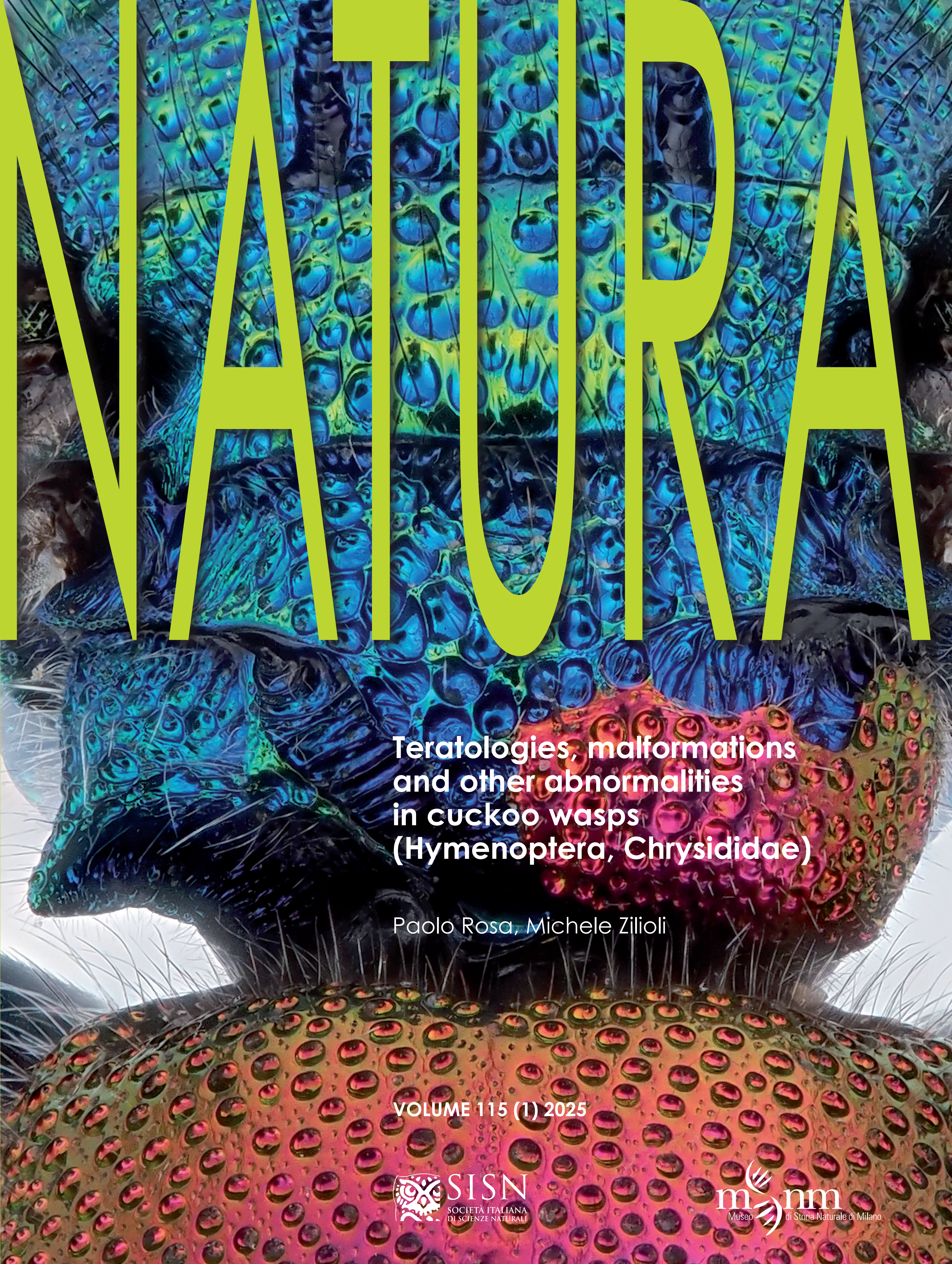

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Paolo Rosa
Laboratory of Zoology, Research Institute for Biosciences,
University of Mons, Belgium
E-mail: paolo.rosa@umons.ac.be

Michele Zilioli
Museo di Storia Naturale, Milan, Italy
E-mail: michele.zilioli@comune.milano.it

In copertina
Case of mesosoma heterotopy in *Chrysura radians*, detail of metasomal tissue on the propodeum. / Caso di eterotopia mesosomale in *Chrysura radians*, dettaglio di tessuto metasomale sul propodeo.
(Foto: Daniele Baiocchi)

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Abstract - The present publication is the first illustrated catalogue of morphological aberrations observed in a family of non-social hymenopterans. Cephalic, thoracic, abdominal, and appendicular aberrations are recorded. Traditionally, only single cases of aberrations are documented in the literature but we here illustrate 163 cases of malformed Chrysididae observed on a total of 809 specimens recorded, including cases of anarthrogenesis, aplasia, asymmetry, atavism, ectromely, epigastrochisis, helicomery, hemiaplasy, heteromorphosis, heterotopy, hypertrophy, microcephaly, nanism, polymelia, polymery, polyocularism, schistomely, somatomely, symphysocery, symphysomery, tumor-like conditions and cuticular perforations, gynandromorphy and other uncategorized aberrations. Coloration abnormalities, like asymmetric coloration, depigmentation, melanism, rufinism and other variations are also reported. Moreover, new teratological cases are reported for Hymenoptera for the first time, such as a specimen with five legs and five wings, the potential development of embryonic, heteromorphic antenna on legs, and the occurrence of metasomal tissue on mesosoma. Based on material recently collected in Italy, malformations in general were observed in 3.72% of the cases (n= 609) on a total of 16,339 examined and 0.13% for the most spectacular cases, which is in any case a considerably higher percentage than those previously recorded in Hymenoptera and Coleoptera studies based on samples exceeding 10,000 individuals.

Key words: aberration, Cuckoo wasps, Deformed Wing Virus, gynandromorph, morphology.

Riassunto - Teratologie, malformazioni e altre anomalie nelle vespe cuculo (Hymenoptera, Chrysididae).

La presente pubblicazione rappresenta il primo catalogo delle aberrazioni morfologiche osservate in una famiglia di imenotteri non sociali, comprendendo malformazioni riscontrate in tutte le parti del corpo.

Vengono registrate aberrazioni cefaliche, toraciche, addominali e appendicolari. Tradizionalmente, in letteratura vengono documentati solo casi isolati di aberrazioni, ma qui illustriamo 163 casi di crisidi malformati osservati su un totale di 809 esemplari registrati, includendo casi di anartrogenesi, aplasia, asimmetria, atavismo, ectromelia, epigastrochisi, elicomeria, semiaplasia, eteromorfosi, eterotopia, ipertrofia, microcefalia, nanismo, polimelia, polimeria, poliocularismo, schistomelia, somatomelia, sinfisoceria, sinfisomeria, condizioni simili a tumori e perforazioni cuticolari, ginandromorfismo e altre aberrazioni non categorizzate. Vengono anche riportate anomalie nella colorazione, come colorazione asimmetrica, depigmentazione, melanismo, rufinismo e altre variazioni. Inoltre, nuovi casi teratologici sono riportati per la prima volta negli Imenotteri, come un esemplare con cinque zampe e cinque ali, il potenziale sviluppo di antenne embrionali eteromorfiche sulle zampe e la presenza di tessuto metasomale nel mesosoma. Basandosi su materiale recentemente raccolto in Italia, le malformazioni in generale sono state osservate nel 3,72% dei casi (n = 609) su un totale di 16.339 esemplari esaminati e nello 0,13% dei casi più spettacolari, una percentuale comunque considerevolmente più alta rispetto a quanto precedentemente registrato in studi su Imenotteri e Coleotteri basati su campioni superiori a 10.000 individui.

Parole chiave: aberrazione, ginandromorfo, morfologia, vespe cuculo, Virus delle Ali Deformi.

INTRODUCTION

Teratologies are structural abnormalities named “monstruosités” by Balazuc (1948, 1958), who provided a complete classification and terminology for the malformations found in arthropods (Balazuc, 1948, 1952, 1969), and Hymenoptera in particular (1958). These so called “monsters” are usually specimens with one or more astonishing anatomical parts incompatible with the diagnosis of the taxon to which the species belongs (Savini & Furth, 2004). Malformations may affect all body segments from head to abdomen, including appendages and genitalia. Gynandromorphy is probably the best-known of these phenomena, in which an organism possesses tissue that is genotypically and phenotypically both male and female (Narita *et al*., 2010), thus showing male and female characters.

Among the other aculeate hymenopterans, a large number of malformations were reported, and historical publications were summarized by Balazuc (1958), while recent ones are reported in the following results and discussion for comparison. In most families, the description of gynandromorphs represent the majority of the contributions; in Anthophila, for example, more than 110 species in 29 genera were recorded (Michez *et al*., 2009; Hinojosa-Díaz *et al*., 2012), and more than another 25 cases were newly recorded in the last years (e.g., Brau & Michez, 2025).

The exact origin of these aberrations is usually challenging to establish, and it is obvious that serious malformations cannot be noticed in nature because deleterious and lethal. They can arise from genetic mutations or morphological disturbances during different developmental stages due to physiological abnormalities in hormonal regulation of molting processes. Moreover, malnutrition, environmental and chemical agents, such as temperature changes, humidity, radiation and pollutants (Safavi, 1968; Berndt & Wisniewski, 1984; Wcislo *et al*., 2004), or even mechanical nest crushes may produce damage or deformations of the adult cuticle (Balazuc, 1958). Other causes may be related to viruses, like the Deformed Wing Virus (DWV), and parasitism as in the case of attack by stylops (Portman & Griswold, 2016) and Nematoda Mermithidae (Laciny, 2021).

Teratological cases are generally considered rare and are traditionally documented on a case-by-case basis (e.g., Engel *et al.,* 2014; Lohrmann & Engel, 2015; Peters & Gibbs, 2024). This publication presents the first comprehensive, illustrated review of morphological aberrations within an entire hymenopteran aculeate family, excluding social species such as honeybees and ants. In social species, major studies have been possible due to the availability of a multitude of specimens and the possibility to breed them in captivity (e.g., Buschinger & Stoewesand, 1971). The aim of the contribution is to provide an illustrated catalog with an overview of teratological cases and various abnormalities observed by the authors, along with a comparative analysis of similar cases documented in other Hymenoptera, or other orders.

The family Chrysididae includes around 3000 aculeate wasps distributed all over the world, and are subdivided into four subfamilies: Amiseginae, Chrysidinae, Cleptinae, and Loboscelidiinae (Kimsey & Bohart, 1991). They are known with the vernacular names of *cuckoo wasps*, for their parasitic and cleptoparasitic behavior, and *jewel wasp*, *gold wasps* or *ruby-tailed* wasps, for their brilliant colorations (Paukkunen *et al*., 2015).

In their larval stages, they develop in the nests of other insects, primarily solitary bees, wasps, and sawflies, exploiting their hosts either as parasitoids or cleptoparasites. Larvae of Cleptinae develop on the prepupae of sawflies (Symphyta, mostly Tenthredinidae); larvae of Chrysidinae parasitize the nests of solitary bees (Megachilidae), solitary wasps (Sphecidae, Crabronidae s.l., and Vespidae, such as Eumeninae and Masarinae) and moths in the family Limacodidae in case of *Praestochrysis species.* The small subfamilies Amiseginae and Loboscelidiinae, which occur only marginally in the Palaearctic and are absent from Europe, are unique in parasitizing the eggs of walking sticks (Phasmatodea). Secondary food sources, when available, may include caterpillars of Lepidoptera, beetle larvae or adults, aphids, or even spiders. Unlike ordinary parasites, parasitoid larvae always kill their host, as they develop at the expense of mature larvae or prepupae. By contrast, cleptoparasitic larvae consume the food supplies collected by the host for its own offspring. In some cases, a cuckoo wasp larva may combine both strategies: first acting as a parasitoid by devouring the host egg or young larva, and later behaving as a cleptoparasite when feeding on the stored provisions (Wiesbauer *et al*., 2020). Oviposition usually takes place directly into the brood cell of the host at a precise moment of the provisioning cycle, or just after the cell has been finally sealed (Wiesbauer *et al*., 2020). Female cuckoo wasps exhibit a remarkable diversity of behaviors related to host detection and egg-laying, reflecting the type of host and the larval feeding strategy.

Despite these general patterns, the biology of Chrysididae remains poorly known. Most studies report only the presumed host identity, while strategies of host location, nest intrusion, host recognition, and larval development are still largely unexplored. Nevertheless, several remarkable behaviours have been revealed in recent years (Kroiss *et al*., 2009; Veenendaal, 2011, 2012; Martynova & Fateryga, 2014; Paukkunen *et al*., 2015; Winterhagen, 2015; Wurdack *et al*., 2015; Bocca *et al*., 2023)

Some teratological cases have been already described and illustrated for cuckoo wasps so far. Recorded aberrations of the head include the unilateral antennal heteromorphosis of a *Chrysis elegans* illustrated by Linsenmaier (1959), the supernumerary antenna of a *Holopyga rubra* illustrated by Linsenmaier (1999), the asymmetric heads of *Rhadinoscelidia malaysiae* illustrated by Kimsey (2018) and a quadriocellar *Hedychridium caeruleum* described by Peters & Gibbs (2024). Numerous cases of metasomal teratologies were also recorded, like the epigastroschisis of two *Holopyga* by Negru (1955, 1958); two aberrant specimens of *Chrysis* by Móczár (1963); the symphysomeries of *Hedychridium* and *Anachrysis* species, some cases of epigastroschisis and helicomery in *Hedychrum* by Rosa (2024a). Finally, Rosa (2024b) illustrated two cases of supernumerary cells in forewings of *Trichrysis*. Gynandromorphs were described by Strumia (2004) and Rosa (2019a) for Cleptinae and by Wolf (2004) and Rosa & Zettel (2018) for Chrysidini and Elampini, respectively. Recently, images of malformed specimens were also published online (www.chrysis.net/forum, www.forumentomologiitaliani.it; www.inaturalist.com) illustrating melanic specimens, cuckoo wasps with deformed eyes, but also interesting aberrations, like a specimen with five wings and five legs (illustrated below).

MATERIALS AND METHODS

This study is based on the following data: i) data taken from literature; ii) exceptional aberrant specimens observed by the first authors in the following museum and private collections: Kyushu University, Faculty of Agriculture, Fukuoka (KUM, Japan); Muséum National d'histoire naturelle, Paris (MNHN, France); Museum für Naturkunde, Berlin (MfN, Germany); Naturhistorisches Museum, Wien (NHMW, Austria); Natur-Museum, Luzern (NMLU, Switzerland); Naturalis, Leiden (RMNH, The Netherlands); Zoological Institute, St. Petersburg (ZISP, Russia), and in the private collections of Daniele Baiocchi (Rome, Italy, DBC), Daniele Sechi (Cagliari, Italy, DSC), Thibault Le Pen (Marseille, France, TLPC) and Marek Halada (Ceske Budejovice, Czech Republic, MHC); (iii) specimens from the collection of the first author (PRC), with some of the illustrated specimens collected by the second author (MZC). When the collection is not given in the text, the specimen is preserved in PRC. The collection of teratologies of the authors has been deposited at the Museo di Storia Naturale di Milano (MSNM, Italy) and kept apart from the general Chrysididae collection; all specimens were encoded as in file provided in the supplementary material.

Terminology and classification for chrysidids follows Kimsey & Bohart (1991). Terminology for teratologies follows partially Balazuc (1948, 1958). Balazuc (1948, 1958) grouped together certain morphological malformations under the name of dysplasia, referring to defects in the maturation of the imago and mechanical crushes. However, in modern usage, the term dysplasia describes the abnormal cellular development of an organ or tissue (Damjanov, 2009) often resulting from exposure to physical chemical or biological agents and this term is not used in the text to avoid confusion. Although Balazuc's dysplasias are not true "monstrosities", they are sometimes comparable to teratologies and may equally affect the abilities of the individuals. They are therefore worth evaluating and illustrating. These malformations are relatively common, and in Chrysididae they are typically visible on the metasoma and likely due to the position of the pupa in the nest or cocoon, and they often result from mechanical pressure exerted by nest crushes at pupal stage leading to malformations in the emerging imago. Other malformations may arise during metamorphosis due to abnormal environmental conditions, such as temperature and humidity at the time of outbreak, which delay skin dehiscence (Earls *et al*., 2023). Additionally, anaemia by haemorrhage caused shortly before pupation can also lead to imaginal malformations. Insects with such deformities often have a precarious life, and become easy prey for predators (e.g., Møller & Swaddle, 1997).

This monograph is based on illustrations and records of teratological cases documented from numerous collections from all over the world, but focusing on Palaearctic specimens. However, to ensure a robust analysis of the frequency of different case types for the final discussion, we focused specifically on the Italian Chrysididae collection of the first author. For this purpose, we carefully examined 16,339 specimens collected over a relatively short time span in the 1990's and from a limited number of localities, allowing us to assess potential trends.

Since the present monograph focuses on morphological aberrations within Chrysididae, the terminology of body parts and appendages used here is schematized to aid the reading and comprehension of the text. The body of cuckoo wasp (Fig. 1) is divided into three parts: head, thorax and abdomen. However, aculeate hymenopterans exhibit a peculiar thoracic-abdominal morphology, commonly known as the "wasp waist". This appears as a conspicuous constriction between the thorax and abdomen. In reality, the first abdominal segment (the propodeum) is fused with the thorax, and the "wasp waist" is therefore located between the first and second abdominal segments, the latter being the first visible segment of the abdomen. For this reason, the thorax-propodeum complex is called the "mesosoma", while the remaining abdominal segments are collectively called the "metasoma".

The head of cuckoo wasps (Fig. 2) always bears by two large compound eyes and three ocelli arranged in a triangle pattern on the vertex. The following parts are of particular systematic value: the shape and sculpture of the facial cavity (or scapal basin); the area between the lower margin of the eye and the insertion of the mandibles, known as malar spaces; and the relative length of the antennal segments. In both sexes, the antennae consist of 13 articles: scape, pedicel and 11 flagellomeres, all with a cylindrical section.

The mesosoma includes the pronotum, mesonotum, metanotum and propodeum. The pronotum has taxonomic significance in members of the genus *Cleptes*. The mesonotum is subdivided in mesoscutum and scu-

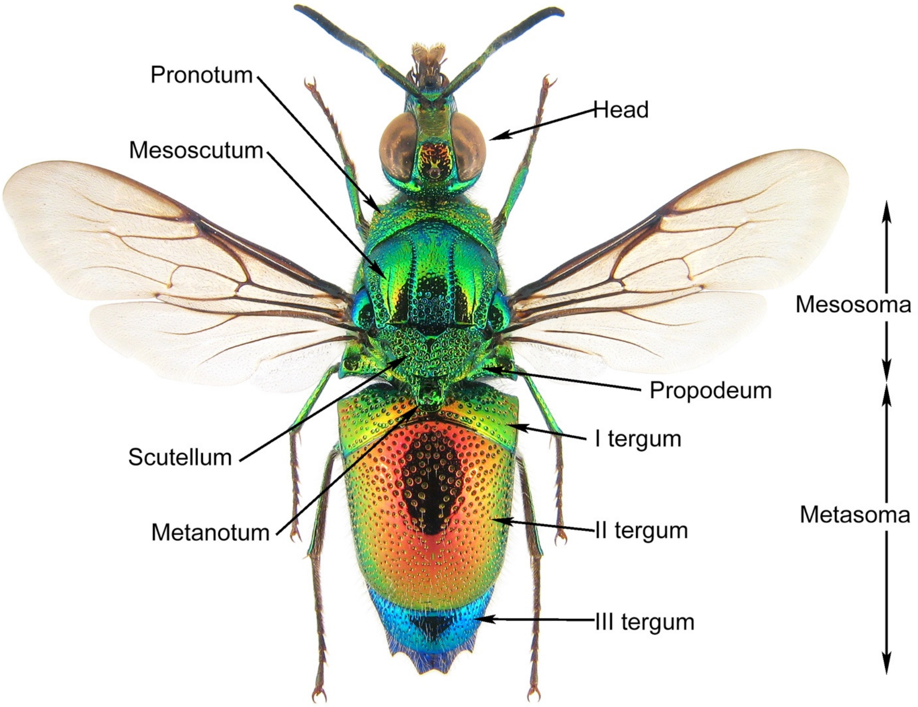

Fig. 1 – Morphological diagram of the Chrysididae body (a specimen of *Stilbum cyanurum* is shown). / Schema morfologico del corpo dei Crisidi (raffigurato un esemplare di *Stilbum cyanurum*).

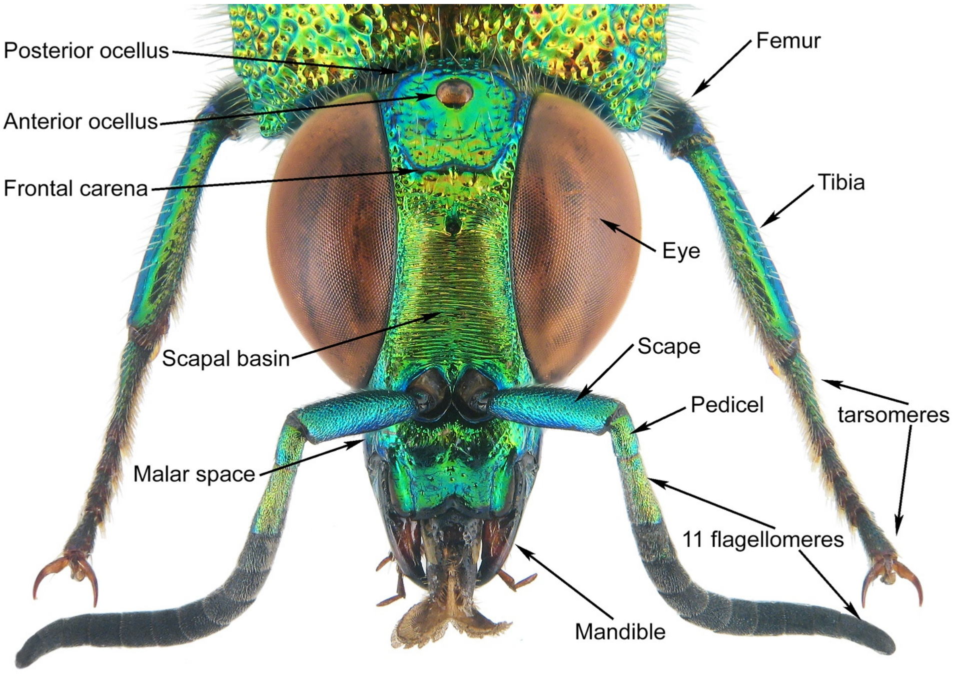

Fig. 2 – Morphological diagram of the Chrysididae head (a specimen of *Stilbum cyanurum* is shown). / Schema morfologico del capo dei Crisidi (raffigurato un esemplare di *Stilbum cyanurum*).

tellum; the former is further divided into three parts by two longitudinal grooves called notauli. The tegulae are strongly developed in *Parnopes*, while in the other genera they cover only the base of the fore wing. The mesopleuron is particularly complex, and its shape and sculpture have diagnostic value. The metanotum is highly modified in the genera *Elampus*, *Stilbum* and *Parnopes* bearing a large, elongated posterior mucron. The propodeum shows two distinct conditions: in *Cleptes* it has a long dorsal surface, whereas in all other chrysidids it appears short and posteriorly subtruncate. Legs are generally simple and unmodified. The wings have reduced venation: the forewing with at most six closed cells, and the hindwing with none.

Chrysidids can be distinguished from other aculeate wasps by the reduced number of visible metasomal segments. Members of the largest subfamily, Chrysidinae, have the metasoma profoundly modified, with only three strongly convex and sclerotized terga (the entire dorsal sclerotized region of a segment is named the tergum, when subdivided, each individual part is called a tergite; in this text we refer to terga rather than tergites, as many malformations involve the whole region); the ventral surface consists of three sterna, and is flat or convex; moreover, the third tergum is the most strongly modified, with its apical margin smooth or variously toothed, and sometimes medially indented. However, males of the tribe Parnopini exhibit four metasomal segments; Cleptinae, Amiseginae and Loboscelidiinae exhibit five visible metasomal segments in males and four in females. Internal metasomal segments are modified to form a telescopic genital apparatus in males and an ovipositor tube in females. The body integument is strongly chitinized and strengthened to protect the cuckoo wasps against their enemies and hosts. Finally, almost all species exhibit metallic coloration, except for Allocoelini (Chrysidinae), Loboscelidiinae and most Amiseginae (Kimsey & Bohart, 1991).

Photographs of the specimens were taken by P. Rosa with a Nikon D-3400 connected to the stereomicroscope Togal SCZ and stacked with the software Combine Z, and with an Olympus OMD E-M1 Mark II photo camera, with the Olympus Zuiko 60 mm objective and a Marumi lens for general habitus, and a Mitutoyo plan achromatic lens LWD 5× for details. These images were stacked with the Helicon© software (Helicon Soft Ltd., Oakland, CA, USA) and then enhanced with Adobe Photoshop© CS6 (Adobe Inc., San Jose, CA, USA). Other digital images were taken by M. Zilioli with a Canon Power-Shot S50 digital camera mounted on a Leica MS5 stereomicroscope and processed through the Combine ZP software, while backscattered images were taken with the scanning electron microscope JEOL JSM 5610 LV of the Museum of Natural History in Milan.

RESULTS

Malformations and anomalies are found in all the body parts of the cuckoo wasps and in their appendages. We here describe and illustrate some of the most astonishing, subdivided according to body parts: head, mesosoma and metasoma. We also describe teratologies, malformations and anomalies affecting the full body: nanism/gigantism, gynandromorphy and abnormal coloration.

Head

The head of Chrysididae is prognathous with the mouthparts placed at the anterior extremity, similarly to other members of the superfamily Chrysidoidea (Lanes *et al*., 2020). In the Chrysidinae, the most noticeable exception to the general structure is given by the dimorphic members of the *Chrysis ehrenbergi* group, whose females have a greatly enlarged head, with a number of exaggerated features such as gigantic mandibles and a swollen, enlarged genal area for the greatly developed mandibular muscles. Other easily recognisable head profiles are those of *Stilbum* Spinola, 1806, which is longitudinally elongate, with a narrow scapal basin and clypeus longer than it is broad, and the head of members in the tribe Parnopini, with unusually elongate mouthparts.

Cephalic aberrations are known in Chrysidinae (Linsenmaier, 1959, 1999; Peters & Gibbs, 2024), both in the tribes Chrysidini and Elampini, and in Losbosceliidinae (Kimsey, 2018). Linsenmaier (1959, 1999) described and illustrated the unilateral heteromorphosis of an antenna of *Chrysis elegans* Lepeletier, 1806, where the tarsi of a leg replaced the last antennal segments, and a supernumerary antenna in *Holopyga rubra* Linsenmaier, 1999. Kimsey (2018) illustrated asymmetries in the head profile in some specimens of *Rhadinoscelidia malaysiae* Kimsey, 1988. Lastly, Peters & Gibbs (2024) reported the first known case of quadriocellar chrysidid, *Hedychridium caeruleum* (Norton, 1879), from Canada. In our survey, a total of 105 cases were observed including anarthrogenesis, asymmetry, aplasy, ectromely, hemiaplasy, heteromorphosis, hypertrophy, microcephaly, schistomely, somatomely, symphysocery, and other small malformations that apparently do not affect the normal life of the cuckoo wasps (Fig. 5A and Fig. 6A), although Safavi (1968) noted that antennal malformations in Hymenoptera might affect the mating behaviour.

We observed 72 cases of cephalic aberrations from the tribe Chrysidini, 32 cases from Elampini, and a single case from Cleptinae; 22 of these cases presented with additional body malformations. Specifically, two cases also exhibited aberrant body coloration, two cases displayed nanism, four cases were affected by multiple body aberrations, three cases showed mesosomal aberrations (e.g., asymmetry), and 11 cases displayed metasomal aberrations, such as symphysocery and other mechanical malformations. Antenna-related anomalies were observed in 46 cases. Of these, five cases showed bilateral antennal aberrations, and 20 cases were characterized by an irregular number of flagellomeres, ranging from fully or partially developed to fused elements. In addition, one case involved an extra antenna while another case was recorded as having a missing antenna. Deformities of the antennal socket and radicle were noted in three cases, and two cases exhibited aberrant scape morphology. Furthermore, 17 cases involved irregular asymmetry or deformation of the flagellomeres. Within this subgroup, four cases appeared to be simple malformations (manifesting as crushed or asymmetrical flagellomeres) that might be attributable to mechanical stress during the pupal stage, whereas the remaining 13 cases likely stem from developmental disturbances, potentially linked to genetic mutations, pollution, or other environmental factors.

Heteromorphosis

Heteromorphosis is one of the most bizarre biological phenomena, in which an organism develops or regenerates a structure that differs from the original in form or function.

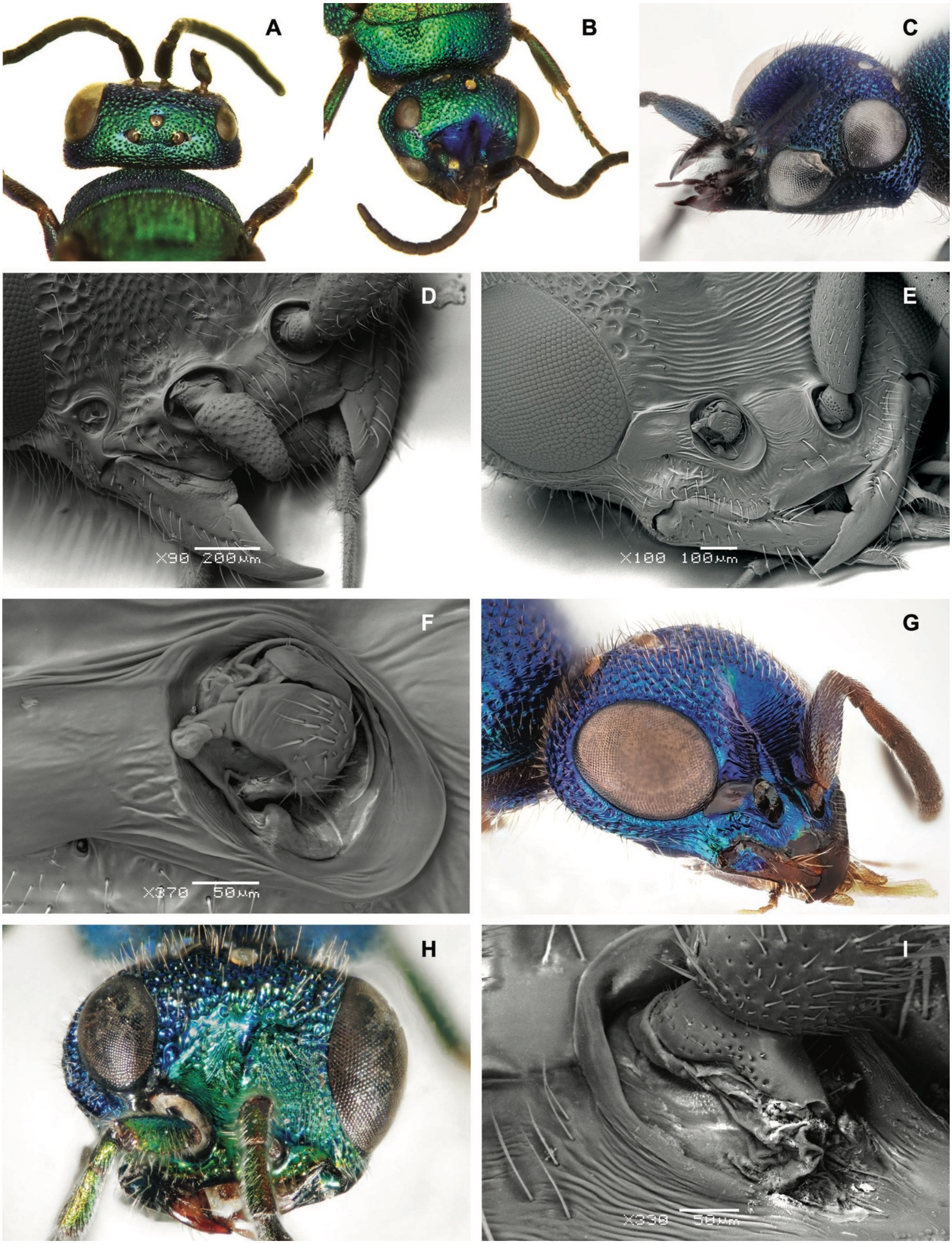

Fig. 3 – Cephalic teratologies. A, B) *Holopyga rubra*, male, head with polymelia (A) and polyocularism (B). C) *Holopyga fervida*, male, head with polyocularism (Photo: Daniele Baiocchi). D) *Chrysis ignita*, female, antennal somatomely and aplasic antenna. E-G) *Hedychrum gerstaeckeri*, female, polymelic mandible and embryonic antenna. H, I) *Chrysis cavalierei*, male, hypotrophic eye, deformed torulus and partially polymelic antennal radicle. / Teratologie cefaliche. A, B) *Holopyga rubra*, maschio, testa con polimelia (A) e poliocularismo (B). C) *Holopyga fervida*, maschio, testa con poliocularismo (Foto: Daniele Baiocchi). D) *Chrysis ignita*, femmina, somatomelia antennale e antenna atrofica. E-G) *Hedychrum gerstaeckeri*, femmina, mandibola polimelica e antenna embrionale. H, I) *Chrysis cavalierei*, maschio, occhio ipotrofico, torulo deformato e radice antennale parzialmente polimelica.

