



An integrative study of *Necremnus* Thomson (Hymenoptera: Eulophidae) associated with invasive pests in Europe and North America: taxonomic and ecological implications

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The species of *Necremnus* attacking two invasive pests of tomato and canola in Europe and North America, respectively, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) and *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), have been revised using an integrative taxonomy approach. Molecular data from the mitochondrial cytochrome oxidase *c* subunit I and the nuclear D2 expansion region of the 28S ribosomal subunit and internal transcribed spacer 2, the discovery of new morphological features, and study of type material resulted in the delineation of three species groups, the *Necremnus artynes*, *Necremnus cosconius*, and *Necremnus tidius* groups, the discovery of four new species, and the resurrection of three taxa from synonymy. Lectotypes have been designated for 13 species originally described in *Eulophus* by Walker. Although *Necremnus* has not been revised, an illustrated key is given to differentiate 23 recognized European species. The key, type images, and treatments of the three species groups will enable more accurate identification of the valid species of *Necremnus* in the future. They will also benefit biological control practitioners of pest species. The ecological consequences of the new taxonomic concepts are discussed.

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INTRODUCTION

Closely related species often display only slight, if any, differences in external morphological traits. If slight differences are misinterpreted as intraspecific variation, this can lead to the lumping of two or more

species under a single taxonomic entity and the underestimation of true species diversity. Mounting evidence, mainly from the use of molecular data, is showing that some recognized morphospecies are in fact complexes of lineages that differ in critical behavioural and ecological features such as host range (Heraty *et al.*, 2007; Gebiola *et al.*, 2009, 2012; Chesters *et al.*, 2012; Hernandez-Lopez *et al.*, 2012). Cryptic diversity is common amongst hymenopteran parasitoids, in which species confusion can have significant economic con-

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sequences because of their wide use as biological control agents. Accurate species identification and host-range assessment of parasitoids, especially when morphological variation is slight or absent, are crucial for the success of biological control attempts and to avoid undesired, potentially deleterious nontarget effects of introduced parasitoids on indigenous hosts (Heraty, 2004).

Europe and North America are currently struggling with major pest problems caused by two invasive species (stage V *sensu* Colautti & MacIsaac, 2004), the tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), and the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae). The tomato pinworm is one of the most devastating pests of tomato in South America (Barrientos *et al.*, 1998; Lietti, Botto & Alzogaray, 2005). It was first reported from Europe in Spain in 2006, and has subsequently spread throughout the Mediterranean Basin, including parts of North Africa and the Middle East. The pest has caused serious damage to tomato crops in invaded areas since its first detection and it is currently considered a key agricultural threat to European and North African tomato production (Desneux *et al.*, 2010; Chailleux *et al.*, 2012). A complex of indigenous natural enemies has been reported since the arrival of *T. absoluta* in the Mediterranean Basin and their suitability for biological control is currently being evaluated (Ferracini *et al.*, 2012; Chailleux *et al.*, 2013). A parasitoid identified as *Necremnus artynes* (Walker) (Hymenoptera: Eulophidae) is one of the most abundant in the field in Italy, Spain, France, and Tunisia (Desneux *et al.*, 2010; Ferracini *et al.*, 2012; Zappalà *et al.*, 2012, 2013; Abbes *et al.*, 2014; Gabarra *et al.*, 2014). *Necremnus artynes* and/or a species close to it (see Ferracini *et al.*, 2012) has high potential as a biocontrol agent in Mediterranean greenhouse tomato production and represents an interesting example of adaptation of an indigenous parasitoid to an invasive pest (Calvo *et al.*, 2013). Inoculative releases conducted in south-eastern Spain have been successful in significantly reducing populations of *T. absoluta*, and some biocontrol companies are already involved in the mass rearing and commercial distribution of *N. artynes* (Urbaneja *et al.*, 2012). Furthermore, Ferracini *et al.* (2012) showed that the effectiveness of a *Necremnus* species near *N. artynes* is even greater than that estimated by parasitization rate alone because its destructive host-feeding behaviour kills additional hosts.

The cabbage seedpod weevil is a pest of canola (oilseed rape), *Brassica napus* L. It was accidentally introduced to North America from Europe by the early 1930s and is now widespread throughout Canada and the USA (Baur *et al.*, 2007; Dossdall *et al.*, 2009). As an exotic pest, *Ce. obstrictus* has long been a prime target for

classical biological control (McLeod, 1951). At least 20 species in five families of Chalcidoidea are recorded as associated with *Ce. obstrictus* in North America (Haye *et al.*, 2013). This surprisingly diverse fauna includes species with both Nearctic and putatively Holarctic distributions, although many of the species appear to have expanded their host ranges to include *Ce. obstrictus* as a host in North America. Some of the species appear to be niche-specific whereas others are more host-specific (Gibson *et al.*, 2005; Dossdall *et al.*, 2006, 2009; Gibson, Gates & Buntin, 2006). Most of the parasitism has been attributed to *Necremnus tidius* (Walker) plus three species of Pteromalidae (Chalcidoidea), *Trichomalus lucidus* (Walker), *Chlorocyclus* sp., and *Pteromalus* sp. (Dossdall *et al.*, 2009; Haye *et al.*, 2013). Within North America, *N. tidius* was identified as *Necremnus duplicatus* Gahan, 1941 prior to 2005 when Gibson *et al.* (2005) concluded that the two names were synonymous, as first suggested by Bouček (1959). The former name was originally described from Europe and the latter from material reared from *Ce. obstrictus* in North America (Gahan, 1941). However, although *N. tidius* has occasionally been reported as a parasitoid of *Ce. obstrictus* in Europe (see references in Gibson *et al.*, 2005), it has never been reported as a principal parasitoid there (Williams, 2003). In North America, Gibson *et al.* (2005) and Dossdall *et al.* (2007) reported *N. tidius* as associated with species of Brassicaceae and Chenopodiaceae. Noyes (2013) listed species of Apionidae, Chrysomelidae, and Curculionidae (Coleoptera), Agromyzidae and Chloropidae (Diptera), Cephidae (Hymenoptera), and Gelechiidae, Scythrididae, and Ypnomeutidae (Lepidoptera) as putative hosts of *N. tidius*, but Dossdall *et al.* (2006) suggested that the noncoleopteran host associations probably result from incorrect identifications of the parasitoid.

Within North America, any biological control measure of *Ce. obstrictus* is inextricably linked to the control of hoary cress, *Cardaria draba* (L.) (= *Lepidium draba*) (Brassicaceae). This invasive species was accidentally introduced from Europe and in North America is an economically important weed, mainly in canola, wheat, and barley, although it is also spreading to natural habitats (Hinz, 2013). *Ceutorhynchus obstrictus* and *T. absoluta* are currently controlled through the use of broad-spectrum chemical pesticides (Cárcamo *et al.*, 2001; Roditakis *et al.*, 2012). Alternative control strategies such as introduced biological control agents are urgently needed to reduce pesticide use and to overcome difficulties in current management strategies (Hinz, 2013). However, introduction of parasitoids for control of *Ce. obstrictus* necessitates these to be host specific so that they do not negatively impact other ceutorhynchine weevils introduced for biocontrol programmes against hoary cress or other invasive

weeds. It is therefore critical that the identity of the parasitoid species and their host ranges be known accurately.

Classical biological control is a cost-effective, permanent, self-sustaining, and ecologically safe option against alien species (Van Driesche *et al.*, 2010). The first essential step in evaluating the potential effectiveness and ecological safety of any biocontrol agent is the correct species delimitation of the parasitoid involved. Recent biocontrol-focused papers have pointed out the existence of species that, although identified as *N. artynes* using available keys, do not fully match the original descriptions or current interpretation of the morphospecies (Ferracini *et al.*, 2012; Zappalà *et al.*, 2012, 2013; Gabarra *et al.*, 2014). Furthermore, apparent anomalies, such as *N. tidius* being a common parasitoid of *Ce. obstrictus* in North America, but not in Europe, and having different postoviposition behaviour in the two regions (Ferracini *et al.*, 2012), bring into question the validity of a single species.

Advancements in molecular techniques for systematics that have occurred over the past decade have provided taxonomists with additional tools to dramatically improve their ability to correctly distinguish species, although not to correctly apply nomenclature, which still requires examination of type material and application of names following the rules of the International Code of Zoological Nomenclature (ICZN). In order to increase the degree of confidence in taxonomic decisions within a general lineage concept (de Queiroz, 2007), it is becoming common for taxonomists to use multiple independent lines of evidence in advancing species hypotheses. Integrative taxonomy provides a good theoretical and practical framework for species delimitation (Dayrat, 2005; Schlick-Steiner *et al.*, 2010). In the present study we used an iterative process (Tan *et al.*, 2010; Yeates *et al.*, 2011; Gebiola *et al.*, 2012) to assess diversity and clarify species limits within two of the principal parasitoids reported for the two pest study systems discussed above. We tested initial species hypotheses based on morphology using three gene regions, the mitochondrial cytochrome *c* oxidase subunit I (*COI*), the D2 expansion region of the 28S ribosomal subunit (*28SD2*), and the ribosomal internal transcribed spacer 2 (*ITS2*), to produce a molecular species hypothesis. We then re-examined a posteriori the morphology of reared specimens belonging to the two complexes to formulate a revised morphological species concept and tested this with further gene sequencing. This iterative process resulted in revised species concepts, which then necessitated the examination of relevant type material, selection of lectotypes to fix and apply existing names, and the formal description of some new species. Clarification of the true species diversity also enabled reassessment of host ranges and

distributional patterns of the delimited species to better explain ecological and behavioural observations.

The primary aim of this study was to clarify the species of *Necremnus* parasitizing two pest species and related hosts rather than a formal revision of the genus. Because of this, species described from North America unrelated to parasitism of the cabbage seedpod weevil and European species that do not affect nomenclature of the *N. artynes* and *N. tidius* complexes were not studied. However, Walker (1839, 1846b, 1848) described several species that have priority within *Necremnus*, and some of these names have been treated as junior synonyms of others, including under *N. tidius* (Noyes, 2013). Study of Walker's type material was therefore necessary to correctly establish nomenclature under our revised species concepts. This resulted in the discovery that some type series consisted of more than one species and that almost none of the names were fixed through formal designation of lectotypes. For these reasons we treated all of the species described by Walker that are now classified in *Necremnus* and provide a revised dichotomous key to the European species of the genus. The European species of *Necremnus* were revised by Bouček (1959) and Graham (1959), but several European species have been described since then (Delucchi, 1962; Bouček, 1974; Hedqvist, 1982; Graham, 1983, 1986; Askew, 1992; Askew, Blasco-Zumeta & Pujade-Villar, 2001; Yefremova, 2007). The key to species is provided not only as a benefit to taxonomists but also for biological control practitioners. However, users should be aware that based on the results of our limited study it is almost certain that additional cryptic species remain to be discovered amongst specimens that we have keyed as single species, but which are morphologically variable.

MATERIAL AND METHODS

SPECIES SAMPLING

Specimens of the putative morphospecies *N. tidius* and *N. artynes* used for this study were obtained from large sampling efforts carried out in Europe (France, Germany, Romania, Spain, and Switzerland), North Africa (Algeria, Morocco, and Tunisia), Canada, and the USA. Although samples of *T. absoluta* were also collected in Argentina during the (austral) summer of 2012, no *Necremnus* were reared in this country. Most specimens of the *N. tidius* complex originated from voucher material of previously published studies of parasitoids associated with *Ce. obstrictus* or related North American and European weevil species associated mainly with *Car. draba* and *Capsella bursa-pastoris* (L.) Medik. Additional samples were reared from canola, hoary cress, shepherd's purse, and other Brassicaceae infested with weevils. Most samples of the *N. artynes* complex were reared from tomato leaves mined by *T. absoluta*, but

more samples were obtained also from native European leafminers in natural ecosystems. A few samples were obtained by sweeping herbaceous layers. In addition, specimens of a few other related *Necremnus* species were used to enhance morphological and molecular analyses, including those identified as *Necremnus leucarthros* (Nees) (morphologically similar to *N. tidius*), *Necremnus metalarus* (Walker) (morphologically similar to *N. artynes*), *Necremnus flagellaris* Askew, and *Necremnus hungaricus* (Erdős). A complete list of the *Necremnus* species, host-plant systems, and sampling localities and dates is given in Table 1. Depending upon the specimen source, reared specimens were preserved initially in 70–95% ethanol prior to DNA extraction and were either air or critical-point dried prior to mounting on points or cards.

SPECIES TESTING

An iterative process was used to discriminate species in the *N. tidius* and *N. artynes* complexes. Specimens were identified to an initial morphological species concept (H_0) using the keys of Gahan (1941) for North American specimens and Askew (1968), Bouček (1959), and Graham (1959) for European specimens, plus comparison with previously identified specimens in North American and European museums. DNA was then extracted and sequenced from identified H_0 individuals that represented a subset of available rearing/collection events to produce an initial molecular species concept (H_1). For instances in which H_1 indicated greater species diversity than H_0 , the sequenced and other nonsequenced specimens from the same collection events were examined to find morphological features that supported H_1 concepts within a revised morphological species concept (H_2). Individuals from rearing/collecting events different from those forming H_0 concepts were then sequenced to test the H_2 concepts. If H_2 agreed with H_1 , then the species hypotheses were considered strongly supported by combined molecular and morphological evidence, and formal taxonomic actions taken.

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

DNA was extracted from whole specimens using a Chelex-proteinase K-based nondestructive protocol (Walsh, Metzger & Higuchi, 1991) modified as in Gebiola *et al.* (2009). The same DNA extraction protocol was used for three dried specimens of *N. leucarthros*, but specimens were kept in Chelex-proteinase K at 55 °C for 5 h instead of 1 h. For each wasp, we amplified the 3' half of fragment of the mitochondrial *COI* gene and two nuclear ribosomal regions, *28S-D2* and *ITS2*. For *COI* amplification, the forward primers C1-J-2195 or C1-J-2183 (Simon *et al.*, 1994) were used with the reverse primer TL2-N-3014 (Simon *et al.*, 1994). *28S-D2* was amplified by using primers D2F and D2R (Campbell,

Stephan-Campbell & Werren, 1993). Primers ITS2F (Campbell *et al.*, 1993) and ITS2RevTrich (Stouthamer *et al.*, 1999) were used for PCR amplification of *ITS2*. For the amplification of dried samples, two *COI* overlapping, shorter fragments of 400 and 570 bp were amplified by using primer pairs C1-J-2195/CO1-Hco-extB (Schulmeister, 2003) and C1-J-2441/TL-N-3014 (Simon *et al.*, 1994), respectively. For *28S-D2* and *ITS2*, a seminested approach was implemented, using internal primer ND2F (Goolsby *et al.*, 2001) in combination with D2R for the second PCR for the former, and external reverse primer ITS2Rev (Campbell *et al.*, 1993) with ITS2F in the first PCR round for the latter. PCR cycles for *COI*, *28S-D2*, and *ITS2* were reported in Gebiola *et al.* (2009) and Gebiola, Bernardo & Burks (2010). Amplicon size was checked on 1.2% agarose gel, purified, and sequenced at XiLin sequencing in Beijing, China. Vouchers of sequenced specimens of the *N. tidius* group are stored at the Canadian National Insect Collection of Insects, Arachnids and Nematodes (CNC) in Ottawa, Canada, and those of the *N. artynes* group at the Natural History Museum, London, UK (BMNH), and at CNC. Chromatograms were unambiguously edited by eye and final sequences aligned using BioEdit (Hall, 1999). Sequences were submitted to GenBank with accession numbers KJ846078–KJ846470 (Table 1). The alignment of *COI* sequences was straightforward, whereas *28S-D2* and *ITS2* sequences were aligned using the G-INS-I algorithm in MAFFT7 (online version; Katoh & Standley, 2013).

PHYLOGENETIC ANALYSES

Phylogenies were obtained using maximum likelihood (ML) in RAxML 7.0.4 (Stamatakis, 2006) and Bayesian inference (BI) in MrBayes 3.2 (Ronquist *et al.*, 2012) on single genes and on a supermatrix concatenated data set that was partitioned by gene, and within *COI*, by first + second codon position, and third codon position. *Hemiptarsenus autonomus* (Mercet) (Hymenoptera: Eulophidae) was used as the outgroup in all analyses. As *28S-D2* and *ITS2* are tightly linked in the ribosome, they were concatenated and analysed as a single ribosomal region. For both ML and BI inferences, the general time-reversible model with gamma distributed rate variation among sites and a proportion of invariable sites was used for both *COI* and *28S-D2* + *ITS2*, as selected by jModeltest (Posada, 2008). ML trees were obtained after 1000 multiple inferences on the original alignment, starting from a random most parsimonious tree and default initial rearrangement settings and number of rate categories. ML branch support was based on 1000 rapid bootstrap pseudoreplicates, and clades were considered as supported when bootstrap > 70%. For BI, two parallel runs of four simultaneous Monte Carlo Markov

Table 1. List of specimens used for both molecular and morphological analyses

Code	Morphospecies	Locality	Country	Host	Plant	Sex	Collection date	GenBank accession numbers		
								28S-D2	ITS2	COI
NA115	<i>Necremnus artynes</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	15. xii. 2011	KJ846222	KJ846353	KJ846091
NA116	<i>Necremnus artynes</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	15. xii. 2011	KJ846223	KJ846354	KJ846092
NA147	<i>Necremnus artynes</i>	Breil-sur-Roya	France	Unknown	Unknown	♀	20. vi. 2012	KJ846231	KJ846382	KJ846100
NA148	<i>Necremnus artynes</i>	Breil-sur-Roya	France	Unknown	Unknown	♀	20. vi. 2012	KJ846232	KJ846383	KJ846101
NA149	<i>Necremnus artynes</i>	Moulinet	France	Unknown	Unknown	♀	21. vi. 2012	KJ846233	KJ846384	KJ846102
NA150	<i>Necremnus artynes</i>	Saint-Etienne-de-Tinée	France	Unknown	Unknown	♀	24. vi. 2012	KJ846234	KJ846385	KJ846103
NA168	<i>Necremnus artynes</i>	Montoliu	Spain	Unknown	Unknown	♀	07. vi. 2013	KJ846385	KJ846466	KJ846204
NA169	<i>Necremnus artynes</i>	Utxesa	Spain	<i>Aproaerema anthyllidella</i>	<i>Astragalus stella</i>	♀	09. vi. 2013	KJ846386	KJ846467	KJ846205
NA170	<i>Necremnus artynes</i>	Aspa	Spain	Unknown	Unknown	♂	09. iv. 2013	KJ846387	KJ846468	KJ846206
NA171	<i>Necremnus artynes</i>	Aspa	Spain	Unknown	Unknown	♂	09. iv. 2013	KJ846388	KJ846469	KJ846207
NA172	<i>Necremnus artynes</i>	Alfés	Spain	<i>Aproaerema anthyllidella</i>	<i>Astragalus sesameus</i>	♂	09. vi. 2013	KJ846389	KJ846470	KJ846208
NA2	<i>Necremnus cosmopterix</i>	Portici	Italy	Unknown	<i>Parietaria judaica</i>	♀	12. iv. 2006	KJ846240	KJ846371	KJ846109
NA3	<i>Necremnus cosmopterix</i>	Moncalieri	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	19. x. 2009	KJ846244	KJ846375	KJ846113
NA10	<i>Necremnus cosmopterix</i>	Moncalieri	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	15. viii. 2010	KJ846210	KJ846341	KJ846079
NA11	<i>Necremnus cosmopterix</i>	Moncalieri	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	04. viii. 2010	KJ846349	KJ846349	KJ846087
NA10	<i>Necremnus cosmopterix</i>	Moncalieri	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	19. x. 2009	KJ846214	KJ846345	KJ846083
NA110	<i>Necremnus cosmopterix</i>	Cariati	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	15. vi. 2010	KJ846215	KJ846346	KJ846084
NA113	<i>Necremnus cosmopterix</i>	Cariati	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	15. vi. 2010	KJ846219	KJ846350	KJ846088
NA112	<i>Necremnus cosmopterix</i>	San Giorgio	Italy	<i>Cosmopterix pulchrimella</i>	<i>Parietaria judaica</i>	♀	25. iv. 2006	KJ846221	KJ846352	KJ846090
NA146	<i>Necremnus cosmopterix</i>	Noli	Italy	<i>Cydia capparidana</i>	<i>Parietaria judaica</i>	♂	13. v. 2006	KJ846220	KJ846351	KJ846089
NA5	<i>Necremnus cosmopterix</i>	Arma di Taggia	Italy	<i>Tuta absoluta</i>	<i>Capparis spinosa</i>	♂	18. ix. 2012	KJ846220	KJ846361	KJ846099
NA105	<i>Necremnus cosmopterix</i>	Bioplanet insectary	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	10. x. 2009	KJ846249	KJ846380	KJ846118
NA106	<i>Necremnus cosmopterix</i>	Bioplanet insectary	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	15. vi. 2010	KJ846214	KJ846345	KJ846083
NA143	<i>Necremnus navonei</i>	Quiberon	France	<i>Dialectica scariella</i>	<i>Solanum lycopersicum</i>	♀	15. vi. 2010	KJ846215	KJ846346	KJ846084
NA153	<i>Necremnus navonei</i>	Fos-sur-Mer	France	Unknown	<i>Echium vulgare</i>	♀	11. vii. 2012	KJ846228	KJ846359	KJ846097
NA16	<i>Necremnus tutae</i>	Marignano	Italy	<i>Tuta absoluta</i>	Unknown	♀	19. viii. 2011	KJ846235	KJ846386	KJ846104
NA23	<i>Necremnus tutae</i>	Pagani	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	20. x. 2010	KJ846238	KJ846369	KJ846107
NA25	<i>Necremnus tutae</i>	Poggromarino	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	20. x. 2010	KJ846242	KJ846373	KJ846111
NA104	<i>Necremnus tutae</i>	Capaccio	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	10. x. 2010	KJ846243	KJ846374	KJ846112
NA4	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	23. x. 2011	KJ846213	KJ846344	KJ846082
NA22	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	08. viii. 2009	KJ846245	KJ846376	KJ846114
NA40	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846241	KJ846372	KJ846110
NA41	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	23. vi. 2010	KJ846246	KJ846377	KJ846115
NA45	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846247	KJ846378	KJ846116
NA57	<i>Necremnus tutae</i>	Pula	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846248	KJ846379	KJ846117
NA108	<i>Necremnus tutae</i>	Bioplanet insectary	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	23. vi. 2010	KJ846250	KJ846381	KJ846118
NA109	<i>Necremnus tutae</i>	Bioplanet insectary	Italy	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	15. vi. 2010	KJ846216	KJ846347	KJ846085
NA96	<i>Necremnus tutae</i>	Antibes	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	15. vi. 2010	KJ846217	KJ846348	KJ846086
NA97	<i>Necremnus tutae</i>	Antibes	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2011	KJ846253	KJ846384	KJ846122
NA89	<i>Necremnus tutae</i>	Berre-l'Étang	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2011	KJ846254	KJ846385	KJ846123
NA100	<i>Necremnus tutae</i>	Berre-l'Étang	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846252	KJ846383	KJ846121
NA101	<i>Necremnus tutae</i>	Berre-l'Étang	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846211	KJ846342	KJ846080
NA156	<i>Necremnus tutae</i>	Berre-l'Étang	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	23. vi. 2010	KJ846212	KJ846343	KJ846081
NA157	<i>Necremnus tutae</i>	Berre-l'Étang	France	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	20. vi. 2011	KJ846236	KJ846367	KJ846105
NA117	<i>Necremnus tutae</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	20. vi. 2011	KJ846237	KJ846368	KJ846106
NA118	<i>Necremnus tutae</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	15. xii. 2011	KJ846224	KJ846355	KJ846093
						♂	15. xii. 2011	KJ846224	KJ846356	KJ846094

