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Gynandromorphism and its Manifestations in Diprionid Hymenoptera (*)

INTRODUCTION

Does gynandromorphism manifest itself in any particular way in Diprionids? How are the male, female or intermediate characteristics as well as other observable morphological alterations distributed in the soma of the individual? An attempt to answer these questions is made in this paper in which three new gynandromorph individuals of *Neodiprion sertifer* (Geoffroy) (Hymenoptera Diprionidae) are also described.

To better understand how gynandromorphism phenomenologically manifests itself in Diprionid Hymenoptera a general overview of the phenomenon and the animals in which it appears is preliminarily called for. The phenomenon can be described as the simultaneous presence within the same organism of genotypically and phenotypically male and female tissues rather than of masculinized or feminized tissues (Laugé, 1985) as is the case with intersexes in which phenotypically male or female regions appear but with an identical chromosomic composition (Whiting *et al.*, 1934).

Gynandromorph forms have been described in the phylum of Arthopods of a number of classes, namely Insects of the following orders: Ephemeroptera (Belfiore, 1979), Blattodea (Graves *et al.*, 1986), Phasmida (Carlberg, 1981), Orthoptera (White, 1968), Hemiptera (Coccoidea) (Miller and Williams, 1993), Trichoptera (Mey, 1982), Lepidoptera (Robinson, 1971; Gemeno *et al.*, 1998), Diptera (Correas *et al.*, 1996), Coleoptera (Ruppel, 1971), Hymenoptera (Watson, 1955; Gordh and Gulmahamad, 1975; Jones and Phillips, 1985; Nilsson, 1987; Halstead, 1988; Heliövaara *et al.*, 1992; Scupola, 1994); Crustaceans of the order of Decapoda (Johnson and Otto, 1981); and Arachnides of the orders of Araneae (Gack, Helversen, 1976) and Acari (Ixodidae) (Clarke and Rechav, 1992). No

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occurrence of the phenomenon has ever been reported for vertebrates (Novak, 1975).

When can an individual be effectively classified as being gynandromorph? Whiting *et al.* (1934) have classified as gynandroid the individuals of *Habrobracon juglandis* (Ashmead) (Hymenoptera Braconidae) which were found to be genetically male but with feminized genitalia. According to Berry (1985) gynandromorphism is restricted only to the case in which the mosaic of cells of both sexes includes the gonads.

There is still speculation as to how this phenomenon originates. It is in any case thought to be ascribable to oogenetic anomalies, fecundation anomalies or cytogenetic aberrations during embryogenesis.

Oogenetic anomalies are essentially connected with the formation of binucleate eggs, whether associated with polyspermy or not. What gives rise to binucleate eggs is not as yet altogether clear. Two possible explanations are postulated for the manifestation of the phenomenon, namely the post-reductional theory according to which the two nuclei are the result of the division of a nucleus of an oocyte (Boveri, 1915) and the pre-reductional theory according to which the two nuclei derive from the second reductional division of oogenesis and therefore consist in the nucleus of the second-order oocyte and in a polar nucleus. The latter clearly highlights the different genotypic contribution made by the male and female somatic characteristics, evidence of which can be found in the gynandromorph forms of *H. juglandis* (Whiting and Stancati, 1931). A binucleate egg of *H. juglandis*, an insect originating from haplo-diploid germ cells, may develop either by parthenogenesis giving rise to a mosaic male (Whiting, 1928) or by fecundation of only one nucleus of the binucleate egg giving rise to a gynandromorph individual (Joly, 1977).

Fecundation anomalies may give rise to gynandromorph individuals. In fact, in an insect originating from haplo-diploid germ cells such as *Apis mellifera* (Linnaeus) (Hymenoptera Apidae), the division of an accessory sperm gives rise to male tissues (Rothenbuler *et al.*, 1952). In the condition of polyspermy and of egg binuclearity, the fecundation of both the nuclei of an egg gives rise to a gynandromorph individual, a phenomenon which has been reported in Lepidoptera with female heterogamy (Joly, 1977).

Cytogenetic aberrations liable to give rise to gynandromorph individuals may originate from different phenomena including: (i) the loss of an X chromosome during the first divisions of a normal female zygote as in *Drosophila (sic)* in which case the male portion in the resulting gynandromorph individual will be so much greater the earlier such an event has occurred in the genoma (Joly, 1977); (ii) accidental meiosis, in which case haploid cells are produced within a diploid embryo in insects where sexual determination is haplo-diploid; (iii) an opposite event which may cause a haploid cell in the embryo to become diploid; (iv) the loss of genes for sexual determination caused either by the elimination of the entire chromosome or more simply of the part containing the loci (Nilsson, 1987).

The facts so far known to lead to the differentiation of gynandromorph individuals essentially relate to atypical conditions of development and consanguinity. The role of the latter has been reported in populations of *Diprion* *pini* (Linnaeus) (Hymenoptera Diprionidae) (Beaudoin et al., 1994). The manifestation of the phenomenon in relation to the first set of causes has been reported in females of *H. juglandis* which, when exposed to temperatures of between 35 to 37°C, more frequently give rise to mosaic males or to gynandromorph individuals (Greb, 1933), as well as in individuals deriving from unfertilized eggs of diploid females of *Athalia rosae* (Linnaeus) (Hymenoptera Tenthredinidae) subjected to a thermal treatment at 36°C and parthenogenetically developed (Hatakeyama *et al.*, 1990).

This paper examines the distribution of the male, female, intermediate and malformed tissues with respect to tagmata and to the bilateral body symmetry in gynandromorph individuals in the family of Diprionids.

MATERIALS AND METHODS

The gynandromorph individuals of Diproinid Hymenoptera for which a sufficient description is available to allow a schematic description of the distribution of male tissues in female forms and vice versa include eight adults of *N. sertifer* (Watson, 1955; Heliövaara *et al.*, 1992), four adults of *D. pini* (Beaudoin *et al.*, 1994) and one adult of *Diprion similis* (Hartig) (Coppel, 1959). To these can now be added three adults of *N. sertifer* as described hereafter.[1]

Specimen A (Figure I, 1). The dimensions of this individual are those of a female. The left parietal side of the head (Figure II, 1) is black while the colour of the right side and of the frons is that typical of females. The frons prevalently comprises female tissues except for a narrow area around the antenna sclerite. The clypeus and the labrum are wholly female. The right mandible is that typical of females while the left one is that typical of males. The entire left mandible is male while only the proximal portion of the cardine of the right one is of the male colour. The left side of the occipital arch is also of the male colour. The left antenna has the dimensions, shape and colour typical of the male, while the right antenna is female. The dorsal area of the entire thorax is typical of that of males, and the fore and hind wings on both sides are also male. Except for the right fore one, which appears to be female, all the other legs are male. Female tissues can be observed in the following areas of the ventral side of the thorax: the right cervical sclerite, the right side of the basisternum, the right ventral side of the pronotum with the exception of a thin line in proximity to the suture with the episternum and the right coxa; all the other parts appear to be male (Figure III, 1). The entire abdomen is of the male type as are the external genitalia which have a normal appearance (Fig. III, 2)[2].

The individual described above was laboratory-reared, emerging on the 1st of April 1998. The parental females and males derived from 2nd instar larvae

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[1] In the graphical representation of the new subjects, broken or missing parts have been omitted, while the appendices and parts thereof which had in a way come off the rest of the body during preparation of the subjects have been shown separately.

[2] The terms used for genitals have been taken from Snodgrass (1935) and those relating to the sternothoracic region from Weber (1927).