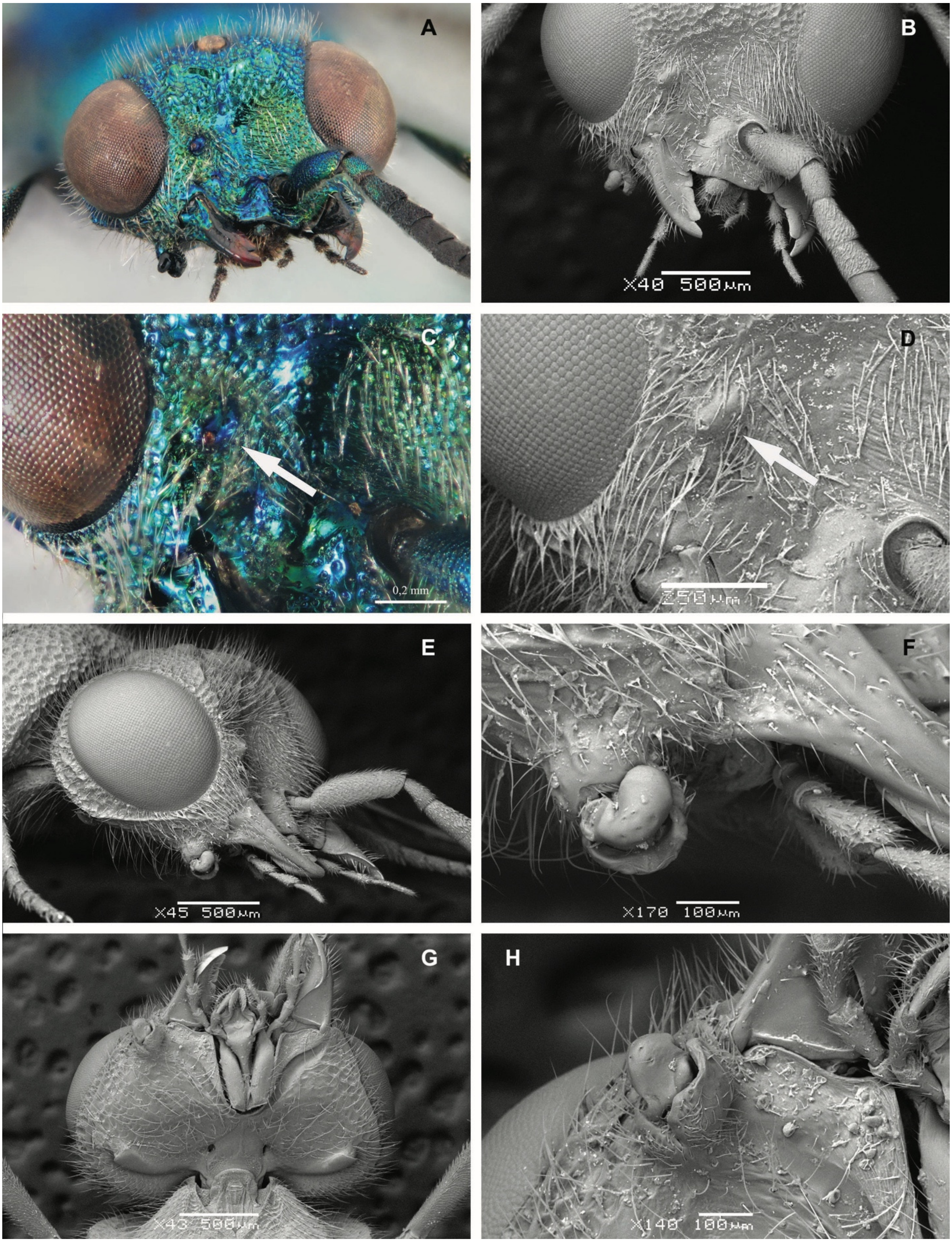

Fig. 4 – Cephalic teratologies. A-H) *Chrysis splendidula*, female, antennal aplasia and supernumerary mandible. A, B) Head, frontal view, C, D) Head, arrow pointing to the possible displaced and non-developed antenna. E) Head, lateral view. F) Detail of the supernumerary mandible, lateral view. G) Head in ventral view. H) Detail of the supernumerary mandible, ventral view. / Teratologie cefaliche. A-H) *Chrysis splendidula*, femmina, aplasia antennale e mandibola soprannumeraria. A, B) Testa, vista frontale. C, D) Testa, freccia che indica la possibile antenna dislocata e non sviluppata. E) Testa, vista laterale. F) Dettaglio della mandibola soprannumeraria, vista laterale. G) Testa in vista ventrale. H) Dettaglio della mandibola soprannumeraria, vista ventrale.

In Hymenoptera it has been documented as the replacement of the last antennal segments with tarsi and onychium, the small appendage of the terminal joint of the fifth tarsus, which includes the two claws found at the end of the leg. This phenomenon has been observed in Symphyta, such as *Cimbex axillaris* (Kraatz, 1876), and wild bees, such as *Bombus variabilis* (Kriechbaumer, 1889) and *Nomada comparata* (Proshchalykin, 2003). These monstrosities, may occur unilaterally or symmetrically, as seen in *Halictus* (Harling, 1902) and in *Andrena clarkella* (Wagner, 1915).

Linsenmaier (1959, Fig. 554) described and illustrated the unilateral heteromorphosis of the antenna of *Chrysis elegans* Lepeletier, 1806. In this aberration, the last flagellomere of the antenna is replaced by an onychium with two fully developed tarsal claws and based on the line drawing, also flagellomeres 9-12 were probably replaced by other tarsomeres because bear setae or spines typical of tarsi. Unfortunately, we could not examine this specimen as it is deposited in an unknown private collection. On the other side, some specimens of *Chrysis gribodoi* Abeille de Perrin, 1879, collected from the same population from Sperone (Abruzzo, Italy), possess a rudimental antenna on the arolium (Fig. 15C-E) (see below under mesosomal anomalies).

The insect leg and antenna are considered homologous structures, evolving from a common ancestral appendage (Cummins *et al*., 2003) and this kind of teratology often results from homeotic mutations, which cause displaced body parts (homeosis), such as leg-like structures growing in place of antennae. These phenomena can originate from mutations in Hox genes that regulate body segment identity, leading to shifts in segmental identity. Similar cases have been studied in the fruit-fly *Drosophila*, where the misexpression of the Antennapedia gene (Antp), which normally controls the development in thoracic segments, leads to ectopic expression of the Antp gene where antennae are normally formed. This misexpression causes the antennae to be replaced by leg-like structures, finally resulting in the transformation of antennae into tarsi (Lewis, 1978).

Polymelia

Polymelia refers to the presence of supernumerary appendages. This condition is considered rare in Hymenoptera (in Balazuc, 1958 under the name somatomely; Lohrman & Engel, 2015) and can involve the development of extra antennae or legs due to developmental errors or genetic mutations. In Chrysididae, a male of *Holopyga rubra* Linsenmaier, 1999, bearing a supernumerary antenna was described and illustrated by Linsenmaier (1999). This Moroccan specimen from Fés (Marrakesh, NMLU) has a third antenna, composed only of the scape (Fig. 3A and B), which has grown on the right margin of the scapal basin. Additionally, in the same specimen, the right eye is replaced by two smaller compound eyes, possibly representing a case of polyocularism (Fig. 3B), condition in which an individual develops extra eyes or additional eye structures. The other morphological parts of this individual do not exhibit aberrations. Another case of polyocularism was observed in a male of *Holopyga fervida* (Fabricius, 1781) from Elche (Fig. 3C) (Alicante, Spain, DBC). In this specimen, the left eye is replaced by two smaller compound eyes, with a similar pattern of the previous case, but without the supernumerary antenna. Similar cases have been documented across various insect orders, and, among Hymenoptera, malformed bilateral supernumerary antennae were recorded, for example, in the wasp *Sulcopolistes sulcifer* Zimmermann, 1930 by Borsato (1995, currently *Polistes semenowii* Dalla Torre, 1894). Tussac & Balazuc (1991) reported a flat wasp *Pseudisobrachium subcyaneum* (Haliday, 1839) with three eyes and a supernumerary ocellus, and tentatively classified this specimen as "*monstre double catadidyme*".

A case of antennal somatomely in Chrysididae was observed in a female of *Chrysis ignita* (Linnaeus, 1758) from Ozein (Aosta Valley, Italy). Multiple aberrations are present on the right lower face of this specimen: the antennal socket is deformed, the antenna is like a stub consisting only of a reduced scape without any other visible segment, and the radicle is doubled (Fig. 3D); on the malar space between the abnormal eye and the mandible there is an embryonic third antennal socket (Fig. 3D).

Another interesting case was observed in a female of *Hedychrum gerstaeckeri* Chevrier, 1869 from Tabiano (Emilia-Romagna, Italy), with an embryonal supernumerary mandible (Fig. 3E-G). The right side of the head is abnormal, displaying a reduced eye and an enlarged antennal socket, with the antenna at embryonic stage. Between the eye and the antennal socket there is a polished, brown tissue resembling that of a mandible. In lateral view, this non-metallic tissue is similar to a supernumerary mandible observed in *Coelinius anceps* [currently *Coelinius parvulus* (Nees, 1881)] (Braconidae) illustrated by Borderá & Tormos (1986).

A different case was observed in a male of *Chrysis cavalierei* du Buysson, 1908, from Guangdong (China). The right eye is dramatically reduced in size, and a brown tissue connects the eye to the antennal socket that is more than three times its normal size (Fig. 3H and I). The right side of the head exhibits additional abnormalities, including irregular facial punctation and a genal carina that deviates from its natural course, reaching the brown tissue instead of the base of the mandible; the radicle of the right antenna is doubled, as observed in the previous case (Fig. 3I).

Additionally, a teratological specimen of *Chrysis splendidula* Rossi, 1790 (from Tuscany, Italy) exhibits a supernumerary right mandible, in embryonic stage, below the right malar area (Fig. 4A, B and E-H).

Aplasia

Aplasia of a specific cephalic organ is another rare condition in Hymenoptera and consists in the complete failure of a tissue to develop. In cephalic aberrations of hymenopterans, this condition has been observed in the eyes [e.g., *Dolerus gonager* (Fabricius, 1781)] and antennae [*Polistes nimpha* (Christ, 1791)] as noted by Balazuc (1958, with the name of atrophy), as well as in the ocelli of various species (Konow, 1900; Lohrmann *et al*., 2016, see below). In Chrysididae, we observed a case of aplasy of the right antenna in a female of *Chrysis splendidula* Rossi, 1790 (Fig. 4A and B) from Vicchio (Tuscany, Italy), where the antenna and the antennal socket are completely absent, resulting in facial asymmetry on the right side (Fig. 4A and B), with reduction in size of the right eye. A small bump is visible in the middle-right portion of the scapal basin (Fig. 4C and D), which may represent the embryonal, undeveloped and displaced antenna. Additionally, the same teratological specimen of *Chrysis splendidula* exhibits a supernumerary right mandible below the right malar area (Fig. 4A and E-H). The supernumerary mandible is at an embryonic stage; however, it is visible and developed enough to show the same brown tissue of the other two fully developed mandibles.

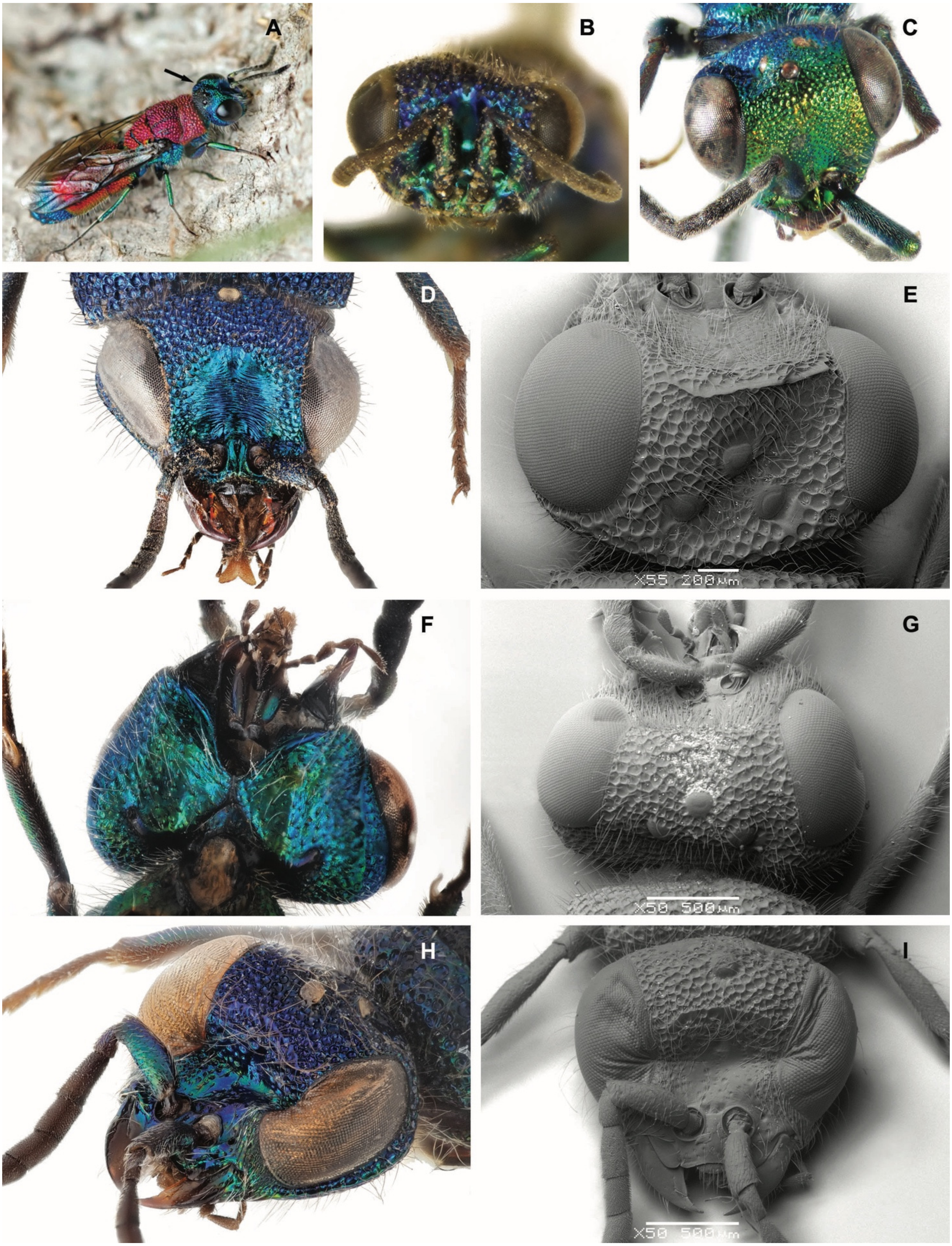

Fig. 5 – Head asymmetry. A) *Chrysis viridula* (photo: Paul Winkler). B) *Pseudomalus auratus*, female. C) *Cleptes auratus*, male. D) *Hedychrum niemelai*, male. E) *Chrysis indigotea*, female. F-G) *Chrysis germari*, male. H) *Chrysis ignita* group, male. I) *Chrysis bicolor*, female. / Asimmetria della testa. A) *Chrysis viridula* (foto: Paul Winkler). B) *Pseudomalus auratus*, femmina. C) *Cleptes auratus*, maschio. D) *Hedychrum niemelai*, maschio. E) *Chrysis indigotea*, femmina. F-G) *Chrysis germari*, maschio. H) Gruppo *Chrysis ignita*, maschio. I) *Chrysis bicolor*, femmina.

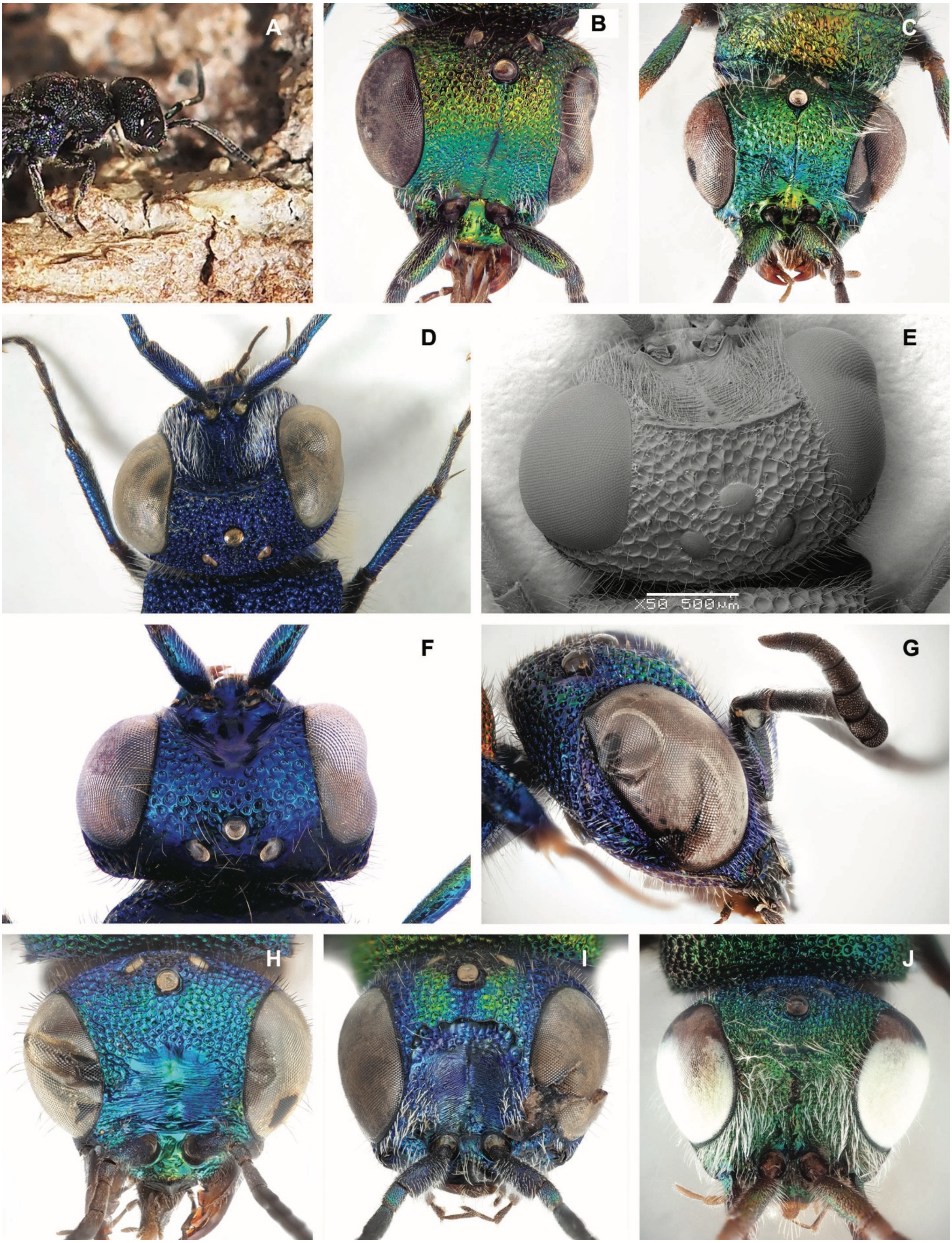

Fig. 6 – Aberrant eyes. A) *Chrysis scutellaris*, female (Photo: from Brigitte Emmery, https://forum.chrysis.net/). B) *Hedychridium aereolum*, female. C) *Hedychridium cupreum*, female. D-E) *Chrysis inaequalis*, female. F) *Pseudomalus auratus*, male. G) *Chrysis chrysostigma*, female. H) *Hedychrum niemelai*, male. I) *Chrysis pulcherrima*, female. J) *Chrysis comparata*, male. / Occhi aberranti. A) *Chrysis scutellaris*, femmina (Foto: da Brigitte Emmery, https://forum.chrysis.net/). B) *Hedychridium aereolum*, femmina. C) *Hedychridium cupreum*, femmina. D-E) *Chrysis inaequalis*, femmina. F) *Pseudomalus auratus*, maschio. G) *Chrysis chrysostigma*, femmina. H) *Hedychrum niemelai*, maschio. I) *Chrysis pulcherrima*, femmina. J) *Chrysis comparata*, maschio.

Other cases of aplasia were observed in a specimen of *Chrysura cuprea* (Rossi, 1790) (from Austria), which lacks the right posterior ocellus (Fig. 7G), also with a small bump in the middle-right portion of the scapal basin, which may represent the embryonal and displaced ocellus; and in a male of the *Chrysis ignita* group (from Japan, KUM), which lacks the anterior ocellus (Fig. 7J).

Asymmetry

Asymmetry of the head is commonly observed in Chrysididae. It was previously described in the literature by Kimsey (2018) for *Rhadinoscelidia malaysiae* Kimsey 1988. This type of malformation does not appear to significantly impact the daily life of specimens, as it has been also documented in photographs of living individuals found online (Fig. 5A and Fig. 6A). Asymmetry occurs both in Elampini and Chrysidini and is usually caused by mechanical factors, such as the compression of the pupa against the cocoon or the collapse of nest wall. These mechanical malformations are rather common (Fig. 5A-C) and can sometimes dramatically alter head structure (Fig. 5C, F and G and Fig. 6H). Other cases of asymmetry may result from incomplete or abnormal development of specific head structures including the eyes (Fig. 3D-F), the antennal socket (Fig. 3D), and the ocelli (Fig. 7D-F). More rarely, asymmetry can be associated with the presence of extra appendages, such as a supernumerary antenna (Fig. 3D) or mandible (Fig. 3G and Fig. 4B).

Eye and ocellar deformities

There are several reports of Hymenoptera with abnormal compound eyes (e.g. Penteado-Dias *et al*., 2005) and ocellar anomalies, such as supernumerary ocelli or reductions in the number of ocelli (Engel *et al*., 2014; Tussac & Balazuc, 1991) or even cyclopia. One of the most striking abnormalities is cyclopia, which is well documented for honey bees (several cases summaries by Haydak, 1948) and wild bees (Hopwood, 2007), and various other hymenopteran families (Balazuc, 1958).

Supernumerary eyes

One of most noticeable aberrations is the polyocularism that we observed in a male of *Holopyga rubra* Linsenmaier 1999 from Morocco, previously cited for antennal somatomely (see above), and in a male of *Holopyga fervida* (Fabricius, 1781) from Spain. In the first specimen, the right eye is replaced by two small compound eyes (Fig. 3A and B), while in the second specimen the same anomaly is present in the left eye (Fig. 3C).

Another remarkable case was observed in a male of *Hedychrum niemelai* Linsenmaier 1959 from Manziana (Lazio, Italy), which exhibits a small supernumerary compound eye between the malformed left eye and the temple (Fig. 7D and E). This anomaly is accompanied by another malformation: the displacement and enlargement of the left posterior ocellus, which is narrowly developed towards the left eye margin. The diameter of this aberrant ocellus is approximately twice the normal size.

Eye malformations

Eye malformations, affecting one or both eyes, are frequently observed in cuckoo wasps. These deformities can arise from mechanical causes, such as pressure from nest walls or the cocoon on the pupa (as supposed for the cases in Fig. 6B and H), genetic factors (Fig. 6D and E), or possibly chemical exposure. A striking case involved a melanic *Chrysis scutellaris* Fabricius 1794 (Fig. 6A) from France (series uploaded by Brigitte Emmery on www.chrysis.net/forum) in which both eyes are collapsed. Similarly, eye malformations were observed in populations of *Hedychridium aereolum* du Buysson 1893 (Fig. 6B) and *Hedychridium cupratum* (Dahlbom 1854) (Fig. 6C) both from Eita (Lombardy, Italy) caught during the same collecting event, with a significant number of specimens affected by the same eye abnormalities. Since a similar malformation was observed in specimens of two different species, the cause could be related to abiotic forces (e.g. temperature changes, environmental pollution) or a virus.

Abnormal growth in specific eye regions has been observed in several (unrecorded) specimens, while it was photographed for two specimens of *Chrysis inaequalis* Dahlbom 1845 (Fig. 6D and E) from Stintino (Sassari, Sardinia) and *Pseudomalus auratus* (Linnaeus 1758) (Fig. 6F) from Sperone (Abruzzo, Italy). In both specimens, the right eye displays a globular protuberance in its ventral region.

Mechanical injuries, such as crushes or attacks by predators can sometimes be self-repaired, as in the case of a female of *Chrysis chrysostigma* Mocsáry 1889 (Fig. 6G) from San Benedetto Belbo (Cuneo, Italy) and a female of *Chrysis pulcherrima* Lepeletier 1806 (Fig. 6I) from Berceto (Emilia-Romagna, Italy). The latter survived despite significant damage to the left eye and part of the mandible possibly caused by a predator or one of his hosts. The repairing tissue is visible on the face and within the eye (Fig. 6I). Although this is not an aberration, it represents a fascinating case which has not been previously documented in Chrysididae.

Ommatidial depigmentation

Both eyes of a male of *Chrysis comparata* Lepeletier 1806 from Tabiano (Emilia-Romagna, Italy), with altered body coloration, exhibit depigmented white ommatidia (Fig. 6J). Similar cases of eye depigmentation were observed in a melanic female of *Pseudochrysis neglecta* (Shuckard 1837) (Fig. 37B), in a male specimen of *Chrysis carinulata* Brullé 1846 from Caaguazú (Paraguay, NMLU) and other unrecorded specimens found in various collections. Interestingly, these specimens retain normal eye pigmentation dorsally, which fades to a pale or completely white coloration ventrally. Reduced ommatidial pigmentation, though not entirely whitish, was also observed in other melanic specimens (see Figs. 36 and 37). Since some specimens partially or fully melanic are affected by eye depigmentation, there could be a relation between the eye depigmentation and melanism. Alterations and loss of pigment in primary pigmentary cells were observed in honeybees by Chaud-Netto & da Cruz-Landim (2000). They documented a reduction in pigment levels within primary and secondary pigmentary cells, as well as receptor cells of mutant eyes, hypothesizing that such changes could lead to visual deficiencies and behavioral modifications. Genetic mutation associated with white-eyed phenotypes were also studied by Whiting (1934) in the parasitic wasp *Habrobracon.* Since ommatidia contain photoreceptor cells responsible for vision, their depigmentation may interfere with proper function, potentially leading to reduced vision or impaired light sensitivity in the affected individuals.

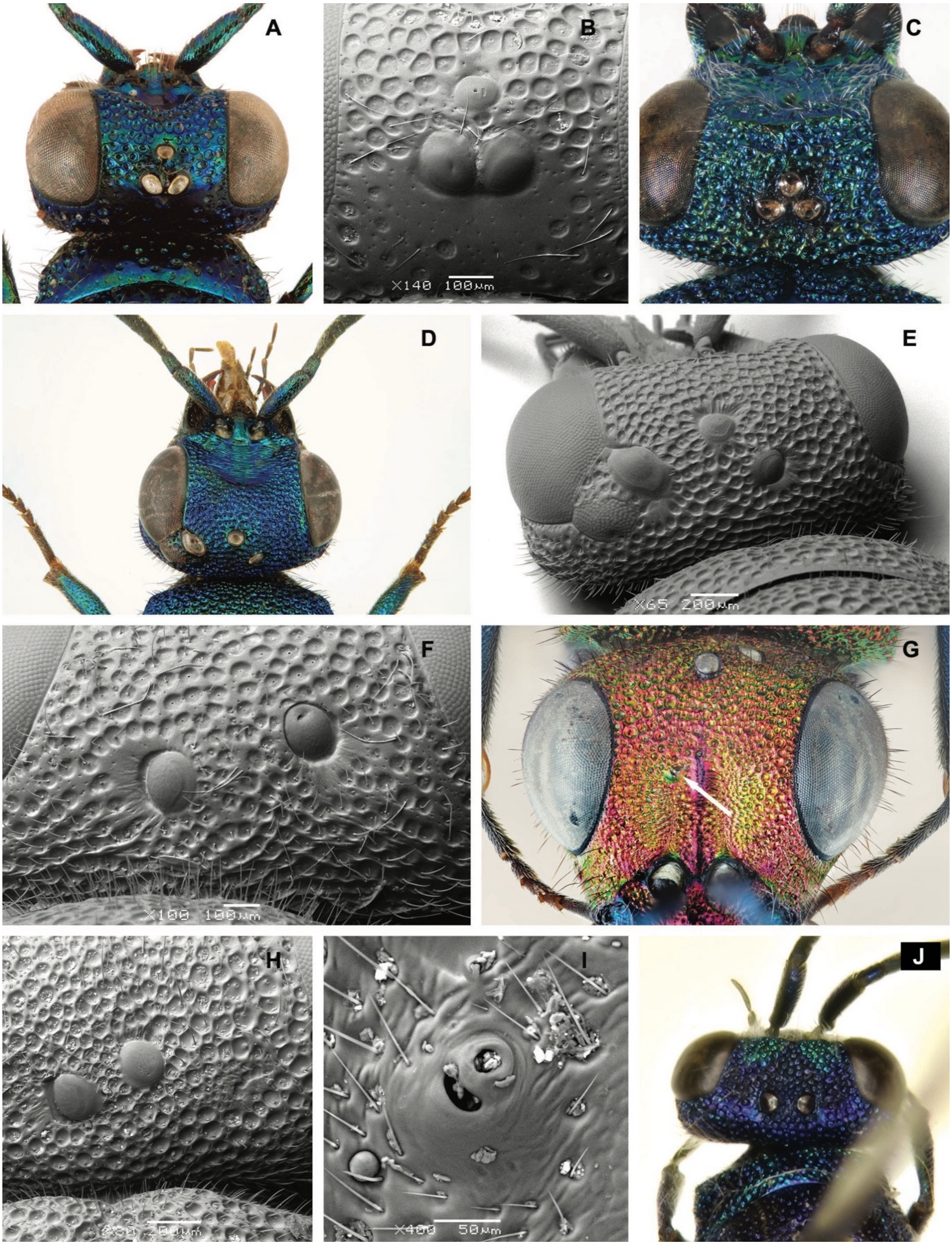

Fig. 7 – Ocellar aberrations. A-B) *Pseudomalus auratus*, male, hypertrophic and displaced posterior ocelli. C) *Chrysis fasciata*, female, displaced ocelli. D-E) *Hedychrum niemelai*, male from Italy, polyocularism and deformed left posterior ocellus. F) *Hedychrum niemelai*, male from Ukraine, aplasy of anterior ocellus and displacement of the posterior right. G-I) *Chrysura cuprea*, female, aplasia of the posterior right ocellus and its possible displacement on face. J) *Chrysis ignita* group, female, aplasia of anterior ocellus. / Aberrazioni oculari. A-B) *Pseudomalus auratus*, maschio, ocelli posteriori ipertrofici e dislocati. C) *Chrysis fasciata*, femmina, ocelli dislocati. D-E) *Hedychrum niemelai*, maschio proveniente dall'Italia, polioculariсmo e ocello posteriore sinistro deformato. F) *Hedychrum niemelai*, maschio proveniente dall'Ucraina, aplasia dell'ocello anteriore e dislocazione di quello posteriore destro. G-I) *Chrysura cuprea*, femmina, aplasia dell'ocello posteriore destro e sua possibile dislocazione sulla faccia. J) Gruppo *Chrysis ignita*, femmina, aplasia dell'ocello anteriore.

Ocellar aberrations

Insect ocelli are simple eyes that collect and focus light through a single lens. These simple eyes assist insects with sun orientation so they can correctly navigate during the day. Ocellar aberrations have been documented in the literature in various hymenopteran families, though they are uncommon as reviewed by Lohrmann & Engel (2015). These aberrations include ocellar aplasia, additional set of lateral ocelli (Tussac & Balazuc, 1991; Engel *et al*., 2014), the presence of two anterior ocelli (Smulyan, 1923; Moller, 1975; Lohrmann & Engel, 2015), cases of three compound eyes and four ocelli (Tussac & Balazuc, 1991), and even complete ocellar aplasia, such as an anocellar tenthredinid and an anocellar polistine wasp, both lacking all three dorsal ocelli (Konow, 1900, Lohrmann *et al*., 2016). Only one case of ocellar aberration has been reported for Chrysididae for a quadriocellar specimen of *Hedychridium caeruleum* (Norton 1879), in which a supernumerary ocellus is positioned to the right of the otherwise normal ocellar triangle. We observed six remarkable cases of teratologies affecting Chrysididae ocelli.

A male of *Pseudomalus auratus* from Nuoro (Sardinia, Italy) exhibits hypertrophic and displaced posterior ocelli, positioned closer together than usual (Fig. 7A and B). A female of *Chrysis fasciata* Olivier, 1790 from Ozein (Aosta, Italy) has all three ocelli displaced and closely grouped, with the characteristic ocellar area absent (Fig. 7C). A male of *Hedychridium niemelai* Linsenmaier 1959 from Manziana (Rome, Italy) has a hypertrophic and displaced left posterior ocellus, positioned closer to the left eye, which is itself malformed and divided into two parts. The smallest of these two parts is as large as the deformed and enlarged left posterior ocellus (Fig. 7D).

Another male of *Hedychridium niemelai* from Dnepropetrovsk (Ukraine) displays an ocellar aplasia, lacking the anterior ocellus; additionally, the right posterior ocellus is displaced, being positioned further anteriorly (Fig. 7F). A female of *Chrysura cuprea* (Rossi 1790) from Stammersdorf (Vienna, Austria) lacks the right posterior ocellus, while the remaining two ocelli are displaced and positioned closer together than their expected placement on the vertex (Fig. 7G and H). A trace of a different sculpture and a slight depression are visible in place of the missing ocellus. Interestingly, a small protuberance, similar in size to an ocellus, is present in the right, median part of the scapal basin (Fig. 7G and I), potentially corresponding to the missing ocellus on the vertex. A male of the *Chrysis ignita* group from Japan (KUM) exhibits another form of aplasia, entirely lacking the anterior ocellus (Fig. 7J). The punctation on the vertex remains unmodified and continuous, without trace of the missing ocellus, structural deformities or alteration in sculpture.

Antennae

Chrysididae males and females have 13 antennal segments: scape, pedicel, and 11 flagellomeres. The morphological structure of the antenna is very simple and, in cross-section, the flagellomeres are usually cylindrical, although in some groups of the genus *Chrysura* Dahlbom 1845 they are lobate beneath. The only noteworthy modification from the original plan is found in the male of a South American cuckoo wasp, *Rhipidochrysis bruchi* (Brèthes 1903), with broad and flabellate male flagellomeres. Sexual dimorphism can be observed in some cases, for example in the genera *Cleptes* Latreille 1802, *Elampus* Spinola 1806 and *Philoctetes* Abeille de Perrin 1879 the male flagellum might be distinctly longer than the female one; in *Chrysellampus* Semenov-Tian-Shanskij 1932 and *Praestochrysis* Linsenmaier 1959, the flagellum may be broad and flattened in male or in both sexes; additionally, in some species groups of the genus *Chrysis* Linnaeus 1761 and *Spintharina* Semenow 1892 males or both sexes have shortened first or first and second flagellomeres. In the subfamily Amiseginae, the female flagellum is unmodified, but males can have elongate and setose flagellomeres. Normally, the relative length of the first three flagellomeres is of specific diagnostic importance. We observed 43 cases of relevant antennal aberrations that could interfere with sensory functions like smell or touch, some of which are discussed below.

Anarthrogenesis

Anarthrogenesis refers to the incomplete development of appendages, such as legs, antennae, or wings, due to genetic mutations or developmental disturbances. We observed two major cases of incomplete antennal development (Fig. 3D and G), in both cases associated to other aberrations. A female of *Chrysis ignita* (Linnaeus 1758) from Ozein (Aosta Valley, Italy) has the antennal socket deformed and the antenna reduced to a stub of the scape, without other visible segment, and with double radicle (Fig. 3D); other aberrations of this specimen are i) the reduced right eye and ii) a third antennal socket on the malar space between the abnormal eye and the mandible. The second case is observed in a female of *Hedychrum gerstaeckeri* Chevrier 1869 from Tabiano (Emilia-Romagna, Italy) (Fig. 3F and G), which is characterized by the incomplete development of the right antenna that remained at embryonic stage inside the antennal socket, with scape and pedicel apparently delineated and the remaining flagellomeres not fully developed. This anomaly occurs in conjunction with other defects: i) the right antennal socket is distinctly enlarged compared to the left one; ii) a raised, smooth, subrectangular and depigmented area is developed between the foramen and the eye; iii) the right eye is considerably smaller than the left one, and the right malar space is widely enlarged compared to the left one, making the lower part of the face distinctly asymmetric.

Schistomely

Schistomely is considered one of the most intriguing teratological anomalies in insects according to Balazuc (1948) and among the first described in entomology (Tiedemann, 1819). This anomaly is characterized by the division or ramification of an appendage, such as antennae, mandibles, or legs, into multiple parts instead of remaining intact. Balazuc (1948) classified schistomely based on the number and symmetry of the branches: if the appendage splits into two branches, it is classified by Balazuc (1948) as binary schistomely, while a three-way split is ternary schistomely. If the two branches are equal in length, the anomaly is classified as homodynamic; if they are unequal, it is classified as heterodynamic.