NA13	<i>Necremnus tutae</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	09.viii.2010	KJ846226	KJ846357	KJ846095
NA14	<i>Necremnus tutae</i>	Cabrils	Spain	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♂	09.viii.2010	KJ846227	KJ846358	KJ846096
NA144	<i>Necremnus tutae</i>	Kairouan	Tunisia	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	25.v.2012	KJ846229	KJ846380	KJ846098
NA8	<i>Necremnus tutae</i>	Agadir	Morocco	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	14.vi.2009	KJ846251	KJ846382	KJ846120
NA162	<i>Necremnus tutae</i>	Mostaganem	Algeria	<i>Tuta absoluta</i>	<i>Solanum lycopersicum</i>	♀	24.iv.2011	KJ846239	KJ846370	KJ846108
NT67	<i>Necremnus aenigmaticus</i>	Bellin	Germany	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♂	04.vii.2010	KJ846308	KJ846439	KJ846177
NT90	<i>Necremnus aenigmaticus</i>	Bellin	Germany	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	04.vii.2010	KJ846330	KJ846461	KJ846199
NT91	<i>Necremnus aenigmaticus</i>	Bellin	Germany	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	04.vii.2010	KJ846331	KJ846462	KJ846200
NT92	<i>Necremnus aenigmaticus</i>	Bellin	Germany	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	04.vii.2010	KJ846332	KJ846463	KJ846201
NT93	<i>Necremnus aenigmaticus</i>	Bellin	Germany	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	04.vii.2010	KJ846333	KJ846464	KJ846202
NT165	<i>Necremnus aenigmaticus</i>	Moulinet	France	Unknown	Unknown	♀	21.vi.2012	KJ846284	KJ846415	KJ846153
NT18	<i>Necremnus duplicatus</i>	Abbots Ford	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	19.vii.2010	KJ846286	KJ846417	KJ846155
NT27	<i>Necremnus duplicatus</i>	Abbots Ford	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	19.vii.2010	KJ846291	KJ846422	KJ846160
NT37	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	26.vii.2010	KJ846301	KJ846432	KJ846170
NT39	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♂	26.vii.2010	KJ846303	KJ846434	KJ846172
NT86	<i>Necremnus duplicatus</i>	Lethbridge	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♂	12.viii.2005	KJ846327	KJ846458	KJ846196
NT17	<i>Necremnus duplicatus</i>	Abbots Ford	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♂	19.vii.2010	KJ846285	KJ846416	KJ846154
NT26	<i>Necremnus duplicatus</i>	Abbots Ford	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	19.vii.2010	KJ846290	KJ846421	KJ846159
NT28	<i>Necremnus duplicatus</i>	Abbots Ford	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	19.vii.2010	KJ846292	KJ846423	KJ846161
NT19	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	26.vii.2010	KJ846287	KJ846418	KJ846156
NT36	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	26.vii.2010	KJ846300	KJ846431	KJ846169
NT38	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	26.vii.2010	KJ846302	KJ846433	KJ846171
NT83	<i>Necremnus duplicatus</i>	Ingersoll	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	25.vi.2010	KJ846324	KJ846455	KJ846193
NT84	<i>Necremnus duplicatus</i>	Ingersoll	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	23.vii.2010	KJ846325	KJ846456	KJ846194
NT85	<i>Necremnus duplicatus</i>	Ingersoll	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♂	16.vii.2010	KJ846326	KJ846457	KJ846195
NT87	<i>Necremnus duplicatus</i>	Stimmie	Canada	<i>Ceutorhynchus obstructus</i>	<i>Brassica napus</i>	♀	12.viii.2010	KJ846328	KJ846459	KJ846197
NT21	<i>Necremnus duplicatus</i>	Centreville	Canada	<i>Ceutorhynchus omissus</i>	<i>Erysimum cheiranthoides</i>	♀	29.vi.2010	KJ846289	KJ846420	KJ846158
NT29	<i>Necremnus duplicatus</i>	Centreville	Canada	<i>Ceutorhynchus omissus</i>	<i>Erysimum cheiranthoides</i>	♂	29.vi.2010	KJ846293	KJ846424	KJ846162
NT30	<i>Necremnus duplicatus</i>	Centreville	Canada	<i>Ceutorhynchus omissus</i>	<i>Erysimum cheiranthoides</i>	♀	29.vi.2010	KJ846294	KJ846425	KJ846163
NT31	<i>Necremnus duplicatus</i>	Centreville	Canada	<i>Ceutorhynchus omissus</i>	<i>Erysimum cheiranthoides</i>	♀	29.vi.2010	KJ846295	KJ846426	KJ846164
NT79	<i>Necremnus duplicatus</i>	Blacks Corners	Canada	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♂	24.vi.2010	KJ846320	KJ846451	KJ846189
NT80	<i>Necremnus duplicatus</i>	Blacks Corners	Canada	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	24.vi.2010	KJ846321	KJ846452	KJ846190
NT81	<i>Necremnus duplicatus</i>	Blacks Corners	Canada	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	24.vi.2010	KJ846322	KJ846453	KJ846191
NT76	<i>Necremnus duplicatus</i>	Edmonton	Canada	<i>Ceutorhynchus neglectus</i>	<i>Rorippa</i> sp.	♀	15.vii.2010	KJ846317	KJ846448	KJ846186
NT77	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus neglectus</i>	<i>Rorippa</i> sp.	♂	21.vii.2010	KJ846318	KJ846449	KJ846187
NT78	<i>Necremnus duplicatus</i>	Saint Célestine	Canada	<i>Ceutorhynchus neglectus</i>	<i>Rorippa</i> sp.	♂	21.vii.2010	KJ846319	KJ846450	KJ846188
NT82	<i>Necremnus duplicatus</i>	Presqu'île Prov. Park	Canada	<i>Ceutorhynchus neglectus</i>	<i>Rorippa</i> sp.	♂	30.vii.2010	KJ846323	KJ846454	KJ846192
NT64	<i>Necremnus hippia</i>	Courchapoix	Canada	<i>Ceutorhynchus</i> sp.	<i>Erucastrum gallicum</i>	♂	18.vi.2010	KJ846305	KJ846436	KJ846174
NT65	<i>Necremnus hippia</i>	Dieterswil	Switzerland	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	22.vi.2010	KJ846306	KJ846437	KJ846175
NT66	<i>Necremnus hippia</i>	Dieterswil	Switzerland	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	22.vi.2010	KJ846307	KJ846438	KJ846176
NT62	<i>Necremnus hippia</i>	Villanova Solaro	Switzerland	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	08.v.2011	KJ846304	KJ846435	KJ846173
NT119	<i>Necremnus hippia</i>	Salusola	Italy	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	11.v.2012	KJ846284	KJ846395	KJ846133
NT120	<i>Necremnus hippia</i>	Salusola	Italy	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♀	11.v.2012	KJ846285	KJ846396	KJ846134
NT121	<i>Necremnus hippia</i>	Cigliano	Italy	<i>Ceutorhynchus</i> sp.	<i>Capsella bursa-pastoris</i>	♂	10.v.2012	KJ846286	KJ846397	KJ846135
NT88	<i>Necremnus hippia</i>	Moretta	Italy	<i>Ceutorhynchus</i> sp.	<i>Capsella bursa-pastoris</i>	♀	11.vi.2011	KJ846329	KJ846460	KJ846198
NT68	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	12.iv.2010	KJ846309	KJ846440	KJ846178

Table 1. Continued

Code	Morphospecies	Locality	Country	Host	Plant	Sex	Collection date	GenBank accession numbers		
								28S-D2	ITS2	COI
NT169	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	19.iv.2010	KJ846310	KJ846441	KJ846179
NT170	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	18.v.2010	KJ846311	KJ846442	KJ846180
NT127	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	14.iv.2010	KJ846270	KJ846401	KJ846139
NT130	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	14.iv.2010	KJ846273	KJ846404	KJ846142
NT134	<i>Necremnus hippia</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	18.v.2010	KJ846277	KJ846408	KJ846146
NT171	<i>Necremnus hippia</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	30.iv.2010	KJ846312	KJ846443	KJ846181
NT172	<i>Necremnus hippia</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	20.vi.2010	KJ846313	KJ846444	KJ846182
NT136	<i>Necremnus hippia</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	20.v.2010	KJ846279	KJ846410	KJ846148
NT139	<i>Necremnus hippia</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	09.v.2010	KJ846282	KJ846413	KJ846151
NT175	<i>Necremnus hippia</i>	Timisesti	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	09.v.2010	KJ846316	KJ846447	KJ846185
NT138	<i>Necremnus hippia</i>	Timisesti	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	20.vi.2010	KJ846281	KJ846412	KJ846150
NT120	<i>Necremnus tidius</i>	Rosetta	Canada	<i>Capsella bursa-pastoris</i>	<i>Capsella bursa-pastoris</i>	♀	30.v.2010	KJ846288	KJ846419	KJ846157
NT132	<i>Necremnus tidius</i>	Rosetta	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♀	30.v.2010	KJ846296	KJ846427	KJ846165
NT133	<i>Necremnus tidius</i>	Rosetta	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♀	30.v.2010	KJ846297	KJ846428	KJ846166
NT134	<i>Necremnus tidius</i>	Rosetta	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♀	30.v.2010	KJ846298	KJ846429	KJ846167
NT135	<i>Necremnus tidius</i>	Rosetta	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♀	30.v.2010	KJ846299	KJ846430	KJ846168
NT123	<i>Necremnus tidius</i>	Ottawa	Canada	<i>Ceutorhynchus typhae</i>	<i>Capsella bursa-pastoris</i>	♂	14.vi.2006	KJ846287	KJ846398	KJ846136
NT125	<i>Necremnus tidius</i>	Agassiz	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♂	04.vii.2009	KJ846288	KJ846399	KJ846137
NT126	<i>Necremnus tidius</i>	Agassiz	Canada	<i>Ceutorhynchus erysimi</i>	<i>Capsella bursa-pastoris</i>	♀	29.v.2009	KJ846289	KJ846400	KJ846138
NT173	<i>Necremnus tidius</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	20.v.2010	KJ846314	KJ846445	KJ846183
NT137	<i>Necremnus tidius</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	20.v.2010	KJ846280	KJ846411	KJ846149
NT131	<i>Necremnus tidius</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	20.v.2010	KJ846274	KJ846405	KJ846143
NT132	<i>Necremnus tidius</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	20.v.2010	KJ846275	KJ846406	KJ846144
NT174	<i>Necremnus tidius</i>	Timisesti	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	09.v.2010	KJ846315	KJ846446	KJ846184
NT195	<i>Necremnus tidius</i>	Timisesti	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	09.v.2010	KJ846334	KJ846465	KJ846203
NT133	<i>Necremnus tidius</i>	Timisesti	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	09.v.2010	KJ846276	KJ846407	KJ846145
NT128	<i>Necremnus tidius</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	18.iv.2010	KJ846271	KJ846402	KJ846140
NT129	<i>Necremnus tidius</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♀	19.iv.2010	KJ846272	KJ846403	KJ846141
NT135	<i>Necremnus tidius</i>	Valea Lupului	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	18.v.2010	KJ846278	KJ846409	KJ846147
NT163	<i>Necremnus tidius</i>	Saint-Etienne-de-Tinée	France	Unknown	Unknown	♀	24.vi.2012	KJ846283	KJ846414	KJ846152
NF154	<i>Necremnus flagellaris</i>	Loubarresse	France	Unknown	Unknown	♀	17.vii.2012	KJ846255	KJ846386	KJ846124
NH166	<i>Necremnus hungaricus</i>	Breil-sur-Roya	France	Unknown	Unknown	♀	22.vi.2012	KJ846256	KJ846387	KJ846125
NH167	<i>Necremnus hungaricus</i>	Sospel	France	Unknown	Unknown	♀	22.vi.2012	KJ846257	KJ846388	KJ846126
NL140	<i>Necremnus leucarthros</i>	Le Chenit	Switzerland	Unknown	Unknown	♀	17.vii.1991	KJ846258	KJ846389	KJ846127
NL141	<i>Necremnus leucarthros</i>	Le Chenit	Switzerland	Unknown	Unknown	♀	22.v.1991	KJ846259	KJ846390	KJ846128
NL142	<i>Necremnus leucarthros</i>	Le Chenit	Switzerland	Unknown	Unknown	♀	24.vii.1991	KJ846260	KJ846391	KJ846129
NL155	<i>Necremnus leucarthros</i>	Cubières	France	Unknown	Unknown	♀	18.vii.2012	KJ846261	KJ846392	KJ846130
NM63	<i>Necremnus metalarius</i>	Valmareno di Follina	Italy	<i>Colophora laricella</i>	Unknown	♀	25.v.2011	KJ846263	KJ846394	KJ846132
NM151	<i>Necremnus metalarius</i>	Sauchières	France	Unknown	Unknown	♀	15.vi.2012	KJ846262	KJ846393	KJ846131
HA1	<i>Hemiptarsenus autonomus</i>	Popricani	Romania	<i>Ceutorhynchus cardariae</i>	<i>Lepidium draba</i>	♂	30.iv.2010	KJ846209	KJ846340	KJ846078

28S-D2, D2 expansion region of the 28S ribosomal subunit; COI, cytochrome oxidase subunit 1; ITS2, internal transcribed spacer 2.

chains (three heated and one cold) were run for 10 000 000 generations, and trees sampled every 10 000 generations. Convergence of the separate runs was checked using the average deviation of split frequencies diagnostic (< 0.02 in all runs), and the potential scale reduction factor (close to 1.00 for all parameters). The burn-in value was set at 25% of sampled topologies, and postburn-in trees were summarized as a 50% majority rule consensus tree with posterior probabilities as nodal support and the threshold for clade acceptance set at 0.95. Trees shown below refer to the final analyses including both 'H₁ specimens' and 'H₂ specimens'. Uncorrected intra- and interspecific *p*-distances based on *COI* were calculated by MEGA4 (Tamura *et al.*, 2007).

MORPHOLOGICAL ANALYSES

A. Ribes was responsible for species treatments within the *N. artynes* group, whereas G. A. P. Gibson was responsible for those of the *Necremnus cosconius* and *N. tidius* groups and treatment of type material of all previously described species. For examination of mounted specimens of the *N. cosconius* and *N. tidius* groups, G. A. P. Gibson used a Nikon SMZ 1500 stereomicroscope allowing magnifications up to 270 ×, and fitted with a 10 mm ocular grid having 100 divisions for measurements. A piece of translucent Mylar tracing acetate was taped to the objective between the specimen and a Leitz 50-watt tungsten halogen light source, which is critical to reduce glare for correct observation of described sculpture. Measurement of lengths of the costal cell, marginal, stigmal, and postmarginal veins for type material of the *N. cosconius* group was carried out at 180 ×. The antennae and wings of most H₂ *N. tidius* group specimens were dissected, the antennae cleared, and the parts slide mounted prior to DNA extraction to obtain comparable relative measurements and examination of the number and arrangement of multiporous plate sensilla (mps) and sensory pores on the scape of the male flagellum. The sensory pores on the scape can only be observed with a compound microscope from cleared antennae. Most H₂ specimens were also imaged prior to DNA extraction using a Philips XL30 environmental scanning electron microscope and a Leica DFC 425C, 5 megapixel digital camera attached to a Leica Z16 APO microscope. A Styrofoam cone placed over the specimen was used to reduce glare from three Leica KL2500 LCD fibre optic light sources fitted with 250-watt cold light reflector lamps. The serial images obtained were combined with Zerene Stacker and digitally retouched using Adobe PHOTOSHOP to enhance clarity. These macroscopic techniques were used to image all specimens used for the plates of illustrations. Excluding primary type specimens, specimens used for photography by G. A. P. Gibson were given a

'CNC Photo' 2012-x or 2013-x specimen number label. This number is cited in the figure captions and if the specimen is not in the CNC then the acronym of the collection is also given so that imaged specimens can be located in the future.

For examination of mounted specimens and type material of the *N. artynes* group, A. Ribes used a stereomicroscope with a maximum magnification of 90 ×, and a 144-light-emitting diode ring as a light source, fitted with a 10 mm ocular grid having 100 divisions for measurements. Descriptions of species include ratios of measurements between various body parts. For the *N. artynes* group, the ranges given are those from usual variations of most specimens examined. If a smaller or larger ratio is rarely possible (often correlated with atypical samples or dwarf body size), this is given in parentheses before or after the typical range to give the possible range. Measurement of the length of the gaster includes the ovipositor sheaths, whereas width of the syntergum is the maximum width between the basal-most visible part laterally, and length of the syntergum is the length measured from its posterior margin to the posterior margin of the previous tergite. Photographs of whole specimens were taken with a compact digital camera placed over a trinocular stereomicroscope. Details of antennae and wings were similarly taken from slides with a trinocular optical microscope, and using polyvinyl alcohol in slides as the mounting and clearing medium. Multiple images of each photograph were combined using CombineZ5 software (Alan Hadley, micropics.org.uk).

Morphological terms mostly follow Gibson (1997). Terms for sculpture used are coriaceous (mesh-like sculpture delimited by impressed lines as if scratched by a pin), alutaceous (similar to coriaceous except sculpture transversely elongate, more leather-like in appearance), reticulate (mesh-like sculpture delimited by raised ridges along all margins), imbricate (sculpture in which one margin is higher than the others but surfaces are flat so as to appear to overlap in a shingle-like manner), reticulate-imbricate (similar to imbricate except surfaces are concave resulting in overlapped U-like depressions, in a more or less 'scalloped' manner), and strigose-imbricate (if raised ridges of imbricate sculpture are more or less aligned longitudinally to form wavy lines). Abbreviations used in the descriptions are: C1–C3, clavomere 1–3; cc, costal cell; F1–F4, funicle segment 1–4; mps, multiporous plate sensilla; mv, marginal vein; OD, ocellar diameter; OOL, ocellular line; pmv, postmarginal vein; POL, postocellar line; R1–3, ramus 1–3 of male flagellum; stv, stigmal vein; T1, first gastral tergite.

TAXONOMIC TREATMENTS

Type material of all species described in *Eulophus* Geoffroy by Walker (1839, 1846b, 1848) that are now classified

in *Necremnus* was examined except for *Eulophus diyllus* Walker, 1839, and *Eulophus zeugma* Walker, 1839, which were not located and are presumed lost. Remaining type material was borrowed from the BMNH and Oxford University Museum of Natural History (Hope Entomological Collections), Oxford, UK (OUMNH). Most of Walker's type material bear M. W. R. de V. Graham lectotype or paralectotype labels, but we do not consider any as valid designations except for that of *Eulophus metanira* Walker 1839 by Graham (1991). In what is essentially a revision of European *Necremnus* and other eulophid genera, Graham (1959: 170) stated in the introduction that 'Where Walker had a mixed series under one name, I have labelled as type that specimen which appears best to fit the description'. However, this is not a valid lectotype designation based on International Code of Zoological Nomenclature Article 74.3, which states that 'lectotypes must not be designated collectively by a general statement; each designation must be made specifically for one nominal taxon and must have as its object the definition of that taxon' (ICZN, 2012). We therefore formally designated lectotypes for each name as necessary in order to stabilize nomenclature within *Necremnus*. To avoid additional labels we did not add our own lectotype and paralectotype labels to type material unless the individuals that we designated differ from those labelled by Graham. In order to assist future revisions and identification of *Necremnus* we provide images of the primary type material of most of the names. For the same reason, we treated each of Walker's valid species regardless of whether they are associated with the two pest species and, for ease of discussion, have treated them in three informal species groups, the *N. artynes*, *N. cosconius*, and *N. tidius* groups. The validity and membership of species groups within *Necremnus* require a formal revision of world species and we have not formally treated species of the *N. artynes* and *N. tidius* groups other than those indicated through molecular evidence, i.e. *N. artynes*, *Necremnus cosmopterix*, *Necremnus navonei*, *Necremnus metalarius*, and *Necremnus tutae* (*N. artynes* group) and *Necremnus duplicatus*, *Necremnus leucarthros*, *Necremnus aenigmaticus*, *Necremnus hippia*, and *N. tidius* (*N. tidius* group).

RESULTS

INITIAL MORPHOLOGICAL IDENTIFICATION

Using the available dichotomous keys, H_0 specimens associated with the two pest species were identified as *N. tidius*, parasitizing various weevil hosts, and *N. artynes* or *N. near artynes*, parasitizing lepidopterous hosts. However, molecular analyses did not support H_0 concepts and indicated that several cryptic species were confused under the morphospecies *N. tidius* and *N. artynes*.

Trimmed *COI* sequences resulted in 744-bp fragments. Alignment was straightforward with no frame shifts, nonsense codons, insertions, or deletions identified in any sequence. Trimmed *28S-D2* sequences ranged from 421 to 428 nucleotides, and the final alignment consisted of 429 bp. No intraspecific variation was detected in any species. Trimmed *ITS2* sequences were 402–489 bp, producing an alignment of 652 bp. No evidence of intraindividual variation (double peaks in the chromatograms) was recorded. In both ML and BI phylogenetic analyses, all gene trees recorded an unexpected genetic diversity within the H_1 concepts of *N. tidius* and *N. artynes*.

In the Bayesian *COI* tree (Fig. S1) specimens initially identified as *N. tidius* formed a monophyletic, yet unsupported, complex that included four highly supported clades. Clade E included specimens collected both in Europe (on weevils attacking *Car. draba*) and Canada (from weevils attacking *Cap. bursa-pastoris*). Clade F included individuals reared mostly from the same host-plant systems as Clade E but only in Europe, with some individuals from the two clades collected in syntopy. Clade G contained specimens reared from Germany and France on *Cap. bursa-pastoris*, whereas Clade H comprised only North American specimens, mostly from *Ce. obstrictus* and from two native Nearctic species, *Ceutorhynchus neglectus* Blatchley and *Ceutorhynchus omissus* Fall, but also from *Ceutorhynchus cardariae* Korotyaev, an introduced biocontrol agent of hoary cress. Similarly, specimens identified as *N. artynes* or as *N. near artynes* revealed four clades. Clade C and Clade D were sister species, the former including parasitoids of *T. absoluta* and *Aproaerema anthyllidella* Hübner (Gelechiidae), and Clade D reared exclusively from *T. absoluta*. Clade A included individuals reared from *T. absoluta*, *Cosmopterix pulchrimella* Chambers (Cosmopterigidae), and *Cydia capparidana* (Zeller) (Tortricidae), whereas clade B included specimens reared from *Dialectica scalariella* (Zeller) (Gracillariidae) and an unidentified host (collected by sweeping). The ML *COI* tree (Fig. S2) slightly differed from the BI tree both in topology and statistical support, with the basal split between the *N. artynes* and *N. tidius* groups unsupported, and different sister relationships within the *N. artynes* group.

The BI and ML ribosomal gene trees (Fig. S3) were nearly identical, and confirmed the existence of the eight clades described above, although with different sister relationships. The main difference from the *COI* trees was in the placement of *N. leucarthros*, which was placed within the *N. tidius* group. The supermatrix concatenated BI and ML trees were fully resolved and with similar topologies, which largely resembled the ribosomal tree (Fig. 1). Uncorrected *COI* *p*-distances showed

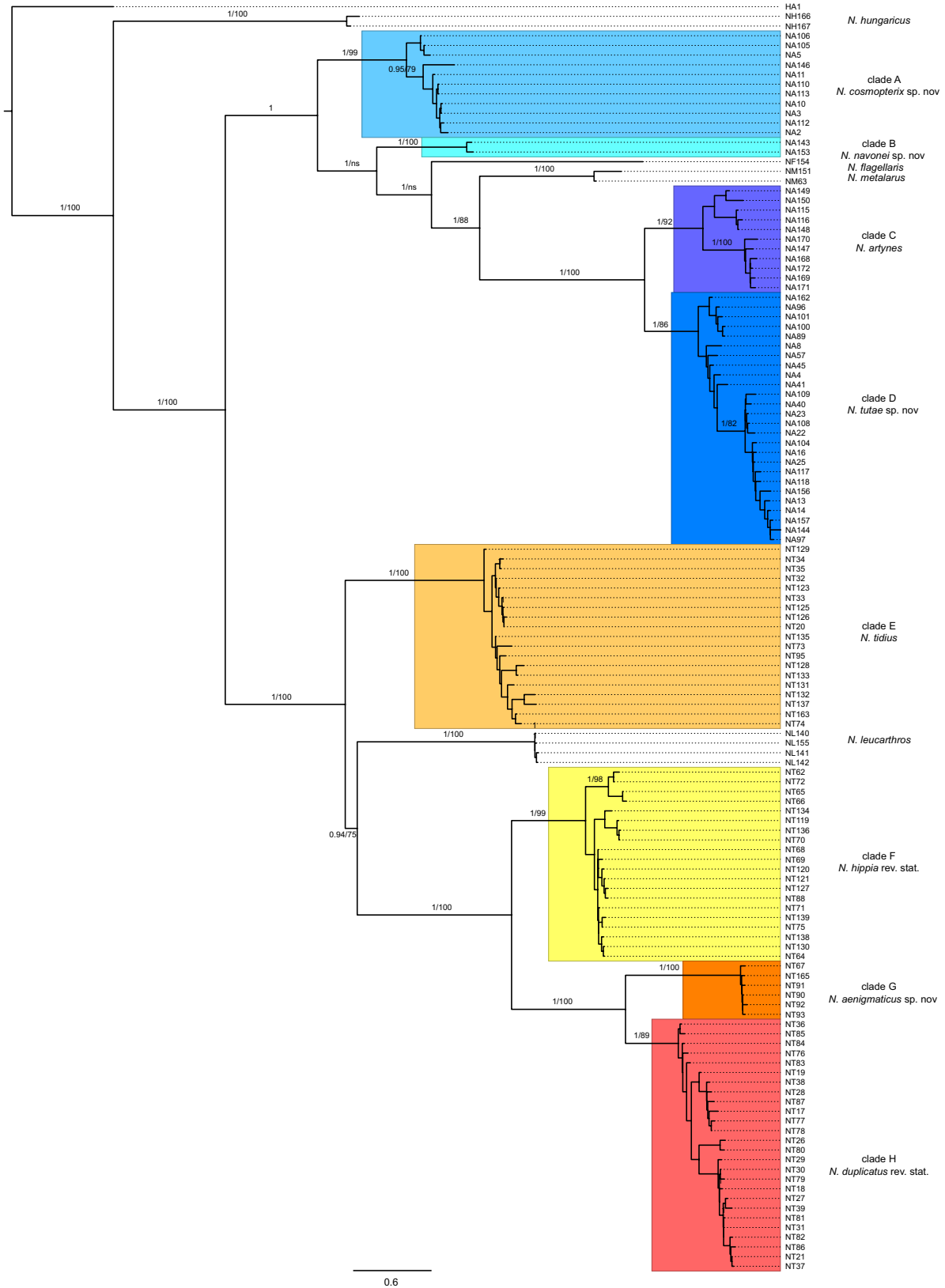


Figure 1. Bayesian majority rule consensus tree based on the concatenated data set. Posterior probabilities > 0.95 above branches.

high intraspecific variation for Clade F, Clade H, Clade A, and Clade D (Table S1).