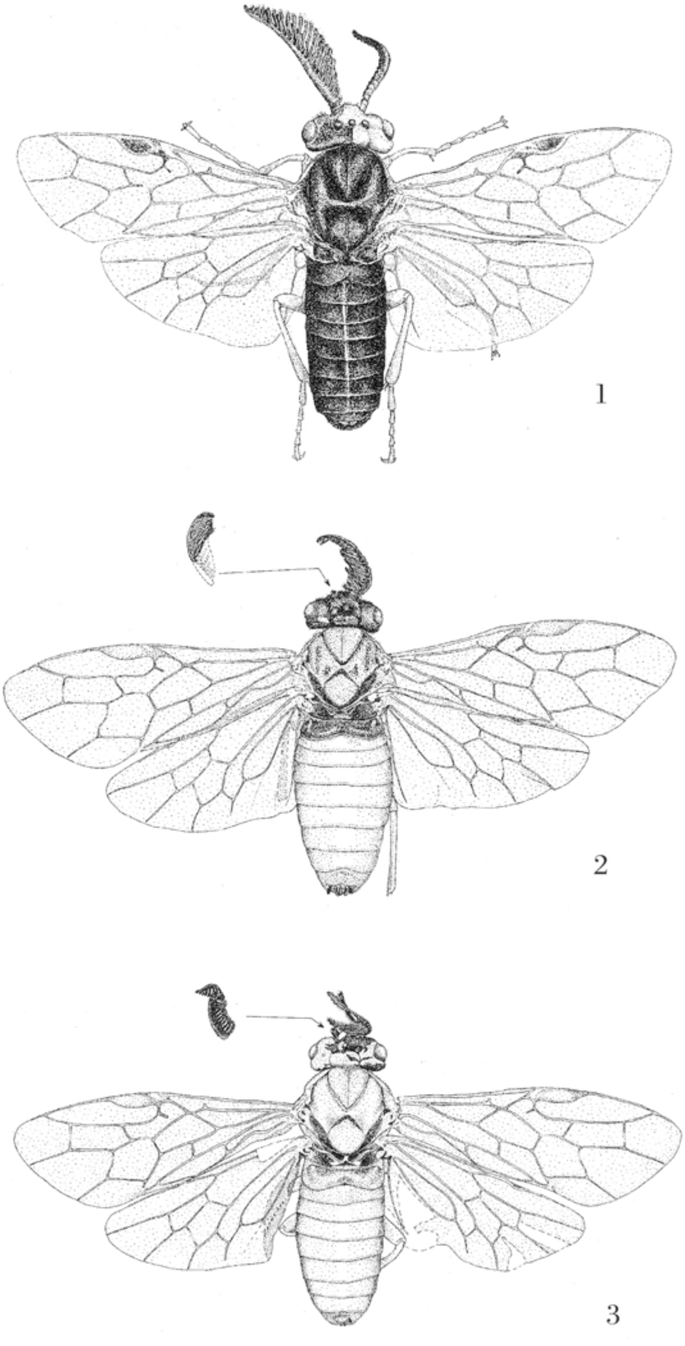

Fig. I. The three gynandromorph individuals described: 1. Specimen A; 2. Specimen B; 3. Specimen C.

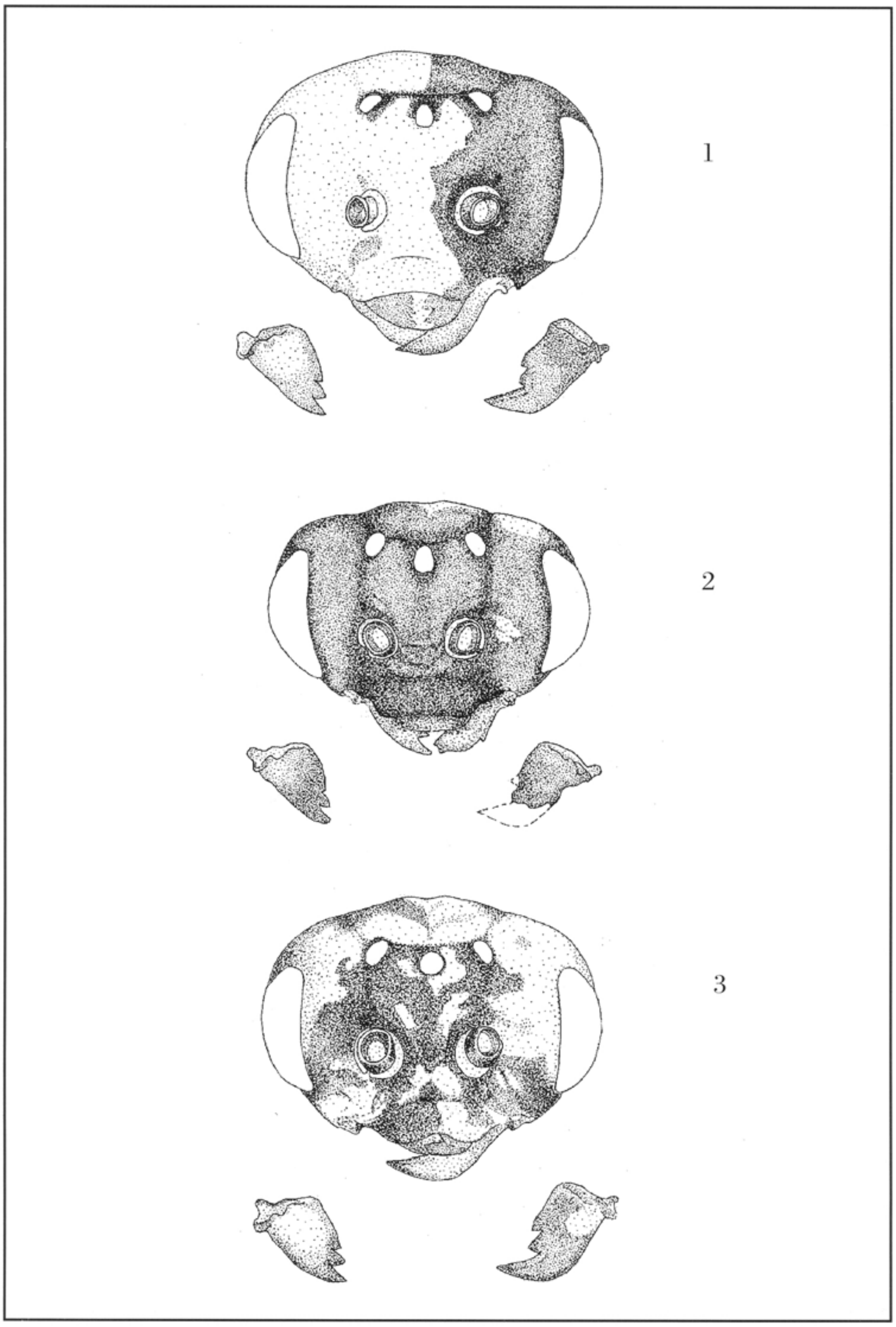

Fig. II. Front view of the crania of the three gynandromorph individuals described: 1. Specimen A; 2. Specimen B; 3. Specimen C.

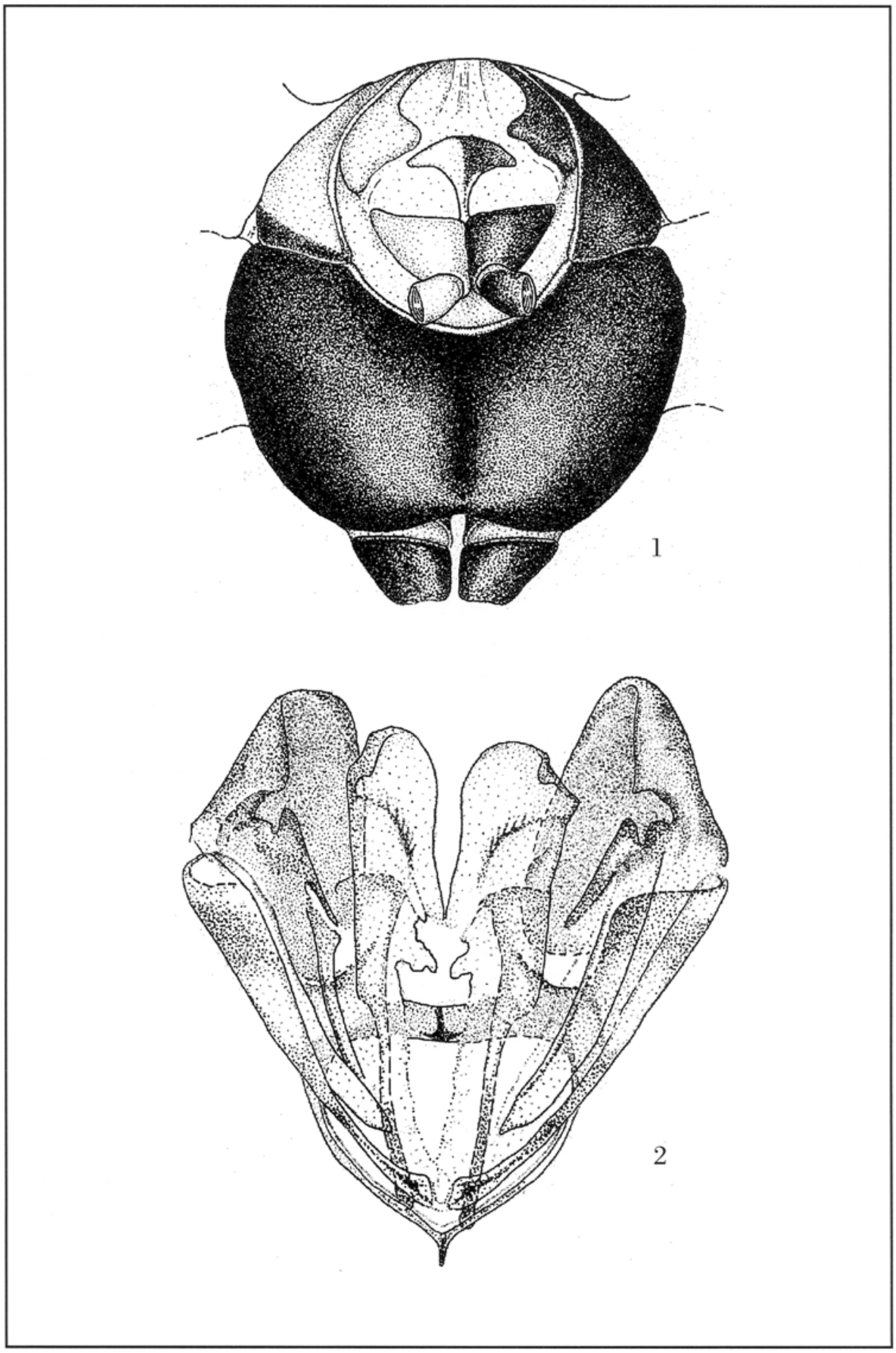

Fig. III. Specimen A: 1. Sternothorax; 2. Genital armature.

collected in a pine forest at Piola in the municipal district of Mercato Saraceno in the province of Forlì-Cesena, and were reared at a temperature of 20°C with a photoperiod of 12 hours. The cocoons were also kept under the same conditions. The adults mated upon being placed in a plastic box kept in an air-conditioned environment at 15°C with a 14-hour photoperiod. The females, kept under similar environmental conditions so as to induce oviposition, were placed together with a pot-reared three-year old sapling of *Pinus sylvestris* Linnaeus. The larvae hatched after 101 days and were kept at 20°C for a photoperiod of 12 hours; the first cocooned eonymph was reported after 45 days.