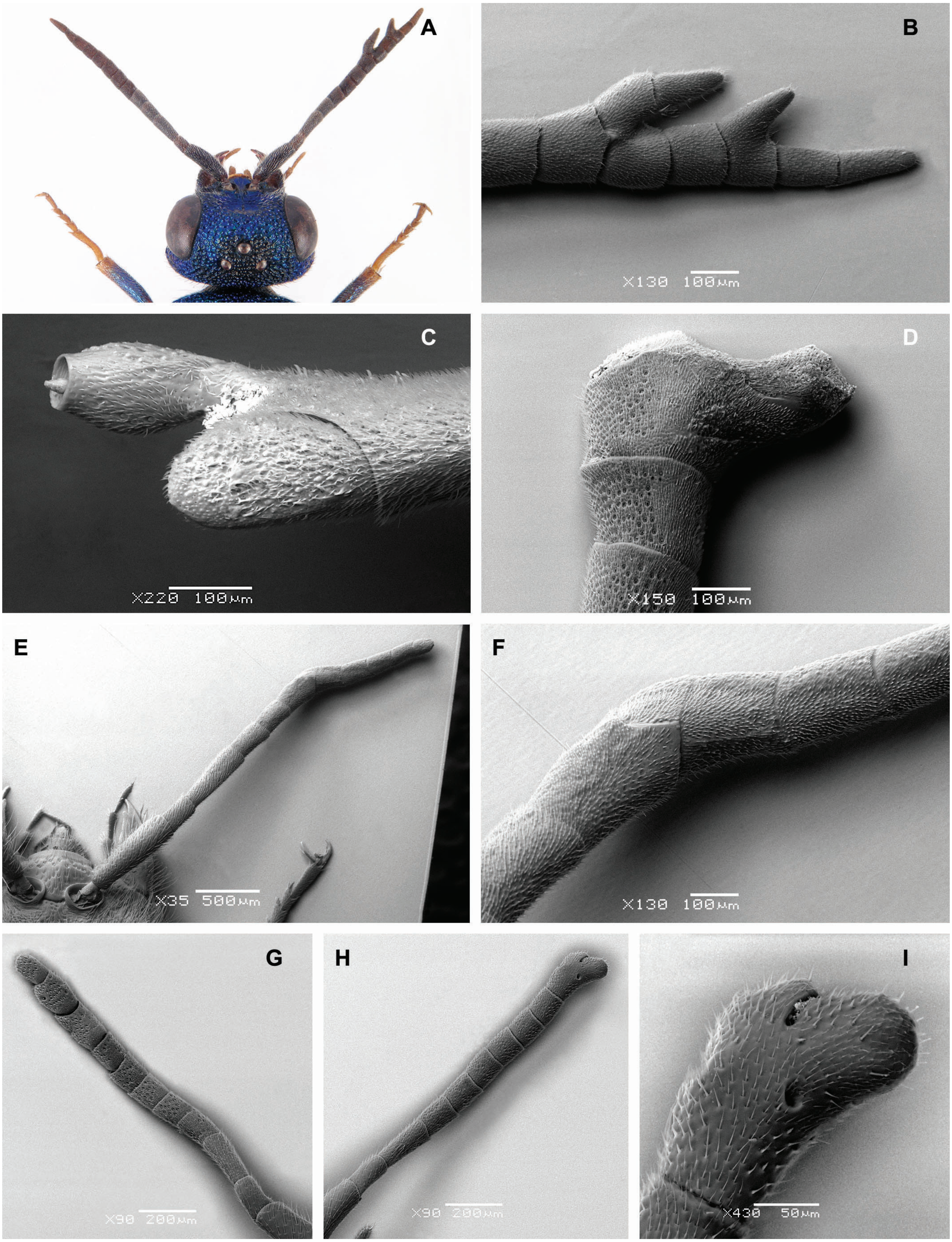

Fig. 8 – Antennal aberrations. A-B) *Hedychridium roseum*, female, heterodynamic ternary schistomely. A) Head, dorsal view. B) Detail of the schistomely. C) *Chrysis ignita*, female, schistomely. D) *Chrysura cuprea*, female, schistomely. E-F) *Chrysura austriaca*, male, ectromely and symphysocery. G-I) *Pseudomalus auratus*, male, ectromely and symphysocery. / Aberrazioni antennali. A-B) *Hedychridium roseum*, femmina, schistomelia ternaria eterodinamica. A) Testa, vista dorsale. B) Dettaglio della schistomelia. C) *Chrysis ignita*, femmina, schistomelia. D) *Chrysura cuprea*, femmina, schistomelia. E-F) *Chrysura austriaca*, maschio, ectromelia e simfisoceria. G-I) *Pseudomalus auratus*, maschio, ectromelia e simfisoceria.

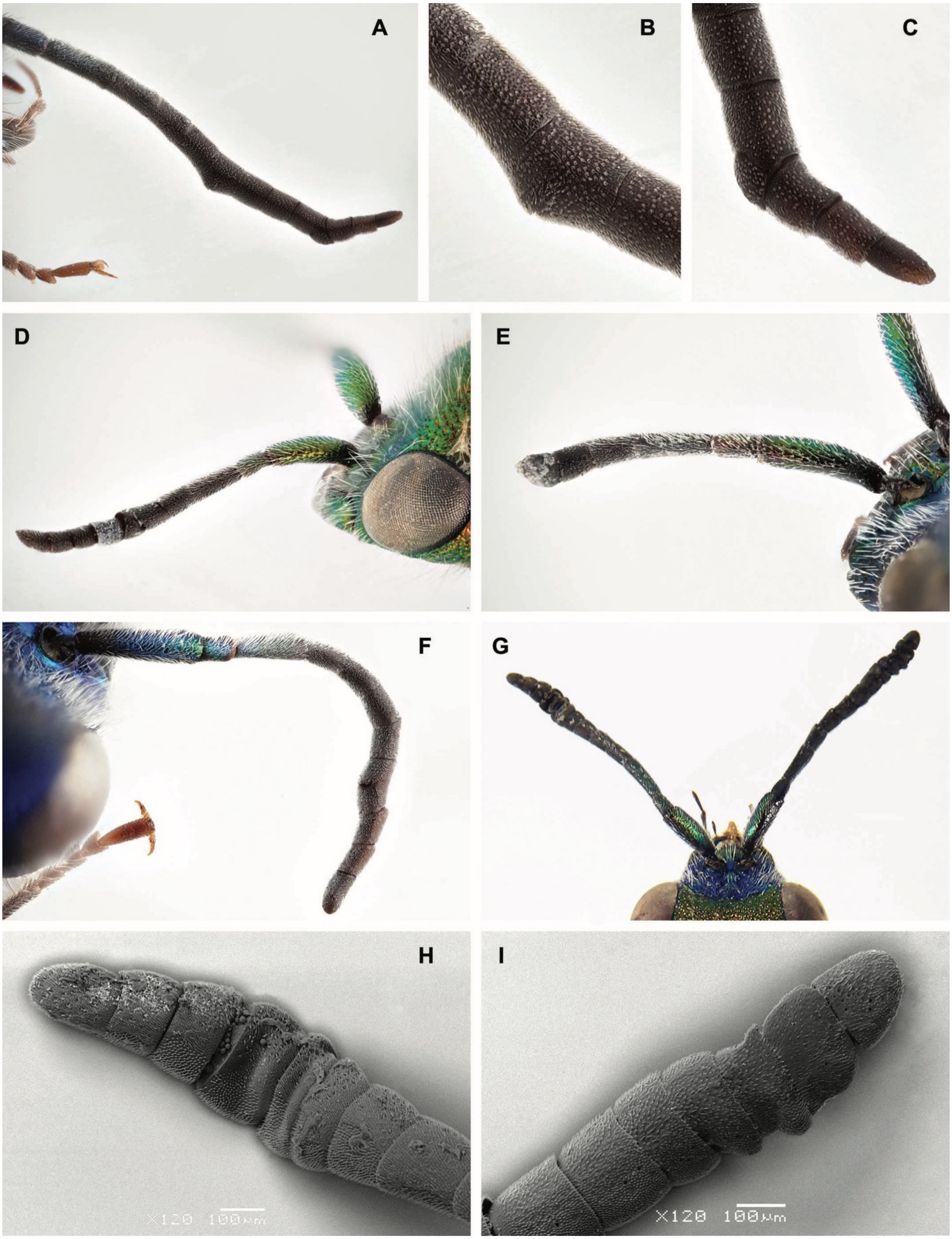

Fig. 9 – Antennal aberrations. A-C) *Chrysis ignita*, female with polymery. A) Flagellum. B) Fifth and sixth flagellomeres partially fused. C) Additional flagellomere between ninth and tenth flagellomere. D) *Hedychridium cupratum*, male, antennal ectromely with 10 articles. E) *Chrysis mixta*, female. F) *Chrysis indigotea*, male, ectromely with ten articles, the sixth and seventh partially fused. G-I) *Chrysura purpureifrons*, female, deformed antennae. / Figura 7. Aberrazioni antennali. A-C) *Chrysis ignita*, femmina con polimeria. A) Flagello. B) Quinto e sesto flagellomero parzialmente fusi. C) Flagellomero aggiuntivo tra il nono e il decimo flagellomero. D) *Hedychridium cupratum*, maschio, ectromelia antennale con 10 articoli. E) *Chrysis mixta*, femmina. F) *Chrysis indigotea*, maschio, ectromelia con dieci articoli, il sesto e il settimo parzialmente fusi. G-I) *Chrysura purpureifrons*, femmina, antenne deformate.

Schistomely may result from genetic mutations in homeotic genes responsible for appendage development, hormones disruptions (e.g., irregular levels of ecdysone or juvenile hormone), or environmental stressor, such as exposure to pollutants or chemicals. Harbeck (1910) reported a case of branched antennae in a tenthredinid with four-branches antennae. Antennal schistomely appears more frequently in Symphyta (Balazuc, 1958), though it has also been recorded in Formicidae and Ichneumonidae (Donisthorpe, 1922; Johnson, 1931). However, this anomaly remains rare in Chrysididae and other hymenopteran families.

We observed a case of schistomely in a female of *Hedychridium roseum* (Rossi 1790) from Manziana (Roma, Italy) (Fig. 8A and B) which exhibits heterodynamic ternary schistomely in the right antenna. This extraordinary aberration includes a ramification of the 7th and 9th flagellomeres which are branched: the 7th flagellomere has a small branch with two segments, whereas the 9th flagellomere is bifurcate, with the inner branch composed of a single segment fused at the base.

Another case of schistomely was observed in a female of *Chrysis ignita* (Linnaeus 1758) from Vertosan (Aosta Valley, Italy) (Fig. 8C) where the left antenna has 11 segments and the 9th flagellomere branched into two final segments, one of which resemble the last flagellomere and the other resembles the penultimate flagellomere but bears a small embryogenic additional flagellomere at its tip.

A female of *Chrysura cuprea* (Rossi 1790) from Oriano (Emilia-Romagna, Italy) (Fig. 8D) exhibits partial schistomely of the right antenna, which terminates at the 7th flagellomere. This flagellomere is distinctly bifurcate, but the subsequent flagellomeres are underdeveloped and fused together.

Ectromely

Ectromely is a type of teratology related to the complete appendage loss or reduction of antennal segments according to Balazuc (1958) who considered it as a relatively common feature in the Hymenoptera. This malformation could be originated by specific mutations in genes involved in segmental development, like Hox genes and Antennapedia. In the Chrysididae it was observed both in Chrysidini and Elampini. More frequent are cases with 10, 11 or 12 segments instead of 13, as we observed, for example, in the case of a male of *Hedychridium cupratum* (Dahlbom 1854) from Eita (Lombardy, Italy) with only eight flagellomeres in the left antenna (Fig. 9D).

A male of *Chrysis indigotea* Dufour & Perris 1840 from Antignano (Tuscany, Italy) (Fig. 9F) has 12 segments in the right antenna and a partial fusion between the sixth and the 7th flagellomere.

In some cases, both antennae may show a reduction in the number of flagellomeres, but this is usually associated with symphysocery (see below), as observed in a male of *Pseudomalus auratus* (Linnaeus 1758) from Torremoella de Mongil (Girona, Andalucia) (Fig. 8G and H). In this specimen, the left antenna has 11 segments, but the 7th is dorsally fused to the 8th and the 9th is fused with the 10th; the right antenna has 10 segments, but the last one consists of three fused segments and is partially schistomelic (Fig. 8I).

In other cases, the flagellum may be shortened from a mechanical damage, such as an enemy attack or the breakout from the nest. In the case of a female specimen of *Pseudomalus auratus* (Linnaeus 1758) from Messina (Sicily, Italy) the antenna ends after the pedicel, and a large, irregular patch of repair tissue is visible, resembling a gall.

In a female of *Chrysis mixta* Dahlbom 1854 from Albenga (Liguria, Italy) the antenna is interrupted at the 5th flagellomere, but the cause is unclear, as the last visible segment is deformed, and the repair tissue is not clearly visible (Fig. 9E).

Symphysocery

Symphysocery is a teratological condition where the antennae have one or more antennomeres partially or completely fused at some point along their length. According to Balazuc (1948), symphysocery in Hymenoptera occurs more frequently from the 6th to 11th flagellomeres, less commonly between the 4th and 5th, and even rarer between the 3rd and 4th. A male of *Chrysura austriaca* (Fabricius 1804) from Bellinzago (Piedmont, Italy) (Fig. 8E and F) exhibits both antennae with 12 segments instead of 13 and a bilateral incomplete symphysocery, with fusion between the ventral part of the 5th and the 6th flagellomere). A female of the same species from Ozein (Aosta Valley, Italy) presents exactly the same aberration on the right antenna. The case of *Pseudomalus auratus* from Torremoella (Fig. 8G-I) has already been discussed above, and additional cases were observed in other species (Fig. 9D).

Polymery

Polymery, also known as hyperantennation or polyantennation, is a teratological condition characterized by the presence of additional antennal segments. This anomaly can result from genetic mutations or developmental anomalies, such as injuries during early stages that lead to atypical regeneration of antennal structures, as studied in the Hemipteran family Aradidae (Taszanowski, 2020). We observed this teratology in two specimens of *Chrysis ignita* (Linnaeus 1758) from Nus and Ozein (Aosta Valley, Italy). In the specimen from Nus (Fig. 9A-C), the right antenna has 15 segments while the left antenna has 14 segments. The right antenna exhibits the 5th flagellomere partially duplicated (Fig. 9B) and an additional, smaller flagellomere developed between the 8th and the 9th flagellomeres (Fig. 9C); the left antenna similarly shows a partially duplicated 9th flagellomere.

Hypertrophy

Hypertrophy refers to an abnormal enlargement of a body part normally due to an increase in the size of its cells and may affects external structures like legs, antennae, wings, or mouthparts. A male of *Hedychrum niemelai* Linsenmaier, 1959 from Pineta di San Vitale (Emilia-Romagna, Italy) displays a case of hypertrophy of the right scape with highly deformed pedicel and some deformed flagellomeres; the left antenna shows some deformed flagellomeres too such as the specimen in Fig. 9E. A female of *Chrysura purpureifrons* (Abeille de Perrin 1878) from Granada (Andalusia, Spain) shows dilated and malformed distal flagellomeres (Fig. 8H and I) possibly due to mechanical stress on pupal stage, but the rest of the specimen is unaltered.

Mouthparts

The mouthparts of Chrysididae are not particularly modified. The tongue protrudes from the oral fossa, and there are five maxillary and three labial palps. The most noticeable modification occurs in Parnopini, where the glossa and galea are greatly elongate, forming a tubular proboscis; moreover, the palpi are greatly reduced, being barely visible or absent. In only one genus, *Allocoelia*, the tongue length is sexually dimorphic, with males possessing considerably longer cardines, stipes, and prementum than females. The labiomaxillary complex may have taxonomic value, as demonstrated in the genus *Hedychrum* by Kilimnik (1993).

Malformations in the mouthparts of Chrysididae appear to be rare or more difficult to detect, primarily due to specimen preparation methods, which often conceal the mouthparts beneath the body or affix them to carton boards, obscuring potential malformations in the palpi and other structures. The few observed malformations include abnormally expanded or reduced galea and glossa (Fig. 10A); deformed mandible (Fig. 10B), which prevent proper closure within the oral fossa; and schistomelic maxillary palps, as shown in Fig. 10C and D.

Microcephaly

Microcephaly is the condition where an individual head is significantly smaller than expected and is a rarely observed malformation. In Chrysididae we observed the interesting case of a male of *Chrysis splendidula chlorisans* du Buysson 1895 from Antakya (Turkey, MHC) with both a microcephalic head and a hypertrophic metasoma with asymmetry of the third tergum (Fig. 11A). The normal habitus of an individual of *Chrysis splendidula splendidula* for comparison can be seen in Fig. 11B.

An unexpected reduction of the head, with anomalous ratio between length and width, may mislead taxonomist in the correct identification of the species. For example, the type of *Chrysis parvicapito* Linsenmaier 1999 from Matmata (Tunisia, NMLU) might have been described on a specimen of the *C. bihamata* group with a microcephalic head (Fig. 11C) and hypertrophic metasoma. Although the head of this specimen is not distinctly smaller as in the previous case, it is clearly reduced compared to the head of other members of the *C. bihamata* group. *Chrysis parvicapito* shows other unusual diagnostic features, such as slight hypertrophic metasoma and edentate apical margin of the third tergum, which could represent another abnormality (Móczár, 1963). Examination of more specimens is needed to correctly evaluate and possibly re-describe this species.

Mesosoma

In hymenopterans like Chrysididae, which belong to the suborder Apocrita (including wasps, bees and ants), the thorax is referred to as the mesosoma because consists of the three thoracic segments and the first abdominal segment, the propodeum. Aberrations in the mesosoma, excluding appendages, are rarely observed compared to those in the head and metasoma. In our survey of teratological anomalies, we observed a total of 83 cases, comprising 74 cases from Chrysidini and 9 from Elampini. Among these, 15 cases were associated with other body malformations. Overall, 58 cases involved abnormalities of the appendages (legs and wings), which also included one case of heteromorphosis, three cases of aberrant coloration, two cases of heterotopy, one case with a supernumerary leg, three cases presenting as tumors, and six cases of mesosoma malformations that might have originated from mechanical stress during the pupal stage. About leg anomalies specifically, 13 cases were observed. Of these, 7 cases involved aberrations of the arolium, while the remaining cases were characterized by hypertrophy, with one case exhibiting a branched leg.

Wing aberrations were the most frequently encountered, with 45 cases documented. Within this group, 32 cases involved abnormalities in the wing venation. More precisely, there were 29 cases of defective veins, including 10 cases affecting the Rs+M vein, 18 cases affecting the m-cu vein, and one case affecting the Cu1 vein. In addition, 11 cases exhibited short, additional spurs (Fig. 17A). We also observed one case of pronotoschisis in a specimen of *Pseudomalus auratus* deposited in the collection of Naturalis (Leiden) (locality not recorded and specimen not photographed). In this specimen, the pronotum was divided into two lateral segments that were not medially fused but connected by a membrane.

Heterotopy

Heterotopy is a teratological phenomenon in which a tissue or anatomical structure develops in an abnormal position relative to its usual location. In insects, this can result to the displacement of abdominal tissues onto the thorax or vice versa. In Chrysididae, we observed two cases of heterotopy.

The first case, one of the most intriguing in our study, involves a female of *Chrysura radians* (Harris, 1776) from France (TLPC) (Fig. 12A and B). In this specimen, metasomal tissue, which is easily distinguishable by its unique coloration and sculpture, has replaced mesosomal tissue on the right side of metapectal-propodeal complex. As a result, the right side of propodeum appears specular to the anterior margin of the first tergum and lacks the typical posterior propodeal projection (propodeal angle), which remains visible on the left side of propodeum. The metasomal tissue covers the right propodeal area, part of the metapostnotum, and interrupts the course of the metapostnotal-propodeal suture.

The second case concerns a female of *Chrysura dichroa* (Dahlbom 1854) from Kalogria (Greece, DBC) (Fig. 12C and D). In this specimen, a triangular area at the base of the left side of the scutellum is replaced by metanotal tissue, which is distinctly recognizable due to its contrasting blue coloration and a different sculpture, characterized by larger, deeper, and more closely spaced punctures compared to the typical scutellar punctation. The presence of metanotal tissue on the scutellum suggests a boundary shift between thoracic segments.

Despite affecting different anatomical regions, these two cases share a common pattern, the displacement of tissue between adjacent segments. In fact, the propodeum is developmentally the first abdominal segment fused to the thorax, and a shift of tissue between adjacent segments is likely structurally and functionally less disruptive than a displacement between non-adjacent segments. This could explain why we were able to find these specimens in nature, because more extreme cases of heterotopy may prevent individuals from surviving. This rare phenomenon could arise from mutations in Hox genes, which regulate segmental identity, and alterations in their expression can cause the abdominal structures to develop in thoracic segments or vice versa (Ronshaugen *et al*., 2002). Alternatively, errors during embryonic development might lead to abnormal cell migration or fusion of adjacent segments. Environmental factors, such as temperature, mechanical stress, or chemical exposure could also potentially induce such malformations during metamorphosis (West-Eberhard, 2003).

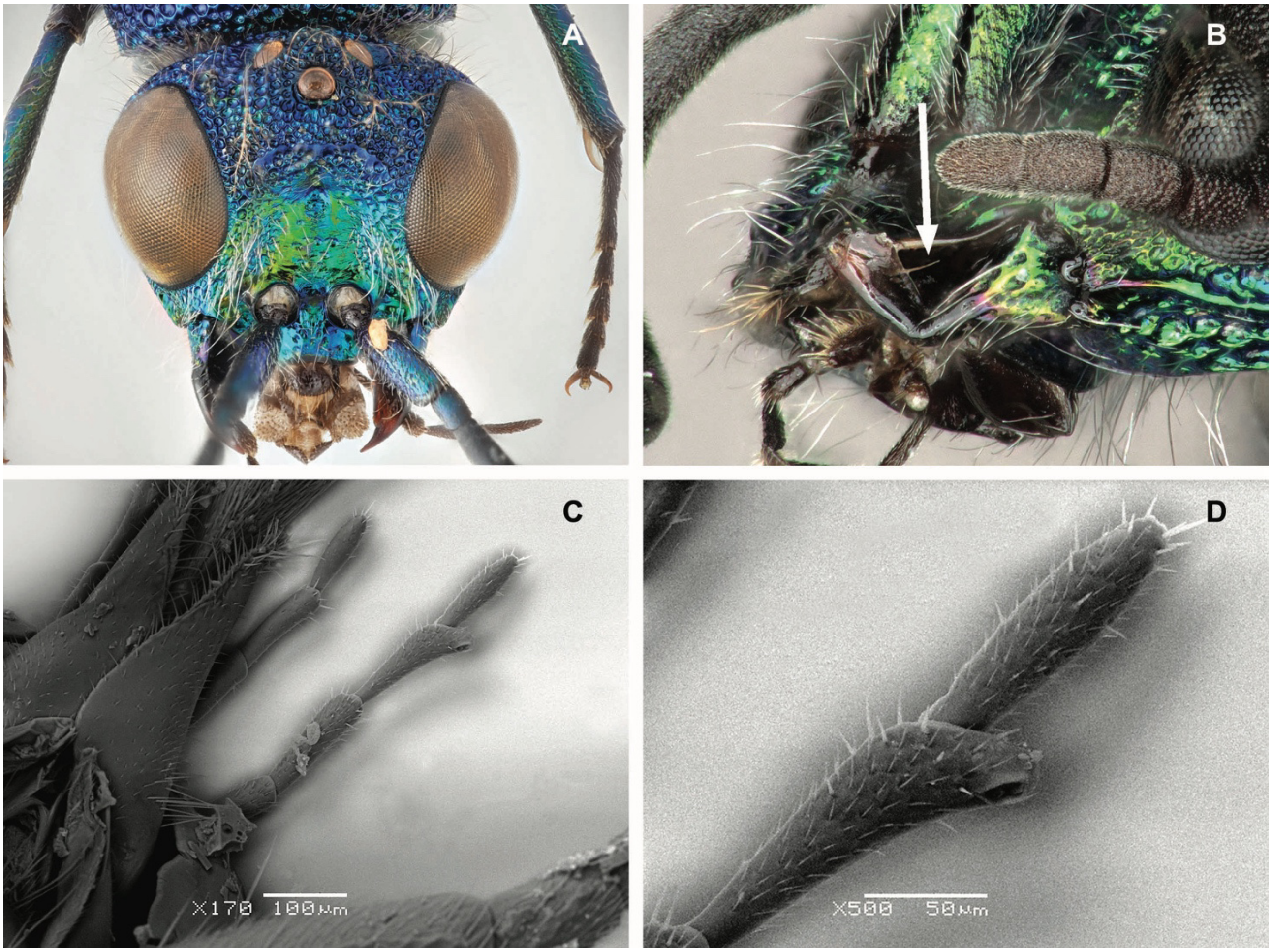

Fig. 10 – Aberrant mouthparts. A) *Chrysis leptomandibularis*, female, galea abnormally expanded. B) *Chrysis angustula*, female, left mandible deformed. C-D) *Pseudomalus auratus*, male, schistomely of maxillary palp. / Parti boccali aberranti. A) *Chrysis leptomandibularis*, femmina, galea anormalmente espansa. B) *Chrysis angustula*, femmina, mandibola sinistra deformata. C-D) *Pseudomalus auratus*, maschio, schistomelia del palpo mascellare.

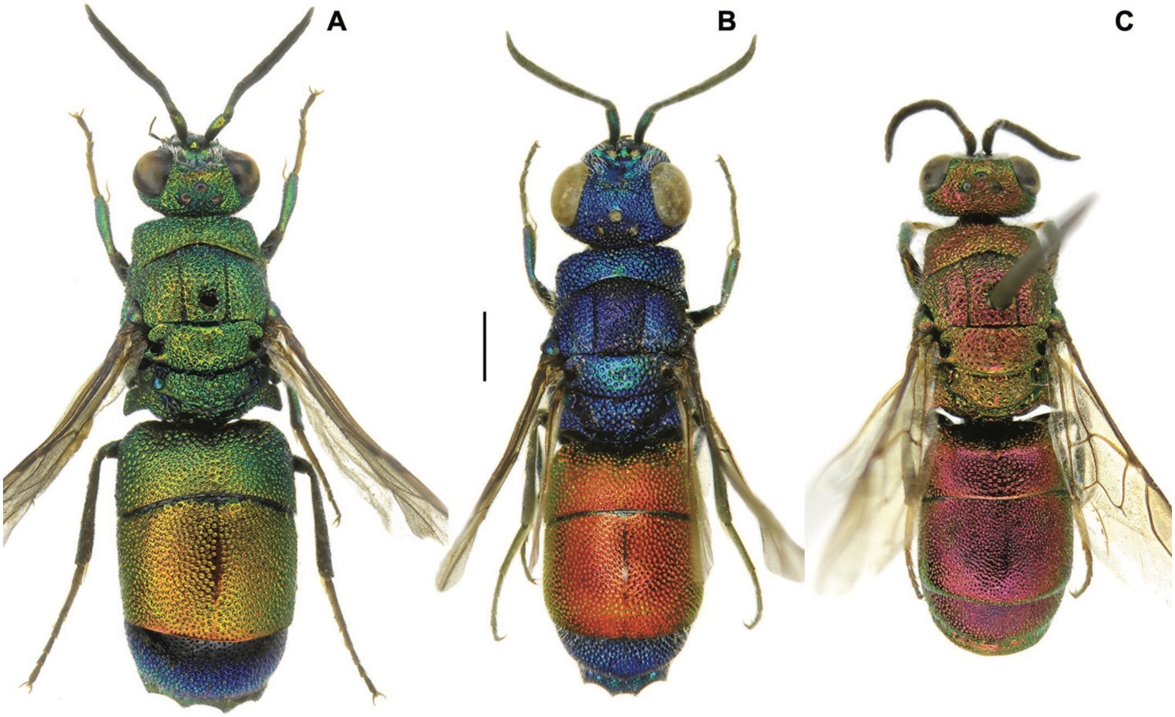

Fig. 11 – Body malformations. A) *Chrysis parvicapito*, male, holotype, dorsal view. B) *Chrysis splendidula chlorisans*, male, dorsal view, microcephalic and hypertrophic metasoma. C) *Chrysis splendidula splendidula*, female, normal habitus. Scale bar: 1.0 mm. / Malformazioni del corpo. A) *Chrysis parvicapito*, maschio, olotipo, vista dorsale. B) *Chrysis splendidula chlorisans*, maschio, vista dorsale, microcefalico e metasoma ipertrofico. C) *Chrysis splendidula splendidula*, femmina, habitus normale. Scala: 1,0 mm.

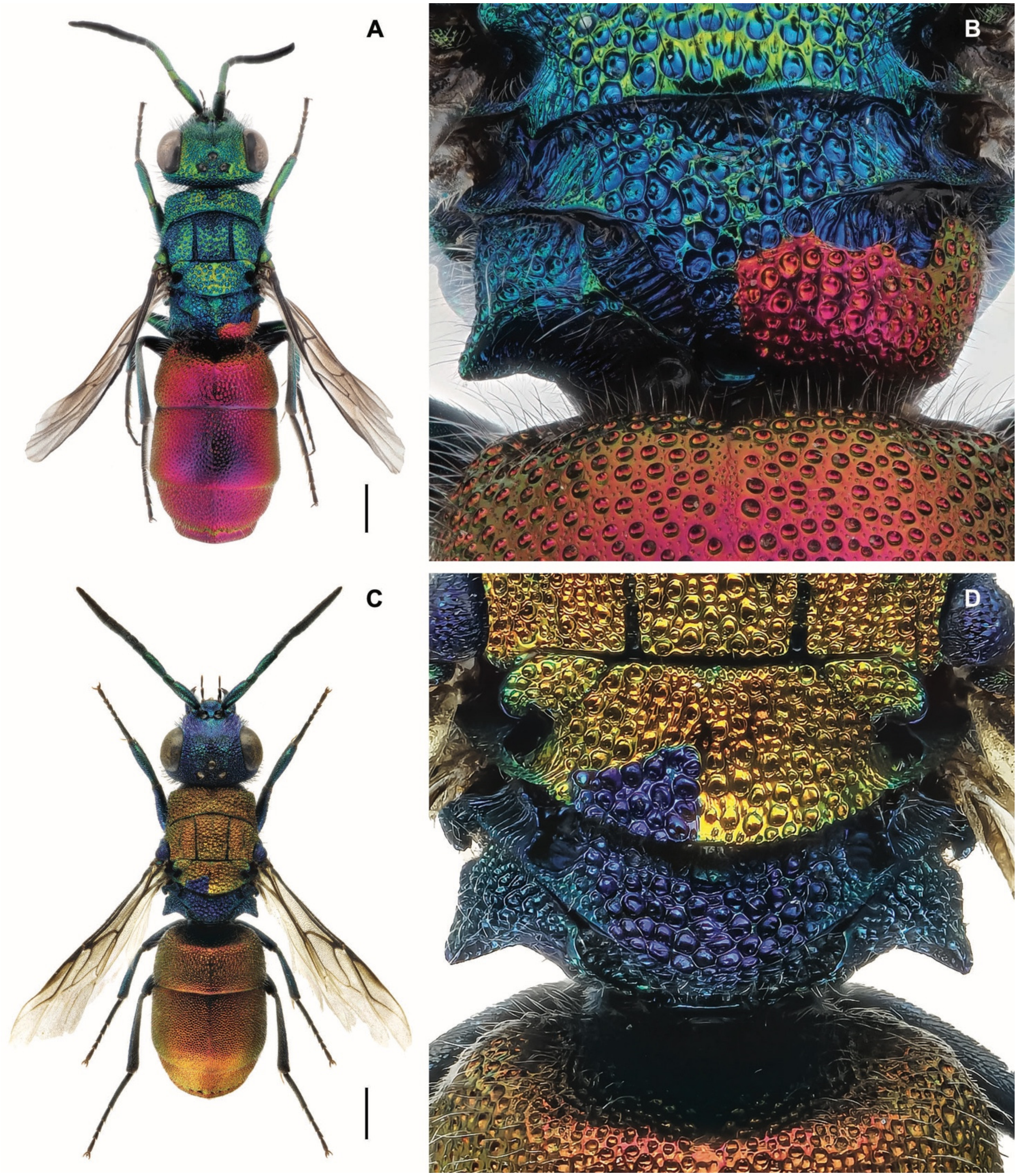

Fig. 12 – Mesosomal heterotopy. A-B) *Chrysura radians*, female. A) Habitus, dorsal view. B) Propodeum (metapectal-propodeal complex), detail, metasomal tissue on propodeum. C-D) *Chrysura dichroa*, female. C) Habitus, dorsal view. D) Scutellum and propodeum, detail, metanotal tissue on scutellum. Scale bars: 1.0 mm. / Eterotopia mesosomale. A-B) *Chrysura radians*, femmina. A) Habitus, vista dorsale. B) Propodeo (complesso metapectus-propodeum), dettaglio, tessuto metasomale sul propodeo. C-D) *Chrysura dichroa*, femmina. C) Habitus, vista dorsale. D) Scutello e propodeo, dettaglio, tessuto metanotale sullo scutello. Scala: 1,0 mm.

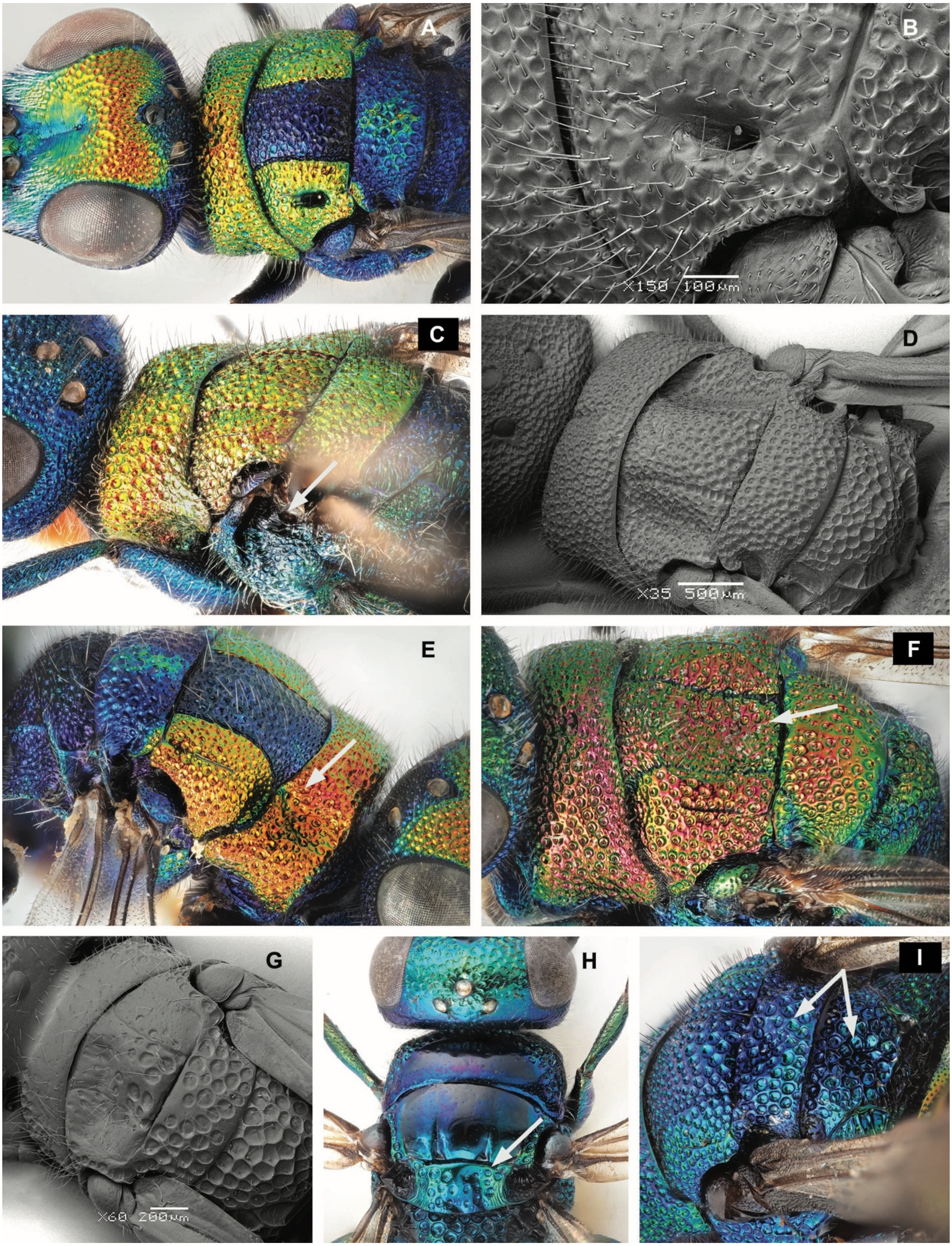

Fig. 13 – Mesosomal malformations. A-B) *Chrysura candens*, male, head and mesosoma, dorso-lateral view. C) *Chrysura dichroa*, male, dorso-lateral view. D) *Chrysis scutellaris*, male, dorsal view. E) *Chrysura candens*, female, dorso-lateral view. F) *Chrysis calimorpha*, male, dorsal view. G) *Pseudomalus auratus*, male, dorsal view. H) *Omalus aeneus*, female, dorsal view. I) *Hedychrum micans*, male, dorso-lateral view. / Malformazioni mesosomali. A-B) *Chrysura candens*, maschio, testa e mesosoma, vista dorso-laterale. C) *Chrysura dichroa*, maschio, vista dorso-laterale. D) *Chrysis scutellaris*, maschio, vista dorsale. E) *Chrysura candens*, femmina, vista dorso-laterale. F) *Chrysis calimorpha*, maschio, vista dorsale. G) *Pseudomalus auratus*, maschio, vista dorsale. H) *Omalus aeneus*, femmina, vista dorsale. I) *Hedychrum micans*, maschio, vista dorso-laterale.