MORPHOLOGICAL RE-EXAMINATION

Following restudy of H₀ individuals based on H₁ results, several features that initially seemed quite variable in the *N. tidius* complex were found to differ in different combinations consistently amongst the clades. These included colour pattern of the tegulae and position of the propodeal spiracles relative to the posterior margin of the metanotum in both sexes, and the number and arrangement of mps on the three rami of the male antenna. Differences in various flagellar and metasomal ratios and setal patterns of the fore wings, particularly for females, also appeared to be useful for differentiating individuals of each clade. Similarly, fore wing colour pattern and different shapes (length/width) of the gaster of females and leg colour pattern of both sexes were found to support the differentiation of four species in what had previously been

considered as or near *N. artynes*. Individuals that subsequently were sorted based on these features (H₂) and newly sequenced resulted in exactly the same clades as from the H₁ sequences. Therefore, H₁ (molecular) and subsequently H₂ (revised morphology) mutually supported a four-species concept within both of what had previously been considered as single species. By comparing sequenced specimens with relevant type material, and after selection of lectotypes to establish valid names, we assigned specimens belonging to Clade C to *N. artynes* and those of Clade E to *N. tidius*, whereas specimens of Clades F and H were determined to be *N. hippia* and *N. duplicatus*, respectively. Furthermore, Clades A, B, D, and G were indicated as undescribed species and we therefore formally describe them as *N. cosmopterix*, *N. navonei*, *N. tutae*, and *N. aenigmaticus*, respectively. The unique combinations of differential features discovered for each clade are included in the key below and detailed in the respective species descriptions.

TAXONOMY

KEY TO EUROPEAN SPECIES OF *NECREMNUS* THOMSON

- | | | |
|------|--|---------------------------------------|
| 1 | Female..... | 2 |
| • | Male..... | 25 |
| 2(1) | Fore wings reduced, extending only to apex of propodeum; pronotum yellow anteriorly; legs yellow; scape yellow..... | <i>Necremnus norvegicus</i> Hedqvist |
| • | Fore wings well developed, extending over gaster; pronotum dark; legs and scape variable..... | 3 |
| 3(2) | Propodeum very coarsely punctate, as strongly as on scutellum, and with step-like elevated plicae and complete median carina; pronotum comparatively elongate, almost as long as mesoscutum and with subparallel sides posteriorly (Bouček, 1959, fig. 18); legs pale yellow beyond coxae; fore wing hyaline..... | <i>Necremnus propodealis</i> Bouček |
| • | Propodeum usually coriaceous (e.g. Figs 13, 53) to reticulate-imbricate (e.g. Figs 45, 110, 147), but if coarsely reticulate then without plicae (e.g. Figs 23, 31, 75), and usually less strongly reticulate than scutellum; pronotum strongly transverse, much shorter than mesoscutum (e.g. Figs 11, 61, 107); legs usually with at least femora infuscate; fore wing sometimes partly infuscate or bimaculate (Figs 12, 29, 43, 52, 59)..... | 4 |
| 4(3) | Gaster short-ovate, at most 1.5 × as long as wide, usually shorter than mesosoma; tibiae usually yellow, femora dark or yellow..... | 5 |
| • | Gaster long-ovate or lanceolate, more than 1.5 × as long as wide; tibiae variable in colour, but dark when gaster relatively short, and femora dark..... | 8 |
| 5(4) | Flagellum filiform, F3 not or barely wider than F1; legs with coxae and femora dark, tibiae usually yellow; postmarginal vein at most 1.4 × length of stigmal vein..... | 6 |
| • | Flagellum fusiform, F3 at least 1.4 × wider than F1; legs with coxae partly yellow, femora dark or yellow, and tibiae yellow; postmarginal vein at least 1.5 × length of stigmal vein..... | 7 |
| 6(5) | Antenna with funicular segments elongate, F1 3 × as long as broad and F3 2 × as long as broad (Bouček, 1959: fig. 19); postmarginal vein very short, 1.15 × as long as stigmal vein; tibiae sometimes dark apically; fore wing hyaline..... | <i>Necremnus capitatus</i> Bouček |
| • | Antenna with funicular segments less elongate, F1 2 × as long as broad and F3 only as long as broad (Bouček, 1974: fig. 4); postmarginal vein 1.2–1.4 × as long as stigmal vein; tibiae yellow; fore wing with very slightly infuscate areas (Bouček, 1974: fig. 3)..... | <i>Necremnus plumiferae</i> Bouček |
| 7(5) | Legs with femora and meso- and metacoxae yellow and procoxa darkened; fore wing with a wide dark area medially (Yefremova, 2007: fig. 2); propodeum with plicae present posteriorly (Yefremova, 2007: fig. 4); antenna with flagellum scarcely compressed (Yefremova, 2007: fig. 1)..... | <i>Necremnus fumipennis</i> Yefremova |

- Legs with femora partly dark and all coxae yellow or sometimes darkened basally; fore wing hyaline; propodeum with plicae absent (Askew, 1992: fig. 1); antenna with flagellum laterally compressed (Askew, 1992: fig. 2)...
.....*Necremnus flagellaris* Askew
- 8(4) Postmarginal vein usually 1.1–1.3 ×, although rarely up to 1.5 × as long as stigmal vein (Figs 63, 70, 76, 81); flagellum with combined length of F1 + anelli at most 1.7 × as long as pedicel (Figs 58, 73); fore wing usually hyaline; frons with distinct piliferous punctures.....9 (*Necremnus cosconius* species group)
- Postmarginal vein usually at least 1.5 × as long as stigmal vein (e.g. Figs 20, 36, 97, 115), but if shorter than frons without piliferous punctures, fore wings bimaculate and flagellum with combined length of F1 + anelli at least 1.8 × as long as pedicel.....12
- 9(8) Mesosoma with scutellum, dorsellum, and propodeum entirely reticulate, the mesh-like sculpture defined by raised ridges, even mesally on propodeum (Figs 74, 75); fore wing hyaline (Fig. 76) and propodeal spiracle separated from metanotum (Fig. 75).....*Necremnus croton* (Walker)
- Mesosoma with at least one or both of dorsellum and propodeum coriaceous to alutaceous-imbricate, the sculpture defined mostly by fine lines (Figs 61, 84, 87); fore wing often variably infusate (Fig. 59) or propodeal spiracle slightly overlapped by metanotum (Figs 90, 91).....10
- 10(9) Anterior margin of propodeal spiracle slightly overlapped by metanotum (Figs 90, 91); scutellum broadly mesh-like coriaceous at least mesally, the sculpture delineated by impressed lines and surfaces flat to slightly convex (Figs 87, 90, 91); fore wing hyaline.....*Necremnus rhaecus* (Walker)
- Anterior margin of propodeal spiracle slightly separated from metanotum (Figs 61, 62, 84); scutellum reticulate-imbricate with at least mesal margins of sculpture delineated by distinct ridges but lateral or basal margins overlapped by raised margins of adjacent sculpture (Figs 60–62, 84); fore wing often with variably distinct infusate regions behind stigmal vein and marginal vein basally (Fig. 59).....11
- 11(10) Fore wing sometimes hyaline but usually either with separate infusate regions behind stigmal vein and base of marginal vein (Fig. 59) or at least quite strongly infusate if extensively infusate behind marginal vein; scutellum mesh-like reticulate-imbricate, the sculpture often appearing somewhat ‘scalloped’ (Fig. 62).....
.....*Necremnus cosconius* (Walker)
- Fore wing hyaline or at most very faintly, uniformly infusate (Fig. 81); scutellum usually with more elongate-narrow, reticulate-imbricate sculpture (Fig. 84).....*Necremnus folia* (Walker)
- 12(8) Meso- and metatibiae at least broadly pale apically and at most narrowly dark basally; flagellum with clava whitish apically (Erdős, 1951: fig. 8c); fore wing with two strongly infusate areas, joined medially (Erdős, 1951: fig. 8d).....*Necremnus hungaricus* (Erdős)
- Meso- and metatibiae almost wholly infusate to almost wholly pale, but if bicoloured then dark apically and pale basally; flagellum uniformly dark or clava only slightly and progressively paler apically; fore wing variable.....13
- 13(12) Antenna with scape reaching beyond level of vertex; flagellum brownish-testaceous; funicular segments narrow, not wider than pedicel, with F1 only slightly longer than pedicel (Graham, 1986: fig. 3); propodeum with spiracles short-oval and separated from posterior margin of metanotum; fore wing with a slight infumation over middle third; gaster 2 × as long as broad; tibiae testaceous (Madeira Island).....*Necremnus alticola* Graham
- Antenna with scape shorter, reaching only level of median ocellus or below; other features variable, but not in above combination.....14
- 14(13) Flagellum short, with combined length of F1 + anelli at most 1.8 × as long as pedicel and usually less than 2.8 × as long as broad (Figs 101, 111, 135, 149, 167), and length of pedicel + flagellum at most 1.2 × as long as breadth of head; fore wing hyaline; mesosoma compact, usually 1.3–1.5 × although rarely up to 1.6 × as long as broad (Figs 92, 103, 125, 145, 165); propodeum sometimes with anterior margin of spiracle slightly overlapped by posterior margin of metanotum (Figs 96, 109, 110, 121, 129–132); meso- and metatibiae with only extreme base (knees) abruptly pale (e.g. Figs 93, 104); hosts usually Coleoptera.....
.....15 (*Necremnus tidius* species group)
- Flagellum usually longer, with combined length of F1 + anelli at least 1.9 × as long as pedicel and usually more than 2.8 × as long as broad (Figs 14, 22, 38, 46, 54), and length of pedicel + flagellum usually more than 1.2 × as long as breadth of head (small specimens rarely with F1 + anelli only 1.6–1.8 × as long as pedicel and 2.4–2.6 × as long as broad, but then fore wing partly infusate or mesosoma elongate); fore wing sometimes variably distinctly infusate behind marginal vein basally and/or behind stigmal vein (Figs 12, 29, 43, 52); mesosoma elongate, 1.5–1.8 × as long as broad (Figs 10, 19, 34, 42, 48); propodeum with spiracle slightly but distinctly separated from posterior margin of metanotum (e.g. Figs 7, 13, 23, 45); meso- and metatibiae sometimes with basal half or more pale (Figs 8, 17, 40, 49); hosts usually Lepidoptera.....
.....18 (*Necremnus artynes* species group)

- 15(14) Propodeum with spiracles slightly separated from posterior margin of metanotum (Figs 147, 172, 174, 175) or if touching (Figs 143, 173) then rim of spiracle uniformly developed; fore wing sometimes with comparatively narrow speculum (Fig. 168).....16
- Propodeum with spiracles slightly overlapped by the metanotum (Figs 96, 109, 110, 129–132) or if only touching metanotum then anterior rim of the spiracle somewhat depressed or sinuate; fore wing always with comparatively broad speculum (Figs 116, 134).....17
- 16(15) Fore wing with speculum comparatively narrow, the dorsal setae extending close to basal fold and subcubital setal line usually composed of two or more rows of setae along most of its length (Fig. 168); tegula sometimes yellowish along inner margin adjacent to mesoscutum; body usually comparatively dark green to blue (Figs 165, 166) or with coppery lustre at least on scutellum (Fig. 173); flagellum with apical two funiculars often quite distinctly oblong, but F3 at least 1.6 × as long as broad (Fig. 167).....*Necremnus tidius* (Walker)
- Fore wing with speculum comparatively broad, the dorsal setae more distant from basal fold, and subcubital setal line at least mostly composed of only one row of setae over at least its basal half (Fig. 148); tegula uniformly dark brown; body comparatively bright green to blue with at most very limited, inconspicuous coppery lustre (Figs 145, 146); flagellum with apical two funiculars less elongate, with F3 at most 1.5 × as long as broad (Fig. 149).....*Necremnus leucarthros* (Nees)
- 17(15) Tegula sometimes entirely yellow (Fig. 95), but most commonly yellow basally and along inner margin and variably extensively darker brown apicolaterally (Fig. 94).....*Necremnus aenigmaticus* sp. nov.
- Tegula uniformly brown (Fig. 120).....*Necremnus hippia* (Walker). [*Necremnus duplicatus* from North America would key here, see discussion under respective species.]
- 18(14) Propodeum uniformly although not strongly reticulate (Fig. 23); tegula uniformly dark (Fig. 21); fore wing hyaline (Fig. 20); postmarginal vein almost always at least 1.8 × as long as stigmal vein (Fig. 20), although very rarely only about 1.7 ×; meso- and metatibiae usually entirely dark, although rarely pale.....*Necremnus cosmopterix* sp. nov.
- Propodeum comparatively smooth and shiny, coriaceous to alutaceous except possibly mesally (Figs 45, 53) or if distinctly reticulate (Figs 31, 35, 37) then tegula bicoloured, yellow, or ochraceous basally and dark apically and fore wing usually with variably distinct infuscate areas behind stigmal vein and/or base of marginal vein (Figs 12, 29, 43, 52); postmarginal vein at most 1.7 × as long as stigmal vein; meso- and metatibiae often widely pale, at least basally.....19
- 19(18) Propodeum uniformly strongly reticulate (Figs 31, 35, 37); tegula testaceous or ochraceous basally, dark brown at apex; tibiae often dark, rarely narrowly pale basally (Figs 27, 32); tarsi with at most basal tarsomeres pale; scape dark; gaster at most 2.3 × as long as broad and hardly longer than head plus mesosoma (Figs 32, 34).....20
- Propodeum usually comparatively smooth and shiny, coriaceous to alutaceous, at most reticulate mesally behind about width of dorsellum (Figs 45, 53); tegula uniformly dark; tibiae usually dark only within apical half or less (Figs 40, 49), although rarely more extensively in small specimens; tarsi at least with basal tarsomeres and often basal two or three tarsomeres pale; scape usually pale (Fig. 14); gaster sometimes longer.....21
- 20(19) Propodeum as strongly reticulate as scutellum, with spiracles round and distant from hind margin of metanotum (Delucchi, 1962: fig. 5); fore wing strongly bimaculate or sometimes with infuscate areas joined; marginal vein 2.7 × as long as stigmal vein; tibiae wholly fuscous; tegula ochraceous basally (Morocco).....*Necremnus rugulosus* Delucchi
- Propodeum less strongly reticulate than scutellum, with spiracles oval and close to hind margin of metanotum (Figs 31, 35, 37); fore wing often with one fuscous blotch at stigma (Fig. 29), although sometimes bimaculate or rarely subhyaline or hyaline (Fig. 36); marginal vein at least 2.8 × as long as stigmal vein (Fig. 36); tibiae usually wholly metallic or fuscous (Fig. 32) except some South European specimens with knees and basal third of metatibia pale; tegula testaceous basally.....*Necremnus metalarus* (Walker)
- 21(19) Propodeum with spiracles small, round, and distant from posterior margin of metanotum by at least half their diameter; gaster usually very long, 3.0–3.6 × as long as broad, and if relatively short then antenna with pedicel + flagellum at most 1.3 × as long as breadth of mesoscutum and F3 at most 1.5 × as long as broad; fore wing sometimes with basal vein bare, speculum open behind, and postmarginal vein only 1.3 × as long as stigmal vein.....22
- Propodeum with spiracles larger, oval, and often very close to posterior margin of metanotum (Figs 7, 13, 45, 53); female gaster usually less elongate, 2.0–3.2 × as long as broad (Figs 10, 42, 48); antenna with pedicel + flagellum at least and usually more than 1.3 × breadth of mesoscutum, and F3 at least and usually more than 1.5 × as long as broad (Figs 14, 46, 54); fore wing with basal vein usually pilose, speculum usually closed behind, and postmarginal vein at least 1.4 × as long as stigmal vein (Figs 12, 43, 52).....23

- 22(21) Gaster very long, $3.6 \times$ as long as broad and $1.6 \times$ as long as head plus mesosoma; syntergum sublinear, $2.7 \times$ as long as broad (Askew *et al.*, 2001: fig. 19); fore wing faintly bimaculate with basal vein bare and speculum open behind; postmarginal vein very short, $1.3 \times$ as long as stigmal vein; meso- and metatibiae yellow, with dark apex.....*Necremnus stylatus* Askew
- Gaster shorter, at most $3.4 \times$ as long as broad and $1.45 \times$ as long as head plus mesosoma; syntergum triangular, as long as broad; fore wing strongly bimaculate with basal vein pilose and speculum closed behind; postmarginal vein at least $1.5 \times$ as long as stigmal vein; tibiae reddish or partly to mainly fuscous (Madeira Island).....*Necremnus fumatus* Graham
- 23(21) Gaster lanceolate, $2.6\text{--}3.2 \times$ as long as broad, $1.5\text{--}1.9 \times$ as long as mesosoma, and $1.2\text{--}1.4 \times$ as long as head plus mesosoma (Figs 8, 10); syntergum elongate or barely transverse, $0.9\text{--}1.3 \times$ as long as broad.....*Necremnus artynes* (Walker)
- Gaster ovate, $1.9\text{--}2.6 \times$ (rarely up to $2.8 \times$) as long as broad, $1.2\text{--}1.6 \times$ as long as mesosoma, and $0.9\text{--}1.3 \times$ as long as head plus mesosoma (Figs 40, 42, 48, 49); syntergum transverse, $0.6\text{--}0.9 \times$ as long as broad.....24
- 24(23) Gaster shorter, $1.9\text{--}2.4 \times$ as long as broad, $1.2\text{--}1.5 \times$ as long as mesosoma and $0.9\text{--}1.2 \times$ as long as head plus mesosoma (Figs 48, 49); antenna with clava at most $3.5 \times$ as long as broad (Fig. 54); meso- and metatibiae variable, but often only slightly darkened apically or almost entirely pale (Figs 48, 49); fore wing coloration variable, but sometimes with strongly infuscate areas (Fig. 52).....*Necremnus tutae* sp. nov.
- Gaster somewhat elongate, $2.4\text{--}2.8 \times$ as long as broad, $1.4\text{--}1.5 \times$ as long as mesosoma and $1.1\text{--}1.3 \times$ as long as head plus mesosoma (Figs 40, 42); antenna with clava usually longer than $3.5 \times$ as long as broad (Fig. 46); meso- and metatibiae often strongly darkened within apical half, the colours sharply contrasted (Figs 40, 42); fore wing with very lightly infuscate areas (Fig. 43).....*Necremnus navonei* sp. nov.
- 25(1) Postmarginal vein usually less than $1.3 \times$, although rarely up to $1.5 \times$ as long as stigmal vein.....26 (*Necremnus cosconius* species group)
- Postmarginal vein usually at least $1.5 \times$, although rarely only about $1.3 \times$ as long as stigmal vein.....27
- 26(25) Antenna without mps on second and third rami, and F4 and clava only about $2.5 \times$ times as long as broad (Fig. 79); body mainly violet- or bronzy-black (Figs 79, 80); scutellum primarily longitudinally reticulate-imbricate to strigose-imbricate (Fig. 80).....*Necremnus folia* (Walker)
- Antenna with mps within basal half of second and third rami (Figs 67, 68), and F4 and clava at least $3 \times$ as long as broad (Fig. 68); body greenish (Figs 65, 66); scutellum more mesh-like reticulate-imbricate or with slightly scalloped sculpture (Fig. 66).....*Necremnus cosconius* (Walker)
- 27(25) Metatibia infuscate within basal quarter and broadly pale apically; gaster with a sub-basal pale fascia; flagellum with rather stiff, bristle-like setae.....*Necremnus hungaricus* (Erdős)
- Metatibia almost wholly infuscate to almost wholly pale, but when bicoloured pale basally and dark apically; gaster without sub-basal pale fascia; flagellum usually with very long, hair-like setae (e.g. Figs 16, 25, 99, 169) although sometimes setae similarly short as dense mps (Fig. 150).....28
- 28(27) Flagellum either with very short setae and dense mps (Fig. 150) or if with conspicuously long setae then at least basal ramus lacking mps (e.g. Figs 136, 137); propodeum sometimes with anterior margin of spiracle slightly overlapped by posterior margin of metanotum (cf. Figs 96, 109, 110); meso- and metatibia with only extreme base (knees) abruptly pale (Figs 98, 106, 151).....29 (*Necremnus tidius* species group)
- Flagellum always with conspicuously long, hair-like setae and all three rami having mps, even though less numerous on basal ramus; propodeum with spiracle slightly but distinctly separated from posterior margin of metanotum (cf. Figs 13, 23, 45, 53); meso- and metatibiae sometimes with basal half or more pale (Figs 9, 41, 50).....32 (*Necremnus artynes* species group)
- 29(28) Flagellum with all rami having numerous mps interspersed with short setae only about as long as mps and width of ramus (Fig. 150).....*Necremnus leucarthros* (Nees)
- Flagellum with at least basal ramus lacking mps and all rami with much longer and more conspicuous hair-like setae (Figs 99, 113, 137, 155).....30
- 30(29) Flagellum with all rami lacking mps (Fig. 99); propodeum with anterior margin of spiracle contiguous with or slightly overlapped by metanotum (cf. Fig. 96); tegula entirely (cf. Fig. 95) to partly yellow, most commonly yellow basally and along inner margin and variably extensively darker brown apicolaterally (cf. Fig. 94).....*Necremnus aenigmaticus* sp. nov. [*Necremnus duplicatus* from North America would key here except tegula entirely brown (cf. Fig. 108).]
- Flagellum with at least one mps on R3 (Figs 113, 155) and often one or more mps on R2 (Figs 136, 170) or if mps absent from all rami then propodeal spiracle with anterior margin quite obviously separated from posterior margin of metanotum (Figs 131, 132) (anterior margin of spiracle more commonly only slightly separated from or contiguous with posterior margin of metanotum); tegula sometimes entirely brown.....31

- 31(30) Propodeum with anterior margin of spiracle at least touching and usually slightly overlapped by metanotum (Figs 131, 132); tegula entirely brown; scape with line of sensory pores along ventral margin obviously more within apical half, the distance between basal-most pore and basal margin much greater than between apical-most pore and apical margin (Fig. 138).....*Necremnus hippia* (Walker)
- Propodeum with anterior margin of spiracle often slightly separated from, but at most touching, posterior margin of metanotum (Figs 174, 175); tegula sometimes partly yellow; scape with line of sensory pores along ventral margin positioned more mesally, the distance between basal-most pore and basal margin similar to or only slightly greater than distance between apical-most pore and apical margin (Fig. 171).....*Necremnus tidius* (Walker)
- 32(28) Tegula bicoloured, yellowish basally and brown apically.....*Necremnus metalarus* (Walker)
- Tegula uniformly dark.....33
- 33(32) Postmarginal vein at least 1.9 × as long as stigmal vein; marginal vein 3.3–4.0 × as long as stigmal vein; costal cell dorsally with a marginal row of 11 or 12 setae apically; propodeum uniformly reticulate, although not strongly so (cf. Fig. 23); antenna with pedicel + flagellum at least 1.9 × as long as breadth of mesoscutum; legs with meso- and metatibiae usually darkened within apical 0.6–0.9, although sometimes paler (Fig. 18).....***Necremnus cosmopterix* sp. nov.**
- Postmarginal vein at most 1.8 × as long as stigmal vein; marginal vein 2.4–3.3 × as long as stigmal vein; costal cell dorsally with a marginal row of three to six setae apically; propodeum coriaceous to only shallowly, superficially reticulate (Figs 13, 45, 53); antenna with pedicel + flagellum usually less than 1.9 × as long as breadth of mesoscutum; legs colour variable.....34
- 34(33) Antenna with clava at most 3.4 × as long as broad and scape 4.2–4.7 × as long as broad (Fig. 47); legs with meso- and metatibiae dark brown over at least about apical half and sharply contrasted with basal pale part (Fig. 41).....***Necremnus navonei* sp. nov.**
- Antenna with clava at least 3.7 × as long as broad (Figs 16, 56) and scape usually broader, 3.5–4.2 × as long as broad (Figs 15, 55); legs sometimes with similar colour pattern as above, but meso- and metatibiae usually more extensively pale or with the dark portion diffuse pale brown (Figs 9, 50).....35
- 35(34) Marginal vein at least 2.8 × as long as stigmal vein; antennal scape with sensorial area wide and paler, reaching 0.4 × width of scape, with sensorial pores larger and densely placed in one irregular row or with some pores arranged in a second irregular row, but with interspaces smaller than pore size (Fig. 55).....***Necremnus tutae* sp. nov.**
- Marginal vein at most 2.7 × as long as stigmal vein; antennal scape with sensorial area narrow and darker, along anterior margin of scape, with sensorial pores smaller, arranged in single row, and with interspaces greater than pore size (Fig. 15).....*Necremnus artynes* (Walker)

NECREMNUS ARTYNES SPECIES GROUP

Diagnosis

Female: fore wing with postmarginal vein usually 1.4–1.8 × (1.25–2.1 ×) length of postmarginal vein; disc usually bimaculate or at least obscurely infuscate behind base of marginal vein and/or behind stigmal vein (Figs 12, 43, 52) (except *N. cosmopterix*, Fig. 20); antenna with flagellum elongate, length of F1 + anelli (1.6)1.9–2.4 × length of pedicel and 2.8–3.8 × as long as broad (Figs 14, 22, 46, 54). Mesosoma elongate, 1.5–1.9 × as long as broad (Figs 11, 21, 44, 51). *Male*: antennal rami with mps and with elongate, hair-like setae (Figs 16, 25, 47, 56). Hosts include Lepidoptera.