Specimen B (Fig. I, 2). Dimensions, shape and colour of the thoracic and abdominal segments are typically female. The darker colour of the first urotergum is deemed to be normal for the females of this species. The appearance of the head, of the right antenna, of the scape and of the distal portion of the left antenna (the proximal portion having been lost) is prevalently male. Only a few isolated areas of the left parietal region are light-coloured. The right mandible appears to be male as also the left one, albeit missing the distal portion (Fig. II, 2). The appearance of the maxillae and the labium has not been described because of their very bad conditions. The external genital structures and the ovipositor exhibit a normal configuration (Figs. IV.1, IV.2, IV.3, IV.4). Mature eggs were found within the ovarioles.

The individual was found on the 23rd of October 1998 on the sticky bottom of a Lund I-type trap which had been set at Sorbano in the municipal district of Sarsina in the Province of Forlì-Cesena. The trap had been set for the purpose of sampling males of *N. sertifer* as part of a study aimed at assessing the efficacy of mating disruption techniques for controlling the population of this diprionid. The trap was baited with a Celluron® dental cotton roll imbibed with 0.1 ml of a solution obtained by diluting 6 mg of the pure isomer (2*S*, 3*S*, 7*S*) of dimethylpentadecanyl acetate in 6 ml of cyclohexane [3].

Specimen C (Fig. I, 3). The dimensions and appearance of the thorax and abdomen of this individual are typically female while the characteristics of the head are intermediate between the two sexes. A closer look at this latter tagma reveals an alternation of areas having a typically female colour with black areas on the frons, clypeus, labrum, parietal regions and occipital arch. The right antenna, which is bipectinate, albeit missing several distal annuli, is of the male type while the structure of the left one would appear to be classifiable as intermediate between that of the male and that of the female given the dimensions of the scape and the fact that it is pectinate. The colour of the right mandible is typically female while that of the left one appears to be male, with the exception of a light-coloured area below the acetabulum (Fig. II, 3). The maxillae and the labium were too damaged to permit a correct interpretation of their morphological structure. The last segments of the abdomen and the external genitalia exhibited

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[3] Supplied by the Department of Chemistry and Process Technology of the Mid Sweden University, Sundsvall, Sweden.

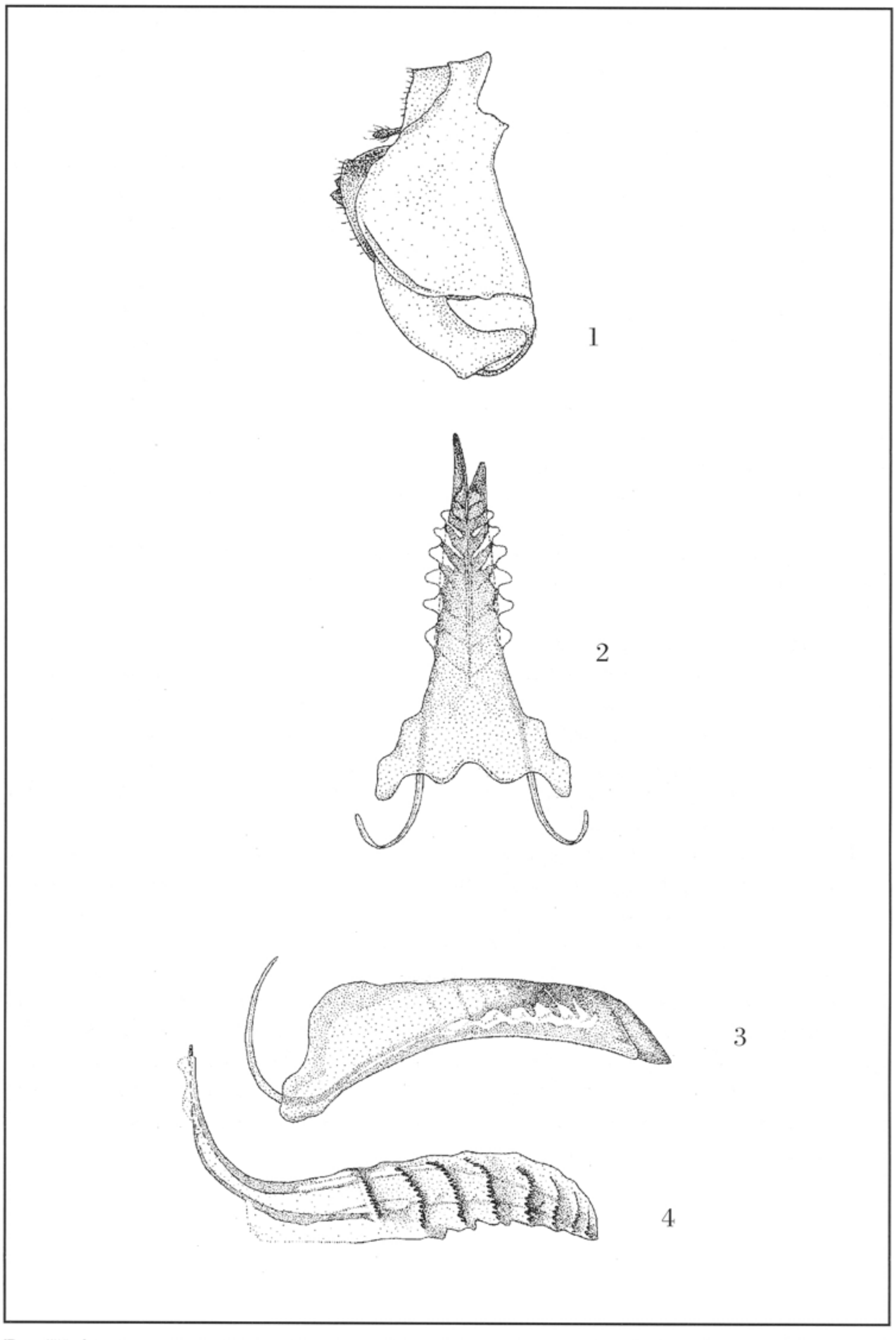

Fig. IV. Specimen B: 1. Right side view of the abdominal extremity; 2. Dorsal view of the second valvulae; 3. Left side view of the second valvulae; 4. Side view of the first left valvula.

ı anomalous asymmetry between the right- and left-hand sides. In particular, the ⟨ tergite was found to be less developed on the right side than on the left one, hile also exhibiting a dark-coloured band down along the dorsal-ventral sides. he first right valvifer has an anomalous conformation and a structure of uncertain ıterpretation. The X tergite, the right cercus and the third valvula appear to be ormal (Fig. V, 1). The entire left side has a normal external conformation (Fig. , 2). Several malformations were however found in the ovipositor, the first alvulae being of more or less normal shape except for the greater length of the rocess linking the right valvula to the valvifer (Figs. V.6 & V.7). Moreover, the econd valvulae, which in this species are merged into a single element distally ivided into two lobes, the right one being longer than the left one, exhibit in this pecimen a left lobe longer than the right one. The latter is wider in the dorso-entral direction and distally divided into three processes. Likewise, the process onnecting the second valvula to the second valvifer runs dorsally and posteriorly ı an anomalous manner (Figs. V.3, V.4 & V.5). The specimen also presents varioles containing mature eggs.

The specimen was found on the 10th of October 1997 in a Lund I-type trap hich had been set at Castello in the municipal district of Mercato Saraceno in ıe Province of Forlì-Cesena as part of a study aimed at monitoring *N. sertifer*. he trap was baited with a polyethylene vial soaked with 1 ml of the pure isomer 2*S*,3*S*,7*S*) of dimethylpentadecanyl acetate [4].

The gynandromorph subjects which were examined to ascertain tissue distribution atterns are schematically represented in Figures VI-XI which clearly show for ach individual the specific way in which the phenomenon manifests itself.

Comparison was made between the cranium, antennae, thorax, wings, legs, bdomen and genital appendices. The following phenotypic expressions were lentified for each of these parts: male-type tissues (**M**), female-type tissues (**F**), ıtermediate tissues (**Int**) and malformations (**Mf**).