Various aberrations

A specimen of *Chrysura candens* (Germar 1817) from Predore (Lombardy, Italy) exhibits a deep perforation in the lateral lobe of mesoscutum, aligned with the left parapsidal line (Fig. 13A and B). A female of *Chrysura dichroa* (Dahlbom, 1854) from Oriano (Emilia-Romagna, Italy) has the mesopleuron deformed beneath the left wings' insertions (Fig. 13C), causing the fore wing to remain in an irregular, vertical position. A male of *Chrysis scutellaris* Fabricius, 1794 from Sperone (Abruzzo, Italy) presents symmetrical depressions on both lateral areas of the mesoscutum, while the median area is normally formed (Fig. 13D). Excluding the cases mentioned above, all other mesosomal malformations observed were of mechanical origin, possibly caused by the position of the pupa in the nest. For example, malformations in a female of *Chrysura candens* from Roccaraso (Abruzzo, Italy), with a depressed right side of pronotum, blocking the articulation with the mesoscutum (Fig. 13E); in a female of *Chrysis calimorpha* Mocsáry 1882 from Ozein (Aosta Valley, Italy) with the mesoscutum largely depressed (Fig. 13F); in a male of *Pseudomalus auratus* from Sperone (Abruzzo, Italy) with the mesoscutum deeply depressed laterally (Fig. 13G); in a female of *Omalus aeneus* (Fabricius, 1787) from Pineta di San Vitale (Emilia-Romagna, Italy) the scutellum is deeply depressed on the right side (Fig. 13H), not clearly visible from the picture); the last specimen worth mentioning is a male of *Hedychrum gerstaeckeri* Chevrier 1869 from Tabiano (Emilia-Romagna, Italy) with the head, scutellum, metanotum and all terga malformed with depressions (Figs. 13I and 26G).

Legs

Legs in Chrysididae are generally unmodified, with few exceptions. In the tribe Elampini the fore femur may be carinate, and the tarsal claws can have different teeth depending on the genus and, in the case of *Holopyga* Dahlbom 1845, on species groups. In a few genera, like *Haba* Semenov-Tian-Shanskij 1954, there are flattened tarsomeres which appear prehensile (Kimsey & Bohart, 1991). Tibial spurs may have diagnostic value (Paukkunen *et al*., 2015) and rake spines can be found on the fore and hind tarsomeres of females in the genus *Parnopes* Latreille 1802. Malformations in legs are less obvious than those in wings, but can be of great interest, particularly in cases involving supernumerary legs.

Somatomely

The presence of a supernumerary leg, also known as teratological polypody or supernumerary leg anomaly, is a rare phenomenon observed primarily in ants (Bateson, 1894; Goss, 1895; Poisson, 1942; Pérez-Lachaud *et al*., 2024) and other hymenopterans, including Symphyta (Balazuc, 1958). Various cases of leg reduplication in Coleoptera, Diptera, and Hymenoptera were described by Cockayne (1937). In Chrysididae, a case of supernumerary leg, or more precisely, reduplication, was observed in a female of *Pseudomalus auratus* collected by M. Jacobs in Belgium (PRC) (Fig. 14). This specimen has two left prothoracic legs with aberrant coxae, trochanters, femora and tibiae (Fig. 14). The anterior foreleg lacks tarsi, while the posterior one has an enlarged, inverted tibia and only two enlarged tarsomeres (Fig. 14B). All other legs and body segments appear unmodified. However, following Bateson's law, the two fore legs are not merely duplicates of the left foreleg; rather, the first one structurally belongs to the opposite side of the body, forming a mirror image. This type of mirror reduplication was previously recorded by Cockayne (1937), who suggested that injury during development could lead to reduplication.

In the case of this *Pseudomalus*, it is likely that the growing point was divided horizontally, parallel to the insect horizontal plane, leading to reduplication below the original appendage. As a result, one appendage has its dorsal surface facing upward, while the other has its ventral surface oriented upwards. Horizontal reduplication was considered the most common form in Coleoptera and the only recorded for Diptera and Hymenoptera (Ichneumonidae) by Cockayne (1937).

Schistomely

Schistomely, like the condition observed in antennae, refers to the division of an appendage into two or more parts. In Chrysididae, we did not examine any complete ramification of the legs as seen in other hymenopterans, particularly in Symphyta (Balazuc, 1958). However, a specimen of *Chrysis bicolor* Lepeletier 1806 from Oriano (Emilia-Romagna, Italy) exhibits partial schistomely in the femur of the right metaleg (Fig. 15A and B), characterized by a rudimental bifurcation of the femur.

Heteromorphosis

As for antennal teratologies, heteromorphosis is the phenomenon in which an organism develops or regenerates a structure that differs in form or function from the original. In Hymenoptera, it is documented by the replacement of antennal segments with leg-like structures, resulting from homeotic mutations that displace body parts. In Chrysididae, we observed three specimens of *Chrysis gribodoi* Abeille de Perrin 1879 from the same population from Sperone (Abruzzo, Italy, PRC) bearing one or two apparently unknown segmented structures on the arolium of the different legs (Fig. 15C-E). In one specimen these structures are present on all legs; in the second specimen on four legs (prolegs, right midleg and right metaleg); in the third one on two legs (right proleg and right metaleg).

A possible interpretation is that these unusual structures may be rudimental antennae composed of 11 segments, possibly homologous to the 11 flagellomeres. Additionally, they are ventrally concave, a characteristic sometimes observed in deformed or dehydrate flagellomeres. This form of heteromorphosis, with antennae developing on the legs is essentially the inverse of the case described by Linsenmaier (1959) for the case of *Chrysis elegans* Lepeletier 1806, where tarsi developed in place of the last flagellomeres. To our knowledge, this phenomenon has not been previously recorded in Hymenoptera.

A somehow comparable case of antennal-like structure grown on a fully developed leg was recorded by Wheeler

(1896) in the dipteran *Dilophus tibialis* Loew 1869, which exhibited a fore coxa bearing a long, nine-jointed antenna. Wheeler hypothesized that the coxa might represent the basal tenth antennal joint; furthermore, he noted that the antennal segments originating from the leg were distinctly longer than broad, differing from those on the head. He speculated that this anomaly could be related to atavism, an evolutionary reversion to a more ancestral structure, as retained by most Nematocera.

We do not have any explanation for this case, which is beyond the scope of this study, but a potential insight may be found in genetic studies (e.g., Schneuwly *et al*., 1987) on the expression of the *Antennapedia* (*Antp*) gene, which suggests that this gene primarily specifies the second thoracic segment where the metalegs are placed. Molecular analysis of dominant gain-of-function mutants has shown that the transformation of antennae into second legs results from the ectopic overexpression of the *Antp*$^+$ protein. They tested this hypothesis by inserting in specimens of *Drosophila* complementary DNA encoding the normal *Antp*$^+$ protein into a heat-shock expression vector, followed by germ-line transformation. As predicted, heat induction at specific larval stages led to the transformation of antennae into second legs. We wonder whether the reverse process might also occur, where antennal-like structures develop on legs under certain environmental conditions, such as heat-shocks. This intriguing possibility warrants further genetic investigation.

Other malformations

A female of *Chrysis splendidula* Rossi 1790 exhibits both metalegs irregularly conformed (Fig. 15F), probably to a defect in drying when the imago was emerging from the exuvia, while the rest of the body is unmodified. A female of *Chrysis gribodoi* from Sperone (Abruzzo, Italy) has dilated arolium (Fig. 15G). A female of *Pseudomalus auratus* has bilateral enlarged metatarsi (Fig. 15H) compared to the normal metatarsi width (Fig. 15I).

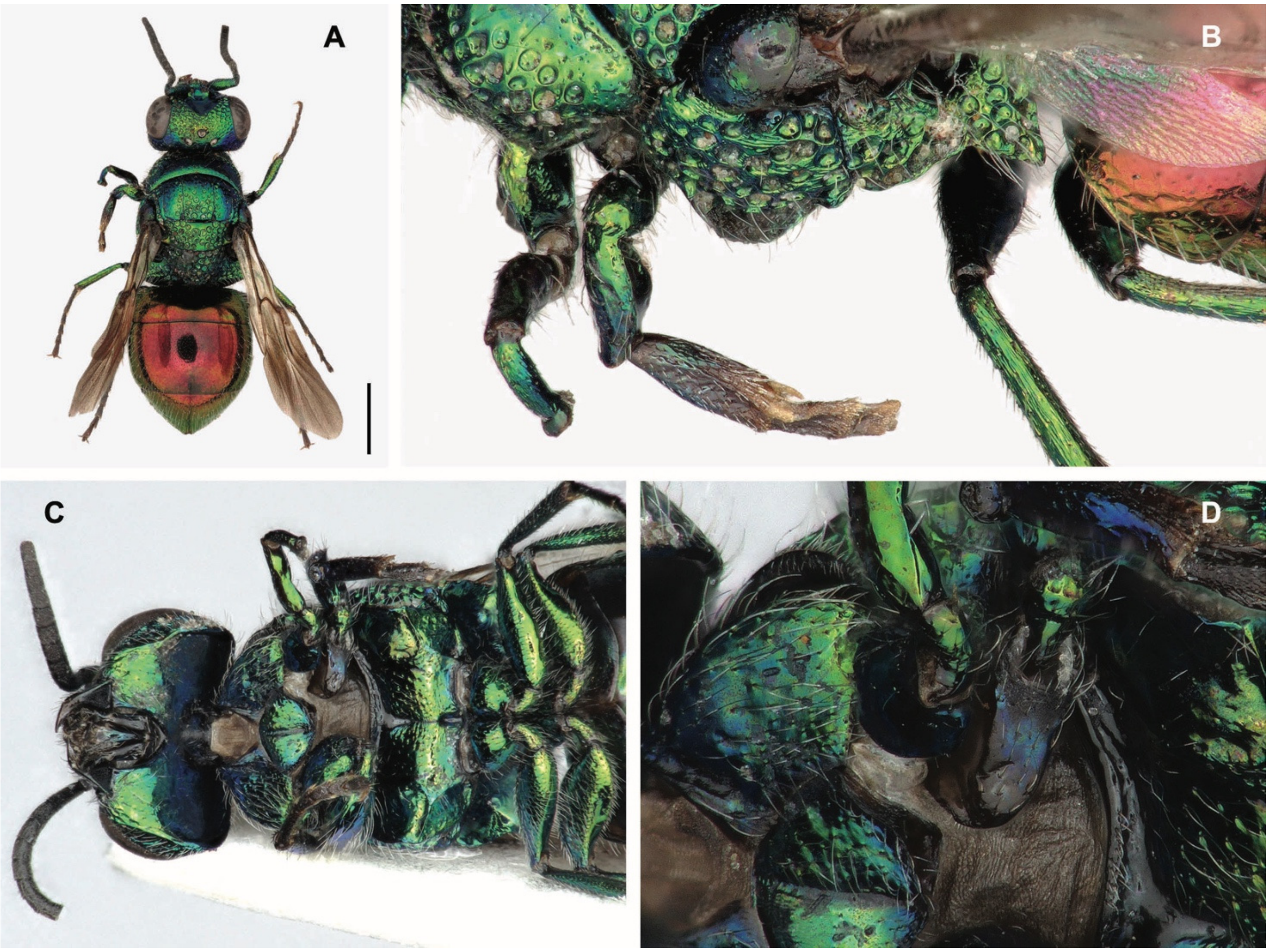

Fig. 14 – Supernumerary leg. A-D) *Pseudomalus auratus*, supernumerary fore leg. A) Habitus, dorsal view. B) Mesosoma, dorso-lateral view, with focus on the two fore legs. C) Head and mesosoma, ventral view. D) Fore legs insertion, ventral view. Scale bar: 1.0 mm. / Zampa soprannumeraria. A-D) *Pseudomalus auratus*, zampa anteriore soprannumeraria. A) Habitus, vista dorsale. B) Mesosoma, vista dorso-laterale, con particolare attenzione alle due zampe anteriori. C) Testa e mesosoma, vista ventrale. D) Inserzione delle zampe anteriori, vista ventrale. Scala: 1,0 mm.

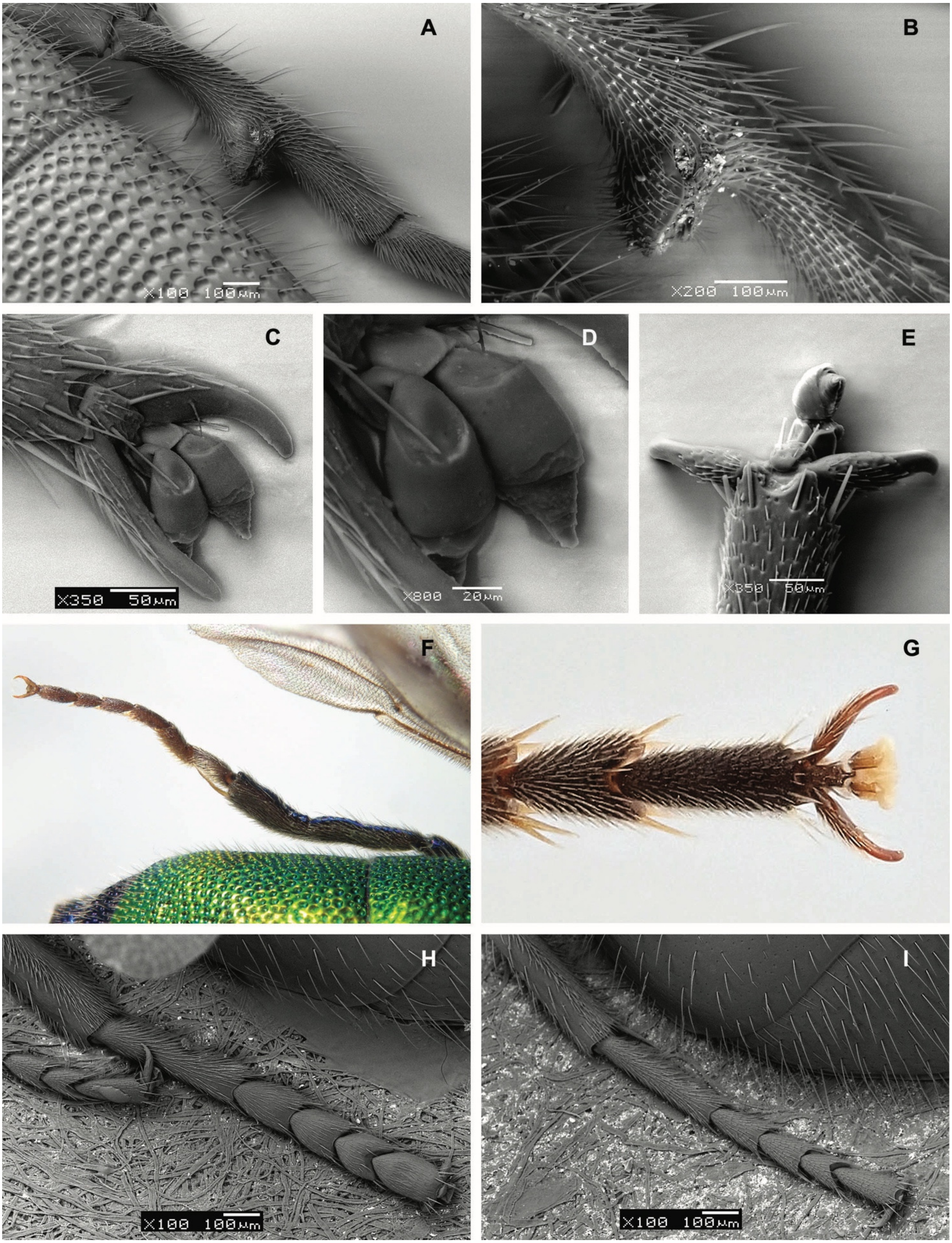

Fig. 15 – Leg aberrations. A-B) *Chrysis bicolor*, hind leg, schistomely C-E) *Chrysis gribodoi*, possible heteromorphosis on arolium. F) *Chrysis splendidula*, malformation of hind legs. G) *Chrysis elegans*, malformation of the arolium. H-I) *Pseudomalus auratus*, hind leg. H) Hypertrophic tarsi. I) Normal condition. / Aberrazioni delle zampe. A-B) *Chrysis bicolor*, zampa posteriore, schistomelia. C-E) *Chrysis gribodoi*, possibile eteromorfosi sull'arolio. F) *Chrysis splendidula*, malformazione delle zampe posteriori. G) *Chrysis elegans*, malformazione dell'arolio. H-I) *Pseudomalus auratus*, zampa posteriore. H) Tarsi ipertrofici. I) Condizione normale.

Wings

Similar to all aculeate Hymenoptera, chrysidid wings are membranous appendages formed by two epidermal layers supported by veins. Veins are subdivided into longitudinal and cross veins, and they form a characteristic network which divide the wing area into cells. With the sole exception of some apterous or brachypterous Amiseginae, Chrysididae typically show fully developed wings, albeit with an extreme reduction of closed cells and veins. Longitudinal veins are robust cuticular tubes that carry the haemolymph, tracheae and sensory nerves associated with wing sensilla. In contrast, cross veins are smaller and connect the longitudinal ones, providing structural support to the membranous wing (Danforth, 1989). The most complete wing venation is found in the tribe Chrysidini with at most six close cells (costal, radial, medial, cubital, discoidal, and submedial; terminology after Kimsey & Bohart, 1991). The posterior wings lack closed cells entirely, showing only faint traces of five veins.

Brachypterous specimens can be observed in the subfamily Amiseginae. Members of this subfamily are parasites of phasmatid eggs and are not distributed in the Palaearctic region, except for a few species recorded in Japan. In most African Amiseginae, both sexes are secondarily apterous or with wings reduced to small pads. In some Oriental and Australian Amiseginae, females are brachypterous, as in *Myrmecomimesis,* or with wings reduced to small pads.

The structure and coloration of the forewing are useful characters for distinguishing genera and, occasionally, species groups. Taxonomical features used in identification keys include the shape of the radial sector, shape of the discoidal and marginal cells, the length of the stigma, and the number and position of recurrent veins. Reductions in venation and number of cells are also important taxonomic characters at the genus level. Vein reduction tends to correlate with body size: the smaller the individual, the more reduced its wing venation tends to be (Kimsey & Bohart, 1991). In fact, the most reduced venation is found in the tribe Elampini, which includes the smallest members of the subfamily Chrysidinae, particularly in the genera *Kimseya* Antropov 1994 and *Microchridium* Bohart 1980. These genera include the smallest known cuckoo wasps, with venation limited to only the basal fourth or fifth of the wing, and with veins that are not clearly defined.

Wing anomalies often attract the attention of entomologists in groups where wing venation is used for taxonomic identification to species level, such as in Tenthredinoidea, where several publications have focused on this topic (Balazuc, 1958). For example, Kloiber (1936) counted 150 cases of wing anomalies among 7,000 sawflies (Symphyta) examined. Anomalies in nervures and cells have been largely discussed in Apoidea (e.g., Tan *et al*., 2008; Maazed, 2011) and are most frequently reported in honey bees (Torres & Ramos, 2000; Penteado-Dias *et al*., 2005; Porporato *et al*., 2014; Comério *et al*., 2015) as well as in other families, including Sphecidae (Gülmez, 2019).

In Chrysididae only one study illustrates the teratological case of an aberrant wing (Rosa, 2024b), specifically the fore wing of *Chrysis curax* Harris 1776 (currently *Trichrysis cyanea* (Linnaeus 1758) which exhibits an additional cell. This limited number of observations may be due to two factors: a) the extremely reduced wing venation and b) the limited attention typically given to chrysidid wing nervures and cells, as they are not used for species-level identification. We observed 44 cases of wing anomalies, all in the tribe Chrysidini but one in Elampini.

The most common anomalies recorded in chrysidid wings are defective diverging veins (25 cases). Other malformations recorded are seven cases of supernumerary vein, 10 cases of supernumerary cells and two possible cases of wing deformed by viruses. Most of the observed anomalies involved the discoidal cell, radial, medial and cubital veins. In 11 cases these aberrations were bilateral, in 6 cases were in association with other malformations of the mesosoma and metasoma; and in one case were associated with melanism.

Supernumerary cells

A male of *Chrysis sexdentata* Christ 1791 from Ventimiglia (Liguria, Italy) (Fig. 16A) exhibits an additional closed cell within the discoidal cell, fully visible in the left wing and less distinct in the right wing. A female of *Chrysura cuprea* (Rossi 1790) from Domica (Slovakia) (Fig. 16B) exhibits a similar additional extra cell, though smaller and only in the right wing. A male of *Chrysis sinuosiventris* Abeille de Perrin 1878 (NMLU) (Fig. 16C) displays a bilateral closed second discoidal cell, which could be an atavistic feature. Another female of *Chrysura cuprea* (Rossi 1790) from Domica (Slovakia) (Fig. 16D) exhibits a small cell in the cubital vein of the right wing. A supernumerary cell was also illustrated by Harris (1776), leading to the description of *Chrysis curax*, a teratological form of *Trichrysis cyanea* (Linnaeus 1758). A supernumerary cell within the discoidal cell was observed in two males of *Chrysis analis* Spinola 1808, from Turlin (Aosta Valley, Italy), collected in different years, one of which exhibiting a bilateral teratology. Similar teratologies were recorded in a female of *Chrysis horridula* from Corfu (Greece); a male of *Chrysis marginata* Mocsáry 1889; a male of *Chrysis phryne* (Abeille de Perrin 1878) from Oriano (Emilia-Romagna, Italy); and a male of *Spintharina versicolor* (Spinola 1808) from Cordenons (Friuli-Venezia Giulia, Italy). A partially developed bilateral supernumerary cell was also observed in a male of *Chrysis mediadentata* Linsenmaier 1951, from Mezzanino Po (Lombardy, Italy) (Fig. 17B).

Defective, irregular and supernumerary veins

Two females of *Chrysura dichroa* (Dahlbom 1854) from Oriano (Emilia-Romagna, Italy), collected in different years, exhibit a defective first segment of the medial vein, resulting in an open discoidal cell (Fig. 16E). Five males and females of *Chrysura dichroa* (Dahlbom 1854) from Oriano (Emilia-Romagna, Italy), Pondel and Ozein (Aosta Valley, Italy), collected in different years, exhibit the same teratology, where a defective m-cu vein leads to an open discoidal cell (Fig. 16F); in three of these cases the defective m-cu is bilateral. A male of *Chrysis chrysostigma* Mocsáry 1889 from Assergi (Abruzzo, Italy) exhibits a deviation of the Rs+M vein from its normal trajectory, preventing the closure of the discoidal cell (Fig. 16G). A female of *Hedychridium roseum* (Rossi 1790) exhibit a spectral external venation of the discoidal cell (Fig. 16H).

Spurs protruding from the m-cu vein were recorded in *Chrysura dichroa* (Dahlbom, 1854) (Fig. 17A), *Chrysis analis* Spinola 1808 (in association with a supernumerary cell), *Chrysis chrysostigma* Mocsáry 1889, *Chrysis gracillima* (Förster 1853) (Fig. 17E), and *Chrysis amasina* Mocsáry 1889.

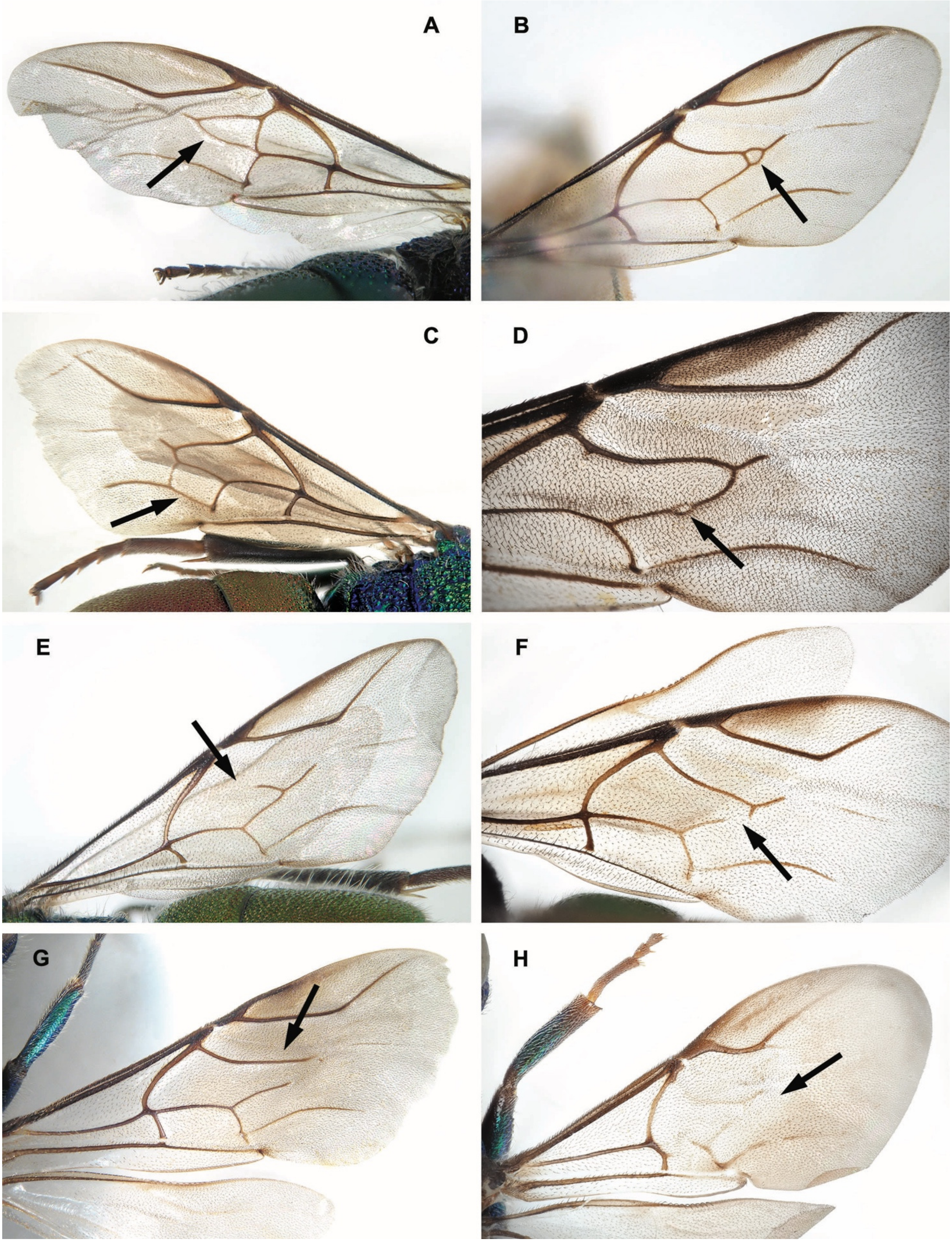

Fig. 16 – Wings, extra cells and defective veins. A) *Chrysis sexdentata*, supernumerary cell. B) *Chrysura cuprea*, supernumerary cell. C) *Chrysis sinuosiventris*, supernumerary cell. D) *Chrysura cuprea*, supernumerary cell. E-F) *Chrysura dichroa*, defective vein. G) *Chrysura dichroa*, deviated vein. H) *Hedychridium roseum*, spectral venation. / Ali, celle soprannumerarie e vene difettose. A) *Chrysis sexdentata*, cella soprannumeraria. B) *Chrysura cuprea*, cella soprannumeraria. C) *Chrysis sinuosiventris*, cella soprannumeraria. D) *Chrysura cuprea*, cella soprannumeraria. E-F) *Chrysura dichroa*, vena difettosa. G) *Chrysura dichroa*, vena deviata. H) *Hedychridium roseum*, venatura spettrale.

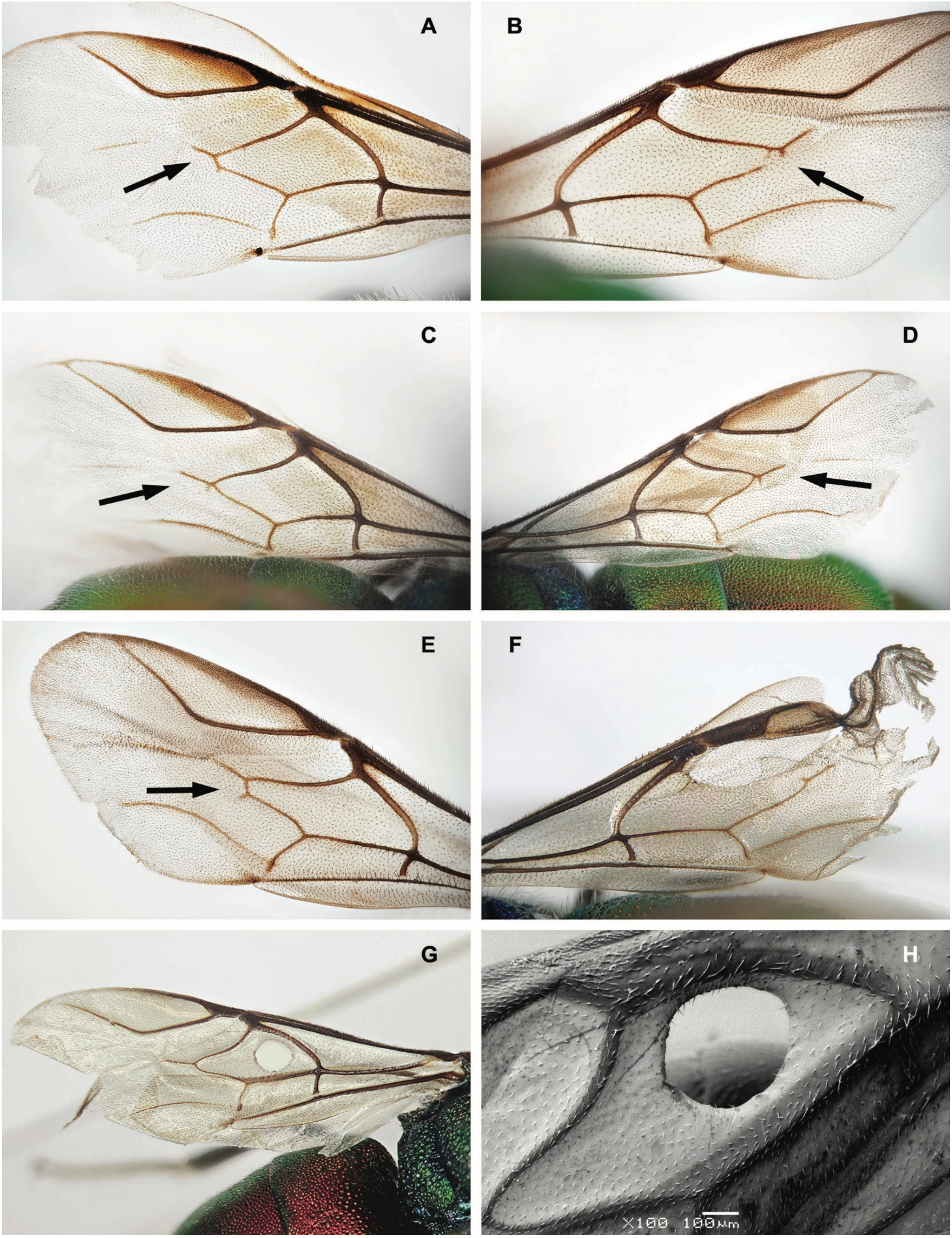

Fig. 17 – Wings, aberrations. A) *Chrysura dichroa*, additional spur. B) *Chrysis mediadentata*, incomplete vein and supernumerary cell. C-D) *Chrysura arcadiae*, deviated vein. E) *Chrysis gracillima*, additional spur. F) *Chrysis leptomandibularis*, crumpled wing possibly due to DWV. G-H) *Chrysura ignifrons*, holed wing possibly due to viral infection. / Aberrazioni alari. A) *Chrysura dichroa*, sperone aggiuntivo. B) *Chrysis mediadentata*, vena incompleta e cella soprannumeraria. C-D) *Chrysura arcadiae*, vena deviata. E) *Chrysis gracillima*, sperone aggiuntivo. F) *Chrysis leptomandibularis*, ala spiegazzata probabilmente a causa di DWV. G-H) *Chrysura ignifrons*, ala forata probabilmente a causa di infezione virale.

Defective veins were observed in seven specimens (four males and three females) of *Chrysis scutellaris* Fabricius 1794 from Pondel and Ozein (Aosta Valley, Italy) and Tabiano (Emilia-Romagna, Italy) collected in different events. These defects resulted in an open discoidal cell due to a defective m-cu vein (five cases) or Rs+M (two cases); in three of them, the aberrations were bilateral (one for m-cu, two for s+M). Additional cases of defective m-cu were recorded in *Chrysis sexdentata* Christ 1790, while defective Rs+M was observed in five males of *Trichrysis cyanea* (Linneus 1758) from Emilia-Romagna (Italy), two of which collected in the same event at Ostellato (Ferrara) and one specimen from Ukraine. In a female of *Chrysura arcadiae* Arens 2001 from Peloponnese (Greece), the trajectory of the m-cu vein is defective (bilateral), failing to meet the Rs+M vein, whose end resembles a short spur (Fig. 17 C and D).

Deformed Wing Virus

The DWV is a highly contagious virus primarily affecting honeybees *Apis mellifera*, but it has been detected in other insects and wasps of the genus *Vespa* and *Vespula* (Forzan, 2017; Martin & Brettell, 2019). Although cuckoo wasps are not parasitized by *Varroa*, the main vector, they might have been indirectly infected by inside the nest of an infected host or by honeybees during pollination. The right fore wing of a *Chrysis leptomandibularis* Niehuis 2000, from Mezzanino Po (Lombardy, Italy), is deformed likely due to the DWV (Fig. 17F), which causes deformed, crumpled, or misshapen wings. Another viral infection could also be responsible for the hole observed in the left wing of a *Chrysura ignifrons* (Brullé 1833) from Peloponnese (Greece) (Fig. 17G and H).

A Rare Monstrosity

Polymely and polyptery are very rare conditions, previously observed in ants with seven legs and five wings, such as in the cases of *Dolicoderus quadripunctatus* (Linnaeus 1771) (Forel, 1920, under *Hypoclinea quadripunctata*) and *Leptothorax acervorum* (Fabricius 1793) (Kutter, 1952).