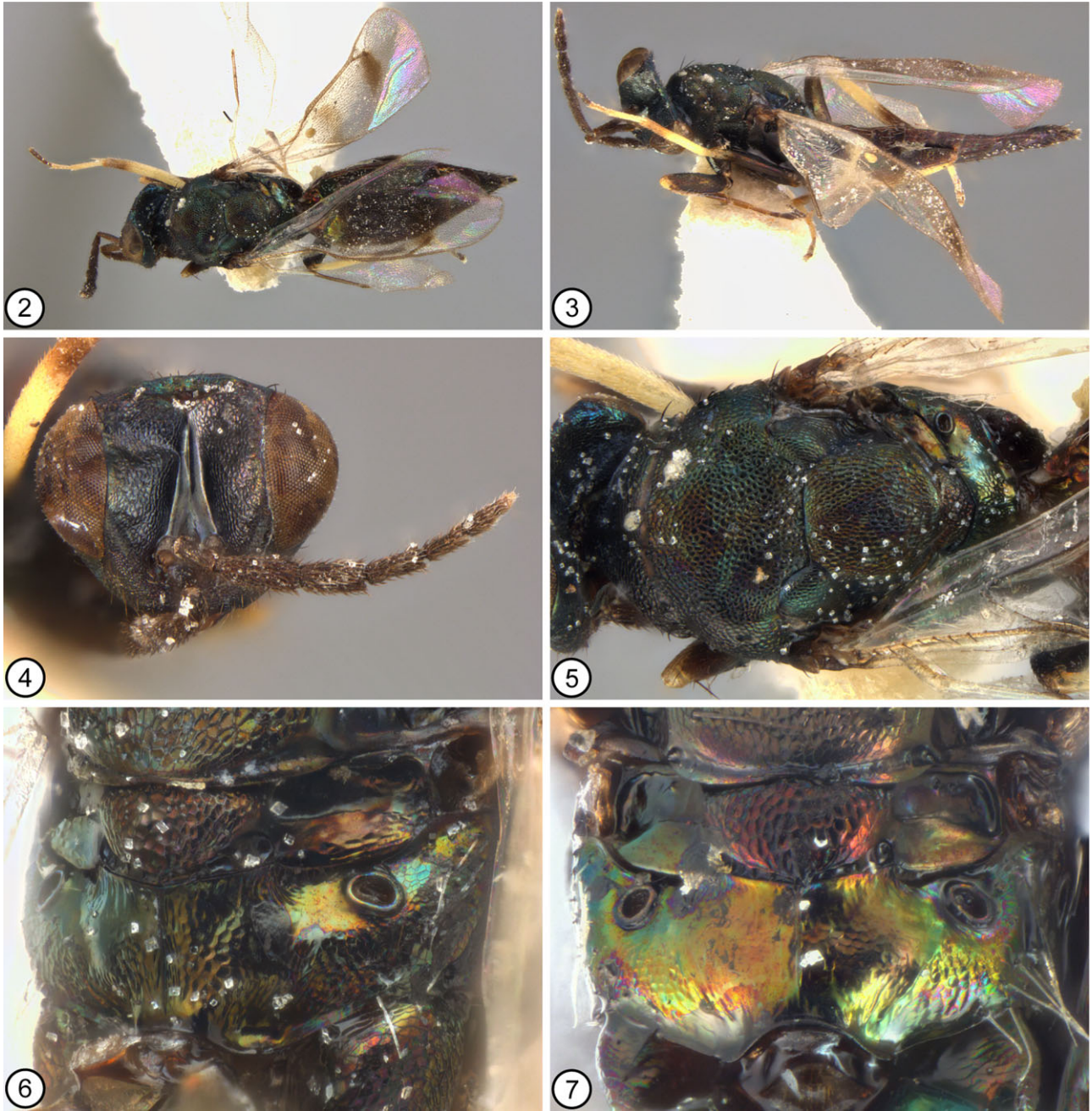
NECREMNUS ARTYNES (WALKER) (FIGS 2–16)

Eulophus Artynes Walker, 1839: 163–164. ♀ lectotype (BMNH, here designated).

Eulophus subcontiguus Thomson, 1878: 231–232. ♀ lectotype (LUZN) designated by Bouček (1959: 150). Synonymy under *N. artynes* by Bouček (1959: 150).

Type material

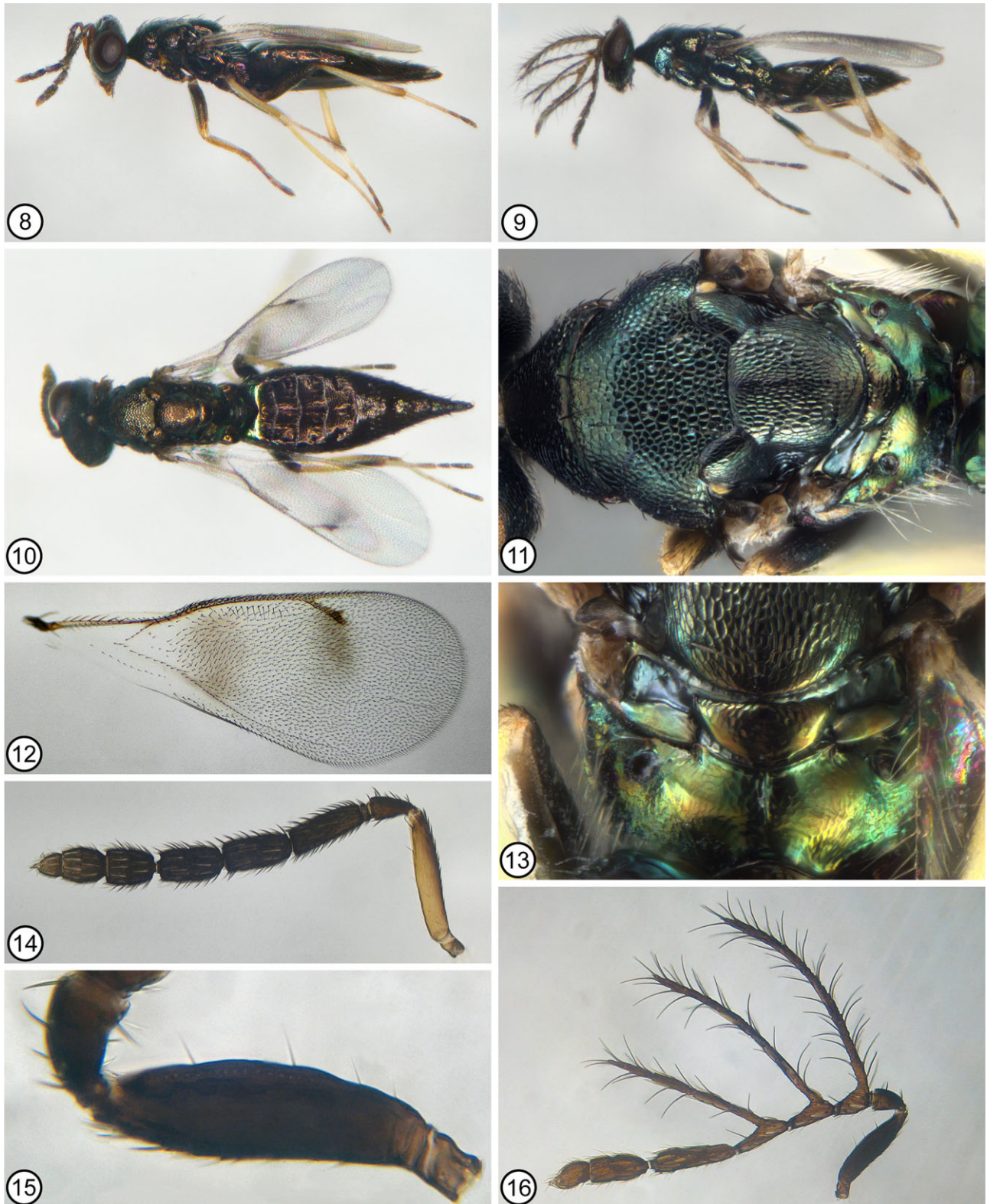
Walker (1839) described *Eulophus artynes* based on at least five females, the description including also four varieties, from material collected on the Isle of Wight, Devon, Cornwall, and Holywood, near Belfast, Northern Ireland. Bouček (1959) stated that he saw one female syntype deposited in Berlin, whereas the BMNH has four females indicated to form part of the type series. One point-mounted female has the following six labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular, handwritten label with what appears to be 'v. 1 [?] w.'; (3) a rectangular label with '*Eulophus Artynes* Walker' handwritten on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse' printed on the other side; (4) a rectangular, handwritten label with '*E. artynes* W. Lectotype M. de V. G.'; (5) a rectangular label with '*Eulophus Artynes* Walker LECTOTYPE: ♀ M. de V. Graham det. 1958' partly printed and handwritten; and (6) a square label with 'B.M. TYPE HYM. 5.2502'. This female lacks antennae except for the scape of the right antenna, the tarsi of both hind legs and the right middle leg,



Figures 2–7. *Necremnus artynes*. 2–6, lectotype ♀: 2, dorsal habitus; 3, lateral habitus; 4, head and antenna; 5, dorsal mesosoma; 6, metanotum and propodeum. 7, paralectotype ♀: metanotum and propodeum.

the tibia and tarsus of the left middle leg, and all wings except for most of the left fore wing. The other three females have circular, blue-bordered labels with 'PARALECTOTYPE' as well as the double-sided label. One of these is card-mounted and also has a rectangular, handwritten label with 'Artynes' and a printed label with 'Walker coll. 1904–120'. It lacks its head, some leg parts, and the gaster, although the right antenna and part of the left antenna are glued

to the card. The other two are point-mounted. One has a circular label with '38/7.12/64' on three separate lines and a small rectangular label with 'Britain' handwritten; it lacks its head and antennae. The third female labelled as paralectotype lacks labels other than the 'PARALECTOTYPE' and the double-sided label, although it has a rectangular card pinned below the specimen to help protect it. It is the only entire specimen.



Figures 8–16. *Necremnus artynes*. 8–10, habitus: 8, ♀ lateral; 9, ♂ lateral; 10, ♀ dorsal. 11, ♀ dorsal mesosoma (2012-5). 12, ♀ fore wing. 13, ♀ metanotum and propodeum (2012-5). 14, ♀ antenna. 15, ♂ pedicel and scape. 16, ♂ antenna.

The initial description for *E. artynes* states that the apices of the mesotibiae are reddish-yellow (fulvae) and those of the metatibiae are dark (fusci), whereas variety β was described as having the mesotibia dark basally and apically, variety γ as having the mesotibia dark apically and the metatibiae black (nigrae) apically, and variety δ as having the mesotibiae black apically. Leg colour was not described for variety ϵ , which was simply described as having the first antennal article (scape) reddish-yellow, dark above. The mesotibiae of the female labelled 'Britain' are entirely yellow, whereas the metatibiae are essentially entirely yellow, with only the extreme apices being very slightly darker reddish-brown and thus might be variety ϵ . None of the other three specimens has the mesotibia dark both basally and apically and thus none fits the description of variety β . The other three females have both the meso- and metatibiae quite obviously infusate apically, although the mesotibia is lighter and somewhat less extensively brownish apically than is the metatibia, the apical darker region of the metatibia encompassing 0.4 of its length. Consequently, the difference between the original description of the legs of *E. artynes* and those of varieties γ and δ is mostly an appreciation of whether apically the mesotibia is reddish-yellow, dark, or black, which may have altered over time in one or more specimens because of fading. Females comprising the type series do differ noticeably in propodeal sculpture. The female that Graham labelled as lectotype has the propodeum quite shiny with subeffaced, mesh-like sculpture anteriorly and posteromesally, and more distinctly although shallowly reticulate between about the level of the spiracle and propodeal foramen posteriorly (Fig. 7). The female labelled as '*Artynes*' also has a finely sculptured propodeum. However, the entire female has the propodeum finely sculptured and shiny only anterolaterally mesal to the spiracle; otherwise it is distinctly reticulate mesally, behind about the width of the dorsellum, and posterolaterally (Figs 5, 6). The female with the 'Britain' label is the only one with distinct plical carinae extending from the propodeal foramen obliquely toward each spiracle. The region lateral to each plical carina is distinctly reticulate whereas the region mesal to the plical carinae is more finely sculptured, although partly shallowly reticulate to coriaceous-reticulate.

Graham did not validly designate a lectotype through publication under ICZN rules and the original description does not describe the propodeal sculpture. Therefore, in order to stabilize the concept of the name, we designate the only complete female (Figs 2, 3) as the lectotype of *E. artynes* (the one lacking labels except for the double-sided label and Graham's paralectotype label). We have added a rectangular, red lectotype label to this female and labelled the others with yellow paralectotype labels.

Although Bouček (1959: 150) did not explicitly state that he was designating the lectotype of *E. subcontiguus*, he stated that he examined 'the lectotype of *Eulophus subcontiguus* Thomson' and provided sufficient details on the condition of the specimen that it could be recognized, which is sufficient to validate the specimen as lectotype. Hansson (1991) subsequently published a separate lectotype designation in order to validate a lectotype designation label by M. de V. Graham on a female. That female bears a printed label 'Lund' and has the LUZN type number 1619:1. We did not examine the lectotype, but according to Bouček (1959: 150) it lacks its gaster and both antennae beyond the pedicel and 'is doubtless the same as the syntype of *E. artynes* Walk. mentioned above'.

Bouček & Askew (1968) stated that *Necremnus comptus* Gahan, 1941, described from North America (California), probably was a synonym of *N. artynes*. Unfortunately, the single type female is badly preserved with only the legs remaining. New material and molecular comparisons are needed prior to any formal synonymy.

Redescription

Female

Body length 2–3.1 mm. Head and mesosoma dark green or sometimes with bluish reflections (Figs 8, 10), mainly at sides, or with bronze reflections on propodeum (Fig. 13), and a small anterolateral part of axillae ochraceous. Antenna with scape brown to black or testaceous-brown ventrally and towards base (Fig. 14); pedicel and flagellum dark brown. Tegula black. Legs (Figs 8, 10) with coxae coloured as body; femora dark with metallic reflections, narrowly testaceous at knees; tibiae whitish-testaceous, protibia with brown stripe on inner surface, meso- and metatibiae pale testaceous and variably darkened apically, the paler forms being entirely testaceous and darker forms being blackish in apical half; protarsus brown, meso- and metatarsi sometimes with only basal tarsomeres pale, but usually basal two tarsomeres whitish-testaceous with apices brownish. Fore wing bimaculate (Figs 2, 12), usually with a brownish area behind stigmal vein reaching half width of disc and another brown stripe behind proximal end of marginal vein reaching cubital row of setae, although infusate areas sometimes reduced or almost absent with only a faint stigmal infuscation; wing venation pale brownish. Gaster dark brown with bronze reflections dorsally on basal tergite (Fig. 10).

Head in dorsal view 1.15–1.25 \times as broad as mesoscutum and 2.3–2.7 \times as broad as long; in frontal view (Fig. 4) transverse-oval, 1.3–1.4 \times wider than high; temple 0.05–0.18 \times as long as eye length. POL 1.65–2.2 \times OOL, OOL 1.9–2.8 \times OD. Eyes 1.3–1.43 \times as high as broad, separated by 1–1.2 \times their height, with very

short, sparse hairs. Gena straight to weakly convex, strongly converging, malar space $0.4\text{--}0.48 \times$ height of eye, malar sulcus present. Mouth opening $1.2\text{--}1.6 \times$ as broad as malar space. Frons flattened on sides, weakly reticulate, with very short hairs, without piliferous punctures. Scrobes depressed, with a median longitudinal carina within scrobal depression. Vertex with short, black setae, occiput densely pilose.

Antennae (Fig. 14) inserted with ventral margins of toruli at level of ventral margins of eyes (Fig. 4). Scape $5\text{--}6.5 \times$ as long as broad, $0.83\text{--}0.9 \times$ as long as height of eye, not reaching median ocellus. Pedicel + flagellum $1.2\text{--}1.3 \times$ as long as breadth of head (Fig. 4) and $1.4\text{--}1.65 \times$ as long as breadth of mesoscutum. Pedicel in profile $1.65\text{--}2.05 \times$ as long as broad. Funicle with two anelli and three funicular segments, the first anellus laminar, the second discoidal; funicular segments decreasing in length, funicle proximally slightly ($1.2\text{--}1.43 \times$) stouter than pedicel, distally very slightly thickened (F3 $1.2\text{--}1.3 \times$ as broad as F1) and slightly compressed; F1 distinctly longer [$(1.45)1.8\text{--}2.15 \times$] than pedicel; F1–F3 (2.35) $2.6\text{--}3.2 \times$, (1.85) $2\text{--}2.4 \times$, and (1.5) $1.7\text{--}2 \times$ as long as broad, respectively. Clava three-segmented, acute apically; $2.8\text{--}3.5(4) \times$ as long as broad; slightly broader ($1\text{--}1.08 \times$) than F3 and $0.8\text{--}0.9 \times$ as long as F2 + F3; with shallow constriction between C1 and C2; C1 $1.15\text{--}1.6 \times$ as long as broad and $0.4\text{--}0.45 \times$ length of clava. Flagellum with sensilla moderately numerous, placed in three or rarely four irregular rows on F1 and F2, in two or rarely three irregular rows on F3, and in two rows on C1 and C2; with short, dense, decumbent setae.

Mesosoma in dorsal view (Figs 10, 11) $1.5\text{--}1.8 \times$ as long as broad, in lateral view (Fig. 8) weakly convex dorsally, $1.7\text{--}1.9 \times$ as long as high with propodeum sloping at about $35\text{--}45^\circ$ with respect to plane of mesoscutum and scutellum. Pronotum $0.2\text{--}0.35 \times$ as long as mesoscutum. Mesoscutum transverse, $1.45\text{--}1.65 \times$ as broad as long, and $1.15\text{--}1.4 \times$ as long as scutellum; notauli visible in anterior half only; slightly shiny, moderately strongly reticulate with isodiametric reticulations; setae sparse, dark, short, and strong. Scutellum convex, $0.95\text{--}1.1 \times$ as long as broad, with two pairs of strong, dark setae; sculpture of scutellum and axillae finer and not as strong as mesoscutum, the scutellum anteriorly with slightly elongate sculpture. Dorsellum (Figs 6, 7) reticulate or coriaceous (Fig. 13). Prepectus strongly reticulate. Legs of moderate length and thickness. Propodeum medially $1.4\text{--}1.7 \times$ as long as dorsellum and $0.43\text{--}0.5 \times$ as long as scutellum; coriaceous (Fig. 13) or with weak, superficial reticulations (Fig. 6), but almost smooth towards nucha and below plical carina, and sometimes with smooth areas on median panels (Figs 7, 13); with fine median carina reaching $0.5\text{--}0.8 \times$ its length; plical carina indistinct, visible only posteriorly; callus with long, white

setae; spiracles of medium size, short-oval, separated from metanotum by $0.3\text{--}0.7 \times$ smallest diameter (Figs 6, 7, 13).

Fore wing (Fig. 12) $2.4\text{--}2.6 \times$ as long as broad. Costal cell $1.05\text{--}1.2 \times$ as long as marginal vein and $8\text{--}9.5 \times$ as long as broad; ventrally with a complete row of setae and some sparse setae apically, and dorsally with a short row of four to eight setae apically. Submarginal vein dorsally with $13\text{--}17$ setae. Marginal vein $2.8\text{--}3.45(3.55) \times$ as long as stigmal vein. Stigmal vein at an angle of $34\text{--}38^\circ$ to the costal wing margin, moderately thin basally; stigma elongate, hardly thickened. Postmarginal vein $1.4\text{--}1.65 \times$ as long as stigmal vein and $0.42\text{--}0.55 \times$ as long as marginal vein. Basal fold pilose; basal cell open posteriorly, bare dorsally and ventrally. Speculum of moderate size, reaching almost to base of marginal vein, closed posteriorly. Cubital row of setae slightly sinuate upward behind speculum; subcubital row of setae in one partial row behind speculum. Admarginal row of setae behind marginal vein with one row of long hairs. Fore wing with moderately dense, dark pilosity beyond speculum; marginal fringe short. Hind wing rounded at apex.

Gaster lanceolate (Figs 2, 10), $2.6\text{--}3.15 \times$ as long as broad, $1.5\text{--}1.9 \times$ as long as mesosoma, $1.2\text{--}1.4 \times$ as long as head plus mesosoma, and $0.85\text{--}1.1 \times$ as broad as mesosoma; acute apically with syntergum usually elongate or barely transverse, $0.9\text{--}1.3 \times$ as long as broad; T1 with posterior margin convex, reaching $0.15\text{--}0.2 \times$ length of gaster. Ovipositor slightly protruding; cercal setae of similar length, not reaching apex of ovipositor. Hypopygium reaching $0.25\text{--}0.35 \times$ length of gaster.

Male (Fig. 9)

Similar to female except in structure of antennae and gaster, and hyaline wings. Body length $1.5\text{--}2.2$ mm. Antenna (Fig. 16) with scape $3.5\text{--}4.5 \times$ as long as broad, sensorial area (Fig. 15) narrow, at margin, with $16\text{--}19$ small sensorial pores placed in one row extending between basal $0.27\text{--}0.3$ and apical $0.75\text{--}0.83$ length of scape, and with interspaces greater than pore size. Pedicel + flagellum $1.35\text{--}1.55 \times$ as long as breadth of head and $1.55\text{--}1.9 \times$ as long as breadth of mesoscutum. Flagellum with one laminar anellus, four funicular segments, and three-segmented clava, with C1 large, reaching $0.6 \times$ length of clava, and C3 reduced apically. Funicular segments increasing in length, F4 $1.35\text{--}1.45 \times$ as long as F3 and $0.8\text{--}0.9 \times$ as long as clava. Funicle with three long, thin, subcylindrical rami on F1–F3, the rami, with long, hair-like setae; funicular segments and all three rami with mps, but denser on all sides of R2 and R3 and sparsely on frontal surface of R1. Fore wing with marginal vein $2.4\text{--}2.7 \times$ as long as stigmal vein; stigmal vein at an angle of $37\text{--}42^\circ$ to the costal wing margin; postmarginal vein 1.3--

1.65 × as long as stigmal vein and 0.5–0.6 × as long as marginal vein. Costal cell dorsally with a short marginal row of four to six setae apically. Legs (Fig. 9) with mesotibia usually pale or sometimes darkened in apical half, metatibia usually with apical 0.2–0.3 or sometimes up to apical half darkened, with dark portions brown to pale brown, or rarely meso- and metatibiae entirely dark; tarsi usually with basal two but rarely only basal tarsomeres pale. Gaster 2–2.8 × as long as broad, 1.1–1.33 × as long as mesosoma, and 0.85–1.05 × as long as head plus mesosoma.

Variation

Variation exists in the amount of leg darkening and fore wing infuscation, depending on distribution, body size, and possibly on seasonal generations. In the type material from England and some specimens from France and Spain the mesotibia is entirely pale, and the apical half of the metatibia is dark (Fig. 3). Other specimens from the same countries have either paler or darker tibiae. Paler forms, frequently in Spain, have the metatibia almost entirely pale with only the apical 0.15–0.3 dark. Darker forms, more frequently in England or France, have the apical half or rarely the mesotibia almost entirely dark. Variation also exists in colour pattern of the fore wings with more or less intense infuscation, and the number of pale basal tarsal segments. Usually the basal two tarsomeres are pale, but sometimes only the basitarsus is pale in small or darker specimens. Antennal segment proportions differ in small or dwarf specimens, these having less distinctly elongate flagellar segments, given in parentheses in the text.

Distribution

Europe (Noyes, 2013). A record from North America requiring confirmation refers to *N. comptus* as a possible synonym of *N. artynes* (Bouček & Askew, 1968).

Hosts

Tuta absoluta on *Solanum lycopersicum* L., and *Ap. anthyllidella* on *Astragalus* spp. (Fabaceae) based on sequenced specimens. Some specimens came from lab culture on *T. absoluta*; one female emerged from *Astragalus stella* Gouan together with *Ap. anthyllidella*, and one male emerged from *Astragalus sesameus* L., possibly associated also with *Ap. anthyllidella*. Another host record based on a specimen in R. R. Askew's collection is *Ap. anthyllidella* on *Anthyllis vulneraria* L. (Penbryn, Cardigan, Wales, vi.1979, leg. A. N. B. Simpson). Noyes (2013) also listed *Cos. pulchrimella* Chambers; however, this is incorrect and is instead the host for one of the cryptic species that we describe, *N. cosmopterix*. Noyes (2013) also listed *Vulcaniella pomposella* (Zeller) (Cosmopterigidae) on *Salvia aethiops* L.; however, according to Koster & Sinev (2003), the

true host may be *Vulcaniella cognatella* Riedl based on the host plant being *Salvia*. In this case, the species status of the parasitoid requires confirmation.