Both mosaic and micromosaic tissues of male and female cells, and tissues xhibiting masculinized or feminized characteristics were classified as intermediate. nly tissues appearing abnormal were classified as malformations. Parts for which o clear-cut description was available were listed as "not described" (**?**) .

The rate of occurrence of any particular type of tissue in each tagma of each ıdividual was assessed by assigning either value 1 when the type of tissue oncerned was observed in at least one of the parts examined or value 0 in the pposite case. The overall frequency for the 16 individuals was thus determined s shown in Table 1. A similar procedure was also applied to determine the equency of the five categories on the right and left sides of the bodies of the pecimens examined (Table 2).

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[4] Supplied by the Department of Chemistry and Process Technology of the Mid Sweden niversity, Sundsvall, Sweden.

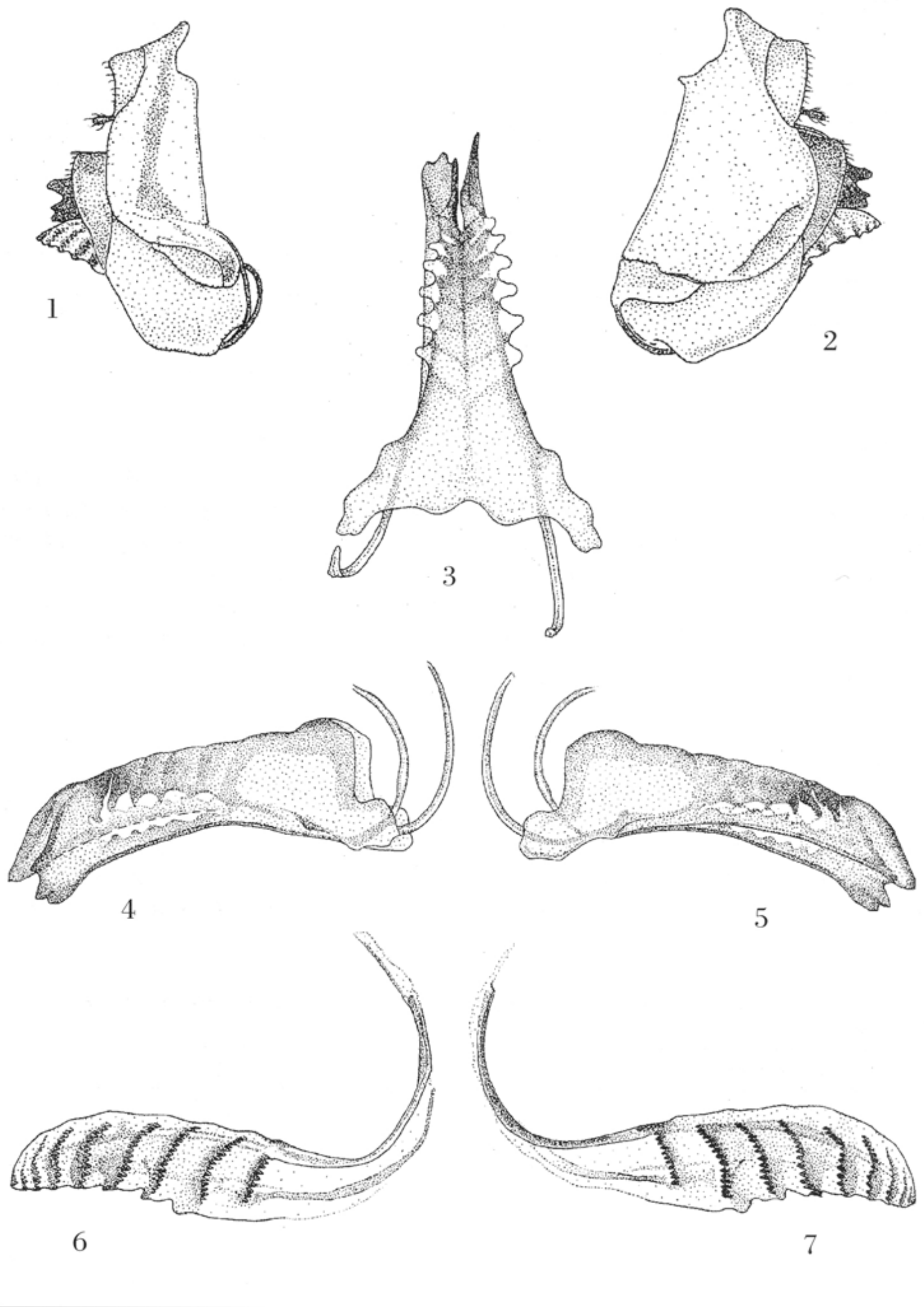

Fig. V. Specimen C: 1. Right side view of the abdominal extremity; 2. Left side view of the abdominal extremity; 3. Dorsal view of the second valvulae; 4. Right side view of the second valvulae; 5. Left side view of the second valvulae; 6. Side view of the first right valvula; 7. Side view of the first left valvula.

Tab. 1. Tissue distribution in the three tagmata (frequency)

TAGMA	M	F	Int	Mf	?
head	14	7	7	0	1
thorax	5	16	2	0	3
abdomen	5	13	3	4	1

Tab. 2. Tissue distribution on the left and right sides (frequency)

SIDE	M	F	Int	Mf	?
right-hand	13	16	9	4	4
left-hand	12	13	8	3	4

The assumption that the rate of occurrence of the different tissues is independent of the tagmata was tested by means of the χ^2 test in a 3x3 contingency table. "**Mf**" and "**?**" were not considered in the test as the frequency of the former was very low while the latter referred to undefinable parts. The hypothesis that the rate of occurrence of the different tissues was independent of the right and left sides was tested by means of the χ^2 test in a 5x2 contingency table (Zar, 1984). The distribution of single tissues between the three tagmata in a specimen was also analysed according to the χ^2 test (Siegel, 1985).

RESULTS

Given the χ^2 value obtained for the frequencies in the three tagmata the null hypothesis of equal distribution can be rejected. Vice versa, the χ^2 test value for the frequencies of the different tissues in relation to the left and right sides points to a symmetrical distribution of these tissues in the specimens examined (Table 3).

Tab. 3. Analysis of the distribution of the different tissues in the three tagmata and on the right and left sides

Comparison	test	g.l.	χ^2	P
Head-thorax-abdomen	3 x 3	4	11.736	< 0.01
Right side-left side	5 x 2	4	0.134	> 0.05

A closer examination of the frequencies of male, female and intermediate tissues in the three regions shows that the recorded dishomogeneity of distribution is ascribable to male type tissues (**M**) which are more frequently located in the head region (Table 4). Vice versa, the deviations from the expected frequencies of the female (**F**) and intermediate (**Int**) tissues in the three tagmata are not significant (Tables 5 & 6).