However, in Chrysididae, we observed an extraordinary case of teratology in a specimen with five legs and five wings. A similar case was described by Richardson (1891) for the moth *Zygena filipendulae* (Linnaeus 1758) and considered by Balazuc (1958) as a case of major heteromorphosis. This highly teratological individual is frequently cited in the literature, and its description and illustration are also reported in Bateson (1894). Our case is somehow comparable to that of *Zygena* and involves a male of *Chrysis sculpturata* Mocsáry 1912 from Perivolia (Arcadia, Greece, leg. F. Izzillo) (Fig. 18). In this individual, the left midleg is completely absent, with a recognizable, sclerotized foramen for the insertion of the midcoxa (Fig. 18E), leading to an asymmetry of the mesosoma. Anteromedially, on the left mesopleuron, there is an additional limb like a somewhat crumpled forewing, in which the main veins and the wing membrane can be recognized (Fig. 18C). The supplementary tegula covering the additional wing insertion has a vaguely normal shape but is thickened and exhibits mesopleural sculpture (Fig. 18B and D). All other body parts are normally developed.

The occurrence of a supernumerary leg or wing is rare phenomenon recorded in various hymenopteran families but an aberration involving the simultaneous aplasia of a midleg and the development of an additional anterior wing on the same segment is documented here for the first time. The origin of this phenomenon remains unclear but may be linked to a genetic mutation affecting the expression of homeotic genes (such as Hox genes), which regulate body segmentation and appendage development. These genes determine the positioning of legs, wings, and other structures, and mutations can result in extra or missing limbs or wings.

Metasoma

In Chrysididae and other hymenopterans of the suborder Apocrita, the first abdominal segment is the propodeum, which is fused with the thorax to form the mesosoma. Consequently, the remaining abdominal segments, from the second to the last, are collectively referred to as the metasoma.

Chrysididae can be distinguished from other aculeate wasps by the reduced number of visible metasomal segments: in the subfamily Chrysidinae only three terga are externally visible, with the exception of Parnopini males, with four visible terga, and Allocoeliini, which have only two; in contrast, Cleptinae, Amiseginae and Loboscelidiinae have five abdominal terga in males and four in females. The internalized metasomal segments are modified to form a telescopic genital apparatus in males and an ovipositor tube in females. Additionally, the ventral surface of the metasoma in Chrysidinae is usually flat to concave, enabling the body to roll up in a defensive ball when they are threatened. The apical margin of the third tergum bears key diagnostic characters for the genus- and species-level identification in the cuckoo wasps. Feature such as the number, position and shape of the apical teeth, the depth of the median notch, and the width of the transparent rim are among the most relevant traits for distinguishing species.

Metasomal aberrations and malformations are relatively frequent in cuckoo wasps. Some of these were previously documented by Negru (1955, 1958), who described and illustrated the cases of epigastroschisis, incomplete fusion of the first (1958) and second (1955) metasomal segments, of *Holopyga chrysonota* Förster 1853 and *Holopyga amoenula* Dahlbom 1845. Móczár (1963), described and illustrated two specimens of *Chrysis ignita* (Linnaeus 1758), one lacking apical teeth on the last visible tergum and another with a malformation on the apical margin of the second tergum. The holotype of *Chrysis gurkoi* Rosa 2019 exhibits an asymmetry in the second metasomal tergum (Rosa, 2019b: Fig. 11). Rosa (2024a) published a series of teratologies affecting the metasoma to justify the synonymization of the genus *Oligogaster* Solimam & Kimsey 2013 with *Hedychridium* Abeille de Perrin 1878. *Oligogaster* was based on a single specimen affected by symphysomery, and Rosa (2024a) illustrated other cases of *Hedychridium* species belonging to different species groups and exhibiting the same teratology - *H. braunsii* (Mócsary 1902) and *H. belokobylskiji* Rosa 2017 - along with another case recorded for an unidentified amisegine wasp of the genus *Anachrysis*. Additionally, Rosa (2024a) reported examples of helicomery in *Hedychrum nobile* (Scopoli 1763) and epigastroschisis in *Hedychrum niemelai* Linsenmaier 1959.

In our survey we observed a total of 565 cases of teratological anomalies, including the absence of terga or hemiterga, fused terga or hemi-terga, spiralled structures, and partial or complete failure of union between the two halves of a tergum. In rare cases multiple abnormalities coexist in the same individual as seen in *C. rutiliventris* Abeille de Perrin 1879 (Fig. 21C). These anomalies comprise 379 cases from Chrysidini, 183 from Elampini, two from Parnopini, and one from *Amiseginae*. Among these, 35 cases were associated with additional body malformations. As many as 342 out of 565 cases, were interpreted as mechanical crush injuries resulting from pupal accidents within the nest or due to the position of the pupa; 223 of these cases involved malformations on the second tergum, with nearly 50% of these cases affecting the dorsal face (Fig. 26A-G). An additional 88 cases of malformations on the second and third terga can be potentially considered to have an embryonic origin. These cases include anomalies such as incorrectly shaped apical teeth, irregular formation of pits in the pit row, or bilateral malformations. Although the exact etiology of these developmental anomalies remains uncertain, they have been documented in the catalogue of teratologies. This inclusion is justified despite their less dramatic appearance compared to other teratological phenomena, such as helicomeries, symphysomeries, epigastroschisis, or gynandromorphs.

Fig. 18 – Mesosomal teratologies. A-F) *Chrysis sculpturata*, polyptery and aplasy. A) Habitus, dorsal view. B) Supernumerary fore wing, lateral view. C) Supernumerary fore wing, dorsal view. D) Supernumerary tegula, dorso-lateral view. E) Mesosoma, ventral view. F) Supernumerary fore wing, ventral view. Scale bar: 1,0 mm. / Teratologie mesosomali. A-F) *Chrysis sculpturata*, polipteria e aplasia. A) Habitus, vista dorsale. B) Ala anteriore soprannumeraria, vista laterale. C) Ala anteriore soprannumeraria, vista dorsale. D) Tegula soprannumeraria, vista dorso-laterale. E) Mesosoma, vista ventrale. F) Ala anteriore soprannumeraria, vista ventrale. Scala: 1,0 mm.

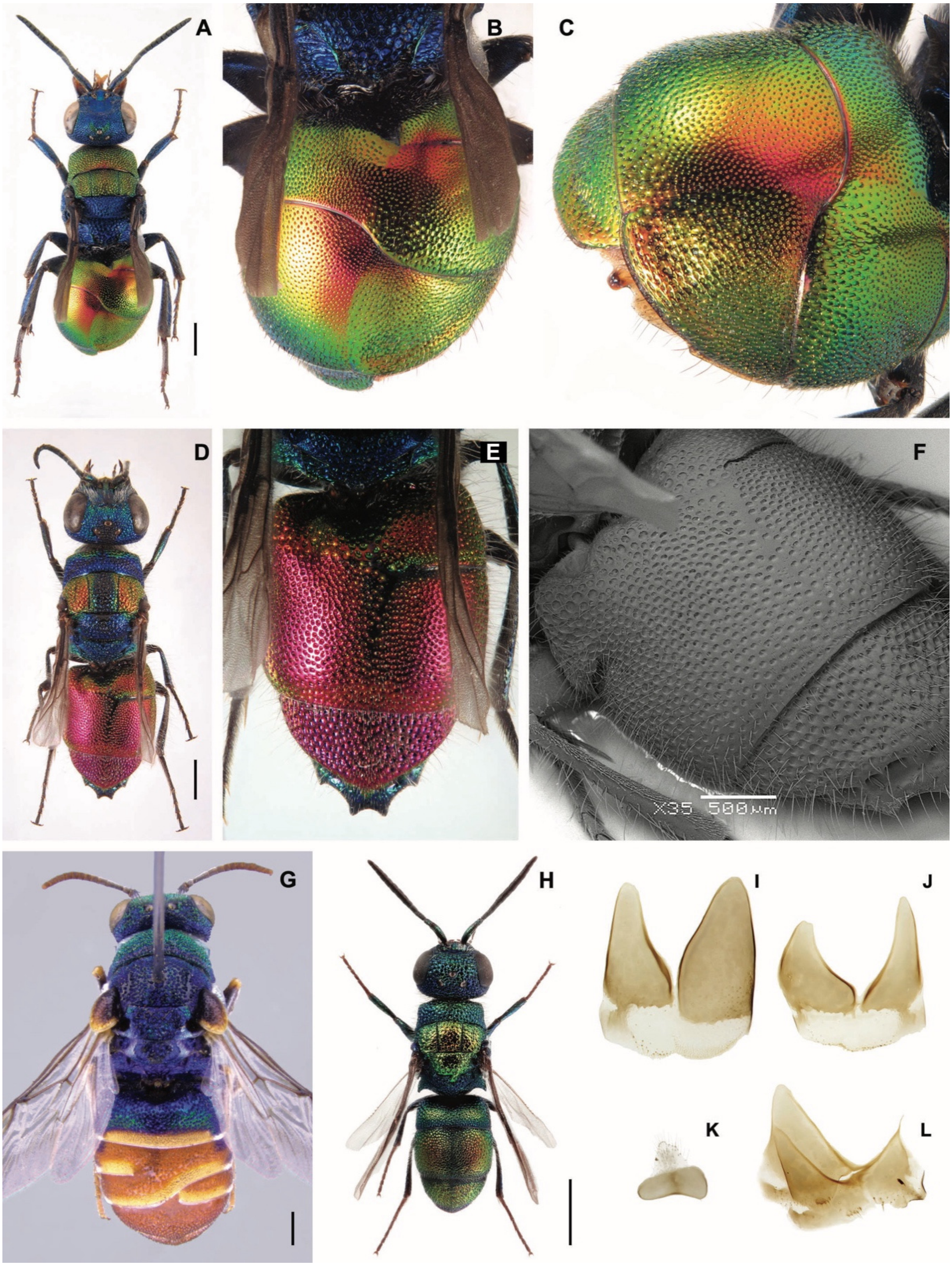

Fig. 19 – Helicomery and epigastroschisis. A-C) *Hedychrum nobile*, female. A) Habitus. B) Metasoma, dorsal view. C) Metasoma, postero-lateral view. D-F) *Chrysis grohmanni*, female. D) Habitus, dorsal view. E) Metasoma, dorsal view. F) Metasoma, dorso-lateral view. G) *Parnopes grandior*, male, dorsal view (Photo: Manuel Brazidec). H-L) *Chrysis leachii* gr., male (Photos: Daniele Baiocchi). H) Habitus, dorsal view. I) Spiral segmentation of S4 and S5. J) Spiral segmentation of S5 and S6. K) Malformed S8. L) T5 and T6 laterally fused. Scale bars: 1.0 mm. / Elicomeria ed epigatroschisi. A-C) *Hedychrum nobile*, femmina. A) Habitus. B) Metasoma, vista dorsale. C) Metasoma, vista postero-laterale. D-F) *Chrysis grohmanni*, femmina. D) Habitus, vista dorsale. E) Metasoma, vista dorsale. F) Metasoma, vista dorso-laterale. G) *Parnopes grandior*, maschio, vista dorsale (Foto: Manuel Brazidec). H-L) *Chrysis leachii* gr., maschio (Foto: Daniele Baiocchi). H) Habitus, vista dorsale. I) Segmentazione a spirale di S4 e S5. J) Segmentazione a spirale di S5 e S6. K) S8 malformato. L) T5 e T6 fusi lateralmente. Scala: 1,0 mm.

Helicomery

Helicomery, or spiral segmentation in the abdominal segments, refers to an unusual developmental or morphological condition where the abdominal segments appear arranged in a twisted or helical pattern rather than in the typical linear arrangement. This condition may result from developmental anomalies, mechanical pressures during pupation, or genetic mutations affecting body patterning. Helicomery is well documented in various hymenopteran families, particularly in wasps, including: Ichneumonidae (Pic, 1922; Constantineanu, 1930); Sphecidae (Cockayne, 1929), Pompilidae (Schneider & Feitz, 2007), and Vespidae (Camerano, 1878; Janet, 1903; With, 1905; Salt, 1927; Cockayne, 1929, 1934; Sart, 1964). The phenomenon is also known in bees, such as Andrenidae (Salt, 1927); Apidae (Sato, 1940); Halictidae (Ornosa *et al*., 2001); Megachilidae (With, 1905; Morice, 1908; Cockayne, 1929).

In the Chrysididae, a case of true, full spiral metasomal segmentation was illustrated by Rosa (2024a) in a female specimen of *Hedychrum nobile* (Scopoli 1763) (Fig. 19A-C) from Pondel (Aosta Valley, Italy); full spiral segmentation of the abdomen is considered rare in insects (Cockayne, 1929). In this specimen, helicomery occurs as a left-handed tricyclic pattern, with a fully developed clockwise spiral segmentation. The spiral is visible only on the dorsal surface, where the left first hemi-tergum is fused with the right first hemi-tergum and the right second hemi-tergum; the left second hemi-tergum is fused with the right third hemi-tergum, while the left third hemi-tergum remains free. The sterna are arranged normally.

A similar condition is observed in a female of *Chrysis grohmanni* Dahlbom 1854 (Fig. 19D-F) from Pineta San Vitale (Emilia-Romagna, Italy), where a left-handed monocyclic helicomery occurs. In this case, the left first hemi-tergum is fused with the second tergum, while the right first hemi-tergum is partially developed and partially fused with the second tergum. The remainder of the body remains unmodified. Right-handed spiral segmentation was also noted in *Parnopes grandior* (Pallas 1771) (Fig. 19G) from Germany where the second right hemi-tergum is fused with the third left hemi-tergum.

Spiral segmentation can also occur exceptionally in internal urites. In a male of *Chrysis* sp. from Elche (Alicante, Spain, DBC) (Fig. 19H), the fourth right hemi-sternum is fused with the fifth left hemi-sternum (Fig. 19I), the fifth right hemi-sternum is fused with the sixth left hemi-sternum (Fig. 19J), the seventh remains unmodified, but the eighth sternum is malformed (Fig. 19K). In the same specimen, the fourth tergum is malformed on the right side, while the fifth and the sixth terga are fused on the right side (Fig. 19L). However, the external three metasomal segments appear normal (Fig. 19H).

Epigastroschisis

Epigastroschisis refers to the incomplete median fusion between two hemi-terga of the metasoma resulting in a longitudinal opening or cleft (Fig. 20A-F). This relatively frequent case of incorrect segmentation has been observed in several Hymenoptera and was previously recorded in Chrysididae by Negru (1955, 1958) for the incomplete fusion of the first and second terga, and by Rosa (2024a) for the third tergum. In fact, this aberration can occur in all metasomal terga. Some illustrated examples are: a female of *Chrysura refulgens* (Spinola 1806) from Kalogria (Peloponnese, Greece), which exhibits partial and fully incomplete fusion of the first hemi-terga (Fig. 20A and B); incomplete median fusion of the first pair of hemi-terga in *Chrysis indigotea* Dufour & Perris 1840 from Bellinzago (Piedmont, Italy) (Fig. 20C); incomplete median fusion of the second pair of hemi-terga in *Chrysis provenceana* Linsenmaier 1959 from Callian (Provence, France, NMLU) (Fig. 20D), where the right hemi-tergum is partially fused with the extended third tergum in a black punctate area corresponding to a spiral segmentation; failed median fusion of the third pair of hemi-terga in *Hedychrum niemelai* Linsenmaier 1959 Issyk (Kazakhstan) (Fig. 20E and F), and in *Chrysis gribodoi* Abeille de Perrin 1877 from Bollano (Tuscany, Italy) (Fig. 21A and B), where the fourth tergum and the tip of the ovipositor are distinctly visible. Additional cases include a male of *Hedychridium krajniki* Balthasar 1953 from Gressan (Aosta Valley, Italy) (Fig. 22A); a female of *Holopyga chrysonota* (Förster 1853) from S. Benedetto Belbo (Piedmont, Italy) (Fig. 22B), where the apical margin of the second tergum is medially interrupted and fused with the third tergum in another case of helicomery; and a female of *Pseudomalus auratus* (Linnaeus 1758) from Trapani (Sicily, Italy) (Fig. 22C), with malformed apical margin of the second tergum. Epigastroschisis was also observed in the subfamily Cleptinae, in a male of *Cleptes splendidus* (Fabricius 1794) from Pondel (Aosta Valley, Italy) (Fig. 22D), where both second hemi-terga failed to fuse, leaving the underlying membrane exposed.

Multiple monstrosities

A female specimen of *Chrysis rutiliventris* Abeille de Perrin 1879 from Roccaraso (Abruzzo, Italy) (Fig. 21C and D) exhibits a unique case of multiple anomalies. In this specimen, the first metasomal tergum is normally developed, but the following two terga are profoundly modified. The metasoma simultaneously presents a right-handed bicyclic helicomery and a reduplication of the third hemi-tergum. The second right hemi-tergum is asymmetrical due to a deeply aberrant left hemi-tergum, which is apically fused with the third left hemi-tergum and medially with the duplicated third hemi-tergum featuring a toothed apical margin. The third right hemi-tergum is fully developed but remains unconnected to the left hemi-tergum. As a result, the metasoma appears to have three toothed apical margins. Despite these malformations, the specimen exhibits no abnormalities in the remaining body structure or in internal segments.

Aplasia and hemiaplasia

In Hymenoptera, in rare cases, an entire tergum or a hemi-tergum may be absent from the metasoma (Cockayne, 1929). In Chrysididae, we observed such rare cases. The first case involves a male of *Euchroeus moricei* du Buysson 1896 (from Morocco, MHC), in which the entire third tergum is missing, while the other two terga and the sterna are correctly and fully developed. The absence of the third tergum exposes the internal urites, which are visible in both lateral and posterior view (Fig. 23A and B). The second case concerns a female of *Chrysura refulgens* (Spinola 1806) from Flassans-sur-Issole (Provence, France), where the second right hemi-tergum is entirely absent (Fig. 23D), as the second left hemi-sternum (Fig. 23E), resulting in an asymmetric and deformed metasoma.

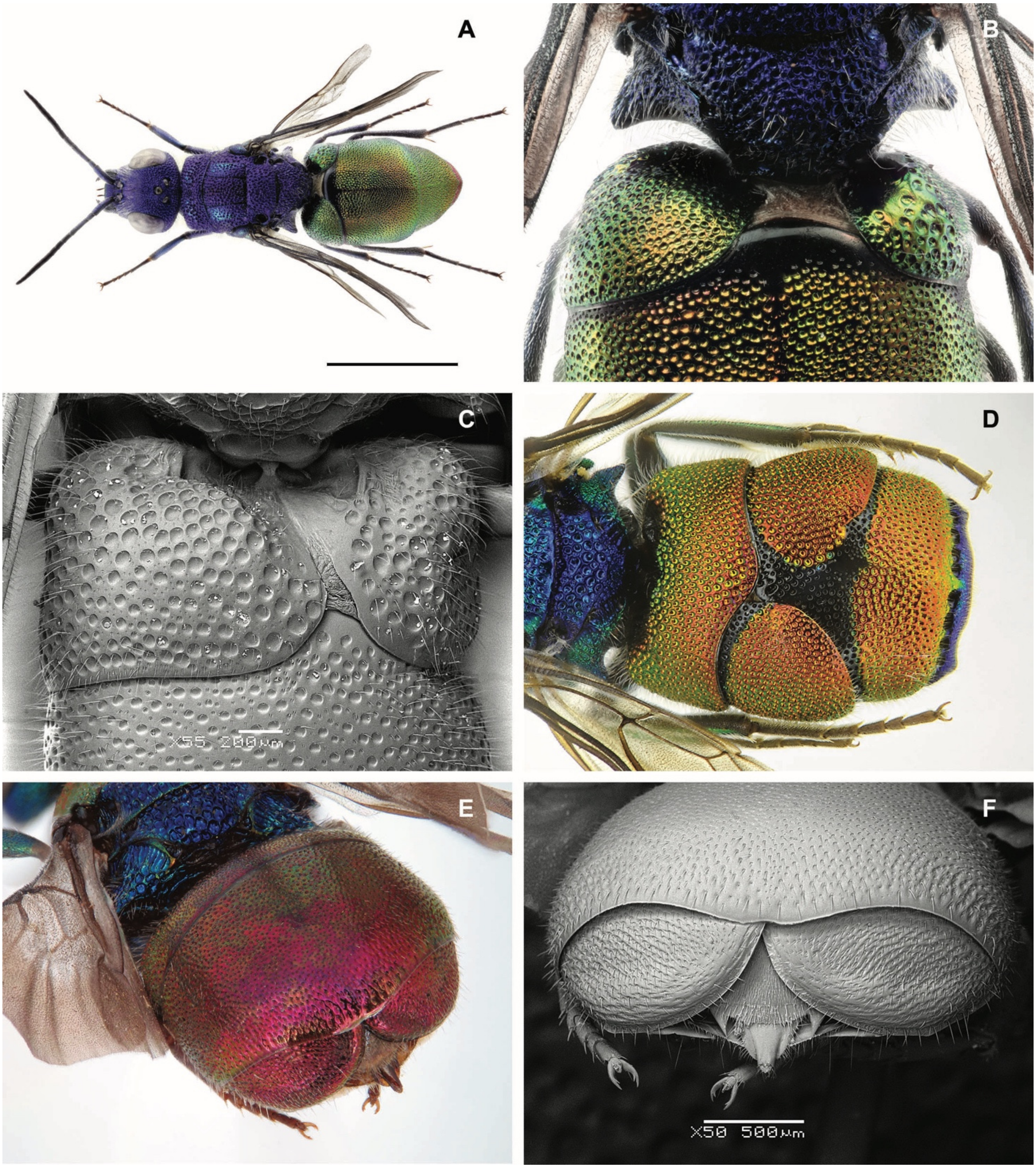

Fig. 20 – Epigastroschisis. A-B) *Chrysura refulgens* (Photo: Daniele Baiocchi), female. A) Habitus, dorsal view. B) Detail on the first tergum. C) *Chrysis indigotea*, female, detail on the first tergum. D) *Chrysis provenceana*, male, metasoma with epigastroschisis on the second tergum and helicomery. E-F) *Hedychrum niemelai*, female, metasoma with epigastroschisis on the third tergum. Scale bar: 5.0 mm. / Epigatroschisi. A-B) *Chrysura refulgens* (Foto: Daniele Baiocchi), femmina. A) Habitus, vista dorsale. B) Dettaglio sul primo tergite. C) *Chrysis indigotea*, femmina, dettaglio sul primo tergite. D) *Chrysis provenceana*, maschio, metasoma con epigatroschisi sul secondo tergite e elicomeria. E-F) *Hedychrum niemelai*, femmina, metasoma con epigatroschisi sul terzo tergite. Scala: 5,0 mm.

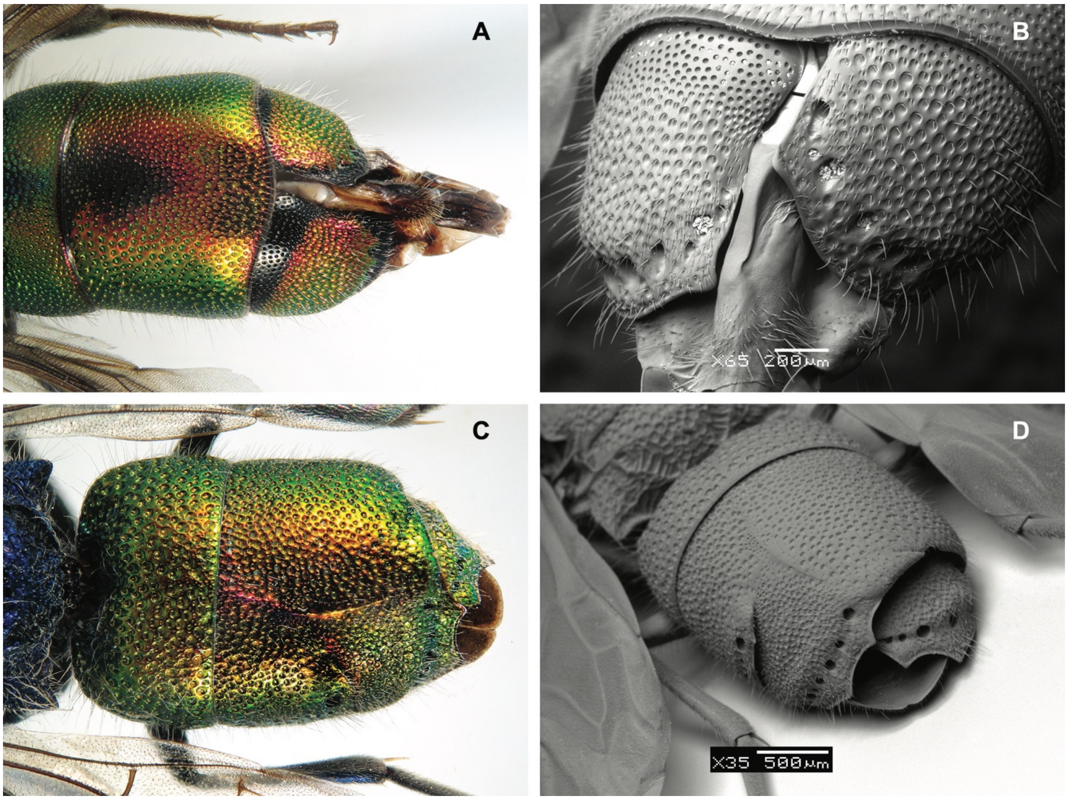

Fig. 21 – Epigastroschisis. A-B) *Chrysis gribodoi*, female, epigastroschisis of the third tergum. A) Metasoma, dorsal view. B) Third tergum, posterior view. C-D) *Chrysis rutiliventris*, multiple aberrations. C) Metasoma, dorsal view. D) Metasoma, postero-lateral view. / Epigatroschisi. A-B) *Chrysis gribodoi*, femmina, epigatroschisi del terzo tergite. A) Metasoma, vista dorsale. B) Terzo tergite, vista posteriore. C-D) *Chrysis rutiliventris*, aberrazioni multiple. C) Metasoma, vista dorsale. D) Metasoma, vista postero-laterale.

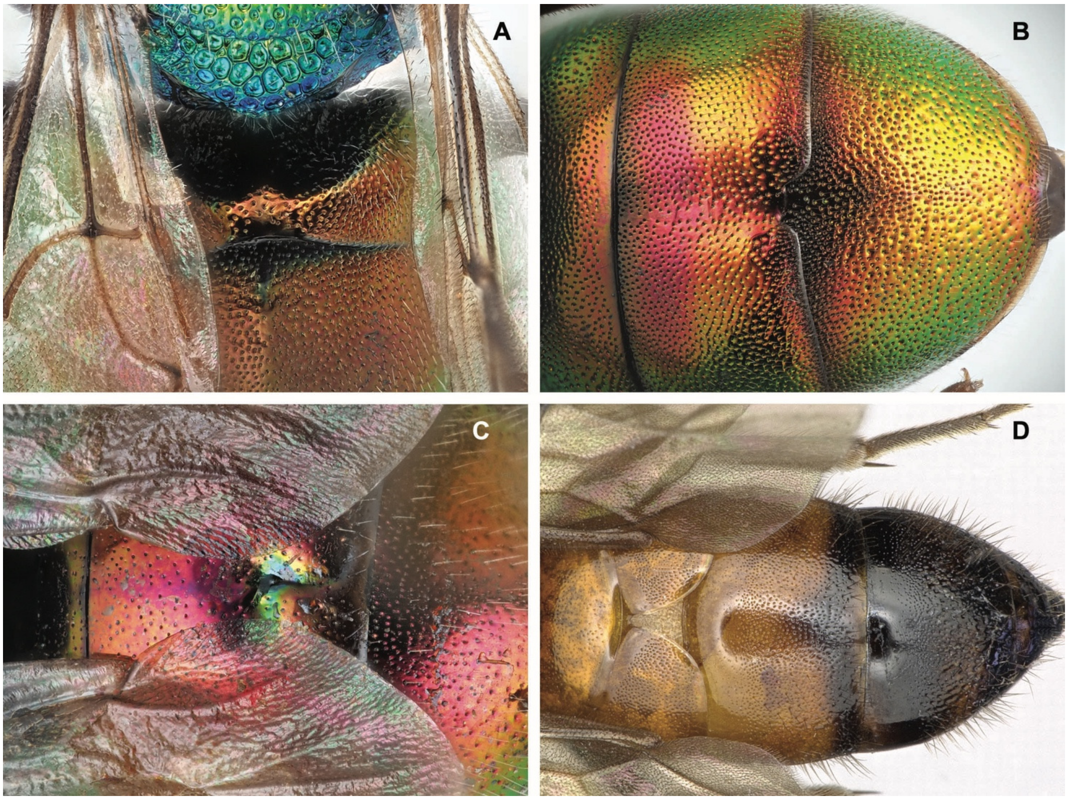

Fig. 22 – Epigastroschisis. A) *Hedychridium krajniki*, male, detail on first tergum. B) *Holopyga chrysonota*, female, detail on second tergum. C) *Pseudomalus auratus*, female, detail on second tergum. D) *Cleptes splendidus*, male, epigastroschisis on second tergum. / Epigatroschisi. A) *Hedychridium krajniki*, maschio, dettaglio sul primo tergite. B) *Holopyga chrysonota*, femmina, dettaglio sul secondo tergite. C) *Pseudomalus auratus*, femmina, dettaglio sul secondo tergite. D) *Cleptes splendidus*, maschio, epigatroschisi sul secondo tergite.

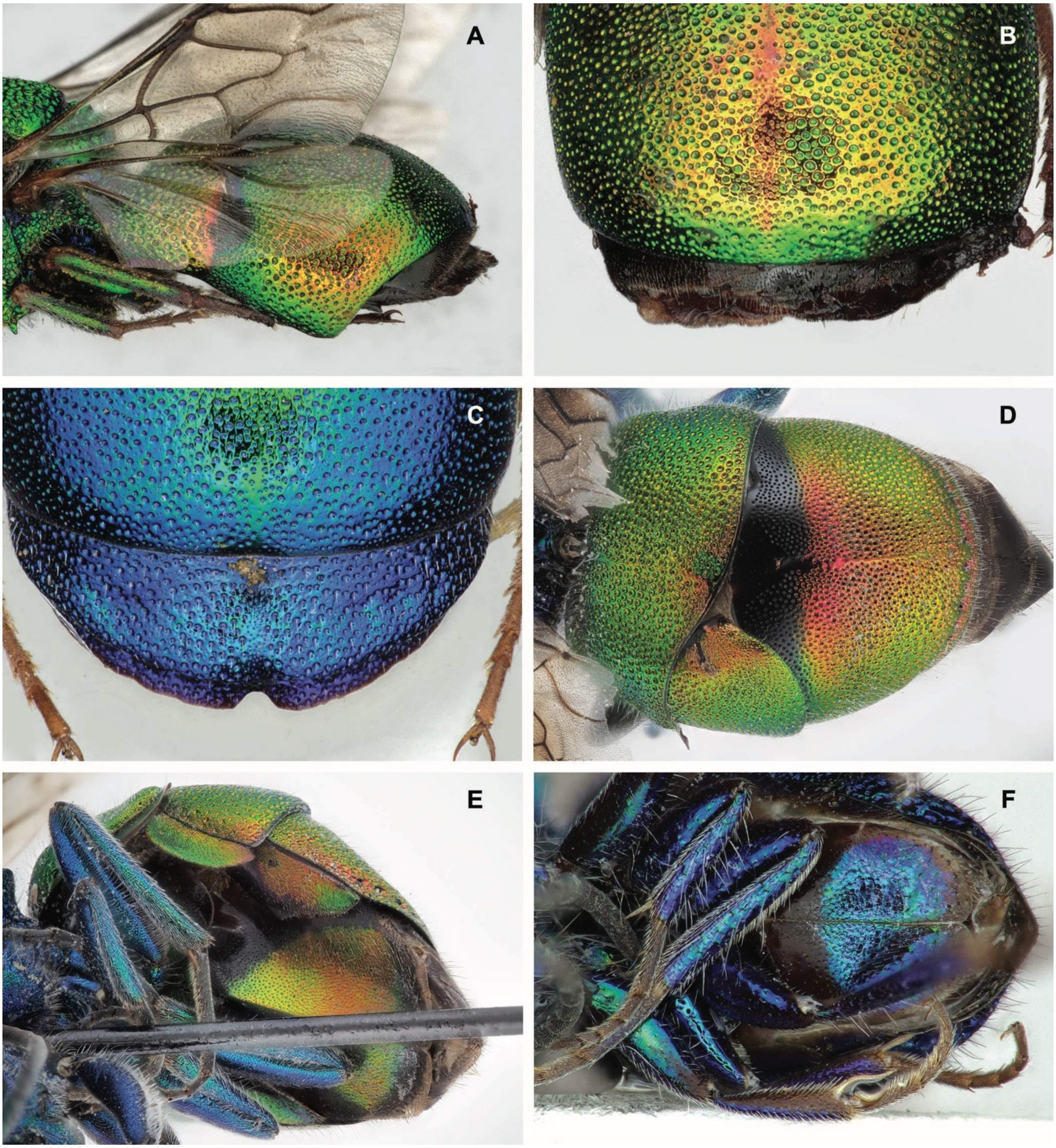

Fig. 23 – Aplasia, hemiaplasia and symphysomery. A-B) *Euchroeus moricei*, male, with aplasia of the third tergum. A) Metasoma, lateral view. B) Second tergum, posterior view. C) *Euchroeus moricei*, male, normal, second and third terga, posterior view. D-E) *Chrysura refulgens*, female. D) Metasoma, dorsal view, hemiaplasia of the right second hemi-tergum. E) Metasoma, ventral view, hemiaplasia of the left second hemi-tergum. F) *Chrysis bilqis*, female, metasoma, ventral view, symphysomery of the second and third sterna. / Aplasia, emiaplasia e simfisoceria. A-B) *Euchroeus moricei*, maschio, con aplasia del terzo tergite. A) Metasoma, vista laterale. B) Secondo tergite, vista posteriore. C) *Euchroeus moricei*, maschio, normale, secondo e terzo tergiti, vista posteriore. D-E) *Chrysura refulgens*, femmina. D) Metasoma, vista dorsale, semiaplasia del secondo emitergite destro. E) Metasoma, vista ventrale, semiaplasia del secondo emitergite sinistro. F) *Chrysis bilqis*, femmina, metasoma, vista ventrale, simfisoceria del secondo e terzo sterno.