Discussion

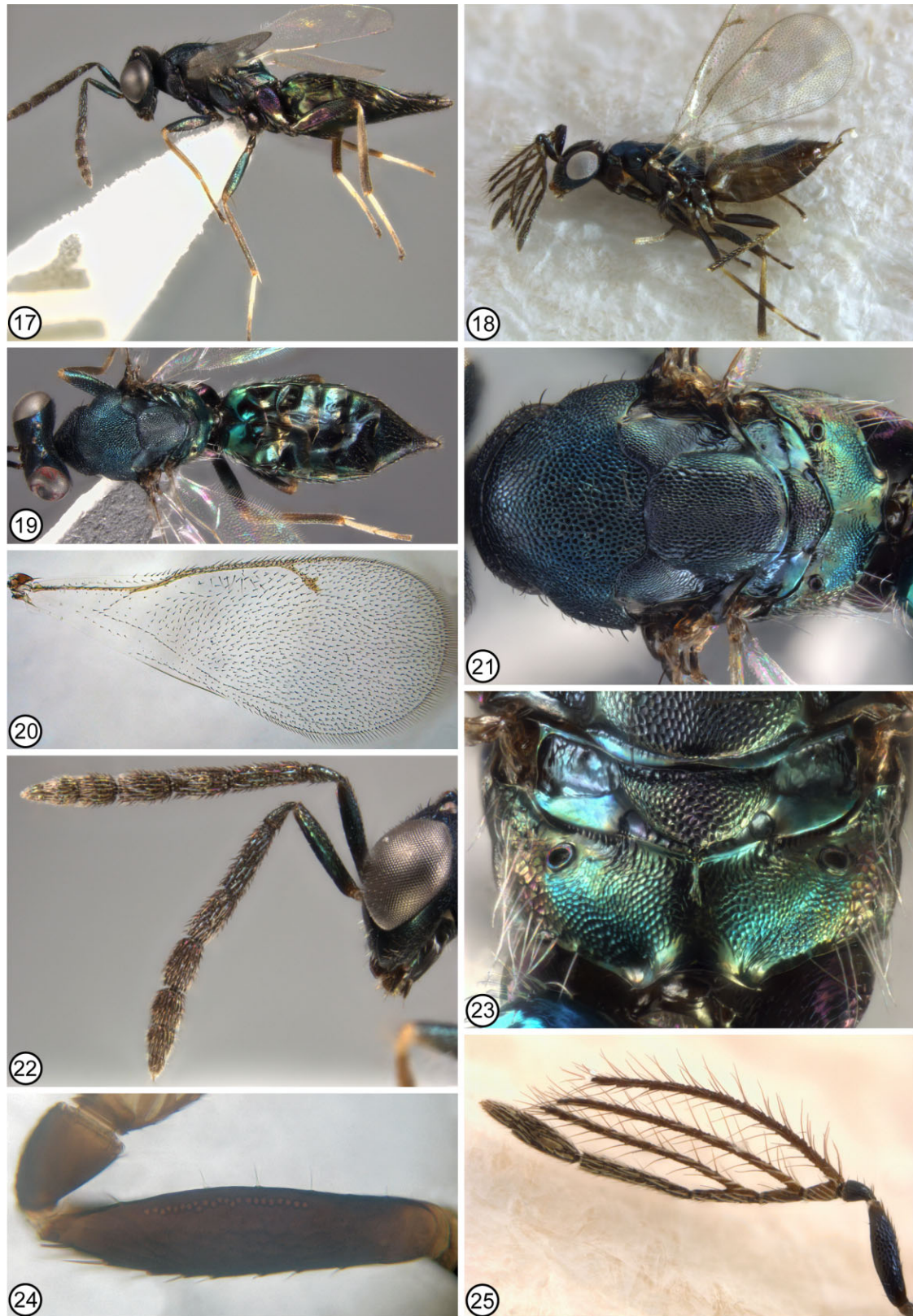
Necremnus artynes is the typical species of the *N. artynes* group, females having bimaculate fore wings (Figs 2, 12), an elongate mesosoma and gaster (Fig. 10), relatively long postmarginal vein, and elongate funicle segments (Figs 4, 14). Within this group, *N. metalarus* and related species are differentiated by their comparatively coarsely sculptured, reticulate propodeum and dorsellum (Figs 31, 37), in combination with almost entirely dark metatibia (Figs 27, 32). Of the species with a weakly reticulate or coriaceous propodeum (Figs 45, 53), *N. artynes* most closely resembles *N. tutae* and *N. navonei*, the former being misidentified frequently in previous surveys of *Tuta* parasitoids. The main diagnostic feature for females of *N. artynes* is the comparatively elongate lanceolate gaster, being 2.6–3.15 × as long as broad. This is clearly longer than for females of *N. tutae* (1.9–2.4 ×, Fig. 48), although not always for females of *N. navonei*, which have the gaster 2.35–2.8 × as long as broad (Fig. 42). When the gaster is collapsed in air-dried specimens, it can appear narrower than its natural shape, but its other proportions with the mesosoma and rest of the body are maintained. The gaster is 1.5–1.9 × as long as the mesosoma in *N. artynes* vs. 1.2–1.5 × in *N. tutae* and 1.45–1.55 × in *N. navonei*. Another feature typical of *N. artynes* females is that the last gastral tergite is usually elongate or barely transverse, 0.9–1.3 × as long as broad, whereas it is clearly transverse, 0.6–0.85 × as long as broad in females of the other species. Other small differences and those of males are detailed in the descriptions of *N. tutae* and *N. navonei*.

We sequenced seven females and four males from France and Spain, but not from type localities in England. Specimens from France are the most similar to the type material. Two females (NA114, NA147) have typical bifasciate fore wing patterns, the mesotibia essentially entirely yellow, and the metatibia with only about the apical quarter brownish. The other three females (NA148–150) have both the mesotibia and metatibia with up to or slightly more than the apical half brown, but only NA150 has a typical fore wing pattern, the other two either having a superficially hyaline fore wing (NA149) or with only a faint brownish region behind the stigmal vein (NA150).

NECREMNUS COSMOPTERIX RIBES & BERNARDO SP. NOV. (FIGS 17–25)

Etymology

Named after the genus of one of its hosts, *Cosmopterix pulchrimella* Chambers.



Figures 17–25. *Necremnus cosmopterix* sp. nov. 17–19, habitus: ♀ lateral (2012-7); 18, ♂ lateral (2013-68); 19, ♀ dorsal (2012-7). 20–23, ♀ (2012-7): 20, fore wing; 21, dorsal mesosoma; 22, antennae; 23, metanotum and propodeum. 24, ♂ pedicel and scape. 25, ♂ antenna (2013-67).

Type material

Holotype ♀: ITALY: Portici (NA), Campania, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, 20.vii.2003, leg. U. Bernardo. *Allotype* ♂: Same data as holotype. *Paratypes* (4♀ 3♂): ITALY: 1♀ 1♂, same data as holotype; 2♀ 2♂, Arma di Taggia, ex. *Tuta absoluta* on *Solanum lycopersicum*, 2009, Bioplanet culture; 1♀, Cariati (CS), Calabria, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, 25.iv.2007, leg. U. Bernardo. The holotype, allotype, and some paratypes are deposited in BMNH, and some paratypes in CNC.

Additional material (8♀ 16♂): ITALY: 1♀ 1♂, Cariati (CS), Calabria, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, 25.iv.2006, leg. U. Bernardo; 2♀ 1♂, Moncalieri (TO), Piemonte, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, 4–15.viii.2010, leg. P. Navone; 3♂, San Giorgio a Cremano (NA), Campania, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, 13.ix.2006, leg. U. Bernardo; 5♀ 10♂, Portici (NA), Campania, ex. *Cosmopterix pulchrimella* on *Parietaria judaica*, v.2006, leg. U. Bernardo; 1♂, Noli (SV), ex. *Selania capparidana* on *Capparis spinosa*, 18.ix.2012, leg. P. Navone.

Diagnosis

Female

Fore wings hyaline (Fig. 20). Postmarginal vein long, (1.65)1.85–2.15 × as long as stigmal vein. Tibiae entirely dark or rarely pale, tarsi usually with only basitarsi pale. Propodeum uniformly reticulate, but not strongly so (Fig. 23). Antenna (Fig. 22) with flagellum elongate, pedicel + flagellum 1.2–1.35 × as long as breadth of head, combined length of F1 + anelli 1.9–2.4 × as long as pedicel, and 2.8–3.4 × as long as broad. Gaster 1.9–2.4(3) × as long as broad (Fig. 19).

Description

Female

Body length 1.8–2.7 mm. Head and mesosoma dark bluish (Figs 17, 19). Antenna (Fig. 22) with scape black, pedicel and flagellum dark brown. Tegula black. Legs (Fig. 17) with coxae coloured as body; femora black with metallic reflections; tibiae usually entirely black, narrowly testaceous on knees, sometimes with basal third testaceous or rarely mainly testaceous in some pale forms; tarsi usually with only basal tarsomeres testaceous, rarely basal two tarsomeres in pale forms. Fore wing (Fig. 20) hyaline; wing venation brownish. Gaster (Fig. 19) dark brown, with violaceous reflections dorsally basally and apically.

Head in dorsal view (Fig. 19) 1.21–1.29 × as broad as mesoscutum and 2.2–2.7 × as broad as long; in frontal view transverse-oval, 1.25–1.38 × wider than high; temple 0.15–0.2 × as long as eye length. POL 1.6–2(2.3) × OOL, OOL (1.25)2–2.3 × OD. Eyes 1.35–1.43 × as high as broad, separated by 0.9–

1.05 × their length, eyes glabrous. Malar space 0.4–0.47 × length of eye, malar sulcus present. Mouth opening 1.3–1.5 × as broad as malar space. Frons flattened on sides, without piliferous punctures.

Antennae (Fig. 22) inserted with ventral margins of toruli at level of ventral margins of eyes. Scape 5–5.5 × as long as broad, 0.85–0.9 × as long as height of eye, not reaching median ocellus. Pedicel + flagellum 1.2–1.35 × as long as breadth of head and 1.5–1.65 × as long as breadth of mesoscutum. Pedicel in profile 1.6–2 × as long as broad. Funicle with two anelli and three funicular segments, the first anellus laminar, the second discoidal; funicular segments decreasing in length, funicle proximally slightly (1.1–1.3 ×) stouter than pedicel, distally very slightly thickened (F3 1.1–1.25 × as broad as F1); F1 distinctly longer (1.75–2.2 ×) than pedicel; F1–F3 2.5–3.1, 2.1–2.35, and 1.8–2.1 × as long as broad, respectively. Clava three-segmented, compact, acute apically, slightly (1.05–1.1 ×) broader than F3, 3.05–3.7 × as long as broad, and 0.8–0.96 × as long as F2 + F3; C1 1.3–1.55 × as long as broad and 0.4–0.45 × length of clava. Flagellum with sensilla placed in four or rarely three irregular rows on F1, in three or rarely two irregular rows on F2 and F3, and in two rows on C1–C2; with short, dense, decumbent setae.

Mesosoma in dorsal view (Figs 17, 21) 1.6–1.8 × as long as broad, in lateral view (Fig. 17) weakly convex dorsally, 1.8–1.93 × as long as high with propodeum sloping at about 40–45° with respect to plane of mesoscutum and scutellum. Pronotum 0.25–0.35 × as long as mesoscutum. Mesoscutum transverse, 1.4–1.5 × as broad as long, and 1.3–1.4 × as long as scutellum; moderately strongly reticulate with isodiametric reticulations. Scutellum convex, 1–1.1 × as long as broad, with two pairs of strong, dark setae; sculpture of scutellum and axillae finer and not as strong as mesoscutum, the scutellum anteriorly with slightly elongate sculpture (Fig. 21). Dorsellum reticulate (Fig. 23). Propodeum (Fig. 23) medially 1.7–1.9 × as long as dorsellum and 0.5 × as long as scutellum; uniformly reticulate, but not strongly so; median carina reaching less than half its length; plical carina indistinct; callus with setae long and white; spiracles of medium size, short-oval, separated from metanotum by 0.5–0.75 × its smallest diameter.

Fore wing (Fig. 20) 2.35–2.4 × as long as broad. Costal cell 1.1–1.2 × as long as marginal vein and 9.5–11 × as long as broad; ventrally with a complete row of setae and another incomplete row in apical half, and dorsally a partial row of six to 13 setae apically. Submarginal vein dorsally with 13–18 setae. Marginal vein 3.35–4 × as long as stigmal vein. Stigmal vein at an angle of 42–46° to the costal wing margin, moderately thin basally; stigma elongate, hardly thickened. Postmarginal vein (1.65)1.85–2.15 × as long as

stigmal vein and $(0.4)0.5\text{--}0.57 \times$ as long as marginal vein. Basal fold rarely glabrous, but usually with one to seven setae; basal cell open posteriorly, with zero to two setae at apex of mediocubital fold; bare dorsally and ventrally. Speculum of moderate size, reaching almost to base of marginal vein, rarely open posteriorly but usually closed by sparse to dense setae, without setae or hair bases at lower surface. Fore wing with moderately dense, dark pilosity beyond speculum; marginal fringe short. Hind wing rounded at apex.

Gaster (Figs 17, 19) long-ovate, $1.9\text{--}2.4(3) \times$ as long as broad, $1.35\text{--}1.55 \times$ as long as mesosoma, $1.05\text{--}1.2 \times$ as long as head plus mesosoma, and $(0.8)1\text{--}1.1 \times$ as broad as mesosoma; acute apically with syntergum transverse, $0.6\text{--}0.7 \times$ as long as broad; T1 with posterior margin convex, reaching $0.15\text{--}0.2 \times$ length of gaster. Ovipositor slightly protruding; cercal setae of similar length, not reaching apex of ovipositor. Hypopygium reaching $0.3\text{--}0.4 \times$ length of gaster.

Male (Fig. 18)

Similar to female except in structure of antennae and gaster. Body length $1.7\text{--}2.25$ mm. Antenna (Fig. 25) with scape $3.7\text{--}4.4 \times$ as long as broad, sensorial area (Fig. 24) narrow, near margin, with 22–25 sensorial pores placed in one irregular row extending between basal 0.3 and apical $0.71\text{--}0.8$ length of scape, and densely placed with interspaces narrower than pore size. Pedicel + flagellum $1.55\text{--}1.65 \times$ as long as breadth of head and $1.9\text{--}2.05 \times$ as long as breadth of mesoscutum. Flagellum with one laminar anellus, four funicular segments, and three-segmented clava; F4 $1.5\text{--}1.7 \times$ as long as F3 and $0.9\text{--}1 \times$ as long as clava. Funicle with three long, thin, subcylindrical rami on F1–F3, the rami with long, hair-like setae; funicular segments and all three rami with mps, but denser on R2 and R3, and sparsely on frontal surface of R1. Fore wing with marginal vein $3.3\text{--}3.45 \times$ as long as stigmal vein; stigmal vein at an angle of 45° to costal wing margin; postmarginal vein $1.9\text{--}2 \times$ as long as stigmal vein and $0.58\text{--}0.6 \times$ as long as marginal vein. Costal cell dorsally with a marginal row of 11 or 12 setae apically. Legs (Fig. 18) with mesotibia darkened in apical $0.6\text{--}0.85$ and metatibia darkened in apical $0.6\text{--}0.75$, with the dark portions dark brown to black; tarsi with basitarsi or rarely basal two tarsomeres pale. Gaster $2.3\text{--}2.5 \times$ as long as broad, $1.05\text{--}1.1 \times$ as long as mesosoma, and $0.85\text{--}0.87 \times$ as long as head plus mesosoma.

Variation

The fore wing usually has the speculum closed by rows of sparse setae basally and posteriorly (Fig. 20), but sometimes it is entirely open with the basal and mediocubital folds bare; this variability is seen also in *N. tutae*. Specimens always have hyaline wings and most have dark tibiae. However, several specimens

reared from *Cos. pulchrimella* under lab conditions, at different temperatures, vary in having the tibiae dark, with the basal third pale, or the tibiae even wholly pale yellow, and with the two basal tarsomeres pale. This variation can be attributed to phenotypic plasticity, as reported also in other Eulophidae by Bernardo, Pedata & Viggiani (2007). Although it has not been seen in specimens collected from the wild, such variation presumably also exists to some degree. Specimens reared under lab conditions from *T. absoluta* always have the tibiae dark. Pale specimens reared from *Cos. pulchrimella* also have some differences in morphological features, having a less elongate ($1.65\text{--}1.9 \times$) postmarginal vein relative to the stigmal vein, pale yellow venation, and finer and paler wing setation, the gaster relatively more elongate ($2.8\text{--}3.05 \times$) and differing values of ocellar ratios (POL $2.2\text{--}2.3 \times$ OOL, OOL $1.25\text{--}1.4 \times$ OD).

Hosts

Cosmopterix pulchrimella on *Parietaria judaica* L. (Urticaceae), *T. absoluta* on *Solanum lycopersicum*, and *Se. capparidana* (Zeller), based on sequenced specimens. The records published as *N. sp. nr. tidius* or *N. tidius* in previous surveys of *Tuta* parasitoids (Ferracini *et al.*, 2012; Zappalà *et al.*, 2012, 2013) belong to *N. cosmopterix*. The record listed in Noyes (2013) as *N. artynes* from *Cos. pulchrimella* also belongs to *N. cosmopterix*.

Discussion

Because of their hyaline wings and dark legs, in general appearance females of *N. cosmopterix* are most similar to *N. tidius* and related species of the *N. tidius* group. However, the elongate antennae, host preferences, and molecular analyses place *N. cosmopterix* in the *N. artynes* group, even though the wings lack an infuscate pattern. This condition is found also in atypical pale specimens of some other *N. artynes*-group species, and a few extralimital species. Females of *N. cosmopterix* differ from those of *N. tidius* in having the pedicel + flagellum $1.2\text{--}1.35 \times$ as long as the breadth of head, the combined length of F1 + anelli $1.9\text{--}2.4 \times$ as long as the pedicel and $2.8\text{--}3.4 \times$ as long as broad (Fig. 22). In *N. tidius* the pedicel + flagellum is $1.1 \times$ as long as the breadth of the head, and the combined length of F1 + anelli is $1.25\text{--}1.6 \times$ as long as the pedicel and $2.1\text{--}2.8 \times$ as long as broad (Fig. 167). Furthermore, the gaster is slightly longer in female *N. artynes*, $1.05\text{--}1.2 \times$ as long as the head plus mesosoma compared with as long as the mesosoma in *N. tidius* (cf. Figs 19, 165). Because of the dark legs and reticulate propodeum females also resemble specimens of *N. metalarus* that have very faint or that lack infuscation from the wings, but females of the latter species always have a more strongly sculptured propodeum, with more distinct plical carinae and

a longer median carina (Fig. 37). Furthermore, females of *N. metalarus* have a shorter postmarginal vein (1.25–1.5 × as long as stigmal vein), shorter marginal vein (2.8–3.4 × as long as stigmal vein), and shorter antenna with the pedicel + flagellum 1.25–1.35 × as long as the breadth of the mesoscutum. Females also resemble atypical specimens of *N. tutae* that have subhyaline fore wings, and atypical *N. artynes* that have pale wings, but these usually have at least some trace of infuscation behind the stigmal vein. Females of *N. cosmopterix* also differ in having the propodeum uniformly reticulate (Fig. 23) compared with weakly, superficially reticulate or coriaceous to partly smooth in *N. tutae* and *N. artynes*, and usually dark although rarely pale tibiae compared with the tibiae always being partly pale in *N. tutae* (Fig. 53) and *N. artynes* (Figs 6, 7). Females of *N. cosmopterix* usually also have a longer antenna (pedicel + flagellum 1.2–1.35 × vs. 1.15–1.27 × as long as breadth of head in *N. tutae*), the marginal vein (3.35)3.55–4 × as long as the stigmal vein vs. 2.8–3.6 × in *N. tutae* and *N. artynes*, and the postmarginal vein (1.65)1.85–2.15 × as long as the stigmal vein vs. 1.4–1.7 × in *N. tutae* and *N. artynes*. Males of *N. cosmopterix* differ from those of *N. tidius* in the presence of mps on the basal ramus, even though these are restricted to the anterior face. Males of *N. cosmopterix* differ from those of *N. artynes*, *N. tutae*, and *N. navonei* by having a longer postmarginal vein, 1.9–2 × vs. 1.3–1.75 × as long as the stigmal vein, longer marginal vein, 3.3–3.45 × vs. 2.4–3.25 × as long as the stigmal vein, and the costal cell being more setose dorsally, with a marginal row of 11 or 12 vs. three to six setae in the latter species, and the propodeum being more strongly reticulate and the legs usually dark in the apical 0.65–0.85.

NECREMNUS METALARUS (WALKER) (FIGS 26–39)

Eulophus Metalarus Walker, 1839: 187–188. ♀ lectotype (BMNH, here designated).

Type material

Walker (1839) described *Eulophus metalarus* based on at least seven females and males, the description also including six varieties, collected from the Isle of Wight, and Holywood, near Belfast, Northern Ireland. The BMNH has at least two females indicated to form part of the type series. Two are point-mounted and have a rectangular card below the point to help protect the specimen. One has the following four labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular, handwritten label with '*Eulophus metalarus* Walker' handwritten on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse' printed on the other side; (3) a rectangular label with '*Eulophus metalarus* Walker LECTOTYPE: ♀ M. de V. Graham

det. 1958' partly printed and handwritten; and (4) a square label with 'B.M. TYPE HYM. 5.2506'. This female is complete (Figs 26, 27) although the head is collapsed and covered with a white substance that obscures the sculpture (Fig. 30). The other has a circular, blue-bordered label with 'PARALECTOTYPE' and the same double-sided label as the specimen labelled as the lectotype. Head sculpture is visible in this female, but it lacks the apical funicular and clava of the left antenna and has the left fore wing torn and curled at the level of the stigmal vein. Both females are typical for the species in having a single infuscate region behind the stigmal vein (Fig. 29), the tegulae dark brown apically but more translucent yellowish basally (Fig. 28), and the dorsellum and propodeum quite strongly reticulate (Fig. 31). In order to stabilize the concept of the name we designate the best-preserved female, the one with Graham's lectotype label, as the lectotype of *E. metalarus*, and the one with his paralectotype label as the paralectotype.

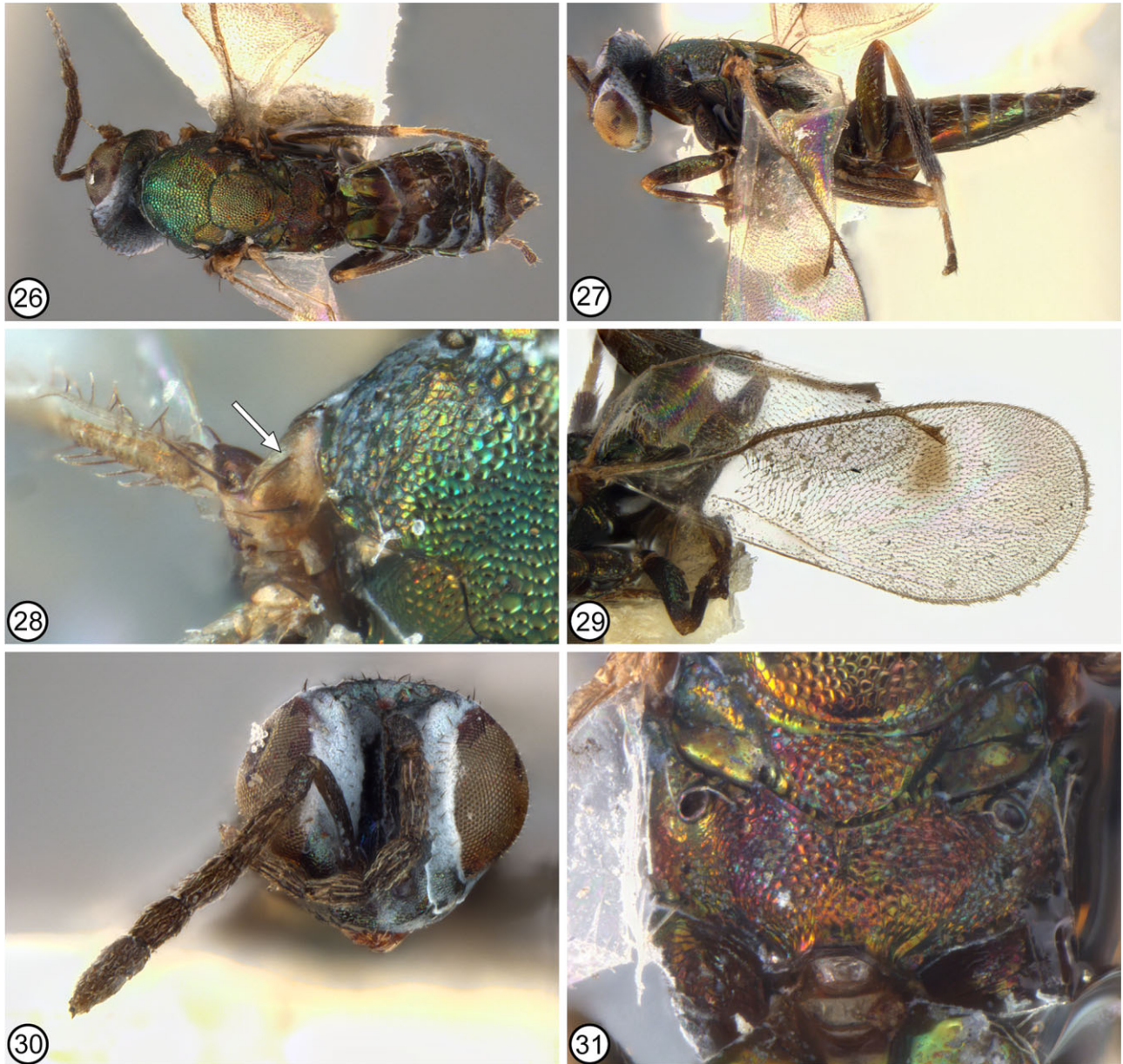
The general collection contains another similar point-mounted female with the same double-sided label as the other two specimens, a circular label with '38/7\12/65' on three separate lines, and a small rectangular label with 'Clermont'. This female is not part of the original type series because it is from Clermont, France (Walker, 1846a).

Redescription

Female

Body length 1.8–3.3 mm. Head and mesosoma dark green, coppery lustre dorsally (Figs 34, 35). Antenna (Fig. 38) with scape dark, pedicel and flagellum dark brown. Tegula partly or rarely entirely yellow, usually dark brown apically and lighter, translucent yellowish basally (Fig. 28). Legs (Figs 27, 32) with meso- and metatibiae almost entirely dark although usually narrowly pale basally, the paler region typically somewhat broader ventrally than dorsally so as not to be distinctly and uniformly differentiated. Hind leg with tarsus sometimes entirely brown, but usually basal tarsomere white to yellowish-brown at least basally and apical three tarsomeres brown or increasingly dark brown. Fore wing usually with at least faint brownish infuscation behind stigmal vein extending at most half width of wing (Fig. 29), although sometimes completely hyaline (Fig. 36) or rarely with broad, faint brownish region behind marginal vein basally, posteriorly the latter region extended obliquely to merge with brownish region behind stigmal vein to form broadly U-shaped infuscate region. Gaster dark brown.