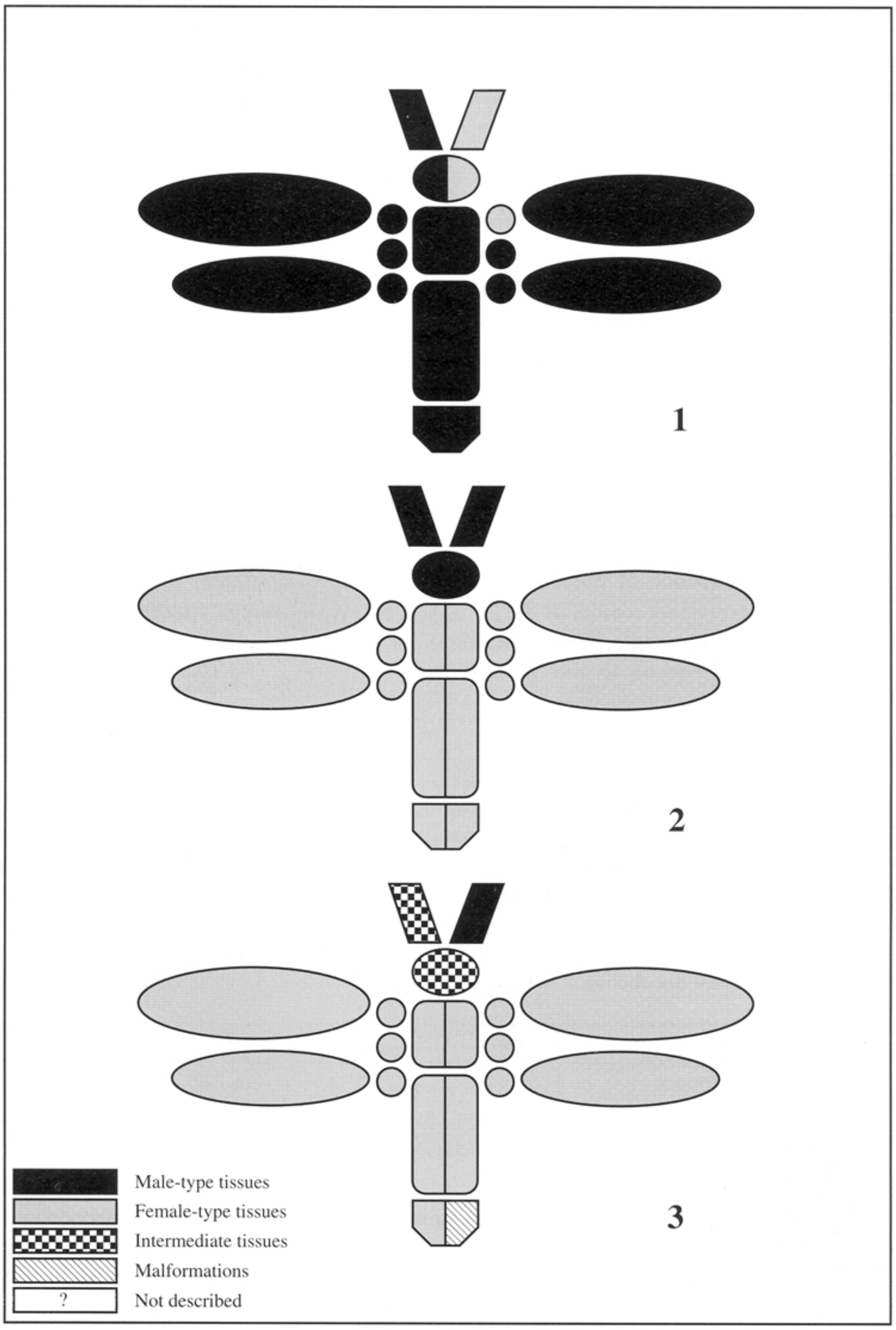

Fig. VI. A schematic representation of the distribution of different tissues in the three new gynandromorph individuals of *N. sertifer*: 1. Specimen A; 2. Specimen B; 3. Specimen C.

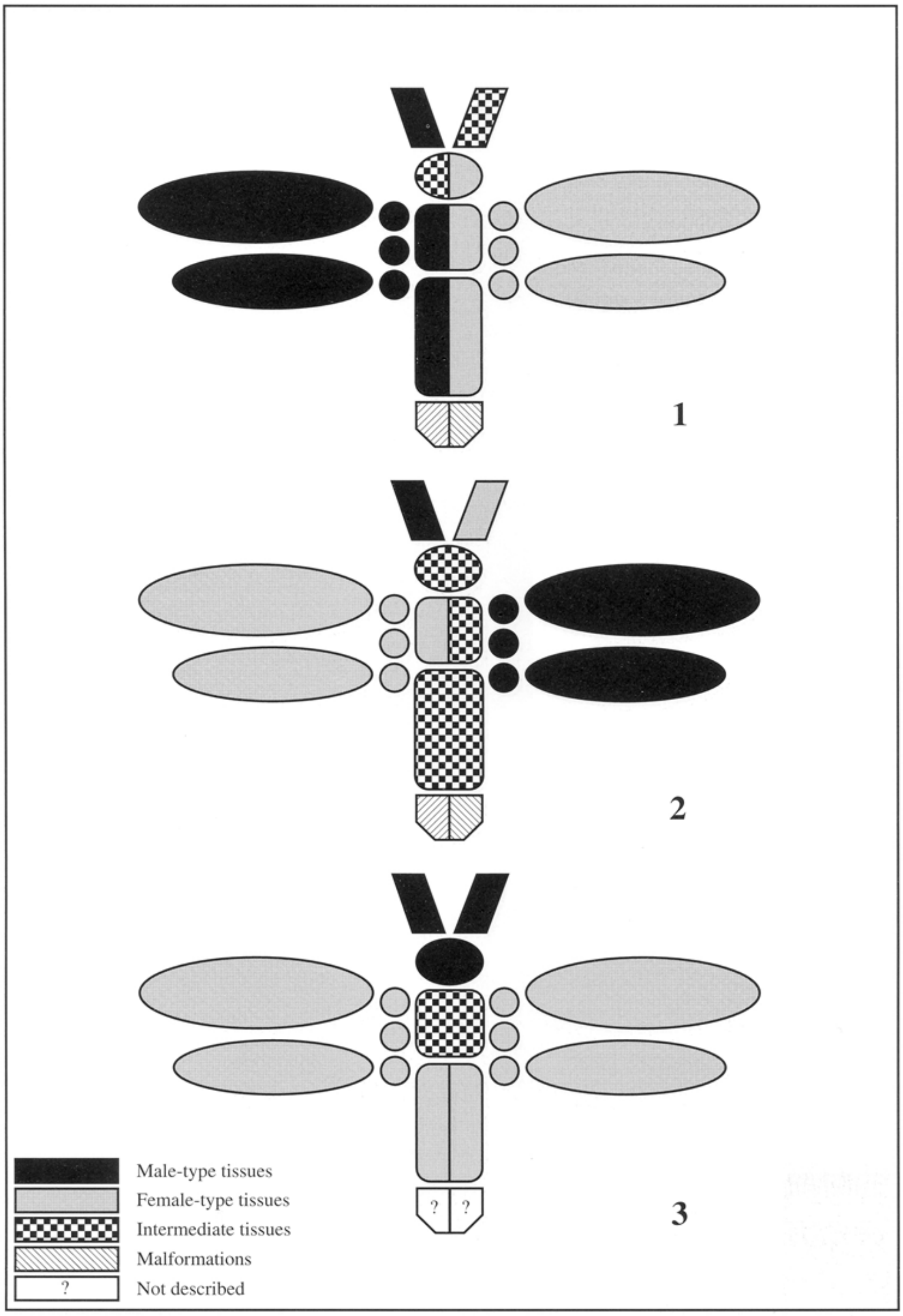

Fig. VII. A schematic representation of the distribution of different tissues in gynandromorph individuals: 1. *N. sertifer*, specimen A (Heliövaara *et al.*, 1992); 2. *N. sertifer*, specimen B (Heliövaara *et al.*, 1992); 3. *N. sertifer*, specimen C (Heliövaara *et al.*, 1992).

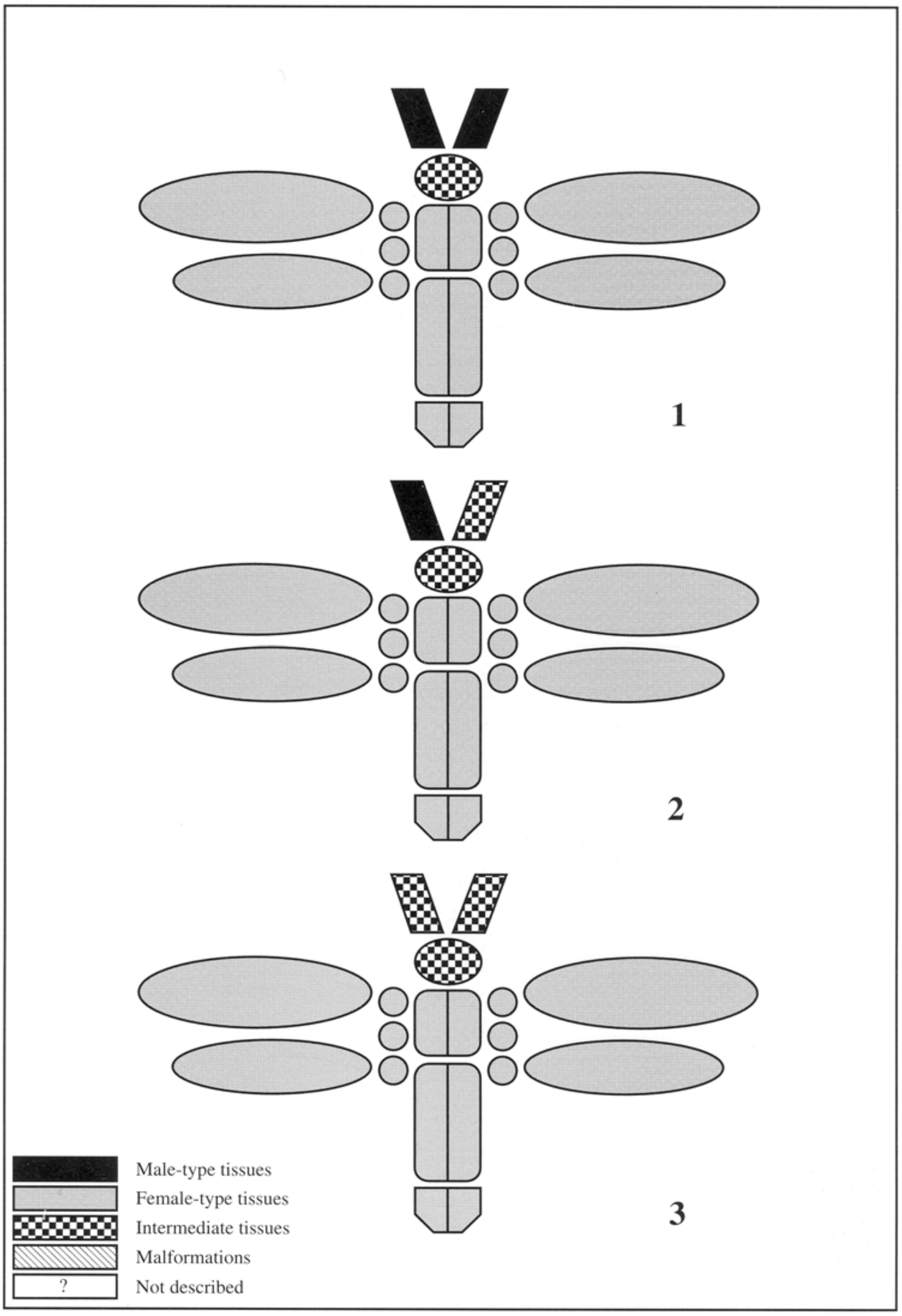

Fig. VIII. A schematic representation of the distribution of different tissues in gynandromorph individuals: 1. *N. sertifer*, specimen D (Heliövaara *et al.*, 1992); 2. *N. sertifer*, specimen E (Heliövaara *et al.*, 1992); 3. *N. sertifer*, specimen F (Heliövaara *et al.*, 1992).