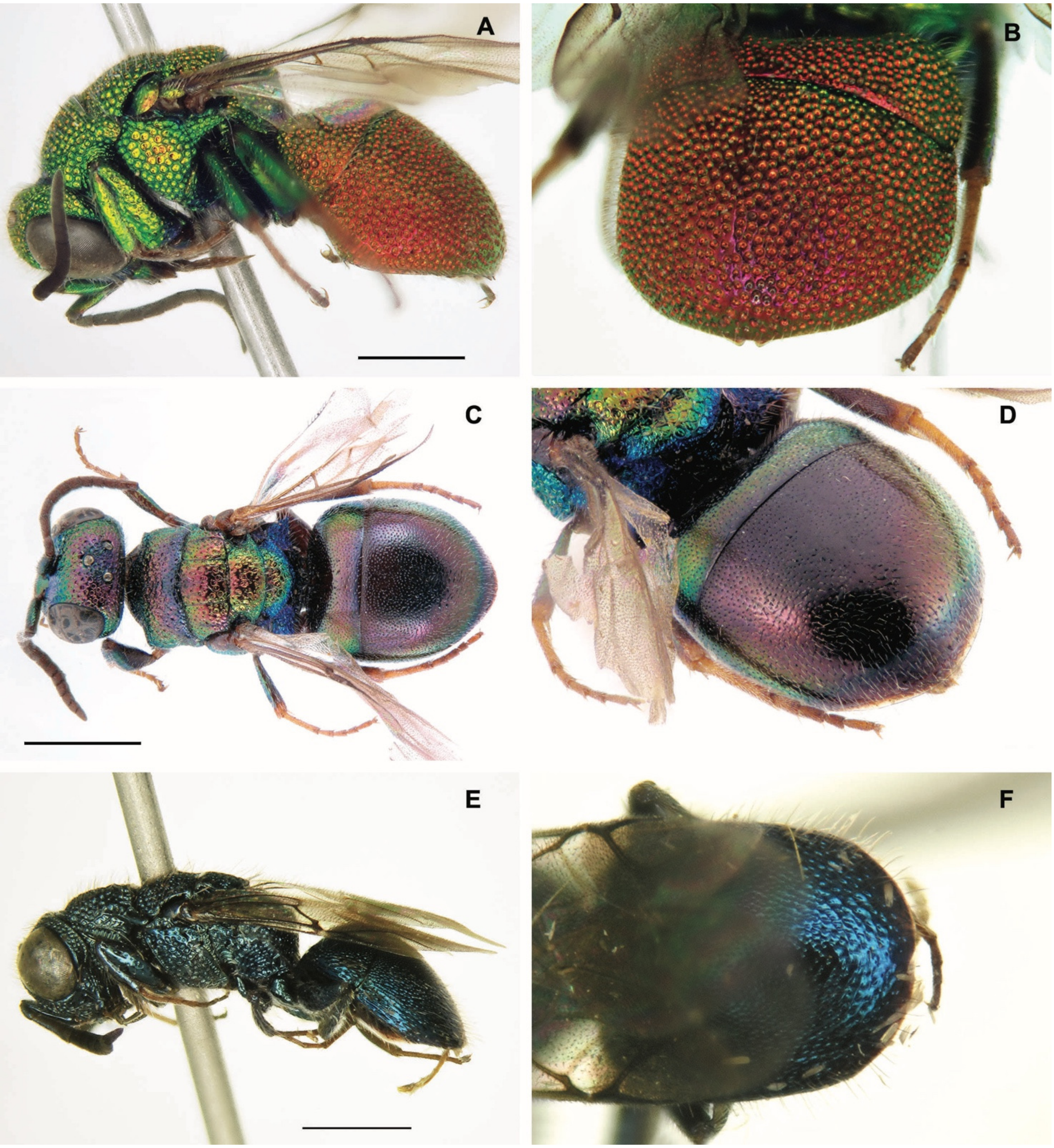

Fig. 24 – Symphysomery. A-B) *Hedychridium braunsi*, male. A) Habitus, lateral view. B) Metasoma, posterior view. C-D) *Hedychridium belokobylskiji*, female. C) Habitus, dorsal view. D) Metasoma, postero-lateral view. E-F) *Anachrysis* sp., female. E) Habitus, lateral view. F) Metasoma, dorsal view. Scale bars: 1.0 mm. / Simfisoceria. A-B) *Hedychridium braunsi*, maschio. A) Habitus, vista laterale. B) Metasoma, vista posteriore. C-D) *Hedychridium belokobylskiji*, femmina. C) Habitus, vista dorsale. D) Metasoma, vista postero-laterale. E-F) *Anachrysis* sp., femmina. E) Habitus, vista laterale. F) Metasoma, vista dorsale. Scala: 1,0 mm.

Symphysomery

Symphysomery is a teratological phenomenon in which two or more normally distinct body parts are merged or fused together. This condition results from developmental abnormalities or malformations during insect growth. In teratological specimens, typical body segmentation may be disrupted, leading to unusual structural combinations, such as fused abdominal segments or incomplete developed parts. In Chrysididae, this rare phenomenon can affect both external and internal segments, and some cases have already been documented by the first author (Rosa, 2024a) to justify the synonymization of the genus *Oligogaster* Soliman & Kimsey 2014 with *Hedychridium* Abeille de Perrin 1878. *Oligogaster* was originally described based on a single aberrant Egyptian specimen characterized by the presence of only two metasomal terga, which were considered by Rosa (2024a) as a result of symphysomery, in which the second and third terga are fused into one. This phenomenon is most prominently observed in the genus *Hedychridium*, with multiple specimens collected from South Africa to Central Asia. A particularly illustrative example is found in *Hedychridium braunsi* Mócsary 1902 from South Africa (MfN) (Fig. 24A and B), which clearly shows the fusion of the second and third tergum. *Hedychridium braunsi*, which belongs to the former subgenus *Acrotoma* Mócsary 1902 (*nec* Boettger 1881), is distinguished by the presence of two small median teeth on the apical margin of the third tergum. In our symphysomeric specimen, however, the second and third terga are fused, and the two small apical teeth of the third tergum are positioned on the apical margin of the second (Fig. 24B). Although all examined *Hedychridium* specimens exhibiting this condition, including *H. kimseyae* Soliman 2023 (type), *H. braunsi* and *H. belokobylskiji* Rosa 2017 from Siberia (Tuva Rep.) (Fig. 24A-D) possess only two terga, they do not belong to the genus *Oligogaster*, but to different species groups within *Hedychridium*, based on other morphological characters, thus showing that the symphysomery is a phenomenon observed across many groups of this chrysidid genus. Other cases were noticed for the allied genus *Prochridium* Linsenmaier 1968 with symphysomeric specimens observed from Mongolia (MHC).

Another case of symphysomery involving fused metasomal terga was observed in a female of *Anachrysis* Krombein, 1986 from South Africa (MfN), a member of the subfamily Amiseginae, which exhibited only two metasomal terga instead of the usual four (Fig. 24E and F).

Symphysomery has also been observed in sternal segments, as in the case of *Chrysis bilqis* Rosa 2024 from Yemen (RMNH), where the second and third metasomal sterna are fused into a single sternal plate (Fig. 23F).

Atavism

Atavism is the reappearance of ancestral characters in an organism that had been lost or significantly modified in its recent evolutionary lineage. This phenomenon occurs when dormant genetic information from distant ancestors is reactivated due to genetic mutations or developmental anomalies. In Hymenoptera, rare cases of atavism are mostly associated with the reappearance of ancestral wing venation patterns (Brown & Nutting, 1949). In Chrysididae, a particularly interesting case involves a female of *Hedychrum rutilans* Dahlbom 1854, which exhibits two distinct teeth or angles and a median notch on the apical margin of the third tergum (Fig. 25A and B). A similar tergal shape, though less pronounced, is known in only one Central Asian species, *Hedychrum concinnum* (Mocsáry 1909), which was described in a different, monospecific genus (*Wollmannia* Mocsáry 1909) exactly for this unique diagnostic trait. However, two small median teeth can be also observed in a few *Hedychridium* included in the subgenus *Acrotoma* Mocsáry 1902, *nec* Boettger 1881. The absence of apical teeth in Chrysidini was considered plesiomorphic by Kimsey & Bohart (1991), whereas Niehuis & Wagele (2004), using molecular analyses, proved that multidentate taxa were already present in the stem groups. The same condition could be valid for Elampini. No molecular or fossil data are currently available for analyzing the evolutionary history of Elampini and their metasomal dentation. However, the morphological trait observed in this *Hedychrum rutilans* specimen is more likely linked to an ancestral character than to a hybrid individual originated from *Hedychrum rutilans* and another unrelated species of Elampini s.str. with a median notch (e.g. *Chrysellampus* Semenov-Tian-Shanskij 1932, *Elampus* Spinola 1806, *Omalus* Panzer 1801, *Philoctetes* Abeille de Perrin 1879 or *Pseudomalus* Ashmead 1902), which are phylogenetically distinct (Pauli *et al*., 2019). It is likely that a mutation reactivated ancestral genes that had remained in the genome but were suppressed in a process known as genetic reversion. Alternatively, the ancestral character may result from an error in embryonic development that mimics an ancestral form.

Asymmetry

Metasomal asymmetry primarily arises from various factors, including external forces that, during the pupal stage, hinder the full development of one or more terga (Fig. 25C and D). This phenomenon may occur, for example, due to the incorrect pupal position, the collapse of the nest chamber or cocoon, or the improper development of a hemi-tergum (Fig. 25D). External factors may also contribute to asymmetric segmentation acting at the early developmental stage, when somites are forming. One case is visible in a male of *Parnopes grandior* (Pallas 1771) from Ozein (Aosta Valley, Italy) (Fig. 25C), where the fourth left hemi-tergum is underdeveloped, distinctly smaller, and exhibits a reduced setose subapical fovea. A more pronounced case is observed in a male of *Chrysis inaequalis* Dahlbom 1845 from Ozein (Aosta Valley, Italy) (Fig. 25D), where incomplete development of the second left hemi-tergum has altered both the punctation, shape and trajectory of the midline. We observed over thirty such similar cases, varying in severity.

Other interesting aberrations involve the incomplete development of apical teeth, angles, or undulations of one or both final hemi-terga. A case of aberrant apical margin of the third tergum has already been described in the literature by Móczár (1963), who reported a specimen of *Chrysis ignita* (Linnaeus 1758) without apical teeth. In our cases, one half of the segment retains a normal shape, while the other half appears straight. These aberrations often occur with other malformations in sculpture [e.g., in a male of *Euchroeus* sp. (ZISP), Fig. 25E] or coloration [e.g., in a male of *Chrysis maracandensis* Radoszkowski 1877 (ZISP), Fig. 25F].

Another form of asymmetry was observed in a male of *Hedychrum cribratum* Mocsáry 1909 from Kazakhstan (ZISP) (Fig. 25G), where the metasoma is hypotrophic, leading to asymmetry and an unusual sculpture. Interestingly,

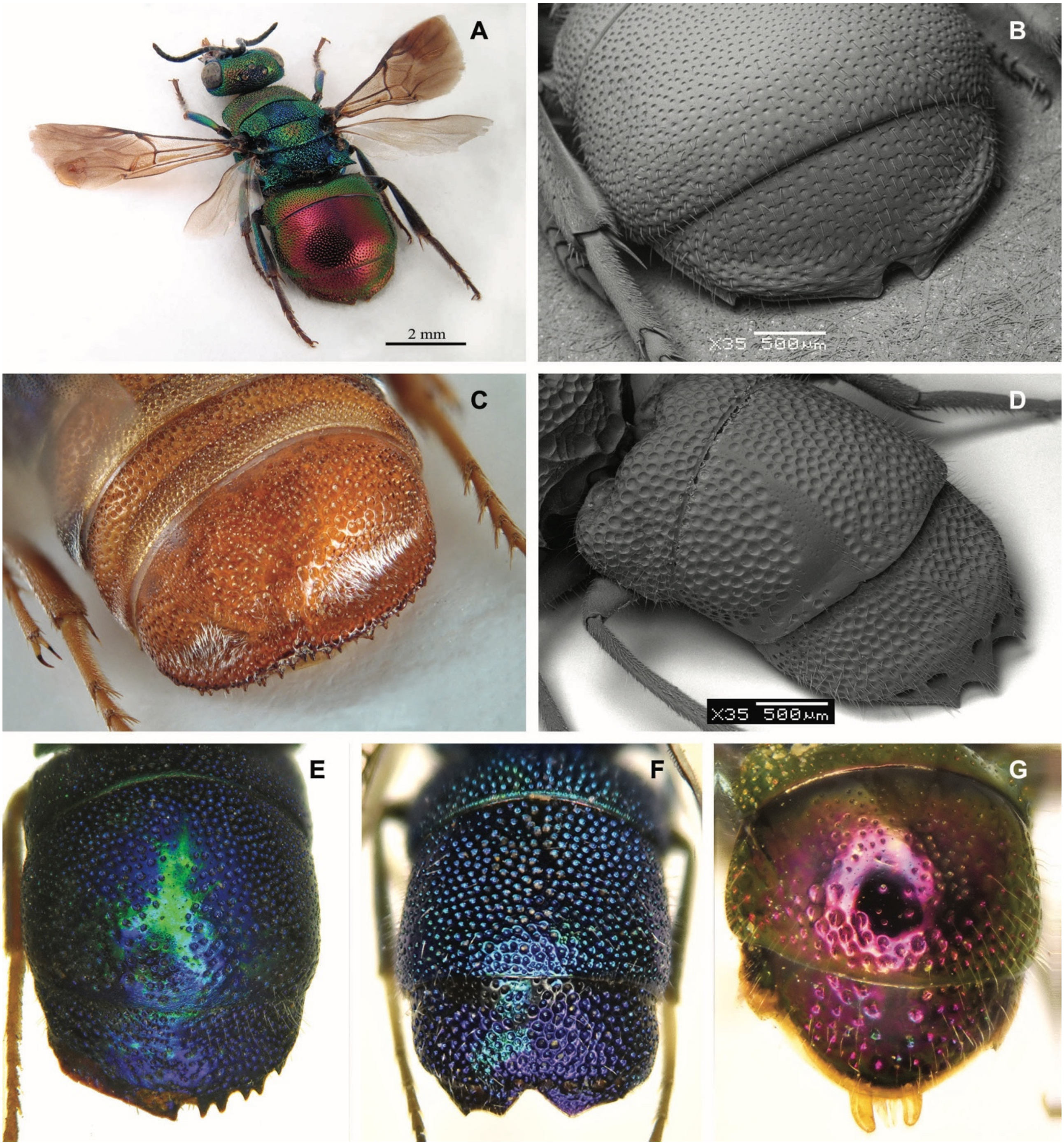

Fig. 25 – Aberrant metasoma. A-B) *Hedychrum rutilans*, atavic female. A) Habitus, postero-lateral view. B) Detail on third tergum. C) *Parnopes grandior*, male, asymmetric, posterior view. D) *Chrysis inaequalis*, male, asymmetric, lateral view. E) *Euchroeus* sp., male, metasoma, posterior view, incomplete development of the apical margin. F) *Chrysis maracandensis*, male, metasoma, posterior view, malformed third tergum with aberrant colour. G) *Hedychrum cribratum*, male, posterior view, hypotrophic metasoma. / Metasoma aberrante. A-B) *Hedychrum rutilans*, femmina atavica. A) Habitus, vista postero-laterale. B) Dettaglio sul terzo tergite. C) *Parnopes grandior*, maschio, asimmetrico, vista posteriore. D) *Chrysis inaequalis*, maschio, asimmetrico, vista laterale. E) *Euchroeus* sp., maschio, metasoma, vista posteriore, sviluppo incompleto del margine apicale. F) *Chrysis maracandensis*, maschio, metasoma, vista posteriore, terzo tergite malformato con colore aberrante. G) *Hedychrum cribratum*, maschio, vista posteriore, metasoma ipotrofico.

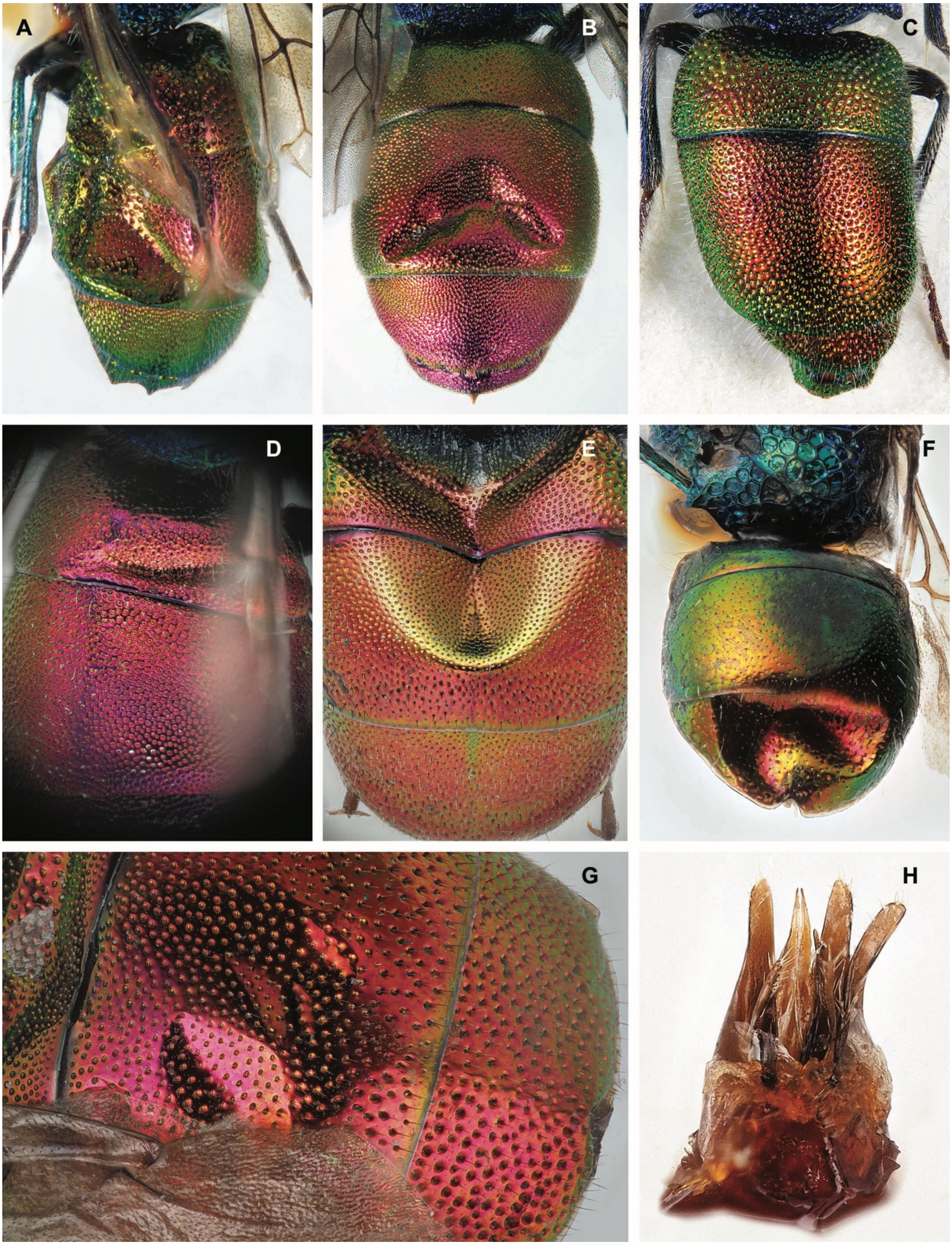

Fig. 26 – Malformed metasoma. A) *Chrysis leptomandibularis*, male, dorsal view. B) *Chrysura purpureifrons*, female, dorsal view. C) *Chrysis sardarica perrecta*, female, dorsal view. D) *Chrysura pyrogaster*, male, first and second terga, dorsal view. E) *Hedychrum niemelai*, male, dorsal view. F) *Pseudomalus auratus*, female, posterior view. G) *Hedychrum gerstaeckeri*, male, dorsal view. H) *Pseudomalus violaceus*, male, aberration of the genital capsule. / Metasoma malformato. A) *Chrysis leptomandibularis*, maschio, vista dorsale. B) *Chrysura purpureifrons*, femmina, vista dorsale. C) *Chrysis sardarica perrecta*, femmina, vista dorsale. D) *Chrysura pyrogaster*, maschio, primo e secondo tergiti, vista dorsale. E) *Hedychrum niemelai*, maschio, vista dorsale. F) *Pseudomalus auratus*, femmina, vista posteriore. G) *Hedychrum gerstaeckeri*, maschio, vista dorsale. H) *Pseudomalus violaceus*, maschio, aberrazione della capsula genitale.

the genital capsule is unaffected by hypotrophy, resulting in a disproportionally large genital capsule that extends beyond the apical margin of the third tergum.

Metasomal asymmetries caused by mechanic pressure or crushing in the nest during the pupal phase are the most frequently observed in Chrysididae, with over 330 recorded cases. Of these, at least fifty resulted in significant body malformations and segmental constrictions, potentially interfering with basic physiological functions such as digestion, respiration, secretion, and haemolymph flow. Examples of severe malformations are illustrated in Fig. 26A-F. The remaining 280 cases involve superficial deformities (e.g., those in Fig. 26G and Fig. 27A-D and I), which appear not to compromise metabolic functions or the individual's ordinary life.

Genitalia aberrations

Malformations can also affect the male genital capsule of Hymenoptera (e.g. Ornosa Gallego, 1985). In Chrysididae, such cases appear to be extremely rare and we observed only one case in a male of *Pseudomalus violaceus* (Scopoli 1763) from Pondel (Aosta Valley, Italy), where one gonostylus is duplicated (Fig. 26H). However, there is an inherent bias, as not all the examined males were dissected, and the genitalia remained concealed within the metasoma. Despite this limitation, this is the only malformation observed among several thousand specimens dissected. Another exceptional malformation was found in a gynandromorphic specimen with a female-like morphology. This individual developed an altered male genital capsule alongside a reduced telescopic ovipositor (Fig. 34).

Cuticular aberrations

The cuticle and sculpture of Chrysididae are key features in their identification. The cuticle is typically highly sclerotized and metallic in most of the species, with characteristic brilliant blue, green, red, or golden colors. These metallic colors are structural and originated thanks to the microscopic epicuticular multilayers in the cuticle that interfere with light (Kroiss *et al.*, 2009). Unlike pigment-based coloration, these structural colors do not fade over time and the ultimate reason for their coloration is still unclear. Their cuticle is also thick and rigid, serving as protection against dehydration and enemies. The whole body is normally covered by punctation (that can be fine or coarse, sparse or dense, even or irregular, etc.), and areolation which are of primary importance in species identification based on density and arrangement.

Cuticular aberrations refer to atypical modifications or irregularities in the cuticle, which can arise from genetic, environmental, or developmental factors. These aberrations may manifest as irregular punctation, deformations, asymmetries, or abnormal structures affecting coloration and identification features.

Occasionally, teratological specimens display aberrant sculpture, characterized by irregular coarse punctures and shinier intervals as in the cases of a male of *Chrysis zonata* Dahlbom 1854 from Greece (normal sculpture in Fig. 27E; abnormal sculpture in Fig. 27F), and in a male of *C. inaequalis* Dahlbom 1845 from Crimea (normal sculpture in Fig. 27G; abnormal sculpture in Fig. 27H). A similar sculpture pattern was also found in specimens with nanism, such as in a male of *Euchroeus limbatus* Dahlbom 1854 from Turkey (MHC) (normal sculpture in Fig. 32E; abnormal sculpture in Fig. 32F). If not carefully evaluated, this altered sculpture might lead to the description of different taxa.

Mechanical damage, such as injuries during pupation or molting, can result in irregular sclerotization, leading to variations in colorations due to the absence of reduced number of cuticular layers. This could be the case of *Chrysis mediadentata* Linsenmaier 1951 from Cassolnovo (Lombardy, Italy) (Fig. 27J), where the first tergum exhibits two wide and deep lateral scratches incised in the cuticle, appearing blue to black in contrast with the normal red to golden coloration. A similar condition is observed in other specimens, such as male of the *Chrysis ignita* group in Fig. 28A, B with a submedian contrasting area, possibly with a reduced number of cuticular layers.

Patchy, asymmetrical punctation may occur in localized areas of the body due to deformed cuticle formations. This phenomenon is observed in a female of *Chrysis illigeri* Wesmael 1839 from Ozein (Aosta Valley, Italy) (Fig. 28C and D), where a swollen cuticular patch displaces the punctation and alters the tergal red coloration to green, generating shinier reflections. Genetic mutations can also lead to irregular punctation, as seen in a male of *Chrysis fulgida* Linnaeus 1761 from Pondel (Aosta Valley, Italy) (Fig. 28E-G). The metasoma of a normal specimen is shown for comparison in Fig. 28E, while Fig. 28F and G illustrate the aberrant specimen, which exhibit an unusual sculpture with sparse, displaced, and irregular punctures on the first tergum and almost no punctures on the second tergum, thus resulting in a shinier cuticular reflection.

Cuticle perforations

Cuticle perforations in Chrysididae are microscopic or macroscopic pathological openings in the cuticle due to damage, developmental defects, or external interactions. These perforations have been observed in all metasomal segments, although they appear to be more common on the second and third terga (Fig. 29A-G). The only case of perforations observed on the first tergum was found in the female of a *Chrysura ignifrons* (Brullé 1833) from the Peloponnese (Greece) (Fig. 29H).

While cuticular perforations are relatively common, their origins are often difficult to determine. Some may result by bacterial or fungal pathogens that degrade the cuticle, leading to visible openings. Specimens with damaged or incomplete sclerotization may exhibit irregular perforations in areas where the exocuticle is weak, as shown in Fig. 29G and 29H. Additionally, some specimens display abnormally irregular perforations likely caused by genetic mutations or stress during the pupal stage. Parasites and predators may also create large openings in the chrysidid cuticle, as observed in *Hedychridium buyssoni* Abeille de Perrin 1887 from Pineta San Vitale (Emilia Romagna, Italy) (Fig. 29I). In this case, the second tergum was likely lost during the emergence from the exuvia or immediately after, and evidence of cuticle repair is visible as a large tumefaction on the margins. The repaired integument appears brown, irregular and lacking an epicuticle, consistent with wound-healing processes documented in other arthropods (Halcrow, 1988). Similar wound-repair tissues have been observed in various part of the body, including the compound eyes of *Chrysis pulcherrima* (Fig. 6I), the antennae, as is the case of a *Pseudomalus auratus* (Linnaeus 1758) missing part of its flagellum, and the legs, where missing tarsi, likely lost during fights with hosts or natural enemies, are commonly seen.

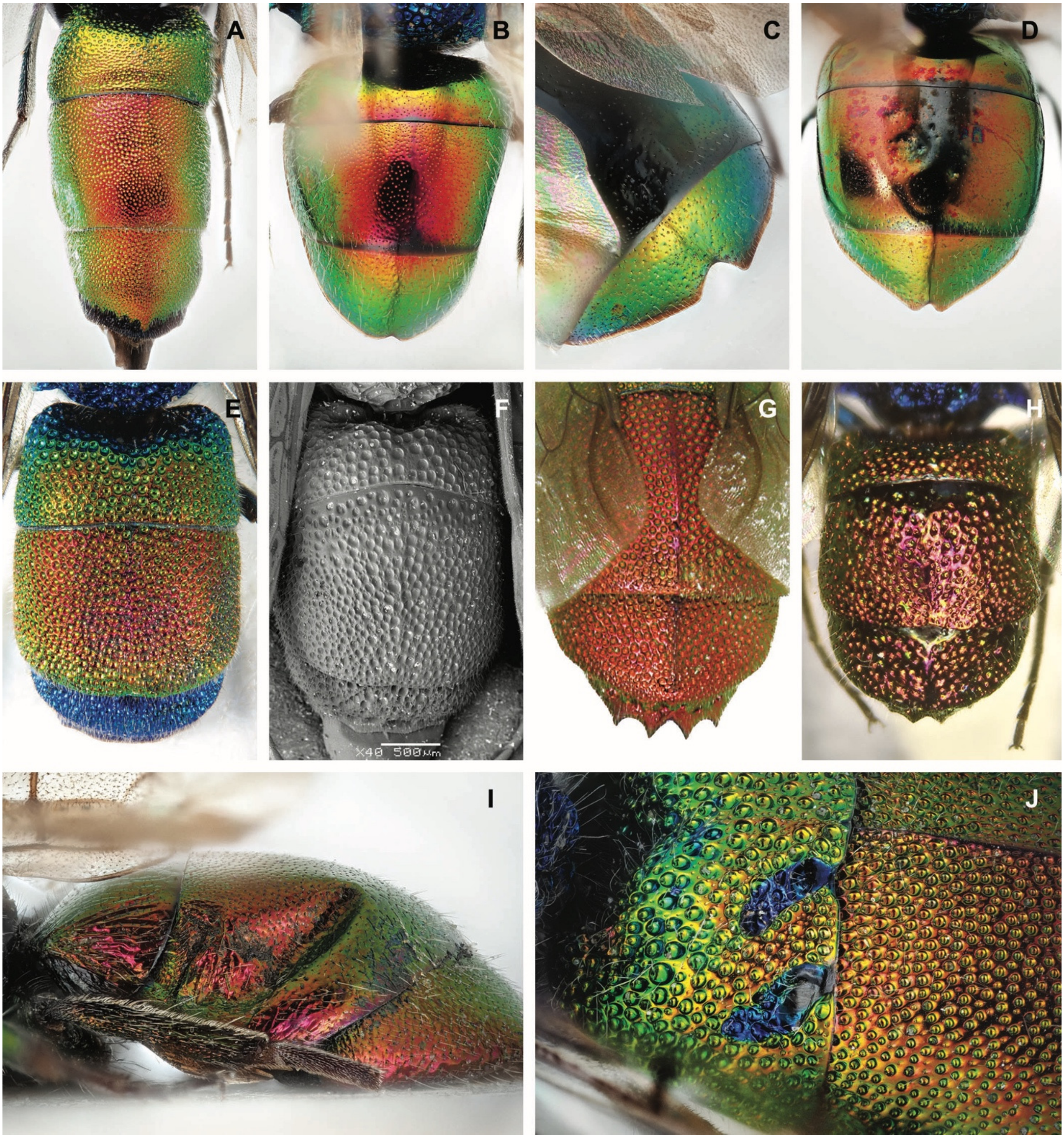

Fig. 27 – Malformed metasoma. A) *Chrysis gracillima*, female, dorsal view. B) *Pseudomalus auratus*, male, dorsal view. C) *Omalus biaccinctus*, female, postero-lateral view. D) *Pseudomalus auratus*, female, dorsal view. E-F) *Chrysis zonata*, male, dorsal view. E) Normal. F) Aberrant sculpture. G-H) *Chrysis inaequalis*, male, dorsal view. G) Normal. H) Aberrant sculpture. I) *Hedychridium cupratum*, female, lateral view. J) *Chrysis mediadentata*, male, detail on first tergum, lateral view. / Metasoma malformato. A) *Chrysis gracillima*, femmina, vista dorsale. B) *Pseudomalus auratus*, maschio, vista dorsale. C) *Omalus biaccinctus*, femmina, vista postero-laterale. D) *Pseudomalus auratus*, femmina, vista dorsale. E-F) *Chrysis zonata*, maschio, vista dorsale. E) Normale. F) Scultura aberrante. G-H) *Chrysis inaequalis*, maschio, vista dorsale. G) Normale. H) Scultura aberrante. I) *Hedychridium cupratum*, femmina, vista laterale. J) *Chrysis mediadentata*, maschio, dettaglio del primo tergite, vista laterale.

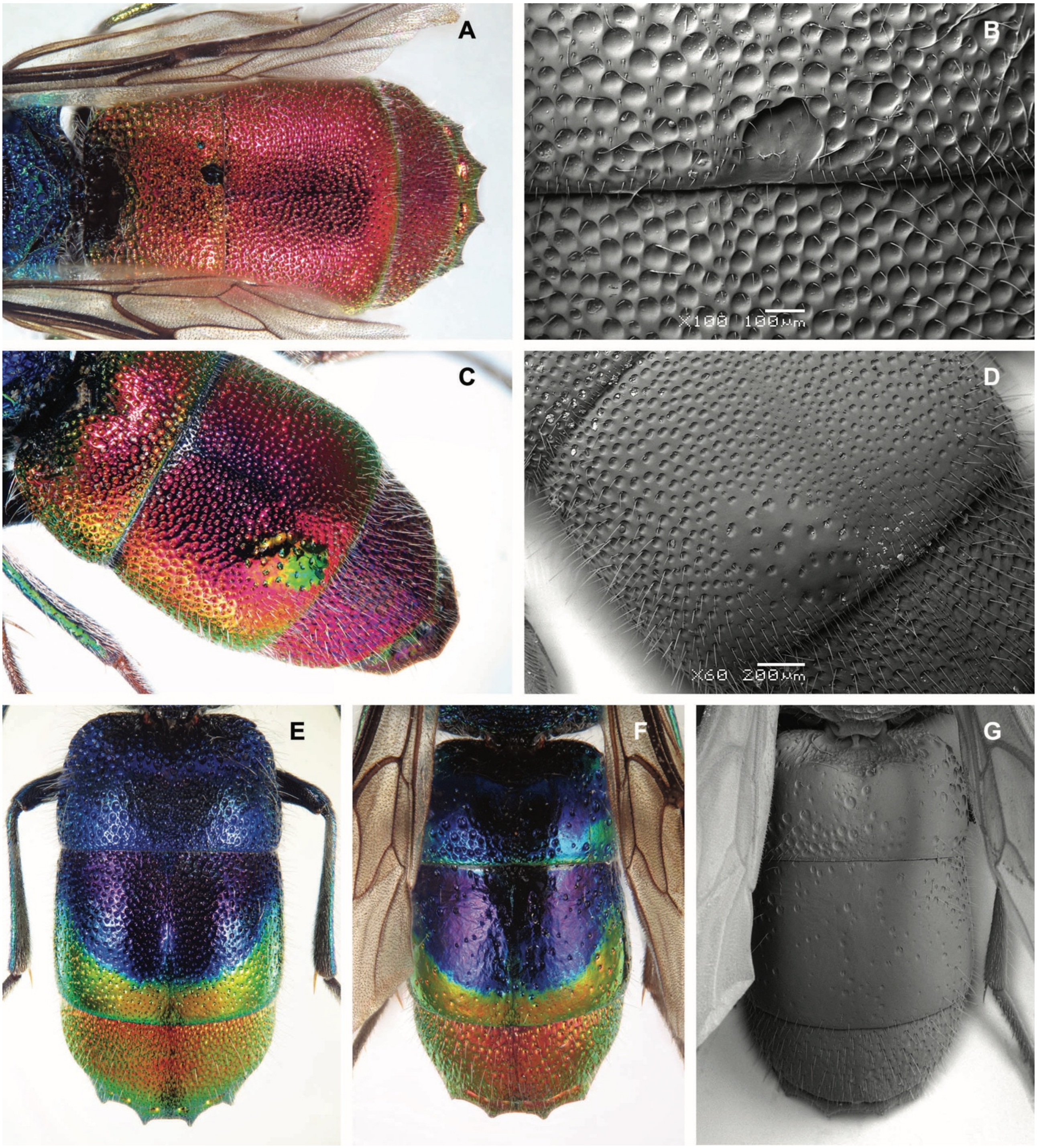

Fig. 28 – Aberrant sculpture. A-B) *Chrysis ruddii*, male. A) Metasoma, dorsal view. B) First tergum, detail. C-D) *Chrysis illigeri*, female. C) Metasoma, dorso-lateral view. D) Detail. E-G) *Chrysis fulgida*, males, metasoma, dorsal view. E) Normal. F) Specimen with abnormal sculpture. G) Same specimen with abnormal sculpture. / Scultura aberrante. A-B) *Chrysis ruddii*, maschio. A) Metasoma, vista dorsale. B) Primo tergite, dettaglio. C-D) *Chrysis illigeri*, femmina. C) Metasoma, vista dorso-laterale. D) Dettaglio. E-G) *Chrysis fulgida*, maschi, metasoma, vista dorsale. E) Normale. F) Esemplare con scultura anomala. G) Stesso esemplare con scultura anomala.