Head in dorsal view (Fig. 34) 1.1–1.2 × as broad as mesoscutum and 2.2–2.5 × as broad as long; in frontal view (Fig. 30) transverse-oval, 1.2–1.35 × wider than high; temple 0.12–0.2 × as long as eye length. POL 1.8–

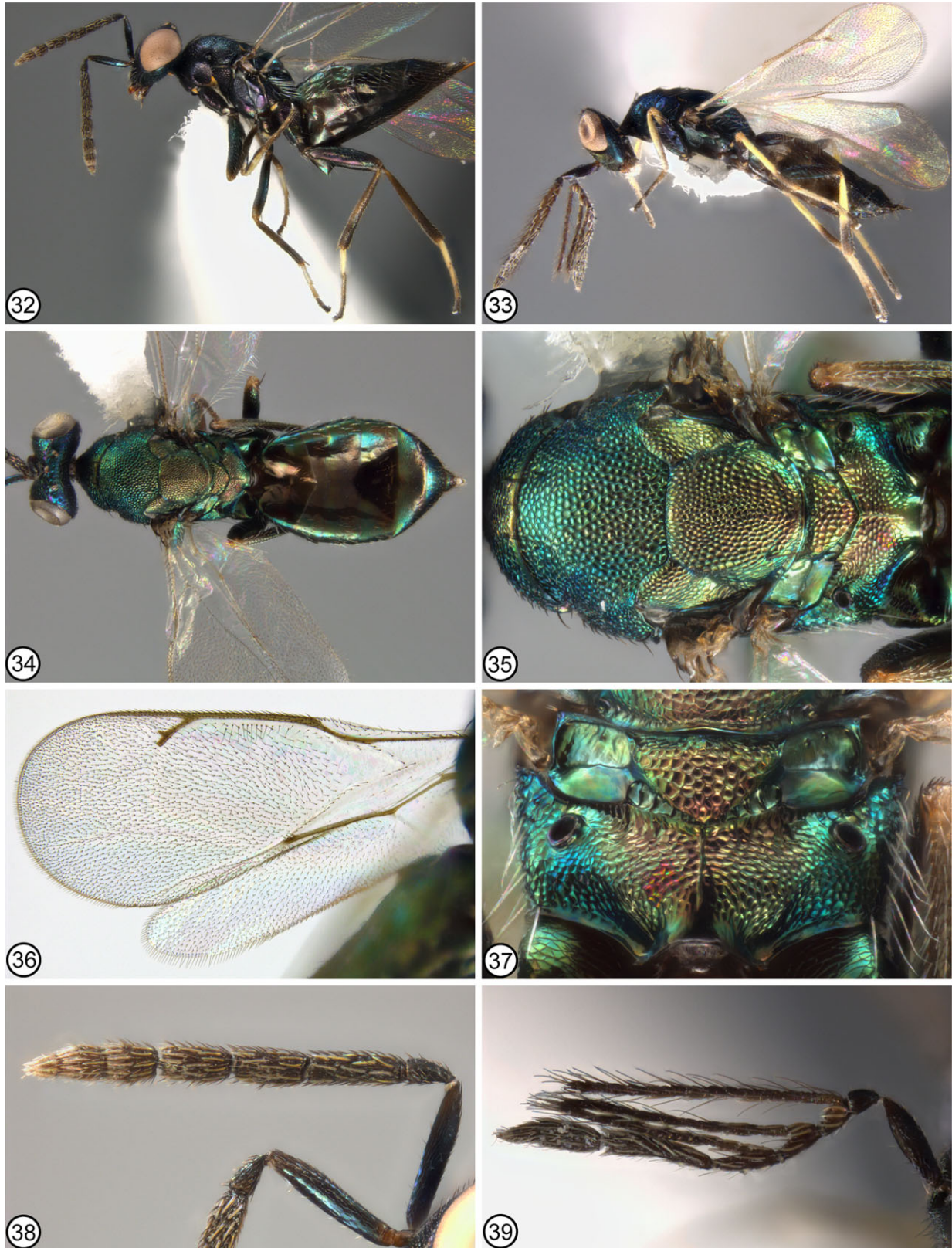


Figures 26–31. *Necremnus metalarus*, ♀ lectotype. 26, dorsal habitus; 27, lateral habitus; 28, tegula (arrow); 29, fore wing; 30, head and antenna; 31, metanotum and propodeum.

$2 \times \text{OOL}$, $\text{OOL } 1.85\text{--}2.15 \times \text{OD}$. Eyes $1.3\text{--}1.5 \times$ as high as broad, separated by $0.9\text{--}1.1 \times$ their height, with very short, sparse hairs. Gena straight to weakly convex, strongly converging, malar space $0.37\text{--}0.42 \times$ height of eye. Mouth opening $1.4\text{--}1.5 \times$ as broad as malar space. Frons flattened on sides, weakly reticulate, with very short hairs, without piliferous punctures.

Antennae (Figs 30, 38) inserted with ventral margins of toruli at level of ventral margins of eyes. Scape $5.5\text{--}6.5 \times$ as long as broad, $0.73\text{--}0.9 \times$ as long as height of eye, not reaching median ocellus. Pedicel + flagellum $1.1\text{--}1.25 \times$ as long as breadth of head (Fig. 30) and

$1.25\text{--}1.35 \times$ as long as breadth of mesoscutum. Pedicel in profile $1.8\text{--}2.15 \times$ as long as broad. Funicle with two anelli and three funicular segments, funicular segments decreasing in length, funicle proximally slightly ($1.1\text{--}1.3 \times$) stouter than pedicel, distally very slightly thickening (F3 $1.1\text{--}1.35 \times$ as broad as F1) and slightly compressed; F1 distinctly longer ($1.7\text{--}2.15 \times$) than pedicel; F1 + anelli $1.8\text{--}2.3 \times$ as long as pedicel; F1–F3 $3\text{--}3.4$, $2\text{--}2.65$, and $1.65\text{--}2.15 \times$ as long as broad, respectively. Clava three-segmented, acute apically, slightly ($1.05\text{--}1.1 \times$) broader than F3, $2.6\text{--}3.15 \times$ as long as broad, and $0.8 \times$ as long as F2 + F3; clava with C1



Figures 32–39. *Necremnus metalarus*. 32–34, habitus: 32, ♀ lateral (2012-9); 33, ♂ lateral (2012-12); 34, ♀ dorsal (2012-8). 35, ♀ dorsal mesosoma (2012-8). 36, ♀ fore wings (2012-9). 37, ♀ metanotum and propodeum (2012-8). 38, ♀ antenna (2012-9). 39, ♂ antenna (2012-10).

1–1.4 × as long as broad and 0.4–0.45 × length of clava. Flagellum with sensilla placed in three or rarely four irregular rows on F1, in two or rarely three irregular rows on F2 and F3, and in two rows on C1; with short, dense, decumbent setae.

Mesosoma in dorsal view (Figs 34, 35) 1.6–1.9 × as long as broad, in lateral view (Fig. 32) 1.9–2.15 × as long as high with propodeum sloping at about 40–45° with respect to plane of mesoscutum and scutellum. Pronotum 0.2–0.3 × as long as mesoscutum. Mesoscutum transverse, 1.5–1.75 × as broad as long, and 1–1.27 × as long as scutellum; with slightly raised, moderately strong reticulation, the reticulations isodiametric. Scutellum convex, 1–1.15 × as long as broad, sculpture of scutellum and axillae finer and not as strong as mesoscutum. Dorsellum (Figs 35, 37) usually quite strongly mesh-like reticulate. Propodeum (Figs 35, 37) medially 1.35–1.7 × as long as dorsellum and 0.4–0.5 × as long as scutellum; typically comparatively strongly sculptured, quite distinctly mesh-like reticulate except sometimes in smaller individuals, with distinct median carina over most of length; without or with variably distinct oblique angulation or carinate plica partly between spiracle and foramen; callus with long, white setae; spiracles obliquely oval, separated from metanotum by 0.3–0.5 × smallest diameter.

Fore wing (Fig. 36) 2.35–2.6 × as long as broad. Costal cell 0.95–1.1 × as long as marginal vein; ventrally with a complete row of setae and some sparse setae apically, and dorsally with a short row of six to eight setae apically. Submarginal vein dorsally with 13–20 setae. Marginal vein 2.8–3.4 × as long as stigmal vein. Stigmal vein moderately thin basally; stigma elongate, hardly thickened. Postmarginal vein 1.25–1.5 × as long as stigmal vein and 0.3–0.47 × as long as marginal vein. Basal fold pilose; basal cell open posteriorly, dorsally bare and ventrally with variable number of minute setae near submarginal vein. Speculum broad, closed posteriorly. Fore wing with moderately dense, dark pilosity beyond the speculum; marginal fringe short. Hind wing rounded at apex.

Gaster (Fig. 34) ovate, 1.9–2.3 × as long as broad, 1.1–1.3 × as long as mesosoma, 0.85–1.05 × as long as head plus mesosoma, and 0.93–1 × as broad as mesosoma; acute apically with syntergum transverse, 0.4–0.55 × as long as broad. Ovipositor slightly protruding. Hypopygium reaching 0.33–0.45 × length of gaster. Other features not detailed in description as in *N. artynes*.

Male (Fig. 27)

Similar to female except in structure of antennae and gaster, and hyaline wings. Antenna (Fig. 39) with flagellar rami long, with long, hair-like setae and with mps. Fore wing hyaline. Tegula variably distinctly and extensively yellow basally to entirely yellow. Legs (Fig. 27) with similar colour pattern as female or up to about

basal half of meso- and metatibiae pale. Metanotum with dorsellum shallowly mesh-like reticulate to mesh-like coriaceous. Propodeum mesh-like coriaceous or at most sculpture defined by very weakly raised lines; spiracle slightly separated from metanotum.

Distribution

Europe, and introduced in North America (Noyes, 2013). We sequenced specimens from France and Italy, the latter a new country record.

Hosts

Coleophora laricella (Hübner) (Lepidoptera: Coleophoridae) on *Larix europaea* Philip Miller (Pinaceae) based on sequenced specimens. Noyes (2013) recorded *Col. laricella* as well as *Coleophora pennella* (Denis & Schiffermüller) [= *Coleophora onosmella* (Brahm)] plus other species in Gelechiidae, Gracillariidae, Lyonetiidae, and Yponomeutidae and plant associates in nine families. Confirmed host records based on examined specimens in the BMNH are *Argyresthia thuiella* (Packard) (Yponomeutidae), *Leucoptera* (= *Lithocolletis*) *spartifoliella* (Hübner) (Lyonetiidae), and *Phyllonorycter scopariella* (Zeller) (Gelechiidae). Other confirmed host records based on specimens in R. R. Askew's collection are *Coleophora serratella* (L.) on *Betula*, *Coleophora vitisella* Gregson on *Vaccinium vitis-idaea* L., *Phyllonorycter quinqueguttella* (Stainton) on *Salix repens* L., and *Mompha miscella* (Denis & Schiffermüller) (Mompidae) on *Helianthemum* sp. (Cistaceae).

Discussion

We sequenced only two individuals that we identified as *N. metalarus* (NM63 and NM151), insufficient to form a proper morphological species concept. Nonetheless, within the *N. artynes* group, typical females of *N. metalarus* are uniquely distinguished by having a comparatively coarsely sculptured, reticulate dorsellum and propodeum (Figs 35, 37) in combination with almost entirely dark metatibia (Figs 27, 32). Owing to their metatibial colour pattern, broad speculum, and propodeal spiracles separated slightly from the metanotum, females, particularly those with entirely hyaline fore wings, could be mistaken for those of *N. leucarthros*. However, females of *N. leucarthros* have a dark brown tegula, whereas in *N. metalarus* the tegula is usually yellowish to variably distinctly bicoloured, brown apically and more translucent yellowish basally (Fig. 28). There is also typically a subtle colour difference between the metatibia of females of the two species. In *N. leucarthros* females, not only is the basal yellow region very short, but it usually is also quite abruptly and uniformly delineated (Figs 145, 146). *Necremnus metalarus* females typically have the pale and dark coloration merging more gradually and the basal pale

region somewhat longer ventrally than dorsally (Figs 27, 32) so as not to be as abruptly delineated as in *N. leucarthros*. Typical *N. leucarthros* females also have a shorter F1 (Fig. 149) and a more finely sculptured, mesh-like coriaceous to coriaceous-imbricate propodeum (Figs 143, 147). However, although most female *N. metalarus* we have seen have F1 about twice the length of the pedicel (Fig. 38), females at the lower end of the size variation can have F1 only about $1.8 \times$ or slightly less than the length of the pedicel, similar to some *N. leucarthros*, as well as a comparatively finely sculptured metanotum and propodeum. This is true for four poorly preserved BMNH females from England associated with several males reared from *Col. laricella*. Males associated with females from this rearing have a similar metatibial colour pattern as females, whereas males associated with females that we identify as *N. metalarus* from other rearings have the metatibia much more broadly pale basally, similar to *N. artynes* males. Most female *N. metalarus* also have the tegula yellowish or noticeably bicoloured, being darker brown apically and lighter and more translucent yellowish to yellowish brown basally (Fig. 28).

NECREMNUS NAVONEI RIBES SP. NOV. (FIGS 40–47)

Etymology

Named after Paolo Navone (Italy), who first collected this species.

Type material

Holotype ♀: FRANCE: Quiberon, Pointe du Conguel, ex. *Dialectica scaliariella* on *Echium vulgare*, col. 11.vii.2012, em. 17.vii.2012, leg. P. Navone. *Allotype* ♂: Same data as holotype. *Paratypes* (6♀): 1♀, same data as holotype; 5♀ progeny of holotype (F1), viii.2012. The holotype, allotype, and some paratypes are deposited in CNC, and some paratypes in BMNH.

Additional material (3♀ 1♂): FRANCE: 1♀ 1♂, same data as holotype; 1♀, Fos-sur-Mer, 19.viii.2011, sweeping herbaceous layer, leg. G. Delvare. ITALY: 1♀, Ventimiglia (IM), Liguria, ex. *Dialectica scaliariella* on *Echium vulgare*, 2.i.2006, leg. P. Navone.

Diagnosis

Female

Gaster (Figs 40, 42) long-ovate, $2.35\text{--}2.8 \times$ as long as broad, $1.45\text{--}1.55 \times$ as long as mesosoma, and $1.1\text{--}1.3 \times$ as long as head plus mesosoma. Propodeum with weak, superficially reticulate or coriaceous sculpture to partly smooth (Fig. 45). Malar space long, $0.48\text{--}0.52 \times$ as long as eye height. Tibiae often very dark with apical half and pale within basal half, the colours sharply contrasted (Figs 40, 42). Fore wing bimaculate

(Fig. 43) to almost hyaline, but at least with very faint infusate areas behind stigmal vein and behind base of marginal vein.

Description

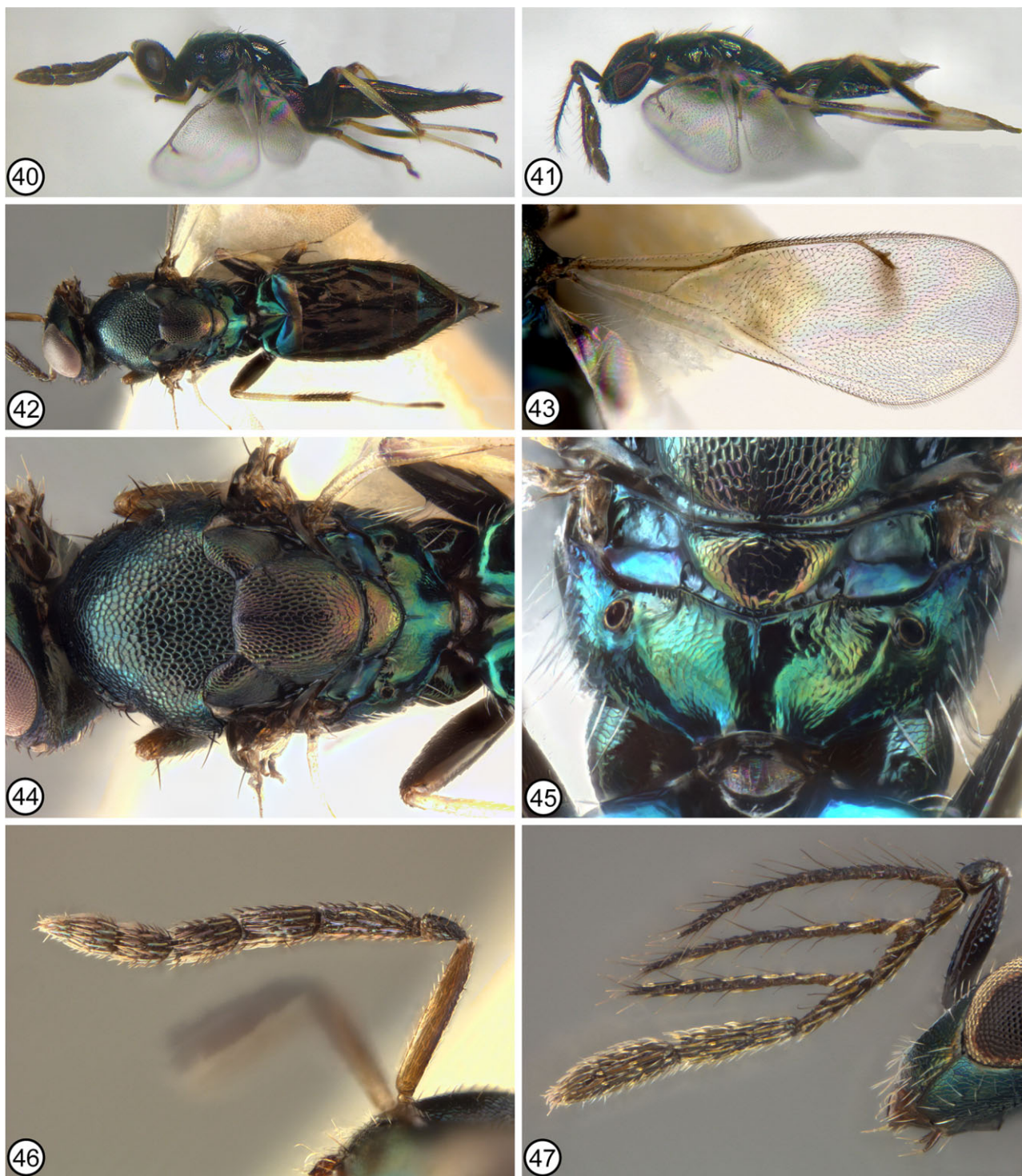
Female

Body length 2.1–2.7 mm. Head and mesosoma dark green, with purplish reflections on scutellum (Figs 42, 44). Antenna (Fig. 46) with scape black or testaceous on anterior margin; pedicel and flagellum dark brown. Tegula black. Legs (Figs 40, 42) with coxae coloured as body; femora black with metallic reflections, narrowly testaceous at knees; tibiae often very darkened in apical half and pale in basal half with colours sharply contrasted; protarsus brown, meso- and metatarsi with basal two tarsomeres testaceous. Fore wing bimaculate (Fig. 43), with a brownish area beneath stigmal vein and another brown stripe under proximal end of marginal vein, although the infusate areas usually very faint; wing venation brownish. Gaster dark brown, dorsally with bronze reflections basally and apically (Fig. 42).

Head in dorsal view $1.2\text{--}1.3 \times$ as broad as mesoscutum and $2.6\text{--}2.7 \times$ as broad as long; in frontal view transverse-oval, $1.2\text{--}1.37 \times$ wider than high; temple $0.1\text{--}0.15 \times$ as long as eye length. POL $1.65\text{--}2 \times$ OOL, OOL $1.75\text{--}2.45 \times$ OD. Eyes $1.3\text{--}1.5 \times$ as long as high, separated by $1\text{--}1.13 \times$ their length, almost glabrous, but with very short, sparse setae. Malar space $0.48\text{--}0.52 \times$ height of eye. Mouth opening $1.2\text{--}1.27 \times$ as broad as malar space. Frons flattened on sides, without piliferous punctures.

Antennae (Fig. 46) inserted with ventral margins of toruli at level of ventral margins of eyes. Scape $6\text{--}7 \times$ as long as broad and $0.9\text{--}0.94 \times$ as long as height of eye, not reaching median ocellus. Pedicel + flagellum $1.15\text{--}1.3 \times$ as long as breadth of head and $1.45\text{--}1.6 \times$ as long as breadth of mesoscutum. Pedicel in profile $1.7\text{--}2 \times$ as long as broad. Funicle with three funicular segments decreasing in length, funicle proximally slightly stouter ($1.2\text{--}1.35 \times$) than pedicel, distally very slightly thickening (F3 $1.15\text{--}1.35 \times$ as broad as F1); F1 distinctly longer ($1.8\text{--}2 \times$) than pedicel, F1–F3 $2.6\text{--}2.9$, $2.15\text{--}2.5$, and $1.7\text{--}2.1 \times$ as long as broad, respectively. Clava three-segmented, compact, acute apically, nearly as broad as F3, $3.4\text{--}3.85 \times$ as long as broad and $0.88\text{--}0.95 \times$ as long as F2 + F3; C1 $1.3\text{--}1.65 \times$ as long as broad and $0.4 \times$ length of clava. Flagellum with sensilla placed in three or rarely two irregular rows on F1–F3, and in two or rarely three rows on C1; with short, dense, decumbent setae.

Mesosoma in dorsal view (Figs 42, 44) $1.67\text{--}1.73 \times$ as long as broad, in lateral view (Fig. 40) weakly convex dorsally, $1.8\text{--}1.85 \times$ as long as high with propodeum sloping at about 45° with respect to plane of mesoscutum



Figures 40–47. *Necremnus navonei* sp. nov. 40–42, habitus: 40, ♀ lateral; 41, ♂ lateral; 42, ♀ dorsal (2013-65). 43–46, ♀ (2013-65): 43, fore wing; 44, dorsal mesosoma; 45, metanotum and propodeum; 46, antenna. 47, ♂ antenna (2013-66).

and scutellum. Pronotum 0.3–0.35 × as long as mesoscutum. Mesoscutum transverse, 1.4–1.7 × as broad as long, and 1.1–1.3 × as long as scutellum; moderately strongly reticulate with isodiametric reticulations; setae sparse, dark, short, and strong. Scutellum convex, 1.05–1.1 × as long as broad, with two pairs of very, dark setae; sculpture of scutellum and axillae finer and not as strong as mesoscutum, the scutellum anteriorly with slightly elongate reticulations. Dorsellum coriaceous (Fig. 45). Propodeum (Figs 44, 45) medially 1.5–2 × as long as dorsellum and 0.45–0.5 × as long as scutellum; with very weak, superficially reticulate or coriaceous sculpture, and shiny and almost smooth posteriorly towards nucha and part of median panels; with fine median carina reaching 0.4–0.5 × its length; plical carina indistinct; callus with long, white setae; spiracles of medium size, short-oval, separated from metanotum by 0.4–0.6 × smallest diameter.

Fore wing (Fig. 43) 2.4–2.5 × as long as broad. Costal cell 1.2–1.3 × as long as marginal vein, 9–11 × as long as broad; ventrally with a complete row of setae and some sparse setae apically, and dorsally with a very short row of usually two or three but rarely up to five setae apically. Submarginal vein with 13–15 dorsal setae. Marginal vein 2.9–3.4 × as long as stigmal vein. Stigmal vein at an angle of 40–43° to the costal wing margin, moderately thin basally; stigma elongate, hardly thickened. Postmarginal vein 1.5–1.7 × as long as stigmal vein and 0.5–0.55 × as long as marginal vein. Basal fold pilose, with four to six setae; basal cell at least mostly open posteriorly, usually with one but sometimes with zero to three setae at apex of mediocubital fold, dorsally bare and ventrally with one to four hair bases near submarginal vein. Speculum of moderate size, reaching almost to base of marginal vein, closed posteriorly by dense or sparse setae, with two to four hair bases at lower surface. Fore wing dark, moderately dense pilosity beyond the speculum; marginal fringe short. Hind wing rounded at apex.

Gaster (Fig. 42) long-ovate, 2.35–2.8 × as long as broad, 1.45–1.55 × as long as mesosoma, 1.1–1.3 × as long as head plus mesosoma, and 0.95–1.05 × as broad as mesosoma; acute apically with syntergum transverse, 0.67–0.8 × as long as broad; T1 with posterior margin convex, reaching 0.2–0.25 × length of gaster. Ovipositor slightly protruding; cercal setae of similar length, not reaching apex of ovipositor. Hypopygium reaching 0.3–0.35 × length of gaster.

Male (Fig. 41)

Similar to female except in structure of antennae and gaster, and hyaline wings. Body length 1.65–1.8 mm. Antenna (Fig. 47) with scape 4.2–4.7 × as long as broad. Pedicel + flagellum 1.6 × as long as breadth of head, and 1.75 × as long as breadth of mesoscutum. Flagellum with four funicular segments and three-segmented

clava, F4 1.3 × as long as F3 and 0.8–0.9 × as long as clava. Funicle with three long, thin, subcylindrical rami on F1–F3, the rami with long, hair-like setae; funicular segments and all three rami with mps, but denser on all sides of R2 and R3, and sparsely on frontal surface of R1. Fore wing with marginal vein 2.7 × as long as stigmal vein; stigmal vein at an angle of 41–43° to the costal wing margin; postmarginal vein 1.5–1.65 × as long as stigmal vein and 0.55–0.6 × as long as marginal vein. Costal cell dorsally with a short marginal row of three to six setae. Legs with mesotibia darkened in apical 0.45–0.6 and metatibia darkened in apical 0.5–0.55, the dark portions dark brown to black; tarsi with basal tarsomeres pale. Gaster 2.35–2.4 × as long as broad, 0.9–1 × as long as mesosoma, and 0.7–0.75 × as long as head plus mesosoma.

Hosts

Dialectica scalarrella on *Echium vulgare* L. (Boraginaceae), based on sequenced specimens.

Variation

There is little variation in the specimens seen.