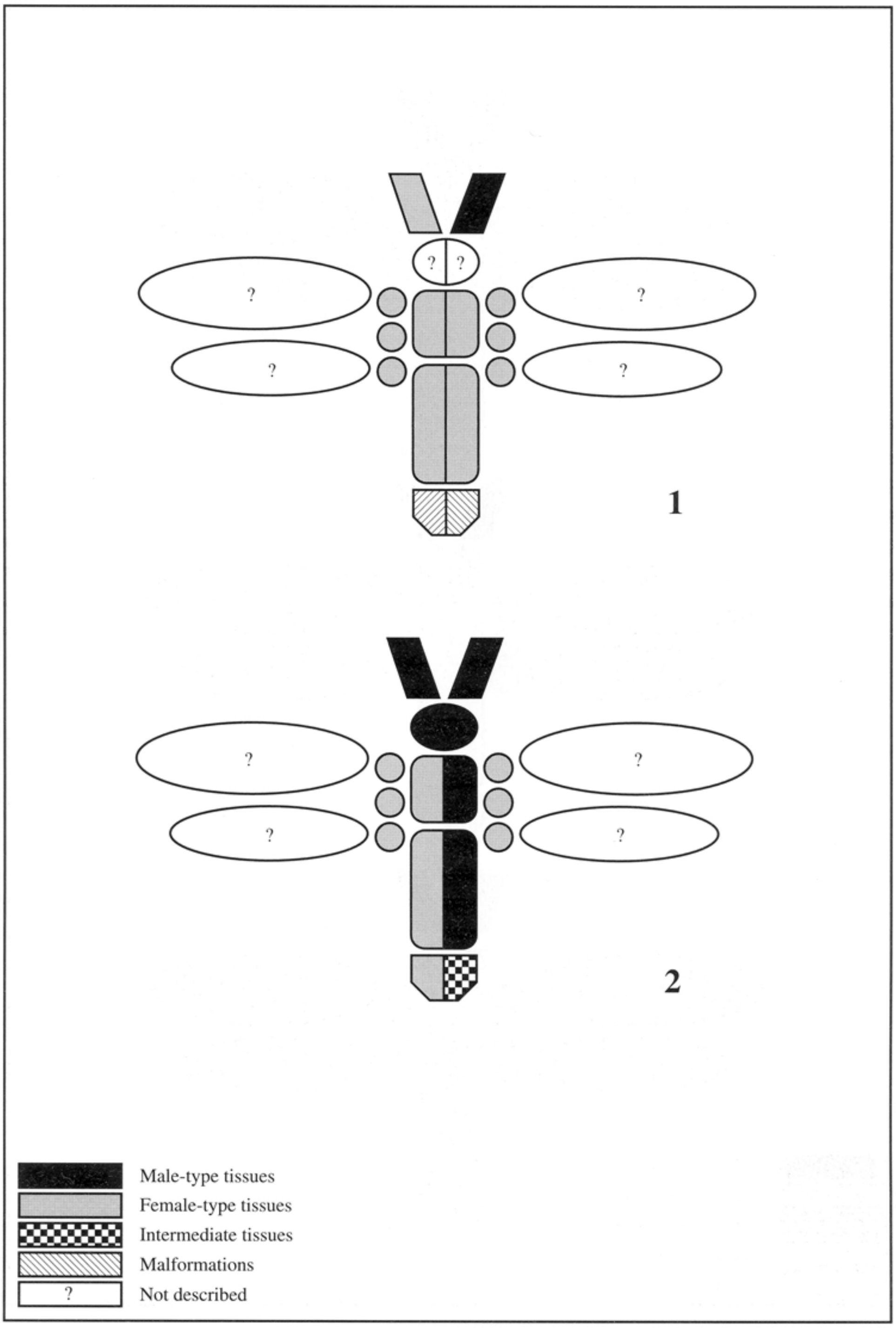

Fig. IX. A schematic representation of the distribution of different tissues in gynandromorph individuals: 1. *N. sertifer*, specimen I (Watson, 1955); 2. *N. sertifer*, specimen II (Watson, 1955).

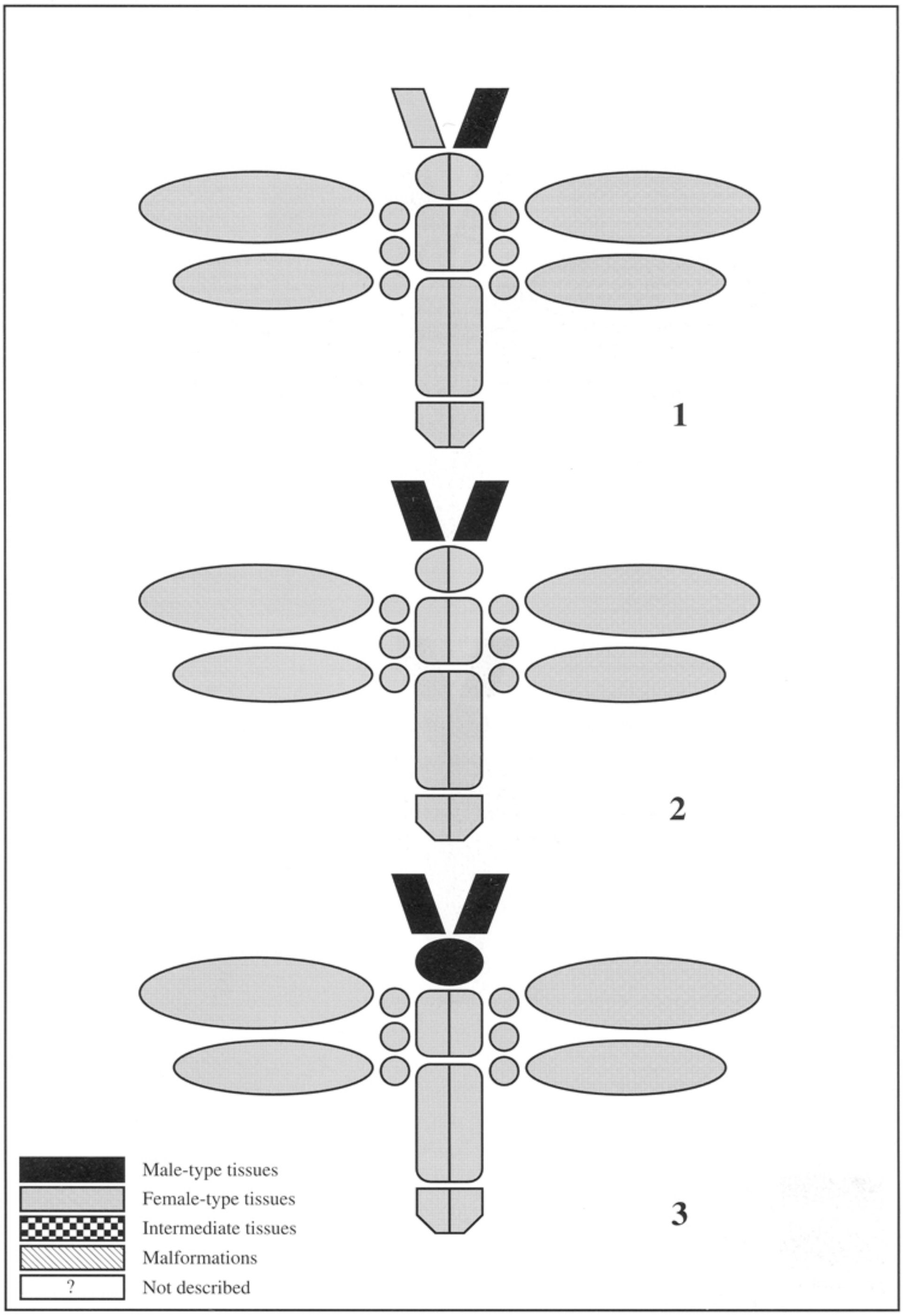

Fig. X. A schematic representation of the distribution of different tissues in gynandromorph individuals: 1. *D. pini*, specimen C (Beaudoin *et al.*, 1994); 2. *D. pini*, specimen D (Beaudoin *et al.*, 1994); 3. *D. pini*, specimen E (Beaudoin *et al.*, 1994).