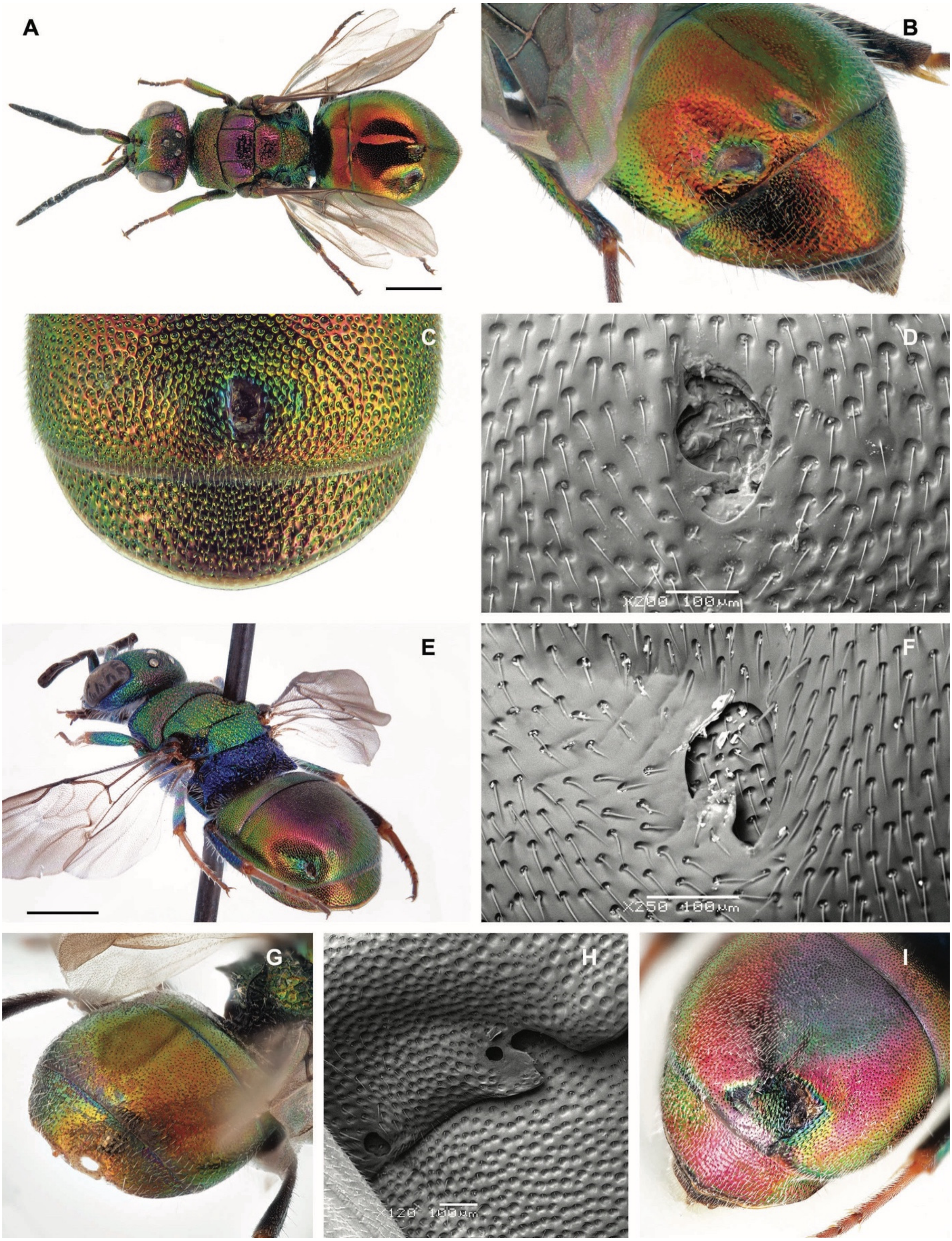

Fig. 29 – Metasoma with perforations. A-B) *Hedychridium cupratum*, female. A) Habitus, dorsal view. B) Metasoma, postero-lateral view. C-D) *Hedychridium sculpturatum*, male. C) Second and third terga, dorsal view. D) Detail. E-F) *Hedychridium jucundum*, female. E) Habitus, postero-lateral view. F) Detail. G) *Hedychridium cupratum*, female, postero-lateral view. H) *Chrysis ignifrons*, female, detail of first tergum, lateral view. I) *Hedychridium buyssoni*, female, metasoma, dorsal view. Scale bars: 1.0 mm. / Metasoma con perforazioni. A-B) *Hedychridium cupratum*, femmina. A) Habitus, vista dorsale. B) Metasoma, vista postero-laterale. C-D) *Hedychridium sculpturatum*, maschio. C) Secondo e terzo tergiti, vista dorsale. D) Dettaglio. E-F) *Hedychridium jucundum*, femmina. E) habitus, vista postero-laterale. F) Dettaglio. G) *Hedychridium cupratum*, femmina, vista postero-laterale. H) *Chrysis ignifrons*, femmina, dettaglio del primo tergite, vista laterale. I) *Hedychridium buyssoni*, femmina, metasoma, vista dorsale. Scala: 1,0 mm.

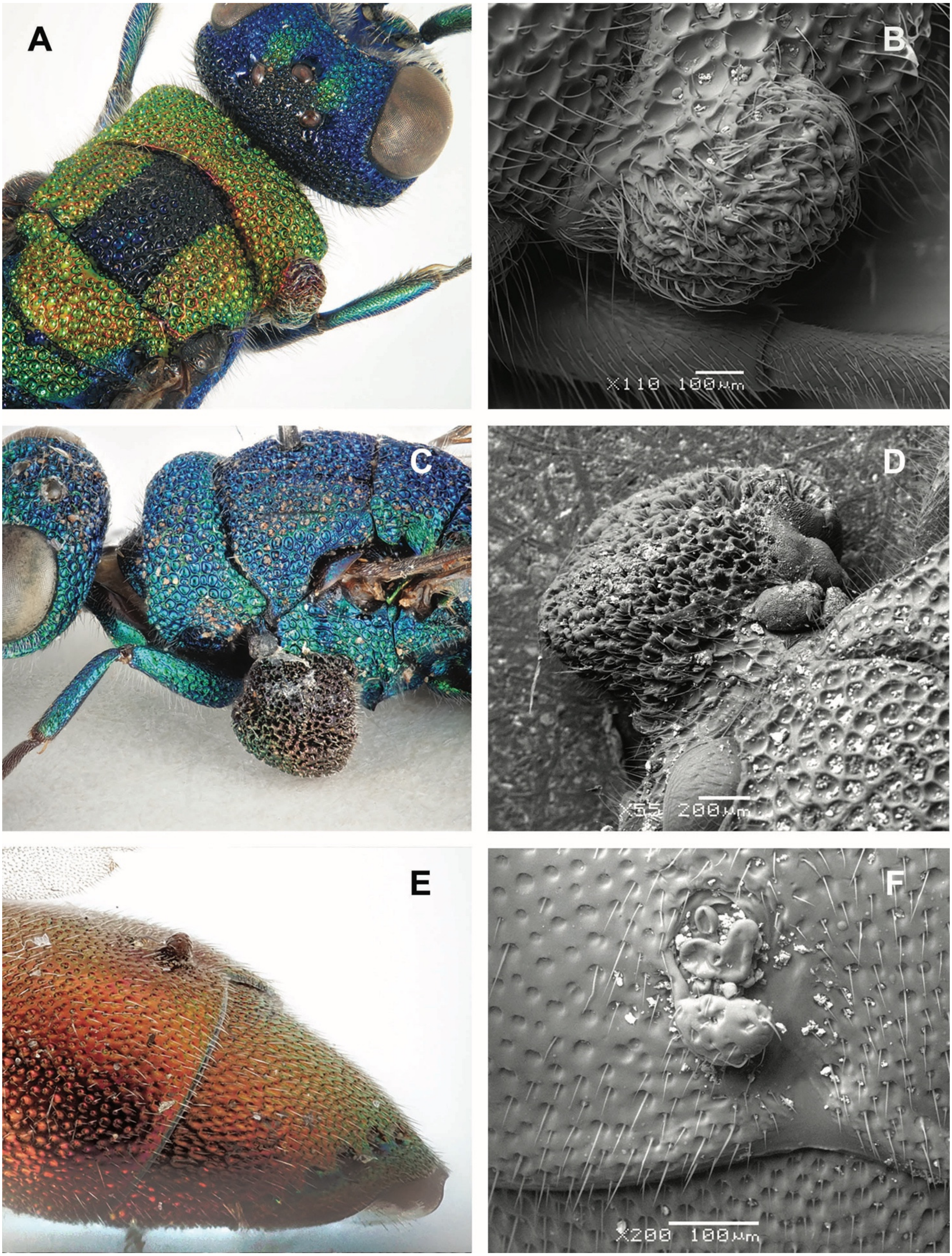

Fig. 30 – Tumor-like structures. A-B) *Chrysis pulcherrima*, male. A) Head and mesosoma, dorso-lateral view. B) Detail. C-D) *Primeuchroeus* sp., male. C) Mesosoma, lateral view. D) Detail. E-F) *Chrysis gracillima*, male. E) Second and third terga, lateral view. F) Detail, dorsal view. / Strutture simili a tumori. A-B) *Chrysis pulcherrima*, maschio. A) Testa e mesosoma, vista dorso-laterale. B) Dettaglio. C-D) *Primeuchroeus* sp., maschio. C) Mesosoma, vista laterale. D) Dettaglio. E-F) *Chrysis gracillima*, maschio. E) Secondo e terzo tergiti, vista laterale. F) Dettaglio, vista dorsale.

Cuticle-like tumors

Cuticle tumors, also known as integumental outgrowths or teratomas, are abnormal growths or protrusions on the exoskeleton. While true malignant tumors are generally rare in insects, documented cases exist of pathological proliferations, tumor-like growths, neoplasms and hyperplasia or hamartoma, which is a benign localized malformation of cells that resembles a neoplasm but results from the overgrowth of multiple aberrant cells.

In Chrysididae, we observed three cases. In the first case, a tumor-like growth protrudes laterally from the right side of the pronotum of a *Chrysis pulcherrima* from Granada (Spain) (Fig. 30A and B) and measures 0.54 mm in length and 0.41 mm in thickness. The outgrowth is metallic with a red dorsal part and a green ventral one. Its sculpture differs from the rest of the propodeum (Fig. 30B), being rugose with irregular punctation that becomes confluent and sulcate. Additionally, the outgrowth is covered by denser silvery setae. We were unable to examine the underlying tissue or conduct a histological analysis of the outgrowth, and therefore we cannot exclude the possibility of infection or the presence of pathogens. However, based on the literature in other Arthropods (e.g. Shields & Small, 2013), we hypothesize that this mass could be a benign papilliform hamartoma. Its exact origin remains unknown but possibly originated from abnormal wound repair.

The second case involves an outgrowth on the left mesopleuron of a female of *Primeuchroeus* sp. from Australia (NMLU). Although structurally similar to the previous case, it differs in several aspects: it is located on a different metasomal segment, is considerably larger, and appears to be composed of two distinct tissues. The outgrowth measures 1.26 mm ×0.85 mm and exhibit a metallic sheen on the intervals between sculptures. As in the first case, the distal part is somewhat rugose, with irregular punctation becoming confluent and sulcate (Fig. 30C and D). However, the anterior portion reveals a differently sculptured, dark brown, non-metallic tissue. This area is further divided into two distinct regions, a larger frontal section with a strigate or costulate sculpture and a smaller dorsal section with papillate sculpture. Since we could not examine the underlying tissue or its histology, we tentatively classify this outgrowth as another benign papilliform hyperplasia or hamartoma.

A third case of a tumor-like outgrowth was observed on the metasoma of a female *Chrysis gracillima* Förster 1853 from Stavropol Krai (Russia) (Fig. 30E and F). However, this case differs from the previous, as it is distinctly smaller and clearly associated with a cuticular aberration. The malformation affects the apical part of the tergum, altering the sculpture of the area. This anomaly may have originated from incorrect cuticular development or, as in the previous cases, from abnormal wound repair during the pupal stage.

Hypertrophy

Developmental anomalies such as abdominal hypertrophy are relatively rare. Abdominal hypertrophy refers to an abnormal enlargement of the abdomen, which can be caused by various factors, including genetic mutations, developmental anomalies, parasitic infections, or environmental stressors. We observed few cases of this condition in Chrysididae including the male of *Chrysis splendidula chlorisans* from Greece and the type of *Chrysis parvicapito* from Tunisia, which also exhibits microcephaly (Fig. 11A). The other two cases occur in the genus *Chrysis*: the first is a male of *Chrysis frivaldszkyi* Mocsáry 1882 from Palermo (Sicily, Italy) (Fig. 31B), which displays an abnormally enlarged metasoma, with a length-to-width ratio of 1.38, whereas in normal males of the same species this ratio is approximately 1.6 (1.64 in the specimen shown in Fig. 31A). No additional anomalies were observed in this individual. The second is a female of *C. succincta* Linnaeus 1767 from Vetan (Aosta Valley, Italy) (Fig. 31D) which exhibits even greater metasoma enlargement than the previous case, with length-to-width ratio of 1.46, whereas in normal females of this species this ratio is around 1.75 (Fig. 31C). These two specimens were collected using a butterfly net, not in pan traps (Moericke traps) which can sometimes induce metasomal enlargement when cuckoo wasps remain in water for too long, causing a distortion that persist after drying. Additionally, they do not show signs of parasitic infestation, suggesting that the anomaly may be the result of genetic factors, hormonal or endocrine dysfunction or environmental stress.

The opposite case is undoubtedly more common in collections, particularly in specimens collected using Malaise traps and/or preserved with an excess of ethanol. In these specimens, the body becomes dehydrated, causing the cuticle, especially that of the metasoma, to appear longer and slenderer in dorsal view due to deformation. This deformation results from distal compression and ventral curvature of the metasoma. This phenomenon is well documented in Kim (2016), where a series of *Omalus aeneus* specimens are illustrated. Kim (2016) initially considered three Korean specimens exhibiting this malformation as a potentially undescribed species. However, after consulting with the first author and recognizing that the head and appendages cannot be entirely concealed within the metasomal venter when the wasp adopts its characteristic defensive posture, it was concluded that this abnormal narrowing of the abdomen was a malformation rather than a valid taxonomic diagnostic character. A similar post-mortem malformation is visible in some specimens illustrated by Wei *et al*. (2014), including *Omalus berezovskii* (Semenov-Tian-Shanskij 1932), *O. probiaccinctus* Wei, Rosa, Liu & Xu 2014, and *O. tibetanus* Wei, Rosa, Liu & Xu 2014. Another example of this deformation is observed in a female of *Omalus aeneus* from Casone Antonucci (Abruzzo, Italy) (Fig. 31F), given in comparison with a normal female (Fig. 31). However, the same malformation may occasionally occur in nature, as observed in a female of *Hedychridium cupratum* (Dahlbom 1854) from Vertosan (Aosta Valley, Italy) (Fig. 31I). This aberration is virtually indistinguishable from that induced by excessive dehydration and may possibly be caused by environmental stress at high altitudes.

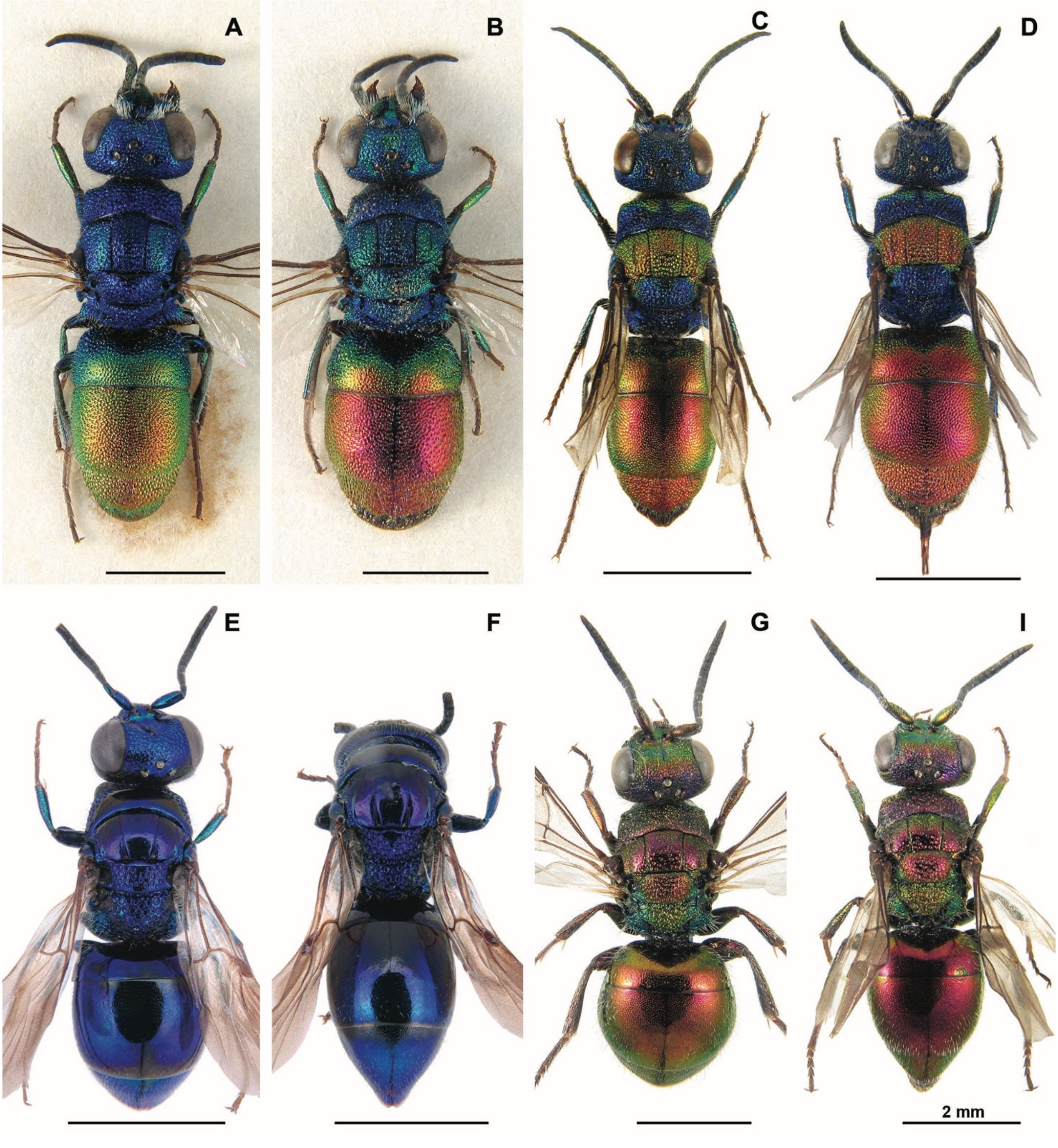

Fig. 31 – Hypertrophic and aberrant metasoma. A-B) *Chrysis frivaldskzyi*, male, dorsal view. A) Normal. B) Specimen with hypertrophic metasoma. C-D) *Chrysis succincta*, female, dorsal view. C) Normal. D) Specimen with hypertrophic metasoma. E-F) *Omalus aeneus*, female, dorsal view. E) Normal. F) Specimen with metasoma malformed post mortem. G-H) *Hedychridium cupratum*, female, dorsal view. G) Normal. H) Specimen with metasoma malformed found in nature. Scale bars: 2 mm. / Metasoma ipertrofico e aberrante. A-B) *Chrysis frivaldskzyi*, maschio, vista dorsale. A) Normale. B) Esemplare con metasoma ipertrofico. C-D) *Chrysis succincta*, femmina, vista dorsale. C) Normale. D) Esemplare con metasoma ipertrofico. E-F) *Omalus aeneus*, femmina, vista dorsale. E) Normale. F) Esemplare con metasoma malformato post mortem. G-H) *Hedychridium cupratum*, femmina, vista dorsale. G) Normale. H) Esemplare con metasoma malformato trovato in natura. Barre di scala: 2 mm.

Nanism and Gigantism

Nanism (microsomia) and gigantism (macrosomia) do not strictly fall within the definition of teratologies. However, specimens with noticeably different body sizes can occasionally be observed. One of the most evident cases occurs in *Stilbum cyanurum* (Forster 1771), the largest species in the family Chrysididae, which typically measures between 12 and 15 mm (Fig. 32A) However, within the same populations occasional small specimens measuring only 5 mm have been recorded by Linsenmaier (1959) and collected by the first author in Sardinia (Fig. 32B). These small individuals exhibit normally developed body parts, with only the overall body size reduced, likely due to limited food resources in the nest.

Other occasional cases are known in the family and can be found in collections. Members of the genus *Pseudochrysis* Semenow 1891 appear to be particularly prone to nanism, as seen in the case of small specimens described under the name *Ps. incrassata minuta* (Mocsáry 1889). Similarly, extreme size variation is evident in *Euchroeus* Fabricius 1809, as exemplified by *Euchroeus limbatus* Dahlbom 1854, in which individuals can exceptionally measure as little as 4.0 mm (Fig. 32D), compared to the normal size range of 8.0–9.0 mm (Fig. 32C-E) and may also exhibit coarser body punctation (Fig. 32F). The insufficient food provisions in the nest could explain the under development of these specimens.

Another case that warrants further study is that of *Chrysura simplex ampliata* (Linsenmaier 1968). *Chrysura simplex* usually ranges from 6.0 to 9.0 mm in length, with small specimens reaching only 4 mm, while giant specimens can grow up to 12 mm (Linsenmaier, 1959). Linsenmaier (1968) described the subspecies *C. simplex ampliata* based solely on its larger size, considering it an "ecological form" more common in mountainous areas (Rosa, 2006), but it may represent a sibling species parasitizing a different Megachilid host, resulting in a phenotypically larger but morphologically similar form. Future molecular analyses, cuticular hydrocarbon studies, or field research on hosts associations may clarify the true taxonomic status of *Chrysura simplex ampliata*.

Gynandromorphs

Gynandromorphism is a phenomenon in which an organism possesses tissue that is genotypically and phenotypically male and female (Michez *et al*., 2009), thus exhibiting a combination of male and female traits. A gynandromorph (or gynander) can display a bilateral or transversal symmetry, when male and female features are clearly developed along a particular axis of the body, or a mosaic pattern, where male and female traits appear as patches distributed across the body (Wcislo *et al*., 2004; Campos *et al*., 2011; Skvarla & Dowling, 2014). Gynandromorphy is widespread in Hymenoptera and many cases have been reported in the last decades (see Michez *et al*., 2009 for Anthophila). Within Hymenoptera, gyn-

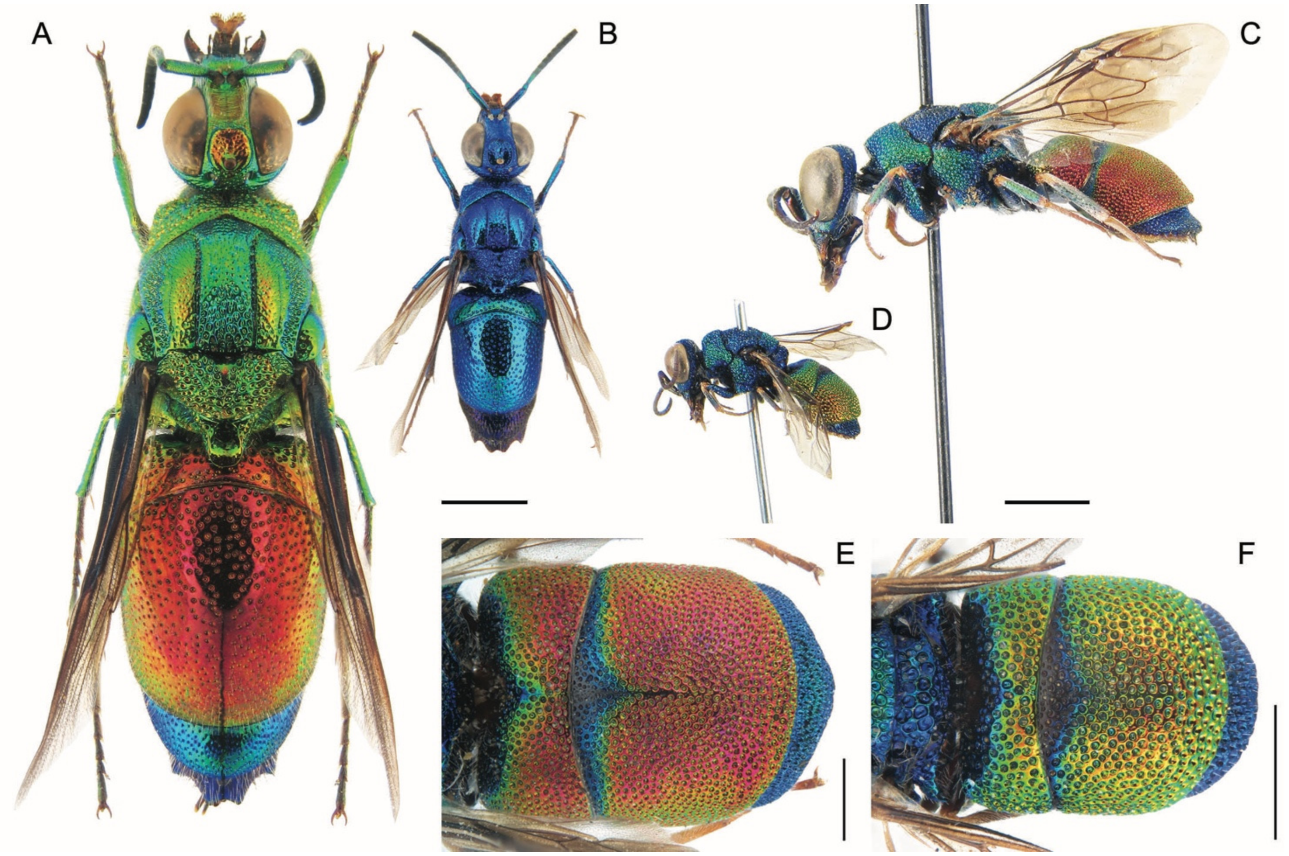

Fig. 32 – Nanism. A-B) *Stilbum cyanurum*, female, dorsal view. A) Normal. B) Specimen affected by nanism. C-D) *Euchroeus limbatus*, male, lateral view. C) Normal. D) Specimen affected by nanism. E-F) *E. limbatus*, metasoma, dorsal view. E) Normal. F) Specimen affected by nanism with aberrant sculpture. Scale bars: 1.0 mm. / Nanismo. A-B) *Stilbum cyanurum*, femmina, vista dorsale. A) Normale. B) Esemplare affetto da nanismo. C-D) *Euchroeus limbatus*, maschio, vista laterale. C) Normale. D) Esemplare affetto da nanismo. E-F) *E. limbatus*, metasoma, vista dorsale. E) Normale. F) Esemplare affetto da nanismo con scultura aberrante. Scala: 1,0 mm.

andromorphy may result from developmental aberrations or *Wolbachia*-induced parthenogenesis; higher temperatures can partially suppress the action of this bacterial symbiont, leading to the formation of gynandromorphs (Bowen & Stern, 1966; Cabello-García & Vargas-Piqueras, 1985; Rafael *et al*., 2017).

In Chrysididae, four cases have been reported in the literature: Wolf (2004) and Rosa & Zettel (2018) documented two Chrysidinae gynandromorphs: *Chrysura pseudodichroa* (Linsenmaier 1959), in the tribe Chrysidini, and *Holopyga fervida* (Fabricius 1781), in the tribe Elampini (Fig. 33A-C). Additionally, Strumia (2004) and Rosa (2019b) described and illustrated two Cleptinae gynandromorphs: *Cleptes triestensis* Móczár 2000 and *Cleptes semiauratus* (Linnaeus 1761) (Fig. 33D and E).

We observed another case of gynandromorphism in a female-like specimen of *Euchroeus rugulosus* (Mocsáry 1909) from Kazakhstan (PRC) (Fig. 35A) which displays an irregularly bicolored head, with the left side of vertex, frons and face and green as a male, while the rest of the body is red like a typical female.

However, when males and females share the same metallic color pattern, gynandromorphy can go unnoticed unless other sexually dimorphic morphological characters are present, as in the case of the female-like of *Chrysis insperata* from Serdiana (Sardinia, DSC) (Fig. 34). The external morphology initially resembles that of an ordinary specimen of *C. insperata*. However, upon dissection, the internal telescopic tube, along with both the terga and sterna, is found to be highly modified, culminating in an aberrant male genital capsule. All terga and the ovipositor are distinctly shorter than in normal specimens (Fig. 34C, G, I and K), whereas the sterna partially exhibit both male and female characteristics (Fig. 34E, K and P); notably, the fourth sternum clearly shows a fusion between male and female structures. The ovipositor is also deformed, as the female's valvula and the male's eight sternite (the subgenital plate) have fused together.

The genital capsule, connected to the ovipositor, is structurally similar to a typical male chrysidid capsule. However, the aedeagus and gonocoxite are extremely elongated (Fig. 34N) compared to the typical morphology of a

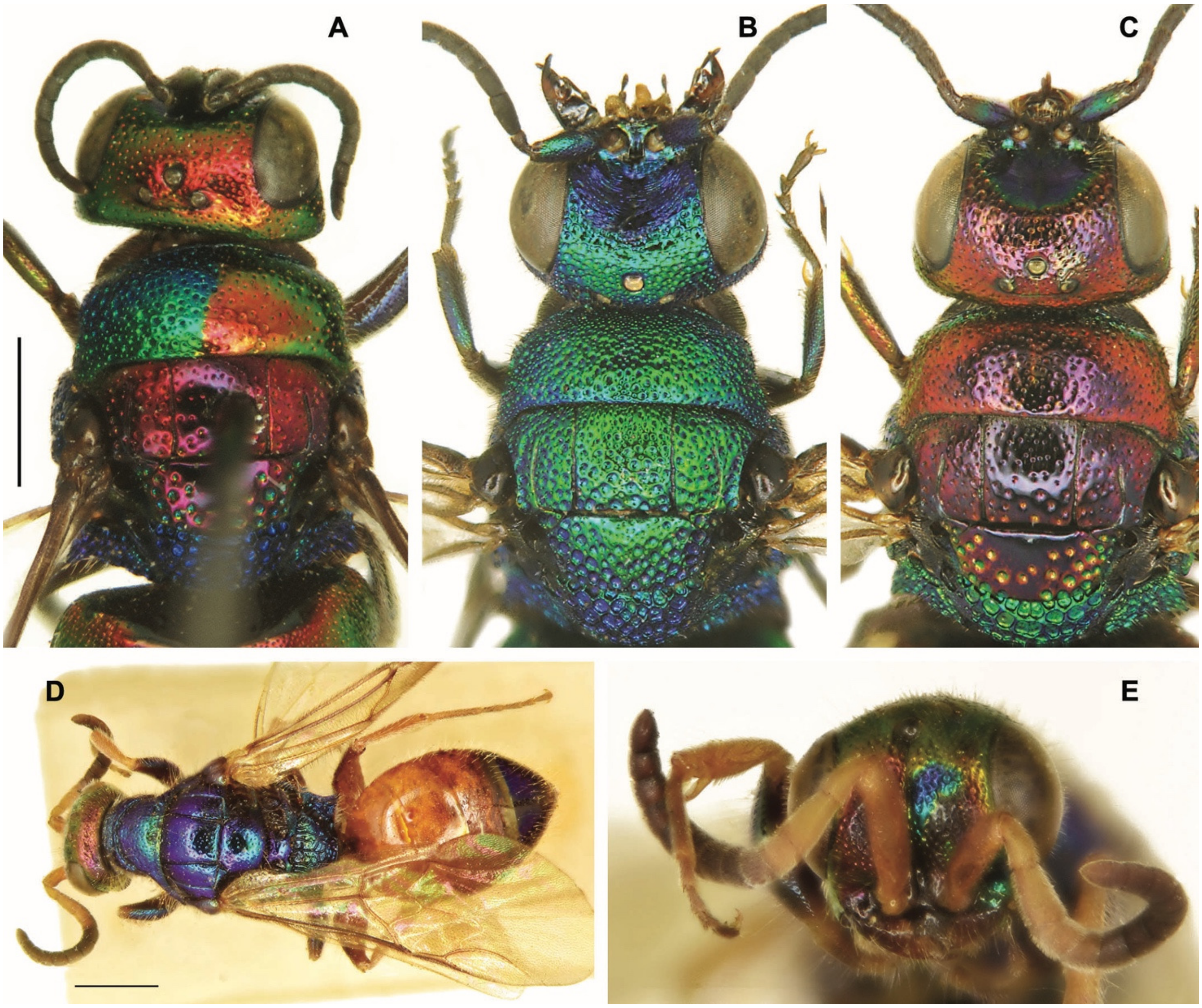

Fig. 33 – Gynandromorphy. A-C) *Holopyga fervida*, head and mesosoma, dorsal view. A) gynandromorph. B) male. C) female. D-E) *Cleptes semiauratus*, gynandromorph. D) Habitus, dorsal view. E) Head, frontal view. Scale bars: 1.0 mm. / Ginandromorfismo. A-C) *Holopyga fervida*, testa e mesosoma, vista dorsale. A) Ginandromorfo. B) Maschio. C) Femmina. D-E) *Cleptes semiauratus*, ginandromorfo. D) Habitus, vista dorsale. E) Testa, vista frontale. Scala: 1,0 mm.

normal aedeagus of *Chrysis insperata* (Fig. 34M). A similar case, with male genital capsule developed at the apex of the female ovipositor, was also observed in the gynandromorph of *Cleptes triestensis* Móczár 2000 by Strumia (2004). The shape of the genital capsule was distinctive enough to accurately identify the specimen, and the simultaneous presence of male and female characteristics on the body allowed for the recognition of the corresponding female. Strumia (2004) was therefore able to describe the female for the first time based on several specimens collected in Tuscany, Sardinia, and Corsica.

The case of *Cleptes triestensis* is a perfect example of a species with strong sexual dimorphism (e.g., differences in body colors), where associating the sexes can be challenging. A gynandromorph, which combines characteristics of both sexes in a single specimen, provides direct evidence of their relationship, helping taxonomists to confidently associate male and female forms.

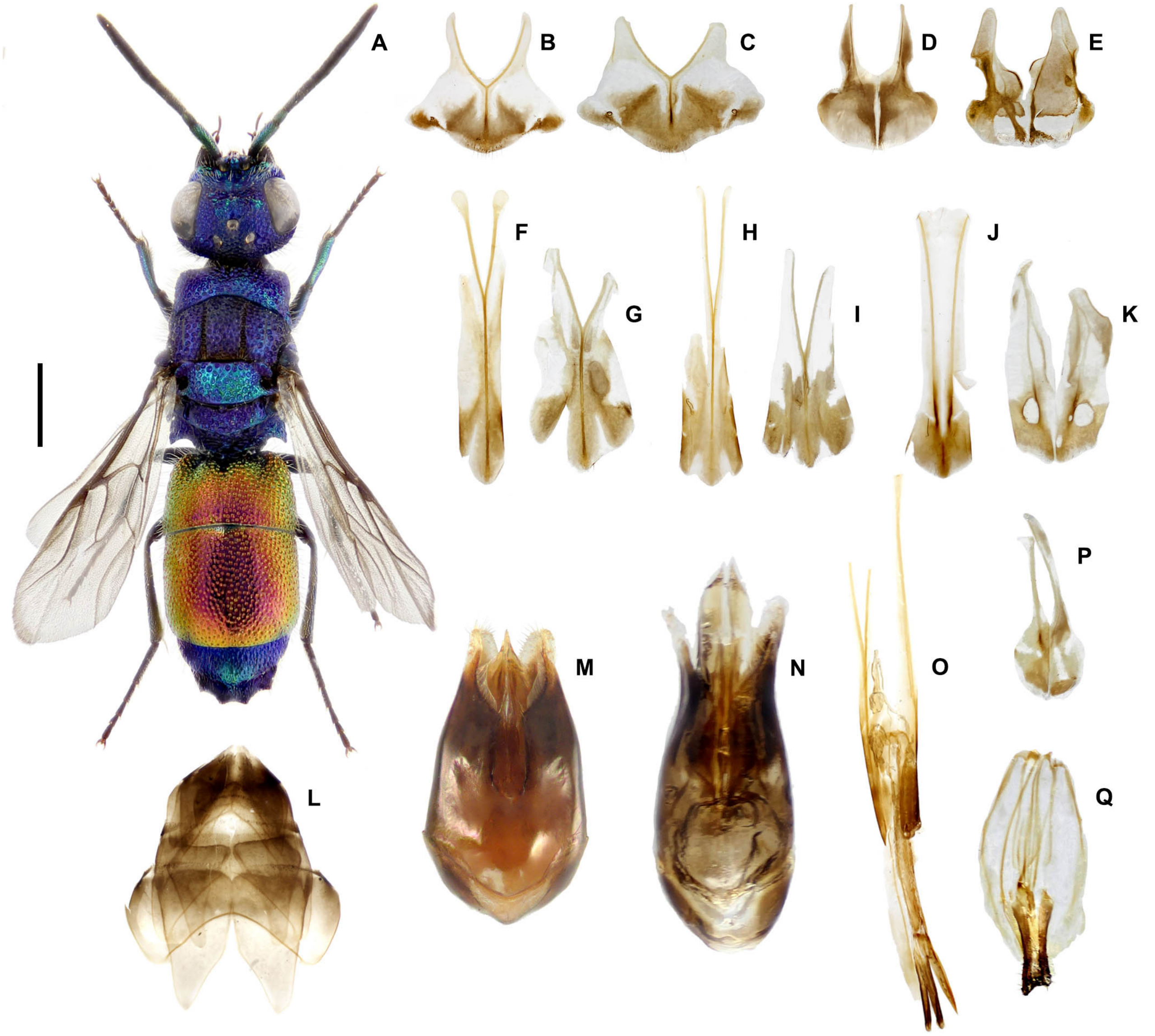

Fig. 34 – Gynandromorphy. *Chrysis insperata*, gynandromorphy, A) Habitus, C) T4. E) S4. G) T5. I) T6. K) S5. P) S6. N) Abnormal genital capsule at top of the ovipositor. Q) Abnormal ovipositor. *Chrysis insperata*, female, normal. B) T4. D) S4. F) T5. H) T6. J) S5. O) T7, S6 and ovipositor. *Chrysis insperata*, male, normal. L) Internal tergites and sternites. M) Genital capsule, normal (Photos: Daniele Sechi). Scale bars: 1.0 mm. / Ginandromorfismo. *Chrysis insperata*, ginandromorfismo. A) Habitus, C) T4. E) S4. G) T5. I) T6. K) S5. P) S6. N) Capsula genitale anomala in cima all'ovopositore. Q) Ovopositore anomalo. *Chrysis insperata*, femmina, normale. B) T4. D) S4. F) T5. H) T6. J) S5. O) T7, S6 e ovopositore. *Chrysis insperata*, maschio, normale. L) Tergiti e sterno interni. M) Capsula genitale, normale (Foto: Daniele Sechi). Scala: 1,0 mm.