Discussion

Females of *N. navonei* have the typical characters of the *N. artynes* group, including bimaculate fore wings (Fig. 43), an elongate body (Fig. 42) and antennae (Fig. 46), and tibiae that are pale basally and dark in the apical half (Figs 40, 42). Females most closely resemble those of *N. artynes* and *N. tutae* in general appearance. Although some features overlap and there are few differences, they are confirmed by the molecular analyses. Furthermore, the host of *N. navonei* is in a different family of Lepidoptera than *N. artynes* and *N. tutae* and it has not been reared as a parasitoid of *T. absoluta*. Even though proportions sometimes overlap, females of *N. navonei* usually differ from those of *N. artynes* in having a slightly less elongate gaster (2.35–2.8 × vs. 2.6–3.15 × as long as broad, 1.45–1.55 × vs. 1.5–1.9 × as long as mesosoma, and 1.1–1.3 × vs. 1.2–1.4 × as long as head plus mesosoma in *N. artynes*). Additionally, the syntergum is transverse, 0.67–0.8 × as long as broad, whereas it is usually slightly elongate or barely transverse, 0.9–1.3 ×, in *N. artynes*. Females of *N. navonei* also usually have fainter fore wing infuscation, and although tibial colour pattern can be similar in both, with the apical half of the meso- and metatibiae being strongly darkened and the colours sharply contrasted, *N. artynes* sometimes has paler tibiae with only the extreme apex dark. Even though proportions sometimes overlap, females of *N. navonei* usually differ from those of *N. tutae* in having a slightly more elongate gaster (in *N. tutae* 1.9–2.4 × as long as broad, 1.2–1.5 × as long as mesosoma, and 0.95–1.2 × as long as head plus mesosoma). Females of

N. navonei also differ in having a longer malar space, 0.48–0.52 × vs. 0.4–0.45 × eye height in *N. tutae*, and a longer clava, 3.4–3.85 × vs. 2.8–3.5 × as long as broad in *N. tutae*. Males of *N. navonei* are very similar to related species. Details of the sensorial pores of the scape were not observed, but observed specimens have a broader clava, 3.1–3.35 × vs. 3.75–5 × as long as broad in related species, usually narrower scape, 4.2–4.7 × vs. 3.5–4.5 × as long as broad in related species, and legs that are darkened in the apical half. Males of related species sometimes have a similar leg colour pattern, although usually they are paler.

NECREMNUS TUTAE RIBES & BERNARDO SP. NOV.
(FIGS 48–56)

Etymology

Named after the genus of its host, *Tuta absoluta* (Meyrick, 1917) (Lep., Gelechiidae).

Type material

Holotype ♀: SPAIN: Cabrils, Barcelona, ex. *Tuta absoluta* on *Solanum lycopersicum*, 17.v.2011, IRTA culture. *Allotype* ♂: same data as holotype. *Paratypes* (28 ♀ 18 ♂): ITALY: 10 ♀ 3 ♂, Liguria, ex. *Tuta absoluta* on *Solanum lycopersicum*, 2012, Bioplanet culture. SPAIN: 5 ♀ 5 ♂, same data as holotype; 13 ♀ 10 ♂, same data as holotype, except dates 29.iii–15.xii.2011. The holotype, allotype, and some paratypes are deposited in CNC, and some paratypes in BMNH and the A. Ribes and U. Bernardo's collection.

Additional material (36 ♀ 31 ♂): ALGERIA: 1 ♀, Mostaganem, ex. *Tuta absoluta* on *Solanum lycopersicum*, 24.iv.2011. FRANCE: 4 ♀ 1 ♂, Berre-l'Étang, Rhone, Provence, ex. *Tuta absoluta* on *Solanum lycopersicum*, 23.vi.2010–20.vi.2011; 2 ♀, Antibes, Alpes Maritimes, ex. *Tuta absoluta* on *Solanum lycopersicum*, 23.vi.2011. MOROCCO: 6 ♀ 6 ♂, Souss-Massa Valley, ex. *Tuta absoluta* on *Solanum lycopersicum*, v.2010, leg. S. Amazouz. ITALY: 2 ♀ 3 ♂, Liguria, Bioplanet culture, ex. *Tuta absoluta* on *Solanum lycopersicum*, 2011–2012; 1 ♀, Pagani (SA), Campania, ex. *Tuta absoluta* on *Solanum lycopersicum*, 20.x.2010, leg. U. Bernardo; 2 ♀, Poggiomarino (NA), Campania, ex. *Tuta absoluta* on *Solanum lycopersicum*, 10–12.x.2010, leg. U. Bernardo; 1 ♂, Marigliano (NA), Campania, ex. *Tuta absoluta* on *Solanum lycopersicum*, 12.x.2010, leg. U. Bernardo; 1 ♂, Capaccio (SA), Campania, ex. *Tuta absoluta* on *Solanum lycopersicum*, 23.x.2011, leg. U. Bernardo; 3 ♀ 2 ♂, Pula (CA), Sardegna, ex. *Tuta absoluta* on *Solanum lycopersicum*, 8.viii.2009–23.vi.2010, leg. F. Sanna; 3 ♀ 1 ♂, Assemini, Sardegna, ex. *Tuta absoluta* on *Solanum lycopersicum*, vii.2009 [BMNH]. LIBYA: 3 ♀, W. of Tripoli, Anjilaa, ex. *Tuta absoluta* on *Solanum lycopersicum*, 15.vi.2010 [BMNH]. SPAIN: 1 ♀ 3 ♂, Cabrils, Barcelona, ex. *Tuta*

absoluta on *Solanum lycopersicum*, 4.x.2010, leg. R. Gabarra, IRTA; 4 ♀ 5 ♂, Blanes, Barcelona, ex. *Tuta absoluta* on *Solanum lycopersicum*, 4.x.2010, leg. IRTA; 6 ♀ 6 ♂, Cabrera de Mar, Barcelona, ex. *Tuta absoluta* on *Solanum lycopersicum*, 4.x.2010, leg. IRTA; 2 ♀, Mareny, Valencia, ex. *Tuta absoluta* on *Solanum lycopersicum*, vi.2008; 9 ♀ 9 ♂, La Mojonera, Almeria, ex. *Tuta absoluta* on *Solanum lycopersicum*, vi.2011. TUNISIA: 1 ♀, Kairouan, ex. *Tuta absoluta* on *Solanum lycopersicum*, v.2012, leg. K. Abbas.

Diagnosis

Female

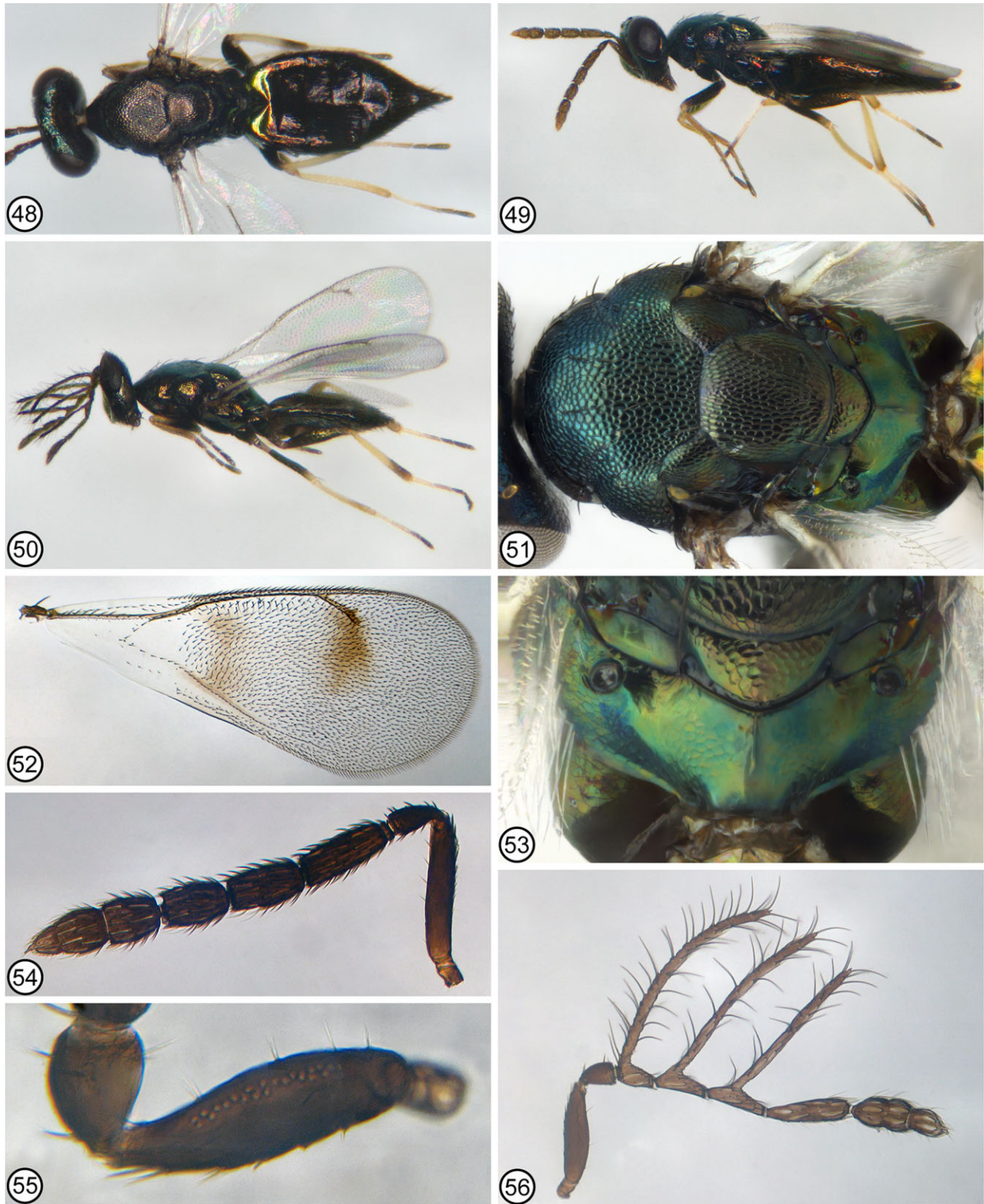
Gaster (Figs 48, 49) ovate, 1.9–2.4 × as long as broad, 1.2–1.5 × as long as mesosoma, and 0.95–1.2 × as long as head plus mesosoma; syntergum transverse, 0.6–0.85 × as long as broad. Propodeum (Fig. 53) with weak, superficially reticulate or coriaceous sculpture to partly smooth; spiracles of medium size, short-oval, and close to metanotum or separated by less than half smallest diameter. Legs (Figs 48, 49) with meso- and metatibiae entirely testaceous to dark over apical half. Fore wing usually bimaculate (Fig. 52), with infusate region behind stigmal vein and behind marginal vein basally, but rarely subhyaline.

Description

Female

Body length 1.7–3 mm. Head and mesosoma dark green, with bronze reflections on propodeum (Figs 48, 51, 53). Antenna (Fig. 54) with scape brown to black or testaceous-brown ventrally and towards base; pedicel and flagellum dark brown. Tegula black. Legs (Figs 48, 49) with coxae coloured as body; femora dark with metallic reflections, narrowly testaceous at knees; tibiae whitish-testaceous, protibia with brown stripe at inner surface, meso- and metatibiae pale testaceous and variable darkened at apex, the paler forms being entirely testaceous and darker forms being mostly blackish; protarsus brown, meso- and metatarsi usually with basal two tarsomeres whitish-testaceous and brownish at apex, but sometimes with only basitarsus or three basal tarsomeres pale. Fore wing bimaculate, usually with a brownish area beneath stigmal vein and another brown stripe under proximal end of marginal vein (Fig. 52), but infusate areas sometimes reduced to almost absent; wing venation pale brownish. Gaster dark brown, with bronze reflections dorsally on basal tergites (Fig. 48).

Head in dorsal view (Fig. 48) 1.1–1.25 × as broad as mesoscutum and 2.3–2.7 × as broad as long; in frontal view transverse-oval, 1.18–1.38 × wider than high; temple reduced, 0.05–0.15 × as long as eye length. POL 1.65–2.1 × OOL, OOL 2–2.8 × OD. Eyes 1.32–1.45 × as high as broad, separated by 0.96–1.15 × their height;



Figures 48–56. *Necremnus tutae* sp. nov. 48–50, habitus: 48, ♀ dorsal; 49, ♀ lateral; 50, ♂ lateral. 51, ♀ dorsal mesosoma. 52, ♀ fore wing. 53, ♀ metanotum and propodeum. 54, ♀ antenna. 55, ♂ pedicel and scape. 56, ♂ antenna.

eyes almost glabrous, but with very short, sparse hairs. Gena straight to weakly convex, strongly converging, malar space $0.4\text{--}0.45 \times$ height of eye. Mouth opening $1.32\text{--}1.55 \times$ as broad as malar space. Frons flattened on sides, without piliferous punctures.

Antennae (Fig. 54) inserted with ventral margins of toruli at level of ventral margins of eyes. Scape $5.25\text{--}6.5 \times$ as long as broad, $0.8\text{--}0.95 \times$ as long as height of eye, not reaching median ocellus. Pedicel + flagellum $1.15\text{--}1.27 \times$ as long as breadth of head, and $1.3\text{--}1.55 \times$ as long as breadth of mesoscutum. Pedicel in profile $1.75\text{--}2.15 \times$ as long as broad. Funicle with two anelli and three funicular segments, the first anellus laminar, the second discoid; funicular segments decreasing in length, funicle proximally slightly stouter ($1.15\text{--}1.4 \times$) than pedicel, distally very slightly thickened (F3 $1.13\text{--}1.3 \times$ as broad as F1) and slightly compressed; F1 distinctly longer ($1.6\text{--}2.1 \times$) than pedicel; F1–F3 $2.55\text{--}3.4$, $2\text{--}2.45$, and $1.65\text{--}2.15 \times$ as long as broad, respectively. Clava three-segmented, acute apically; $2.8\text{--}3.5 \times$ as long as broad; slightly broader ($1\text{--}1.13 \times$) than F3 and $0.8\text{--}0.95 \times$ as long as F2 + F3; compact or with shallow constriction between C1 and C2; C1 $1.15\text{--}1.47 \times$ as long as broad and $0.4\text{--}0.45 \times$ length of clava. Flagellum with sensilla usually placed in three irregular rows, rarely in two or four rows on F1 and F2, in two or rarely three irregular rows on F3, and in two rows on C1 and C2; with short, dense, decumbent, setae.

Mesosoma in dorsal view (Fig. 48) $1.47\text{--}1.7 \times$ as long as broad, mesosoma, in lateral view (Fig. 49) weakly convex dorsally, $1.73\text{--}1.95 \times$ as long as high with propodeum sloping at about $40\text{--}45^\circ$ with respect to plane of mesoscutum and scutellum. Pronotum $0.2\text{--}0.3 \times$ as long as mesoscutum. Mesoscutum transverse, $1.5\text{--}1.63 \times$ as broad as long, and $1.2\text{--}1.4 \times$ as long as scutellum; moderately strongly reticulate. Scutellum convex, $0.95\text{--}1.05 \times$ as long as broad, with two pairs of strong dark setae; sculpture of scutellum and axillae finer than and not as strong as mesoscutum, the scutellum anterior with slightly elongate sculpture. Dorsellum reticulate (Fig. 51) or coriaceous. Propodeum (Figs 51, 53) medially $1.5\text{--}1.83 \times$ as long as dorsellum and $0.43\text{--}0.52 \times$ as long as scutellum; with weak, superficial reticulations or coriaceous but almost smooth towards nucha and behind plical carina, and sometimes with smooth areas on median panels; with fine median carina reaching $0.5\text{--}0.75 \times$ its length; plical carina indistinct, indicated only posteriorly; callus with long, white setae; spiracles of medium size, short-oval, separated from metanotum by $0.3\text{--}0.5 \times$ smallest diameter.

Fore wing (Fig. 52) $2.3\text{--}2.45 \times$ as long as broad. Costal cell $1.07\text{--}1.23 \times$ as long as marginal vein and $8\text{--}9.3 \times$ as long as broad; ventrally with a complete row of setae and some sparse setae apically, and dorsally usually with a short row of three to six or rarely up to eight setae apically. Submarginal vein dorsally usually with

$12\text{--}15$ but rarely up to 18 setae. Marginal vein $2.9\text{--}3.6 \times$ as long as stigmal vein. Stigmal vein at an angle of $37\text{--}44^\circ$ to the costal wing margin, moderately thin basally; stigma elongate, hardly thickened. Postmarginal vein $1.35\text{--}1.7 \times$ as long as stigmal vein and $0.43\text{--}0.55 \times$ as long as marginal vein. Basal fold pilose, rarely with only one or two but usually with three to eight setae; basal cell open behind, bare dorsally and ventrally. Speculum of moderate size, reaching almost to base of marginal vein, rarely almost open but usually closed posteriorly by sparse to dense setae; speculum not effaced at lower surface. Fore wing with moderately dense, dark pilosity beyond speculum; marginal fringe short. Hind wing rounded at apex.

Gaster (Figs 48, 49) ovate, $1.9\text{--}2.4 \times$ as long as broad, $1.2\text{--}1.5 \times$ as long as mesosoma, $0.95\text{--}1.2 \times$ as long as head plus mesosoma, and $0.95\text{--}1.13 \times$ as broad as mesosoma; acute apically with syntergum transverse, $0.6\text{--}0.85 \times$ as long as broad; tergite T1 with posterior margin convex, reaching $0.2\text{--}0.25 \times$ length of gaster. Ovipositor slightly protruding; cercal setae of similar length, not reaching apex of ovipositor. Hypopygium reaching $0.3\text{--}0.4 \times$ length of gaster.

Male (Fig. 50)

Similar to female except in structure of antennae and gaster, and hyaline wings. Body length $1.2\text{--}1.9$ mm. Antenna (Fig. 56) with scape $3.5\text{--}4 \times$ as long as broad, sensorial area (Fig. 55) wide and pale, reaching $0.4 \times$ width of scape, with $20\text{--}26$ relatively large sensorial pores densely placed in one irregular row, the interspaces smaller than pore size, and usually some pores arranged in a second irregular row, the pores extending between basal $0.23\text{--}0.27$ and apical $0.76\text{--}0.78$ of the length of scape. Pedicel + flagellum $1.45\text{--}1.6 \times$ as long as breadth of head and $1.75\text{--}1.85 \times$ as long as breadth of mesoscutum. Flagellum with one laminar anellus, four funicular segments, and three-segmented clava; F4 $1.25\text{--}1.65 \times$ as long as F3 and $0.75\text{--}1.05 \times$ as long as clava. Funicle with three long, thin, subcylindrical rami on F1–F3, with long, hair-like setae; funicular segments and all three rami with mps, but denser on all sides of R2 and R3, and sparsely on frontal surface of R1. Fore wing with marginal vein $2.8\text{--}3.25 \times$ as long as stigmal vein; stigmal vein at an angle of $40\text{--}45^\circ$ to the costal wing margin; postmarginal vein $1.45\text{--}1.75 \times$ as long as stigmal vein and $0.52\text{--}0.6 \times$ as long as marginal vein. Costal cell dorsally with a short marginal row of three to six setae apically. Legs (Fig. 50) variably darkened with mesotibia usually pale or sometimes dark in apical 0.5 ; metatibia usually dark in apical $0.3\text{--}0.5$ or sometimes pale, the dark portions brown to pale brown; tarsi with one or two basal tarsomeres pale. Gaster $2\text{--}2.9 \times$ as long as broad, $0.9\text{--}1.2 \times$ as long as mesosoma, and $0.7\text{--}0.95 \times$ as long as head plus mesosoma.

Variation

Variation exists in the extent of leg darkening, depending on distribution, body size, and possibly on winter/summer generations. Usually the meso- and metatibiae are whitish-testaceous, with only the metatibia darkened pale brown in the apical 0.2–0.3. The fore wings of this form have moderately intense infuscate areas. However, some specimens have darker legs with up to 0.2–0.6 or rarely 0.9 of the mesotibia apically blackish and 0.35–0.5 or rarely 0.7 of the metatibia apically blackish, and sometimes also darker fore wing infuscation. Paler forms occur in southern areas in which the tibiae are almost entirely whitish-testaceous, only slightly darkened apically on the inner side, and usually having fore wings with less intense infuscate areas or with only one slightly infuscate area behind the stigmal vein, to almost entirely hyaline. These paler forms usually also have the basal fold and the cubital fold behind the speculum less setose, with the speculum almost open posteriorly and on the inner side, although sometimes as setose as in darker forms. Variation in antennal segment proportions occurs in small or dwarf specimens, with less distinctly elongate flagellar segments; dwarf specimens also have darker coloured tibiae.

Hosts

Tuta absoluta on *Solanum lycopersicum*, based on sequenced specimens. No native host is known. The records published as *Necremnus* sp. nr *artynes*, and most of the records published as *N. artynes* in previous surveys of *Tuta* parasitoids (Desneux *et al.*, 2010; Ferracini *et al.*, 2012; Zappalà *et al.*, 2012, 2013; Gabarra *et al.*, 2014) belong to *N. tutae*. The records of *N. metalarus* parasitizing *T. absoluta* in Spain (Urbaneja *et al.*, 2012; Zappalà *et al.*, 2013) probably also refer to dark forms of *N. tutae*, as for a similar specimen seen from Algeria.

Discussion

Necremnus tutae belongs to the *N. artynes* group of species based on females having bimaculate fore wings (Fig. 54), an elongate mesosoma and gaster (Fig. 48), relatively long postmarginal vein, and elongate funicle segments (Fig. 54). They are similar to *N. artynes* in having the propodeum (Fig. 53) weakly reticulate or coriaceous to partly smooth, the spiracles oval and placed near the metanotum, and the meso- and metatibiae variably darkened apically (Figs 48, 49). Although the differences are small, they are confirmed by the molecular results. Females also resemble those of *N. navonei*, the differences detailed in the description of the latter species. Females of *N. tutae* differ from *N. artynes* mainly in the shape of the gaster (1.9–2.4 × vs. 2.6–3.15 × as long as broad, 1.2–1.5 × vs. 1.5–1.9 × as long as mesosoma, and 1–1.2 × vs. 1.2–1.4 × as long as rest of body) compared with *N. artynes*. When the gaster is collapsed it can appear narrower than

its natural shape (appearing 2.6–3.2 × as long as broad), but its other proportions with the mesosoma and rest of body are maintained. Additionally, in females of *N. tutae* the syntergum is distinctly transverse, 0.6–0.85 × as long as broad, compared with usually slightly elongate or barely transverse, 0.9–1.3 × as long as broad in *N. artynes*. Males of *N. tutae* are very similar to those of *N. artynes*, differing in the scape having a broader sensorial area with the sensorial pores of larger size and densely placed in one irregular row such that the interspaces are smaller than pore size, and usually with some pores arranged in a second irregular row (Fig. 55). In males of *N. artynes* the sensorial area is narrow and although the sensorial pores are placed in one row they are smaller such that they are separated by interspaces greater than a pore width (Fig. 15). In addition, males of *N. tutae* have a longer marginal vein, 2.8–3.25 × compared with 2.4–2.7 × as long as the stigmal vein in *N. artynes*, and the postmarginal vein is frequently longer, 1.45–1.75 × compared with 1.3–1.65 × as long as the stigmal vein in *N. artynes*.

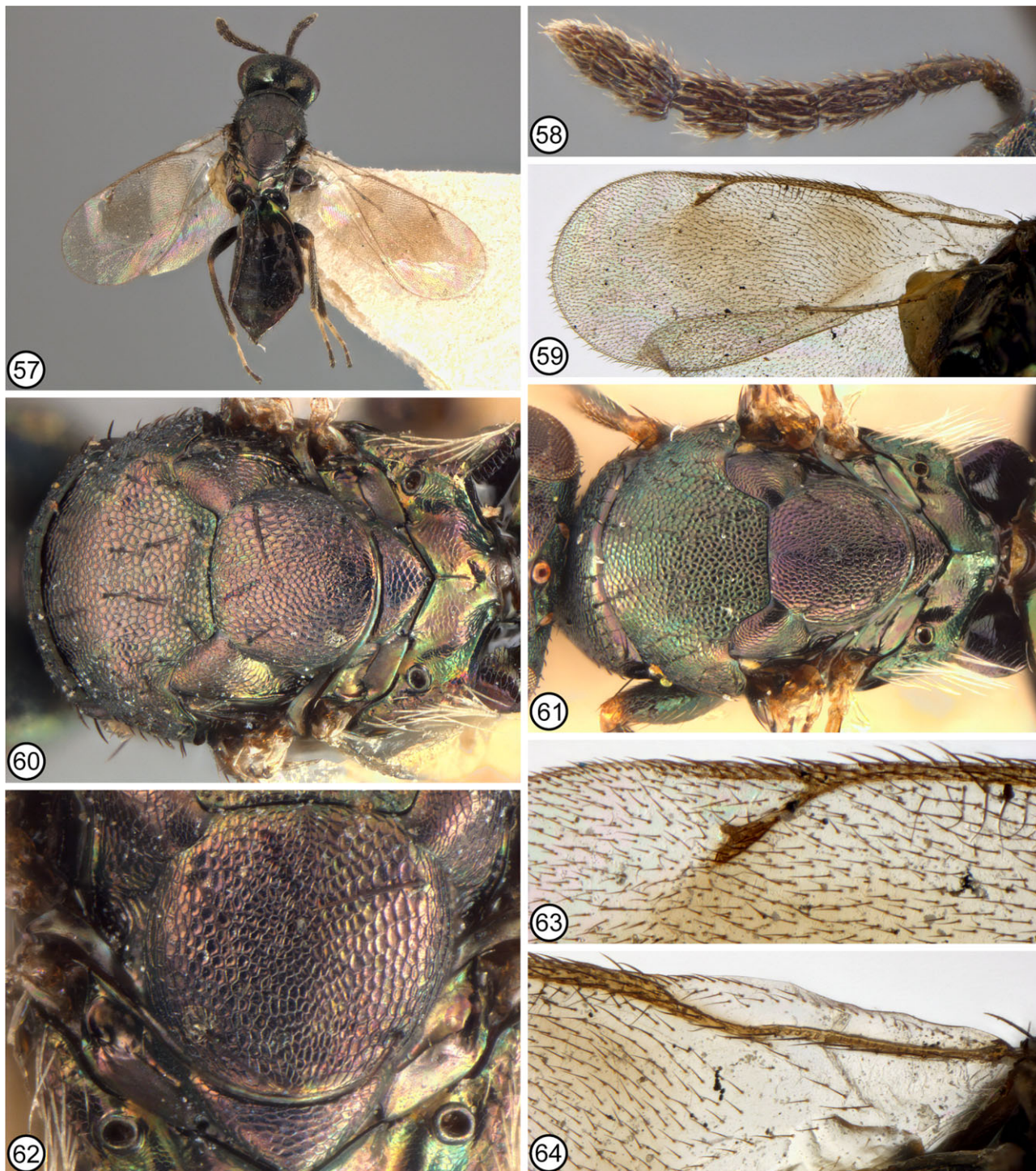
Atypical small females of *N. tutae* with dark legs also resemble *N. metalarus*, being similar in shape of the gaster and the tibiae being partly to almost entirely blackish. However, they differ in having weak, superficially reticulate or coriaceous sculpture on the propodeum and indistinct plical carinae (Fig. 53). The propodeum in *N. metalarus* is strongly reticulate and the plical carinae are distinct (Fig. 37). Colour of the tibiae and the fore wings are also usually different in typical *N. tutae*, with the meso- and metatibiae mainly pale testaceous, only darkened apically (Figs 48, 49), and the fore wings bimaculate (Fig. 52). In *N. metalarus* the meso- and metatibiae are usually dark brown from the base to the apex (Figs 27, 32) (rarely basal third testaceous), and the fore wings have only one dark area behind the stigmal vein (Fig. 29) (usually faint, but sometimes darker with indication of a second dark area behind the base of marginal vein). Consequently, colour similarities exist only in atypical specimens of both species.

