliator Thyrinteina arnobia (Stoll, 1782) (Lepidoptera: Geometridae). *Anais da Academia Brasileira de Ciências* **79**: 235–237.

BÉTHOUX O. 2010: Alteration of sex-related developmental modules: a case of "feminized" male wing morphology in Creobroter gemmatus (Mantodea: Hymenoptera). *European Journal of Entomology* **107**: 133–135.

COCKAYNE E. A. 1916: VIII. Gynandromorphous Agriades coridon, Poda; A. coridon ab. oystonensis, Pickett. *Transactions of the Royal Entomological Society of London* **64**: 243–263.

COCKAYNE E. A. 1922: VII. Intersexual forms of Plebeius argus L. (aegon. Schiff.). *Transactions of the Royal Entomological Society of London* **70**: 225–239.

COCKAYNE E. A. 1927: Colias lesbia. Description of genitalia of a gynandromorph. *Entomologist's Record and Journal of Variation* **39**: 99–100.

COCKAYNE E. A. 1935: The origin of gynandromorphs in the Lepidoptera from binucleate ova. *Transactions of the Royal Entomological Society of London* **83**: 509–531.

CRAIG D. A. & CROSBY T. K. 2008: Gynandromorphs of New Zealand Austrosimulium spp. (Diptera: Simuliidae). *Zootaxa* **1811**: 57–68.

DAVIS D. R. 1994: A bilateral gynandromorphic Harmaclona tephrantha from Indonesia (Lepidoptera: Tineidae). *Tropical Lepidoptera* **5**: 117–122.

DAVIS D. R. 1998: A world classification of the Harmacloninae, a new subfamily of Tineidae (Lepidoptera: Tineoidea). *Smithsonian Contributions to Zoology* **597**: 1–81.

DODSON M. E. 1935: Development of the female genital ducts in Trichoptera. *Quarterly Journal of Microscopical Science* **77**: 383–403.

GEMENO C., ANTON S., ZHU J. W. & HAYNES K. F. 1998: Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, Agrotis ipsilon (Haufnagel) (Lepidopotera: Noctuidae). *International Journal of Insect Morphology and Embryology* **27**: 185–191.

HELLBERG H. & TORSTENIUS S. 1974: Genitalia hos en gynandromorf Euxoa adumbrata Ev. (Lep. Noctuidae). *Entomologisk Tidskrift* **95**: 125–127 (in Swedish, English abstract).

HODGES E. & BROWN J. W. 2007: A remarkable genitalic gynandromorph of Acleris celiana (Robinson) (Lepidoptera: Tortricidae: Tortricini) from Texas. *News of the Lepidopterists' Society* **49**: 79, 85.

HODGES R. W. 1998: Gelechioidea. Pp. 131–158. In: KRISTENSEN N. P. (ed.): *Lepidoptera, Moths and Butterflies. Vol 1. Evolution, Systematics and Biogeography*. Handbuch der Zoologie/Handbook of Zoology. Vol. IV/35. Walter de Gruyter, Berlin & New York, 491 pp.

JOSEPHRAJKUMAR A., SUBRAHMANYAM B. & RAMAMURTHY V. V. 1998: Gynandromorph of Helicoverpa armigera [Lepidoptera: Noctuidae]. *Entomological News* **109**: 288–292.

KAGEYAMA D., NARITA S. & WATANABE M. 2012: Insect sex determination manipulated by their endosymbionts: incidences, mechanisms and implications. *Insects* **3**: 161–199.

KNOTS A. B. 1956: Lepidoptera. Pp. 97–111. In: TUXEN S. L. (ed.): *Taxonomist's Glossary of Genitalia in Insects*. Ejnar Munksgaard, Copenhagen, 284 pp.

KRISTENSEN N. P. 2003: *Lepidoptera, Moths and Butterflies. Vol 2. Morphology, Physiology and Develompment*. Handbuch der Zoologie/Handbook of Zoology. Vol. IV/35. Walter de Gruyter, Berlin & New York, 564 pp.

KUIJTEN P. J. 1973: A gynandromorph of the small ermine moth, Yponomeuta cagnogellus (Hb.) (Lepidoptera, Yponomeutidae). *Entomologische Berichten* (Amsterdam) **33**: 221–222.

KUZNETSOV N. J. 1916: Contributions to the genital apparatus in Lepidoptera: some cases of gynandromorphism. *Revue Russe d'Entomologie* **16**: 151–191 (in Russian, English abstract).

MEHTA D. R. 1933: On the development of the male genitalia and the efferent genital duct in Lepidoptera. *Quarterly Journal of Microscopical Science* **76**: 35–61.

MILLER J. S. 1988: External genitalic morphology and copulatory mechanism of Cyanotricha necyria (Felder) (Dioptidae). *Journal of the Lepidopterists' Society* **42**: 103–115.

MORGAN T. H. 1907: The cause of gynandromorphism in insects. *American Naturalist* **41**: 715–718.

MORGAN T. H. & BRIDGES C. B. 1919: The origin of gynandromorphs. Pp. 1–122. In: BRIDGES C. B., MORGAN T. H. & STURTEVANT A. H. (eds.): *Contributions to the genetics of Drosophila melanogaster*. Carnegie Institution of Washington, Washington, 388 pp.