Abnormal colorations

The metallic colors of Chrysididae are a spectacular feature that has inspired both their scientific and common names, such as "jewel wasps" and "ruby-tailed wasps" in English-speaking countries, or "golden wasps" in many other countries, e.g. "*Goldwespen*" in German, "*осы-блестянки*" [*osy-blestjanki,* = glittering wasps] in Russian, "*guêpe dorée*" in French, "*vespe dorate*" in Italian, "*Goudwespen*" in Dutch, "*Guldvepse*" in Danish, "*guldsteklar*" in Swedish, "*Zlatih os*" in Slovenian, "*Zlotolitki*" in Poland, "*Zlatěnky*" or "*Zlatěnkovití*" in Czech etc. (Agnoli & Rosa, 2024). Nevertheless, some species in the subfamilies Amiseginae and Loboscelidiinae have brownish to dull black coloration. Despite the prominence of these structural colors, their ultimate function remains unclear. Several hypotheses suggest that they may serve as aposematic signal to deter predators; indicate indigestibility or even be an epiphenomenon, a secondary effect of structural adaptations in the cuticle originally selected for other purposes (Kroiss *et al*., 2009).

The metallic iridescence in Chrysididae results from structural coloration, produced by an epicuticular multilayer in which microscopic nanostructures, like cuticular ridges and air spaces, create optical effects through thin-film interference and diffraction, generating intense, shimmering colors (Kroiss *et al*., 2009). These colors shift depending on the angle of incidence of the light and the point of observation, making individuals appear different hues varying lighting conditions.

Color anomalies are uncommon. We recorded more than 40 specimens exhibiting unusual coloration, associated with gynandromorphism, melanism, rufinism, as well as rare cases of color depigmentation, dyschromy, asymmetry, or insertions of different color patches. The origin of these aberrant colors includes genetic mutations, like alterations in genes regulating chitin deposition and cuticular ultrastructure; mechanical damage during development, when the cuticle is physically disrupted during pupation and the normal structure of reflective layers is altered, leading to dull or patchy coloration (Fig. 35B). We hypothesise that stress conditions caused by temperature or humidity during the pupation stage may affect the fine structure of the cuticle, producing unexpected colour variations. Furthermore, irregular tissue differentiation caused by teratological factors due to developmental abnormalities could lead to localised colour malformations (Fig. 35C-F).

Transparent or pale metallic structures

A male of *Chrysis splendidula* Rossi 1790 from Italy, Parma (Fig. 35B) has a depigmented patch on the right lateral area of mesoscutum, likely originated from a mechanical damage during the pupal development. In some cases, the epicuticle does not fully develop, leading to weakened or translucent reflection (Fig. 35C), like in a female of *Chrysis insperata* Chevrier 1870 from Crete (Greece).

Patchy or asymmetric metallic patterns

Some specimens exhibit abnormal patches or asymmetries where metallic coloration is altered, possibly due to localized developmental disruptions. These color anomalies are rare in cuckoo wasps and therefore particularly striking when they occur, as in the illustrated cases of a male of *Chrysura refulgens* (Fig. 35D), a female of *Holopyga generosa* (Förster 1853) (Fig. 35E), a male of *Holopyga fervida* (Fabricius 1781) (Fig. 35F). Dyschromic patches appear in numerous specimens, such as in *Hedychrum nobile* (Scopoli 1763) from Girona (Catalonia, Spain) (Fig. 35G), where an elongate darker stripe on the red third metasomal tergum features different, with fine and dense punctation, unlike the rest of the metasomal sculpture. The origin of this anomaly is unclear, and possibly not a case of gynandromorphy, as male and female of *H. nobile* exhibit similar metasomal coloration and sculpture. Similar patches, varying in shape, can also be observed on the mesosoma.

In other cases, abnormal color patterns are symmetric, as in the case of a male of *Chrysis emarginatula* Spinola 1808, from Granada (Andalusia, Spain) (Fig. 35H) with symmetric blue patches on metasoma, while the normal color is uniformly red; and in a female of *Chrysura refulgens* (Spinola 1806), from Imperia (Liguria, Italy) (Fig. 35I) where geometric, symmetric patterns are visible on the metasoma, which is normally uniformly red. These specimens deviate from the typical different color pattern, and in both asymmetric and symmetric cases, the anomalies could be teratological, possibly caused by genetic mutations affecting the cuticular nanostructure.

Unusual hue variations

Some individuals display unexpected shifts in metallic coloration, as seen in aberrant specimens of *Philoctetes bidentulus* (Lepeletier 1806), a species which is normally blue on the head and mesosoma, with a red to golden-red metasoma. Two aberrant specimens from Aosta Valley (Italy) exhibit a bronze or light olive-green body color. Similarly, in rare specimens of the *Chrysis succincta* group and *C. scutellaris* group, both males and females may exhibit an entirely blue mesosoma, lacking the characteristic red mesoscutum (in the *succincta* group) or scutellum (in the *scutellaris* group).

Melanism

Melanism is the increased deposition of dark pigments (usually melanin) in the cuticle, leading to darker or completely black individuals and is well-documented in many insect groups (True, 2003). Melanism in Chrysididae specimens is particularly intriguing because their coloration is structural rather than pigment-based. We observed melanic specimens in almost all genera, including *Chrysis* Linnaeus 1761, across different species groups (Fig. 36B, D and F, and Fig. 37F and G), *Chrysura* Dahlbom 1845 (Fig. 36H), *Pseudochrysis* Semenow 1891 (Fig. 37B), *Stilbum* Spinola 1806 (Fig. 37D), *Primeuchroeus* Linsenmaier 1968 (Fig. 37E).

The possible origins of these melanic aberrations may be disruption of cuticular nanostructures, or melanin deposit in between layers altering or obscuring these structures. In this case the iridescence may be reduced or completely lost, making the insect appear black or dull. Actually, many observed melanic specimens still retain weak iridescence. Other possible origins are changes in cuticle thickness; developmental abnormalities, such as improper cuticle formation during pupation; and environmental temperature effects, such as low temperatures that can increase melanin production, potentially affecting metallic reflections.

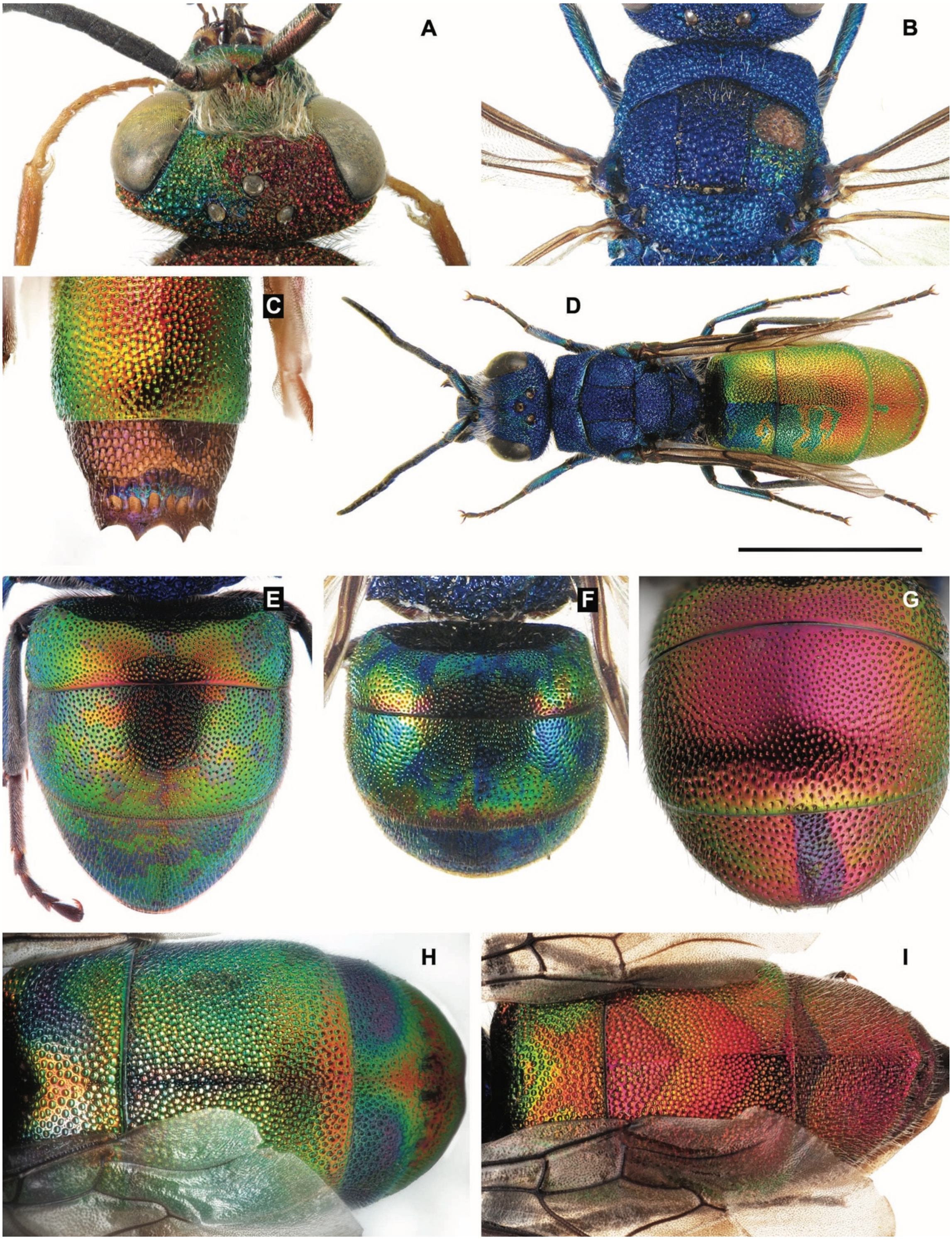

Fig. 35 – Aberrant coloration. A) *Euchroeus rugulosus*, gynandromorph, female-like with green colour corresponding to masculine tissue. B) *Chrysis splendidula*, male with depigmented patch on mesoscutum. C) *Chrysis insperata*, female, third tergum with colour aberration. D) *Chrysura refulgens*, female, metasomal colour aberration. E) *Holopyga generosa*, female, metasomal colour aberration. F) *Holopyga fervida*, male, metasomal colour aberration. G) *Hedychrum niemelai*, female, dyschromy. H) *Chrysis emarginatula*, male, metasomal colour aberration I) *Chrysura refulgens*, female, metasomal colour pattern aberration. Scale bar: 5.0 mm. / Colorazione aberrante. A) *Euchroeus rugulosus*, ginandromorfo, simile alla femmina con colore verde corrispondente a tessuti maschili. B) *Chrysis splendidula*, maschio con macchia depigmentata sul mesoscutum. C) *Chrysis insperata*, femmina, terzo tergite con aberrazione di colore. D) *Chrysura refulgens*, femmina, aberrazione di colore del metasoma. E) *Holopyga generosa*, femmina, aberrazione di colore del metasoma. F) *Holopyga fervida*, maschio, aberrazione di colore del metasoma. G) *Hedychrum niemelai*, femmina, discromia. H) *Chrysis emarginatula*, maschio, aberrazione di colore del metasoma. I) *Chrysura refulgens*, femmina, aberrazione del pattern di colore del metasoma. Scala: 5,0 mm.

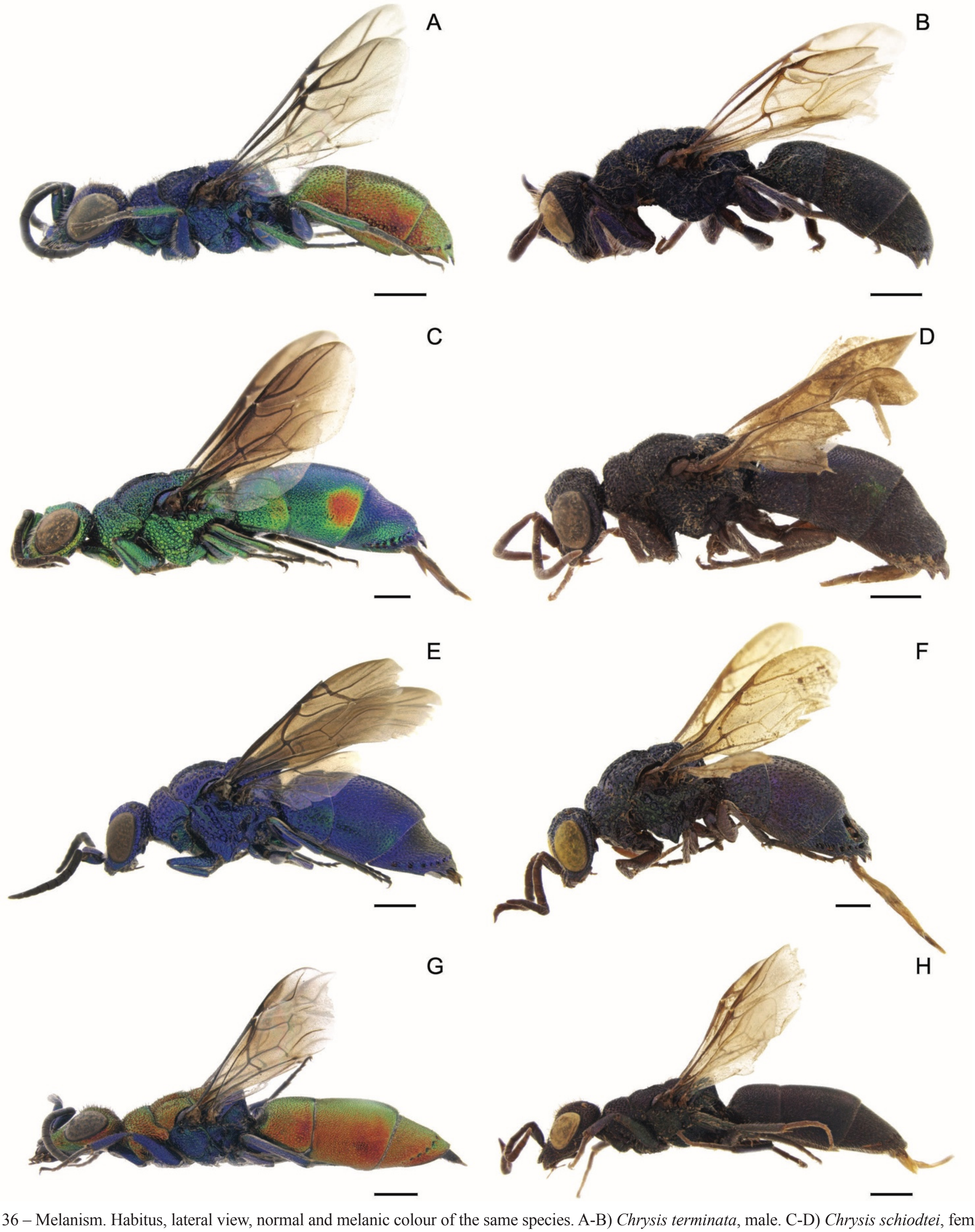

Fig. 36 – Melanism. Habitus, lateral view, normal and melanic colour of the same species. A-B) *Chrysis terminata*, male. C-D) *Chrysis schiodtei*, female. E-F) *Chrysis stilboides*, female. G-H) *Chrysura cuprea*, female. Scale bars: 1.0 mm. / Melanismo. Habitus, vista laterale, colore normale e melanico della stessa specie. A-B) *Chrysis terminata*, maschio. C-D) *Chrysis schiodtei*, femmina. E-F) *Chrysis stilboides*, femmina. G-H) *Chrysura cuprea*, femmina. Scala: 1,0 mm.

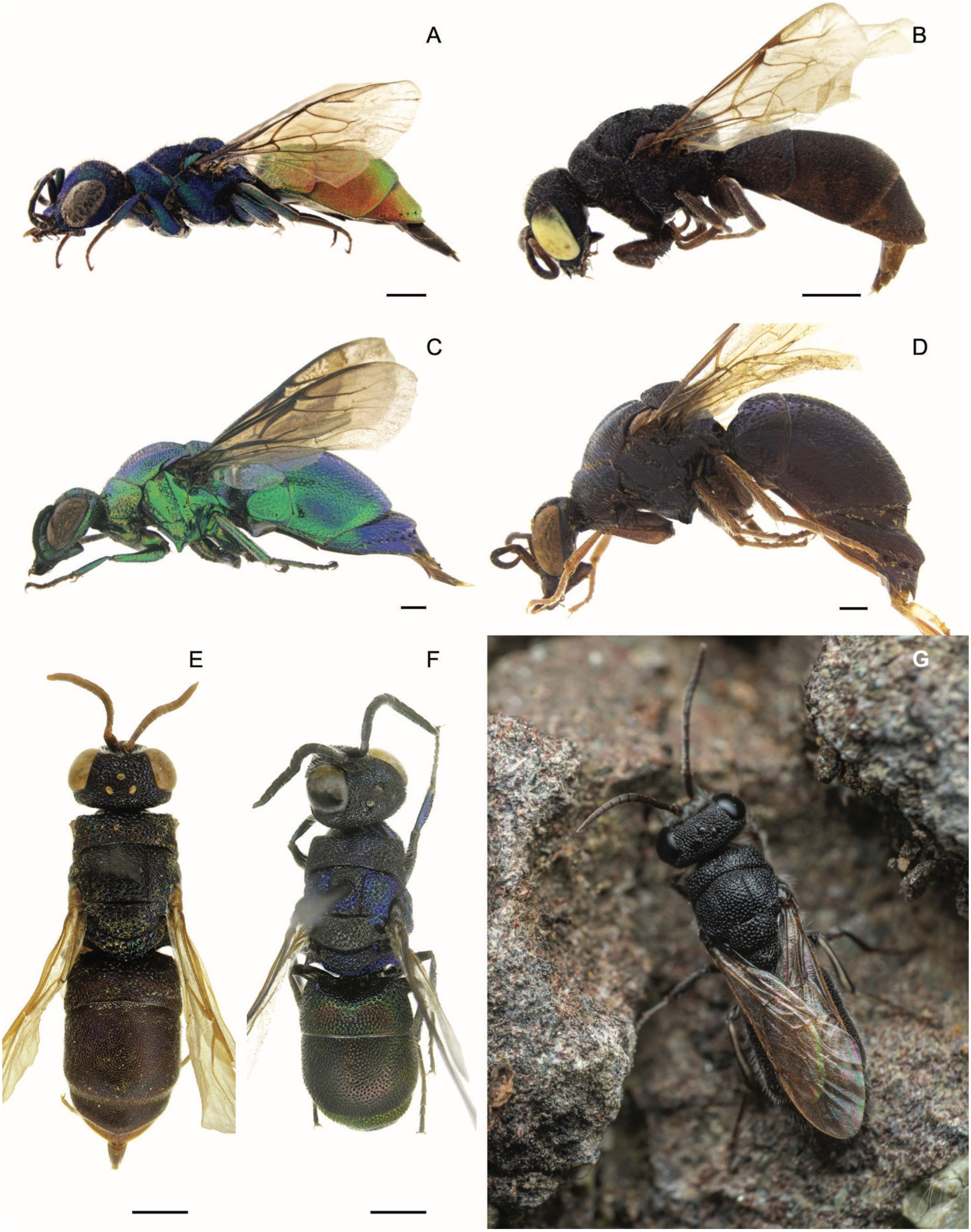

Fig. 37 – Melanism. A-D) lateral view, normal and melanic colour of the same species. A-B) *Pseudochrysis neglecta*, female. C-D) *Stilbum cyanurum*, female. E-G) Habitus, dorsal view. E) *Primeuchroeus papuanus*, female. F) *Chrysis scutellaris*, male. G) *Chrysis ignita* group, female (Photo: Joshua Clarke). Scale bars: 1.0 mm. / Melanismo. A-D) Vista laterale, colore normale e melanico della stessa specie. A-B) *Pseudochrysis neglecta*, femmina. C-D) *Stilbum cyanurum*, femmina. E-G) Habitus, vista dorsale. E) *Primeuchroeus papuanus*, femmina. F) *Chrysis scutellaris*, maschio. G) *Chrysis ignita* gruppo, femmina (Foto: Joshua Clarke). Scala: 1,0 mm.

Melanic specimens have led to the description of new species and varieties such as *Chrysis kuthyi* Mocsáry 1889 [currently *Pseudochrysis neglecta* (Shuckard 1837)], *Chrysis wuestneii* Mocsáry 1889 [currently *C. subsinu*ata Marquet 1879], *Chrysis ignita lugubris* du Buysson 1895 [including several melanic individuals of different taxa of the *ignita* group], *Holopyga hortobagyensis* Móczár 1983 [currently *H. generosa* (Förster 1853)], and others.

The phenomenon of melanism in Chrysididae was neglected in the past. We hypothesize that there may be a relationship between black colouration in some species and the geological environment. As a matter of fact, many species found in the Canary Islands are entirely or largely black. This is the case of *Chrysis atrocomitata* Linsenmaier 1993; *C. canaria amaurotica* Linsenmaier 1993; *C. globiscutella* Linsenmaier 1993; *C. magnifacialis* Linsenmaier 1993; *C. umbofacialis* Linsenmaier 1993; *Philoctetes caudatus ortegai* Linsenmaier 1993; and *P. tenerifensis* Linsenmaier 1959. We posit that black body colour serves a cryptic function, allowing them to blend in with the dark volcanic terrain. The igneous Canary archipelago still shows regular volcanic activity, and large areas are covered with basaltic lava, volcanic ash, and tephra, giving the landscape a naturally dark or black background. The presence of dark pigmentation in insects inhabiting volcanic regions is often an adaptive response to this unique environment. This phenomenon is sometimes referred to as "fire melanism" and was already observed in other insects like Coleoptera (Selander, 1958).

Rufinism

Rufinism refers to an increased presence of reddish, rufous, or rusty brown colouration. This can manifest as an abnormal and rare reddish colouration, differing from the typical colour pattern of a species. Rufinism is less frequent than melanism, and we observed only a few completely rufinic specimens in Chrysidinae. Examples include a male of *Elampus panzeri* (Fabricius 1798) (NHMW) (Fig. 38A, B) and a female of *Pseudomalus auratus* (Linnaeus 1758) (NHMUK) (Fig. 38C, D) which are entirely rufinic with weak opalescent reflections. We also observed fully rufinic specimens of *Stilbum cyanurum* (Forster 1771) (NMLU and other museums), which lack any 'normal' metallic hue. Another taxonomic case involves the taxon *Stilbum cyanurum leveillei* du Buysson 1896, whose holotype has melanic head and mesosoma combined with a rufinic metasoma, completely devoid of metallic hues.

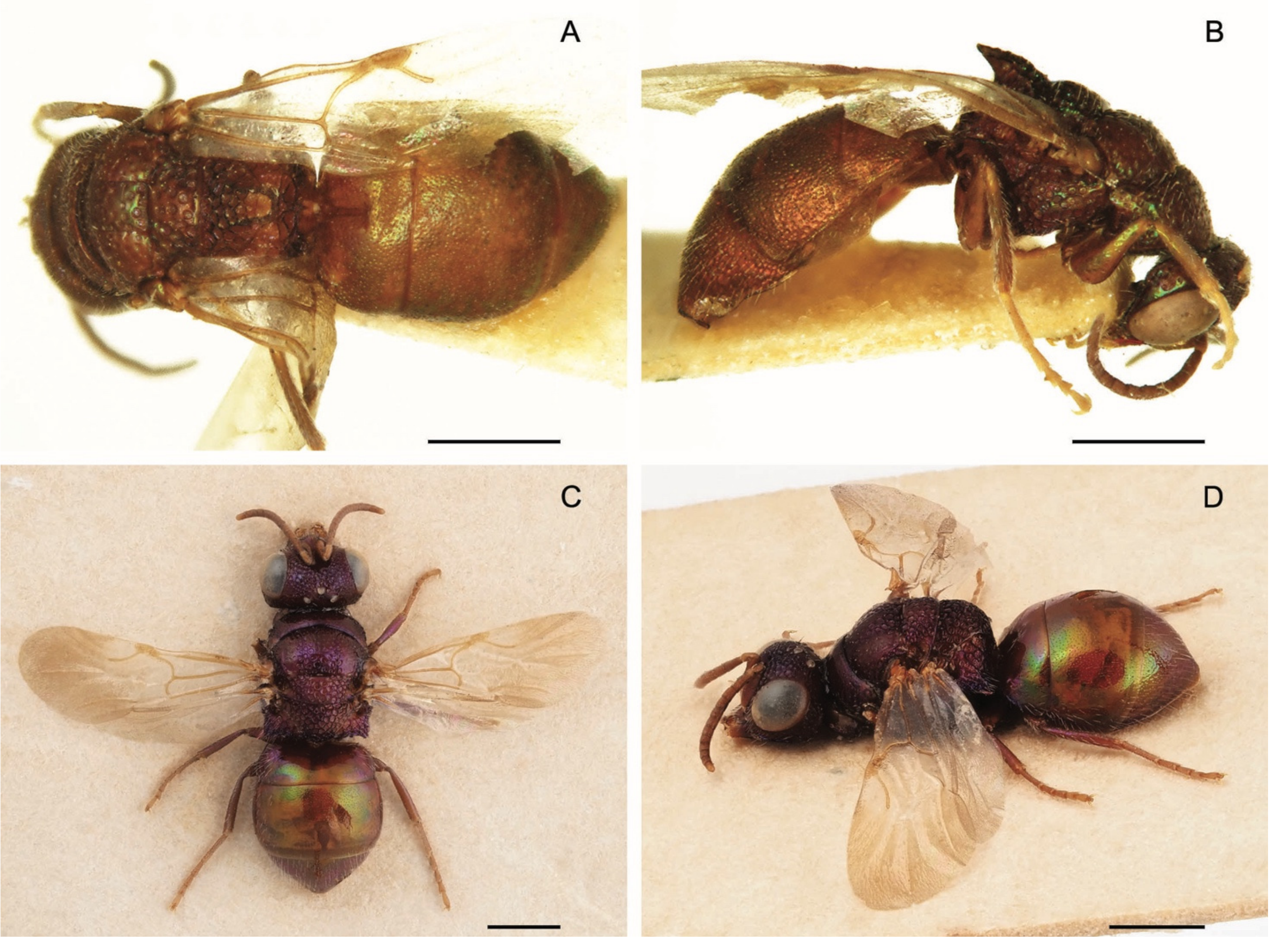

Fig. 38 – Rufinism. A-B) *Elampus panzeri*, male. A) Habitus, dorsal view. B) Habitus, lateral view. C-D) *Pseudomalus auratus*, female. C) Habitus, dorsal view. D) Habitus, lateral view. Scale bars: 1.0 mm. / Rufinismo. A-B) *Elampus panzeri*, maschio. A) Habitus, vista dorsale. B) Habitus, vista laterale. C-D) *Pseudomalus auratus*, femmina. C) Habitus, vista dorsale. D) Habitus, vista laterale. Scala: 1,0 mm.

DISCUSSION

Despite the scarcity of described records, some aberrations can be frequently observed in cuckoo wasps, particularly in their head and metasoma. These anomalies were probably neglected by other researchers for several reasons. For example, because of the small size of the majority of the species, or because they are hard to pin out due to poor preparation of the specimens. Indeed, chrysidids in collections are often clumsily pinned in the mesosoma with the body almost rolled up, the head facing the bottom of the entomological box, the antennae positioned under the specimen, the wings obscuring each other and hiding the metasoma, and the legs hidden under the ventral part of the body. It is also conceivable that researchers have thought that no significant conclusions could be obtained from isolated aberrant individuals and therefore they were simply not reported, excluding a few exceptional cases.

Frequency of teratological cases

Evaluating the occurrence of aberrations from the Hymenoptera literature is challenging for several reasons: i) there is a significant publication bias favouring only the most spectacular teratological cases; ii) eusocial species, such as honeybees and ants, may produce a higher number of both viable and teratomorphic individuals due to their social structure (Balazuc, 1958; Buschinger & Stoewesand, 1971; López & Ortuño, 1992); iii) organisms that are particularly susceptible to parasitism are more likely to develop into teratomorphic individuals (Balazuc, 1948; Espadaler & Riasol, 1983); iv) insects with highly mobile preimaginal stages, such as those in Tenthredinoidea, face an increased risk of trauma that may lead to abnormal regenerations (Balazuc, 1948); v) finally, cleptoparasites and predators are less abundant than herbivorous, and aberrations are normally less evaluated in these groups.

In social Hymenoptera, Buschinger & Stoewesand (1971) recorded 97 teratologies in a sample of approximately 250,000 ants (0.039%); of these 84 were presumed to have resulted from environmental causes, 11 were gynandromorphs and two cases were interpreted as atavistic. In Sphecidae wasps, Gülmez (2019) observed an extremely high frequency of forewing teratologies (6.7%), with 112 cases out of 1,682 specimens belonging to 42 species. However, this high rate could be influenced by a methodological bias, as collections have focused on agricultural land, a habitat that having been extensively modified by humans could have contributed to the increased occurrence of such malformations. In contrast, our study mainly examined specimens from natural environments.

In general, teratologies are rarely recorded even in large datasets. For example, in the case of Coleoptera, Balazuc (1948) analysed data from the Perty insect collection and estimated that one anomalous individual occurs per 17,000 specimens (approximately 0.006%). Similarly, in a study of Caraboidea collected in the Iberian Peninsula, Ortuño & Vique (2007) examined 29,186 specimens developed under natural conditions and observed only 10 teratological cases, roughly one teratomorph individual for every 3,000 individuals (0.034%).

Frequency in Chrysididae

Móczár (1963) provided the only available analysis of teratologies for the family Chrysididae. For his revision of the Magyar Fauna, Móczár (1963, 1967) examined approximately 10,000 specimens housed at the Hungarian Museum of Natural History in Budapest, and observed only two teratological cases, yielding a frequency of 0.02%.

In our study, we recorded 808 specimens exhibiting morphological anomalies of various ontogenetic origins. However, some of these anomalies were photographed in museums or in private collections and specimens were collected from various countries in the Palearctic region; although these images serve as examples of specific aberrations, they cannot be reliably used to assess frequency. We can probably assess only the frequency of gynandromorphy, because we observed only four cases among more than 275,000 specimens examined. Although many gynandromorphs may have gone unnoticed due to the lack of clear sexual dimorphism between the sexes, the frequency of this teratology can be estimated at one in every 68,750 specimens, with a frequency of 0.00145%.

To provide a robust analysis for Chrysididae, we examined data from the first author's collection (PR), based on specimens collected in nature in Italy over a decade between 1990 and 2000, and supplemented by other Italian records collected with less frequency in the following years, from the same localities in Abruzzo, Aosta Valley, Emilia-Romagna, Lazio, Liguria, Lombardy, Piedmont, Sardinia and Sicily. In total, we analysed 16,339 specimens, of which 609 exhibited malformations (3.72%) due to various causes. Specifically:

- 74 specimens exhibited malformations on the head (0.46%), including 16 cases in combination with malformations in other body parts;
- 68 specimens exhibited malformations on the mesosoma (0.41%), including 19 in combination with malformations in other body parts;
- 458 on the metasoma (2.8%), including 23 in combination with malformations in other body parts, of which 260 possibly with simple mechanical malformations (1.59%).

When excluding specimens with a malformation of doubtful origin, possibly only related to pupal positioning in the nest or mechanical crushing (284 cases across all body parts), the number of cases reduces to 324, corresponding to a frequency of 1.98%. The most spectacular teratological cases, such as those illustrated in this article, constitute only a small fraction (22 specimens, with a frequency of 0.13%). This frequency is anyway considerably higher than those previously recorded in Hymenoptera and Coleoptera studies based on samples exceeding 10,000 individuals (Balazuc, 1948; Móczár 1963; Buschinger & Stoewesand 1971; Ortuño & Vique, 2007).

Based on our overall observations, the tribe Chrysidini exhibited a higher frequency of anomalies (69.9%) compared to Elampini (29.04%)%), Parnopini and Cleptinae (both with only one specimens observed). Additionally, anomalies were more prevalent in males (57.82%) than in females (42.18%).

Time trends in teratologies cannot be reliably assessed over the relatively short period of time, around a decade, during which the Italian specimens were collected. However, evaluating such trends is essential for understanding the underlying mechanisms and patterns that generate teratologies. This requires a larger dataset to determine whether there is an increase at specific times, either regionally or on a global scale.

CONCLUSIONS AND PERSPECTIVES

Our findings reveal relatively high frequencies of abnormal specimens, ranging from 1.98% to 3.72% (depending on the definitions), 0.13% for the most spectacular cases. These observations raise several questions: why are cuckoo wasps particularly affected? Could their parasitoid lifestyle be a contributing factor? For instance, might parasitization of an inappropriate host induce hormonal, genetic or developmental modifications in the emerging imago? Conversely, are the observed aberrations more frequent because Chrysididae are inherently more resilient than other hymenopteran groups? Or could these patterns simply reflect increased environmental pollution and climate change?

We encourage both morphologists and geneticists to pursue further investigations into these questions. Teratological data bridge the gap between morphology, genetics, and developmental biology, highlighting how deviations from the "norm" can illuminate the processes that generate it. Therefore, contributing new observations of teratological specimens is not merely of anecdotal interest, it represents a step toward building a comprehensive framework for understanding morphological variation and its evolutionary implications. Even the documentation of single cases contributes to the gradual accumulation of larger datasets, which in turn supports the formulation and testing of explanatory hypotheses. Beyond their immediate descriptive value, such records form the empirical foundation necessary for recognizing recurrent morphological trends, developmental constraints, or lineage-specific predispositions to certain anomalies. As the dataset grows, it will eventually allow for more rigorous statistical and phylogenetic analyses, helping to reveal whether particular teratologies are random, lineage-linked, or correlated with specific ecological or developmental factors, underlying genetic or environmental causes of such abnormalities.

SUPPORTING INFORMATION

Excel file including taxonomic information of the studied specimens, code number, figure published, sex, locality, date of the collecting event, collector, type of aberration and body part affected.

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