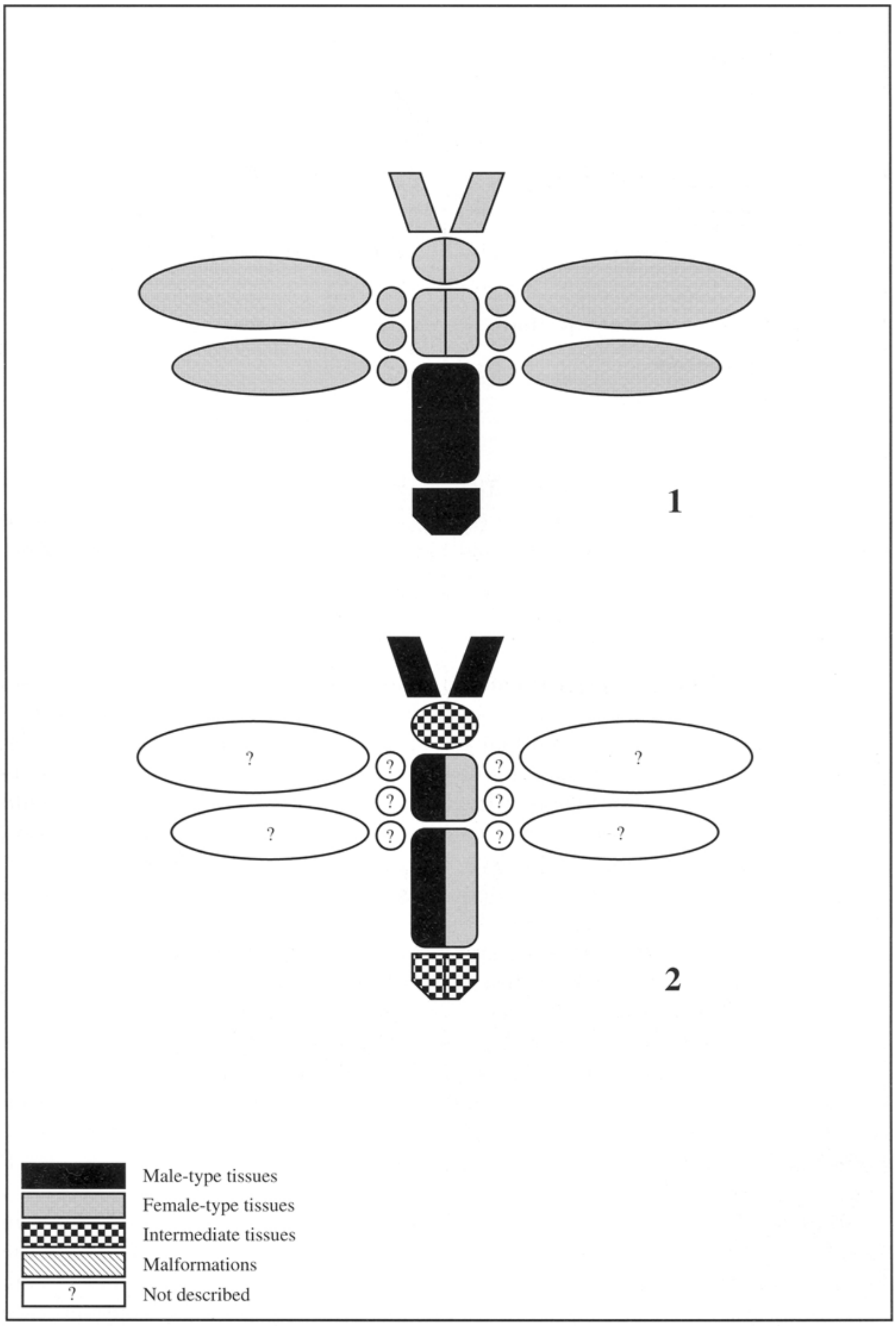

Fig. XI. A schematic representation of the distribution of different tissues in gynandromorph individuals: 1. *D. pini*, specimen F (Beaudoin *et al.*, 1994); 2. *D. similis*, (Coppel, 1959).

Tab. 4. Analysis of male type (**M**) tissue distribution in the three tagmata

Comparison	g.l.	χ^2	P
Head-thorax-abdomen	2	6.75	< 0.05

Tab. 5. Analysis of female type (**F**) tissue distribution in the three tagmata

Comparison	g.l.	χ^2	P
Head-thorax-abdomen	2	3.63	> 0.05

Tab. 6. Analysis of intermediate type (**Int**) tissue distribution in the three tagmata

Comparison	g.l.	χ^2	P
Head-thorax-abdomen	2	3.50	> 0.05

With regards malformed tissues (**Mf**), even though these were exclusively found to be located in the genitals, their frequency was so low that it was not possible to determine whether their predominant manifestation is in the abdominal region.

CONCLUSIONS

Tissue distribution in gynandromorph individuals of Diprionids clearly shows that male-type tissues are located more frequently in the head of the insect.

It can thus be safely assumed that gynandromorphism manifesting itself in the juxtaposition of male and female tissues is not a casual phenomenon but occurs according to a certain rationale which as yet cannot be explained. It would therefore be worthwhile to examine more closely the indefinite number of ways of tissue distribution reported by Nilsson (1987) for 12 individuals of different species of Aculeate Hymenoptera which, like Symphyta, are characterized by a haplo-diploid sexual determination.

Moreover, a more analytic examination of the way gynandromorphism manifests itself in the three new subjects described in this paper, is revealing.

With regards specimen A, it is first and foremost worth noting that 85% of the individual is made up of male tissues and that it is larger than a normal male. This may be accounted for by the diploidy of the male parts. Such a finding however has not as yet been reported for *N. sertifer* but it has already been observed for *Neodiprion nigroscutum* Middleton (Smith and Wallace, 1971). Then, again, dimensional anomalies have been observed also in specimens E and F (Figs. X & XI) of *D. pini* (Beaudoin *et al.*, 1994).

It should also be noted that the malformations were recorded exclusively in the abdominal region and in particular in the genitalia (Table 4). This specific location, albeit not borne out by statistical findings, may not be altogether casual.

Finally, the specimens collected at Sorbano and Castello were captured in a trap baited with synthetic sexual pheromones, similarly to the three individuals described by Heliövaara (1992). This behaviour highlights the male nature of these individuals which are otherwise prevalently female but with antennae wholly or partially of the male kind.

ACKNOWLEDGEMENTS

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SUMMARY

Gynandromorphism is a phenomenon which entails the simultaneous presence of phenotypically and genotypically male and female tissues in the same organism. The phenomenon probably results from anomalous oogenesis or fecundation or from cytogenetic aberrations during embryogenesis, and would appear to be favoured by atypical developmental conditions and consanguinity. Three new individuals of *Neodiprion sertifer* (Hymenoptera, Diprionidae) are described. The distribution of male, female, intermediate tissues and of malformations in the body of these individuals and in another eight gynandromorph specimens of the Diprionids family, is examined. The different types of tissues are symmetrically distributed on the right and left sides of the body, but male tissues are more frequently found in the head, a fact which suggests a polarity. The phenomenon is also often associated with malformations apparently limited to the genitalia. Individuals prevalently comprising female tissues but with male antennae were found to be able to detect a source of synthetic female sexual pheromone.

KEY WORDS: Gynandromorphism, Hymenoptera Diprionidae, *Neodiprion sertifer.*

Il ginandromorfismo e le sue manifestazioni negli Imenotteri Diprionidi

RIASSUNTO

Il ginandromorfismo è la condizione per cui nello stesso organismo sono presenti contemporaneamente tessuti fenotipicamente e genotipicamente maschili e femminili. Tale manifestazione è probabilmente dovuta ad anomalie della oogenesi, della fecondazione o ad aberrazioni citogenetiche durante l'embriogenesi, e pare favorita da condizioni atipiche di sviluppo e dalla consanguineità.

Tre nuovi individui di *Neodiprion sertifer* (Hymenoptera, Diprionidae) sono descritti e viene presa in esame la distribuzione nel corpo dei tessuti maschili, femminili, intermedi e delle malformazioni in questi e in altri otto esemplari ginandromorfi della famiglia dei Diprionidi.

I diversi tipi di tessuto sono distribuiti in maniera simmetrica nel lato destro e sinistro, ma quelli maschili risultano localizzati con maggior frequenza nella testa, mettendo in evidenza l'esistenza di una polarità. Il fenomeno è inoltre spesso accompagnato da malformazioni apparentemente limitate ai genitali. Gli individui, composti prevalentemente da tessuti femminili ma con antenne maschili, si sono dimostrati capaci di identificare una sorgente di feromone sessuale femminile sintetico.