MUTUURA A. 1972: Morphology of the female terminalia in Lepidoptera, and its taxonomic significance. *Canadian Entomologist* **104**: 1055–1071.

NARITA S., NOMURA M. & KAGEYAMA D. 2007: A gynandromorph of Eurema hecabe (Lepidoptera: Pieridae) from Japan. *Entomological News* **118**: 134–191.

NARITA S., PEREIRA R. A. S., KJELLBERG F. & KAGEYAMA D. 2010: Gynandromorphs and intersexes: potential to understand the mechanism of sex determination in arthropods. *Terrestrial Arthropod Reviews* **3**: 63–96.

NEKRUTENKO Y. P. 1965: Three cases of gynandromorphism in Gonepteryx: an observation with ultraviolet rays. *Journal of Research on the Lepidoptera* **4**: 103–108.

NIHEI S. S. & CARVALHO C. J. B. 2002: Occurrence of gynandromorphism in Polietina orbitalis (Stein, 1904) (Diptera: Muscidae: Muscinae). *Studia Dipterologica* **9**: 73–81.

NUPPONEN K. 2009: Scythris antisymmetrica Nupponen, sp. n. from Central Spain, an example of antisymmetric male genitalia in the order Lepidoptera (Lepidoptera: Scythrididae). *SHILAP Revista de Lepidopterologia* **148**: 439–444.

OGATA M., OKADA Y., OKAGAKI H. & SIBATANI A. 1957: Male genitalia of Lepidoptera: morphology and nomenclature III. Appendages pertaining to the tenth somite. *Annals of the Entomological Society of America* **50**: 237–244.

OKAGAKI H., SIBATANI A., OGATA M. & OKADA Y. 1955: Male genitalia of Lepidoptera: morphology and nomenclature II. Morphological significance of sacculus and furca. *Annals of the Entomological Society of America* **48**: 438–442.

OKUMURA T., UTSUNO H., KURODA J., GITTENBERGER E., ASAMI T. & MATSUNO K. 2008: The development and evolution of left-right asymmetry in invertebrates: lessons from Drosophila and snails. *Developmental Dynamics* **237**: 3497–3515.

PASSERIN D'ENTRÈVES P. 1985: Il genere Enolmis Duponchel (Lepidoptera, Scythrididae): sistematica, ipotesi filogenetiche e note biogeografiche. Pp. 261–265. In: *Atti XIV Congresso Nazionale Italiano di Entomologia (Palermo, 28.v-1.vi.1985)*. Palermo, 918 pp.

PASSERIN D'ENTRÈVES P. 1991: Description de six nouvelles Episcythris Amsel (Lepidoptera, Scythrididae) avec quelques remarques phylogénétiques et systématiques sur ce genre. *Nota Lepidopterologica* **14**: 53–68.

PASSERIN D'ENTRÈVES P. & ROGGERO A. 2009: Eastern Palaearctic Scythrididae (Lepidoptera: Gelechioidea): description of a new genus and some new species. *Zootaxa* **2263**: 1–20.

PASSERIN D'ENTRÈVES P. & ROGGERO A. 2012: Taxonomic account of Scythris caramani species-group, with the description of a new species from Turkey (Lepidoptera, Gelechioidea, Scythrididae). *SHILAP Revista de Lepidopterologia* **40**: 409–418.

POSADA F. J., VIRDIANA I., NAVIES M., PAVA-RIPOLL M. & HEBBAR P. 2011: Sexual dimorphism of pupae and adults of the cocoa pod borer, Conopomorpha cramerella. *Journal of Insect Science* **11(52)**: 1–8.

PURI I. M. 1933: A case of gynandromorphism in Simulium. *Indian Journal of Medicine Research* **20**: 801–802.

ROBINSON G. S. 1976: The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist’s Gazette* **27**: 127–132.

SENDI J. J., SRIVASTAVA K. P. & SINGH M. R. K. 1993: Postembryonic study on the development of the female efferent genital system in the lemon-butterfly, Papilio demoleus L. (Lepidoptera). *Journal of Research on the Lepidoptera* **32**: 162–169.

SIBATANI A., OGATA M., OKADA Y. & OKAGAKI H. 1954: Male genitalia of Lepidoptera: morphology and nomenclature I. Division of the valvae in Rhopalocera, Phalaenidae (=Noctuidae) and Geometridae. *Annals of the Entomological Society of America* **47**: 93–106.

SILVA DIAS F. M., CASAGRANDE M. M. & HENDRIK MIELKE O. H. 2012: Description of a new species of the genus Zaretis Hübner, [1819], with taxonomic notes on Z. itys and Z. itylus, stat. rev. (Lepidoptera: Nymphalidae: Charaxinae) and illustration of a gynandromorph. *Zootaxa* **3382**: 29–40.

SPENCER W. P. 1927: A gynandromorph in Drosophila funebris. *American Naturalist* **61**: 89–91.

YANG A. S. & ABOUHEIF E. 2011: Gynandromorphs as indicators of modularity and evolvability in ants. *Journal of Experimental Zoology, Part B (Molecular and Developmental Evolution)* **316**: 313–318.

ZHANG J. & LI H. 2010: Review of the sinensis group of the genus Scythris (Lepidoptera: Scythrididae) from China. *Entomological News* **12**: 63–68.