PAROLE CHIAVE: Ginandromorfismo, Hymenoptera Diprionidae, *Neodiprion sertifer.*

REFERENCES CITED

BEAUDOIN L., GERI C., ALLAIS J.P., GOUSSARD F., 1994. - Influence of consanguinity on the sex-ratio and diapause of *Diprion pini* L. (Hym., Diprionidae) populations. - *J. Appl. Ent.* 118(3): 267-280.

Belfiore C., 1979. - A gynandromorph *Baetis pavidus* Grandi M. 1949 (Ephemeroptera: Baetidae). *Bollettino- Associazione Romana di Entomologia* 33 (1/4): 50-52. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

Berry S.J., 1985. - Reproductive system: Sex determination. In: Blum, 1985. - Fundamental of Insect Physiology. 598 pp. - *John Wiley & Sons Ed.* New York.

Boveri Th., 1915. - Über die Entstehung der Eugsterschen Zwitterbienen. *Arch. f. Entw. Organismen*, 41: 264. - In: Whiting P.W., Stancati M.F., 1931. - A gynandromorph of *Habrobracon* from a post-reduced binucleate egg. - *Biol. Bull.* 61: 481-484.

Carlberg U., 1981. A gynandromorph specimen of *Extatosoma tiarum* (MacLeay) (Insecta: Phasmidae). *Zoologischer Anzeiger* 207 (5/6): 320-322. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

Clarke F.C., Rechav Y., 1992. - A case of gynandromorphism in *Amblyomma hebraeum* (Acari: Ixodidae). *Journal of Medical Entomology* 29 (1): 113-114. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

Coppel H.C., 1959. - A Sex Anomaly of the introduced Pine Sawfly, *Diprion similis* (Htg.) (Hymenoptera: Diprionidae). *Entomol. News* 70 (8): 223.

Correas C.L., Mora D.G., Carricondo F.J., 1996. - Un ginandromorfo de *Culex pipiens* Linnaeus, 1758 (Diptera, Culicidae) en Madrid (España). *Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.)* 92 (1-4): 221-223.

Gack C., von Helversen O.V., 1976. - Behaviour of a gynandromorph wolfspider (Arachnidae: Araneae: Lycosidae). *Entomologia Generalis* 3 (1/2): 109-118. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

Gordh G., Gulmahamad, H., 1975. - A bilateral gynandromophic *Xylocopa* taken in California (Hymenoptera: Apidae). - *Proc. Entomol. Soc. Wash.*, 77 (3): 269-273

Graves R.C., Yoon J.S., Durbin E.J. 1986. - A gynandromorph in the Madagascar Hissing Cockroach, *Gromphadorhina portentosa* (Blattodea: Blaberidae). *Ann. Entomol. Soc. Am.* 79 (4): 662-663.

Greb R. J., 1933. - Effects of temperature on production of mosaics in *Habrobracon*. *Biol. Bull.* 65: 179-186.

Halstead J.A., 1988. - A gynandromorph of *Hockeria rubra* (Ashmead) (Hymenoptera: Chalcididae). - *Proc. Entomol. Soc. Wash.* 90 (2): 258-259.

Hatakeyama M., Nakamura T., Kim K.B., Sawa M. Naito T., Oishi K., 1990. - Experiments inducing prospective polar body nuclei to partecipate in embryogenesis of the sawfly *Athalia rosae* (Hymenoptera). - *Roux's Arch. Dev. Biol.* 198(7): 389-394.

Heliövaara K, Väisänen R., Varama M., and Viitsaari, M., 1992. - Gynandromorphic individuals of *Neodiprion sertifer* (Hymenoptera, Diprionidae). - *Entomologica Fennica*, 3 (3): 149-153.

Johnson P.T., Otto S.V., 1981. - Histology of a bilateral gynandromorph of the Blue Crab, *Callinectes sapidus* Rathbun (Decapoda: Portunidae). - *Biol. Bull.* 161(2): 236-245.

Joly P., 1977. -Le développement postembryonnaire des insectes: la différenciation sexuelle. In P.P. Grassé: Traité de zoologie, Tome VIII, fascicule V-A, *Masson Ed.*

Jones S.R., Phillips S.A.Jr., 1985. - Gynandromorphism in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). - *Proc. Entomol. Soc. Wash.*, 87 (3): 583-586.

Laugé G., 1985. - Sex Determination: Genetic and Epigenetic Factors. In: Kerkut G.A., Gilbert L.I., Comprehensive Insect Physiology Biochemistry and Pharmacology, Vol. 1 Embryogenesis and reproduction. - *Pergamon Press*, Oxford.

Maxwell D.E., 1956. - Sawfly Cytology with Emphasis Upon the Diprionidae (Hymenoptera: Symphyta). - *Proceed. Tenth Int. Congr. Ent.* 2: 961-978.

Mey W., 1982. - A bilateral gynandromorph of *Anabolia lurcata* Brauer (Insecta, Trichoptera). *Zoologischer Anzeiger* 209 (5/6), 394-396. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

MILLER D.R., WILLIAMS D.J., 1993. - Systematic revision of the Family Micrococcidae (Homoptera: Coccoidea), with a discussion of its relationships, and a description of a gynandromorph. *Boll. Lab. Ent. agr. Filippo Silvestri*, 50: 199-247.

NAITO T., SUZUKI H., 1985. - Sex determination in sawflies (Hymenoptera). - *Jpn. J. Genet*. 60: 646. - Citato da: HATAKEYAMA M., NAKAMURA T., KIM K.B., SAWA M. NAITO T., OISHI K., 1990. - Experiments inducing prospective polar body nuclei to partecipate in embryogenesis of the sawfly *Athalia rosae* (Hymenoptera). - *Roux's Arch. Dev. Biol.* 198(7): 389-394.

NAITO T., SUZUKI H., 1991. - Sex determination in Sawfly, *Athalia rosae ruficornis* (Hymenoptera): Occurence of Triploid Males. - *Journal of Heredity* 82: 101-104.

NILSSON G.E. 1987. - A gynandromorphic specimen of *Evylaeus albipes* (Fabricius)(Hymenoptera, Halictidae) and a discussion of possible causes of gynandromorphism in haplo-diploid insects. - *Notulae Entomologicae*, 67: 157-162.

NOVÁK V.J.A. 1975. - Insect hormones. - *Chapman and Hall*, London.

ROBINSON R., 1971. *Lepidotera Genetics*. Pergamon Press, Oxford. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

ROTHENBUHLER W.C., 1952. - Androgenesis with zygogenesis in gynandromorphic honeybees (*Apis mellifera* L.). - *Science*, 115: 637-638.

RUPPEL R.F., 1971. - An asymmetrical gynandromorph of *Cerotoma facialis* (Coleoptera: Galeruceidae). *Michigan Entomologist* 4 (1): 1-2. In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

SCUPOLA A., 1994. - Un caso di ginandromorfismo in *Myrmica* Latr. (Hymenoptera Formicidae). - *Boll. Soc. ent. ital. Genova*, 125 (3): 252-254.

SIEGEL S., 1985. - Statistica non parametrica: per le scienze del comportamento. XVI + 269 pp. - *Organizzazioni Speciali*, Firenze.

SMITH S.G., WALLACE D.R., 1971. - Allelic sex determination in a lower Hymenopteran, *Neodiprion nigroscutum* Midd. - *Can. J. Genet. Cytol.* 13: 617-621.

SNODGRASS R.E., 1935. - Principles of Insect Morphology, *Mc Graw-Hill Book Company*, New York and London, 1935.

WATSON W.Y., 1955. - Two gynandromorphic sawflies. *Bim.Progr. Rep. Div. For. Biol. Dep. Agric. Can.* 11 (3): 1.

WEBER H., 1927. - Die Gliederungder Sternalregion des Tenthredinidenthorax. *Allgemeine Zeitschrift fur Entomologie*, Bd. XXII, 6/8: 161-198.

WHITE M.J.D., 1968. - A gynandromorphic grasshopper produced by double fertilisation. *Australian Journal of Zoology* 16 (1), 101-109. - In: Gemeno C., Anton S., Zhu J.W. e Haynes K.F.,1998. - Morphology of the reproductive system and antennal lobes of gynandromorphic and normal black cutworm moths, *Agrotis ipsilon* (Hufnagel)(Lepidoptera: Noctuidae). - *Int. J. Insect Morphol. & Embryol.*, 27 (3): 185-191.

WHITING P.W., 1943. - Mosaicism and mutation in *Habrobracon*. - *Biol. Bull.* 54: 289-306.

WHITING P.W., 1943. - Multiple alleles in complementary sex determination of *Habrobracon*. - *Genetics* 28: 365-382.

WHITING P.W., STANCATI M.F., 1931. - A gynandromorph of *Habrobracon* from a post-reduced binucleate egg. - *Biol. Bull.* 61: 481-484.

WHITING P.W., GREB R.J., SPEICHER B.R., 1934. A new type of sex-intergrade. *Biol. Bull.* 66: 152-165.

ZAR J.H., 1984. - Biostatistical Analysis. 718 pp. - *Prentice Hall*, New Jersey.

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