Females of *N. tutae* with subhyaline wings can also resemble atypical specimens of *N. cosmopterix* that have pale tibiae, particularly because both species have the same host, *T. absoluta*. Differences are detailed in the description of the latter species, although females of *N. tutae* have at least some traces of fore wing infuscation behind the stigmal vein, whereas those of *N. cosmopterix* have entirely hyaline wings. Typical female *N. cosmopterix* also have entirely dark tibiae.

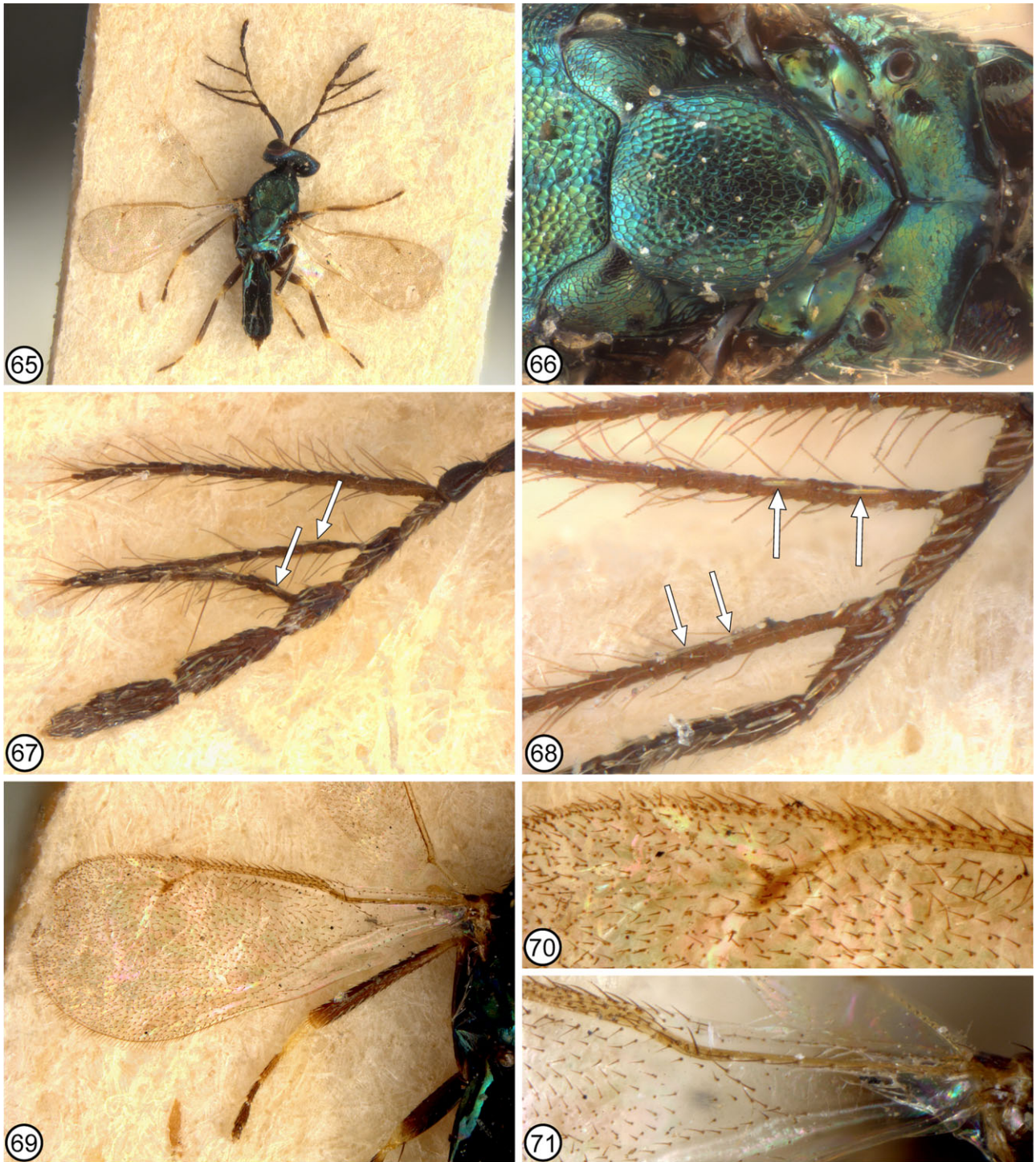
NECREMNUS COSCONIUS SPECIES GROUP

Diagnosis

Both sexes: Fore wing with postmarginal vein often a little longer than stigmal vein, but less than 1.3 × as long as stigmal vein (Figs 63, 70). *Female:* tegula



Figures 57–64. *Necremnus cosconius*. 57–60, *Eulophus amempsimus*, lectotype ♀: 57, dorsal habitus; 58, antenna; 59, left fore wing; 60, dorsal mesosoma. 61; ♀ dorsal mesosoma (2013-44). 62–64, *E. amempsimus*, lectotype ♀: 62, scutellum and dorsellum; 63, stigmatal and postmarginal veins; 64, base of fore wing.



Figures 65–71. *Necremnus cosconius*, ♂ lectotype (LT) or paralectotype (PLT). 65, LT dorsal habitus; 66, PLT scutellum-propodeum; 67, LT flagellum; 68, PLT R2 and R3; 69, LT fore wing; 70, stigmatal and postmarginal veins; 71, base of fore wing. Arrows point to multiporous plate sensilla in 67 and 68.

uniformly yellowish brown to dark brown; propodeal spiracle separated from posterior margin of metanotum (except *N. rhaecus*); fore wing hyaline to partly infuscate, most often behind marginal vein or separate regions behind stigmal vein and base of marginal vein; composite length of F1 + anelli at most about 1.7 × length of pedicel. *Male*: with elongate-slender rami having long, hair-like setae and with or without mps on R2 and R3.

NECREMNUS COSCONIUS (WALKER) (FIGS 57–71)

Eulophus cosconius Walker, 1839: 145. ♂ lectotype (BMNH, here designated).

Eulophus amempsimus Walker, 1839: 186–187. ♀ lectotype (BMNH, here designated); synonymy under *N. leucarthros* by Bouček (1959: 151), and under *N. cosconius* by Bouček & Askew (1968: 65).

Necremnus punctifrons Thomson, 1878: 235. ♀ lectotype (LUZN, not examined); lectotype designation by Hansson (1991: 33); synonymy under *N. folia* by Bouček, 1959: 152, and under *N. cosconius* by Bouček & Askew (1968: 65).

Necremnus cosconius; Graham, 1959: 184.

Type material

Walker (1839) described *Eulophus cosconius* based on at least six males, the description including also five varieties, from material collected in May and September near London, Isle of Wight, Dorsetshire, Cornwall, and Ireland. The BMNH has three males indicated to form part of the type series. A card-mounted male (Fig. 65) has the following seven labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a circular label with '38-/7.12/4' on three separate lines; (3) a small, rectangular handwritten label with 'Britain'; (4) a rectangular label with '*Eulophus Cosconius* Walker' written on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (5) a rectangular label with 'Britain' handwritten; (6) a rectangular label with '*Eulophus Cosconius* Walker LECTOTYPE: ♂ M. de V. Graham det. 1958' partly printed and handwritten; and (7) a square label with 'B.M. TYPE HYM. 5.2504'. The lectotype is entire. The other two males have a circular, blue-bordered 'PARALECTOTYPE' label. Both have the 'Britain' label, one also has a circular label with '38/7.12/3', and the other has a handwritten label with '*Cosconius*'. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate the male with Graham's lectotype label as the lectotype and the other two males as paralectotypes of *E. cosconius*.

Walker (1839) described *Eulophus amempsimus* based on at least ten females, the description also including nine varieties, from material collected April to October

from near London, Isle of Wight, Wales, and Scotland. The BMNH has six females indicated to form part of the type series. A point-mounted female (Fig. 57) has the following six labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a circular label with '38./4.5/411' on three separate lines; (3) a rectangular label with '*Eulophus Amempsimus* Walker' written on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (4) a rectangular label with 'Britain' handwritten; (5) a square label with 'B.M. TYPE HYM. 5.2503'; and (6) a rectangular label with '*Eulophus amempsimus* Walker LECTOTYPE: ♀ M. de V. Graham det. 1958' partly printed and handwritten. Of the other five females, one has a circular, red-bordered label with 'Type' and a handwritten label with '*Amempsimus*'. The other four females have the same double-sided label as the one labelled as lectotype, one also has a circular label with '38/4.5/410', one a similar label with '38/7.12/66', one a small rectangular label with '2', and one a similar label with '977'. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate the female with his lectotype label as the lectotype. We designate the other five females as paralectotypes of *E. amempsimus* and have labelled them as such because they did not previously have paralectotype labels.

Description

Female (lectotype of *E. amempsimus*)

Body (Fig. 57) about 2.4 mm in length. Head primarily dark green with coppery lustre, particularly face, under some angles of light. Antenna (Fig. 58) with scape similarly dark as flagellum; length of flagellum + pedicel about 0.9 × width of head; flagellum with length of F1 + anelli about 1.7 × dorsal length of pedicel and about 2.4 × as long as wide, F2 about 1.4 ×, F3 funicular about 1.3 ×, and clava about 2.3 × as long as wide. Mesosoma dark green with variably distinct and extensive coppery to violaceous-coppery lustres under different angles of light (Figs 57, 60); tegula uniformly dark brown. Mesonotum (Fig. 60) with mesoscutum mesh-like reticulate; scutellum reticulate-imbricate lateral to midline with only mesal margins of reticulations distinct and surfaces only slightly concave (Fig. 62). Fore wing faintly but distinctly bimaculate, with brownish infuscation behind stigmal vein and base of marginal vein (Fig. 59); basal cell apically and speculum posteriorly delineated by complete rows of setae, but mediocubital fold with only one seta basal to setae marking juncture of basal and mediocubital folds (Fig. 64); speculum broadly bare dorsally (Fig. 64); approximate ratio of cc : mv : stv : pmv = 79:75:20:24. Legs dark except with protibia dorsolongitudinally, knees narrowly, and basal

two tarsomeres of middle and hind legs pale. Metanotum with dorsellum very shallowly reticulate-imbricate to imbricate-alutaceous (Figs 60, 62). Propodeum (Figs 60, 62) with median carina over slightly more than basal half, otherwise entirely or mostly mesh-like alutaceous to alutaceous-imbricate, the sculpture sometimes stronger, with raised ridges, only posterolaterally; spiracle comparatively large, separated from posterior margin of metanotum by about $0.5 \times$ minimum internal diameter. Gaster (Fig. 57) brown with slight greenish lustre basally; about $1.9 \times$ as long as wide and about $1.3 \times$ length of mesosoma; syntergum short.

Male (lectotype of *E. cosconius*)

Body (Fig. 65) about 1.6 mm in length. Head primarily bright green with bluish purple lustre within scrobal depression. Antenna (Fig. 65) with scape about $4.1 \times$ as long as wide; length of funiculars and clava about 1.2, 1.6, 1.6, 2.3, and $2.8 \times$ length of pedicel, with F4 about $3 \times$ and clava about $3.4 \times$ as long as wide; rami with long, hair-like setae, elongate-slender with R1 about $2.3 \times$ length of scape, R1 without mps, R2 with single mps on either side near base, and R3 with one or two mps on either side near base (Fig. 67). Mesosoma bright green similar to head, without distinct coppery lustre (Fig. 65); tegula uniformly brown. Mesonotum with mesoscutum mesh-like reticulate; scutellum lateral to midline imbricate to very shallowly reticulate-imbricate, the reticulations flat or with only mesal margins slightly raised (Fig. 66). Fore wing hyaline (Fig. 65); basal cell apically and speculum posteriorly delineated by complete rows of setae, but mediocubital fold with only one or two setae basal to seta marking juncture of basal and mediocubital folds (Fig. 71); speculum broadly bare dorsally (Fig. 71); approximate ratio of $cc : mv : stv : pmv = 61:54:17:22$. Legs (Fig. 65) dark except with protibia dorsolongitudinally, knees and basal tarsomeres pale, the second tarsomeres yellowish to brown and apical two tarsomeres brown. Metanotum with dorsellum mesh-like coriaceous-imbricate (Fig. 66). Propodeum (Fig. 66) with median carina over less than basal half, otherwise mesh-like coriaceous to alutaceous-imbricate; spiracle comparatively large, separated from posterior margin of metanotum by about $0.5 \times$ minimum internal diameter.

Distribution

Europe (see Noyes, 2013).

Hosts

Unknown (see Noyes 2013 for plant associates).

Discussion

The paralectotypes of *N. amempsimus* vary in the colour of the mesosoma, sometimes being more extensively dark green with less distinct violaceous-coppery lustre

(Fig. 61) than for the lectotype (Fig. 60). Some also have the second tarsomeres yellowish to brown, the fore wing infuscation less distinct or the mediocubital fold with up to two setae basal to the seta that delimits the junction of the basal and mediocubital folds. However, all of the females designated as paralectotypes of *E. amempsimus* seem to be conspecific except for the one with the circular label stating '38/4.5/410', which is *N. tidius* based on fore wing setal pattern (narrow speculum and more extensively setose mediocubital fold) in combination with length of the postmarginal vein. The species identity of the '38/7.12/66' female is less certain because it lacks evident fore wing infuscation and appears to have a somewhat longer postmarginal vein, making it more similar to *N. tidius*-group females, although the propodeal spiracle is slightly separated from the metanotum and the mesosoma is comparatively darkly coloured.

Eulophus amempsimus was first synonymized under *N. leucarthros* by Bouček (1959) and subsequently under *N. cosconius* by Bouček & Askew (1968) based on the opinion of Marcus Graham, but in both instances without giving reasons for the synonymy. Even though males are a much brighter green than are females (cf. Figs 57, 65), the sex association between *N. amempsimus* (female) and *N. cosconius* (male) is probably correct based on type material of both apparently having a comparatively short postmarginal vein, the propodeal spiracles being slightly separated from the metanotum (cf. Figs 62, 66), and having similar scutellar sculpture patterns. Females of the type series of *N. amempsimus* have the scutellum quite distinctly reticulate-imbricate (Fig. 62) or even somewhat scalloped in appearance. Males of the type series of *N. cosconius* have a similar pattern although the sculpture is shallower and therefore less distinct (Fig. 66), but this is probably correlated with their smaller body size relative to females.

Differentiation of female *N. cosconius* and *N. leucarthros* can sometimes be questionable, particularly for females in which the length of the postmarginal vein cannot be measured accurately. Females are similar in colour pattern, sculpture, and structure, including both having the propodeal spiracles slightly separated from the metanotum and uniformly dark tegulae. Although *N. leucarthros* females have a longer postmarginal vein, the apical limit of this vein can sometimes be difficult to discern, particularly card-mounted females with the wings glued to the card, and some females that we identify as *N. cosconius* have the postmarginal vein approaching $1.3 \times$ the length of the stigmal vein. However, those *N. leucarthros* females for which the postmarginal vein cannot be measured accurately always have entirely hyaline fore wings and usually are much brighter green to bluish-green without extensive coppery lustre (Figs 140, 141, 145). Typical females that we identify

as *N. cosconius* have the fore wings at least faintly, inconspicuously infuscate behind the base of the marginal vein and/or the stigmal vein and usually are a darker green with variably extensive coppery to violaceous-coppery lustres (Figs 57, 60–62). Females of both species appear to have a variable number of setae on the mediocubital fold basal to the basal fold, with up to four setae within about its basal half in *N. cosconius*. The morphological limits of *N. cosconius* and *N. folia* are also not fully resolved because of presence or absence and variation in fore wing infuscation and the reliability of scutellar sculpture and protibial colour pattern for differentiating females of the two species (see under *N. folia*). The fore wing colour pattern of typical *N. cosconius* females (Fig. 59) is similar to some *N. artynes*-group females, but the latter have F1 comparatively much longer (cf. Figs 14, 58).

Paralectotype males of *N. cosconius* have one or two mps on either side of the second and third ramus within the basal half of the respective ramus (Fig. 68). As all have their fore wings glued to the card mounts (Figs 69, 70), we are unsure of the exact length of the postmarginal vein relative to the stigmal vein.

NECREMNUS CROTON (WALKER) (FIGS 72–77)

Eulophus croton Walker, 1839: 182. ♀ lectotype (BMNH, here designated).

Necremnus croton; Graham, 1959: 184.

Type material

There is no indication in the original description of whether the type series consisted of more than a single female. The original description stated that the species was collected near London. The BMNH has a single, card-mounted female (Fig. 72) with the following five labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular label with 'Croton' handwritten on one side and '[?]ENT GAR' printed on the other side; (3) a rectangular label with 'Pteromalus Croton Walker' handwritten on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (4) a rectangular label with 'Eulophus Croton Walker LECTOTYPE: ♀ M. de V. Graham det. 1958' partly printed and handwritten; and (5) a square label with 'B.M. TYPE HYM. 5.2501'. The lectotype is entire, but the head is collapsed and the flagellum is mostly covered in glue (Fig. 73). As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate this female as the lectotype of *E. croton*.

Description

Female (lectotype)

Body (Fig. 72) almost 1.5 mm in length. Head strongly collapsed, but primarily dark brown with very slight

violaceous lustre under some angles of light. Antenna (Fig. 73) with scape similarly dark as flagellum; length of flagellum + pedicel at most about 1.2 × width of head (head strongly collapsed and width estimated); flagellum with length of F1 + anelli about 1.5 × length of pedicel and about 2.1 × as long as wide, F2 about 1.8 ×, F3 about 1.5 ×, and clava about 2.6 × as long as wide. Mesosoma (Figs 72, 74) with mesonotum bluish-green to purple under some angles of light, but dorsellum and propodeum more distinctly green (Fig. 75); tegula uniformly yellowish brown. Mesonotum (Fig. 74) with mesoscutum distinctly mesh-like reticulate; scutellum entirely, distinctly reticulate, the reticulations somewhat larger and more elongate laterally than along midline. Fore wing (Figs 72, 76) hyaline; basal cell and speculum posteriorly delimited by complete rows of setae (Fig. 77); speculum broadly bare dorsally; approximate ratio of cc : mv : stv : pmv = 53:36:15:[?]. Legs (Fig. 72) with profemur dark brown, protibia and protarsus lighter brown with knee and tibia dorsolongitudinally pale; meso- and metafemora dark brown, metatibia brown except extreme base and apex pale, but mesotibia with about basal half more brownish yellow, and meso- and metatarsi with basal two tarsomeres pale and apical two tarsomeres brownish. Metanotum with dorsellum distinctly reticulate (Fig. 75). Propodeum (Fig. 75) with entire median carina, otherwise reticulate to more reticulate-imbricate toward spiracles; spiracle comparatively small, separated from posterior margin of metanotum by about minimum internal diameter. Gaster (Fig. 72) brown; about 1.9 × as long as wide and about 1.25 × length of mesosoma; syntergum short.

Male

Unknown.

Distribution

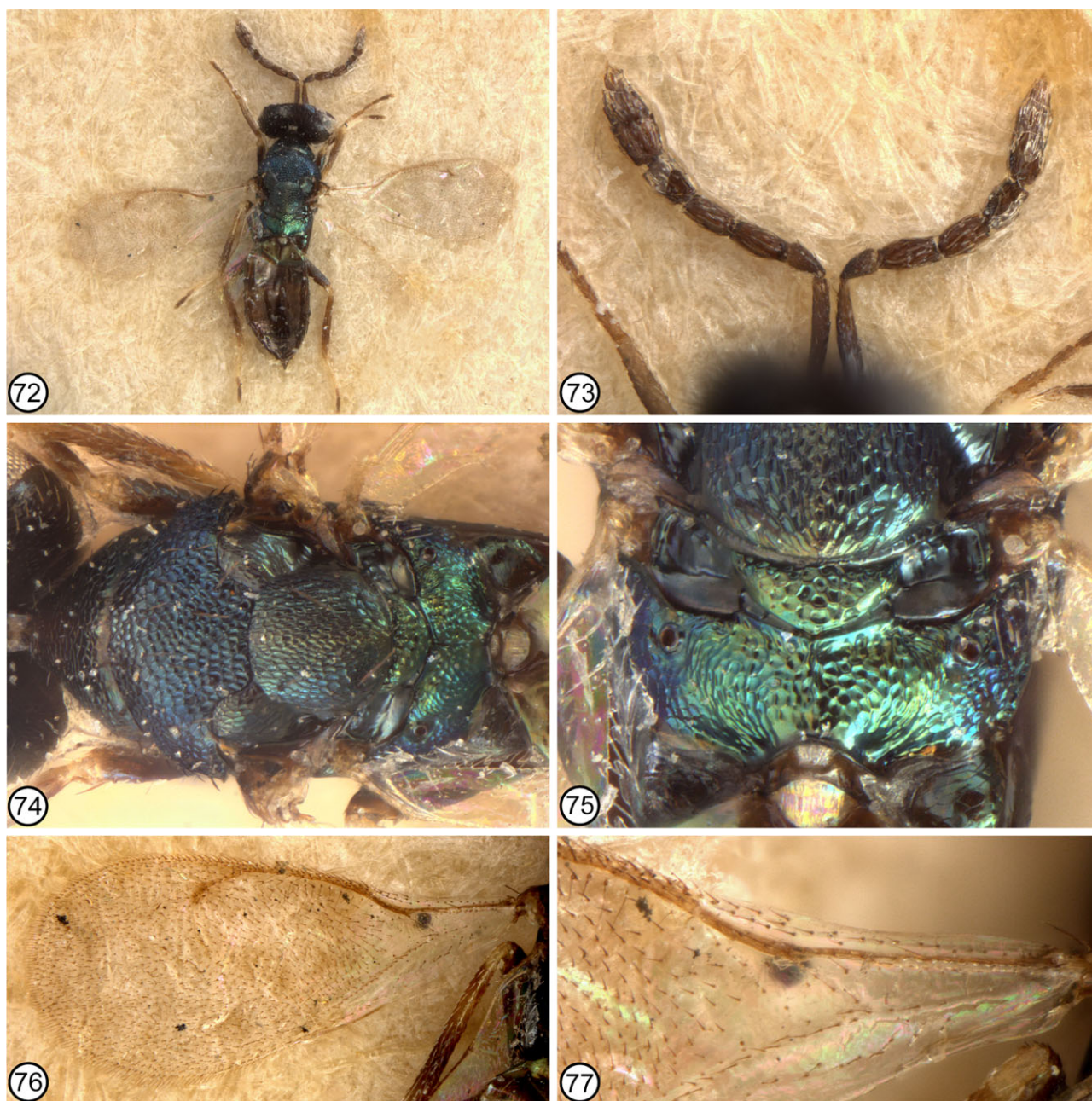
England, Macedonia, Sweden, Turkey (Noyes, 2013).

Hosts

Pseudobankesia macedoniella (Rebel) (Lepidoptera: Psychidae) (Bouček, 1977).

Discussion

Females of *N. croton* and *N. capitatus* Bouček differ from those of other described *Necremnus* (except *N. propodealis* Bouček, which has pale legs beyond the coxae) by their comparatively strongly sculptured mesosoma (Fig. 74), particularly the propodeum (Fig. 75). Accurate measurement of the length of the postmarginal vein of the lectotype of *N. croton* is questionable because the wing is glued to the card and the exact apical extent of the vein is not clear (Fig. 76), although the vein appears to be relatively short compared with the stigmal vein. Askew (1964) stated that both *N. croton* and



Figures 72–77. *Necremnus croton*, ♀ lectotype. 72, dorsal habitus; 73, antennae; 74, dorsal mesosoma; 75, metanotum and propodeum; 76, fore wing; 77, fore wing base.

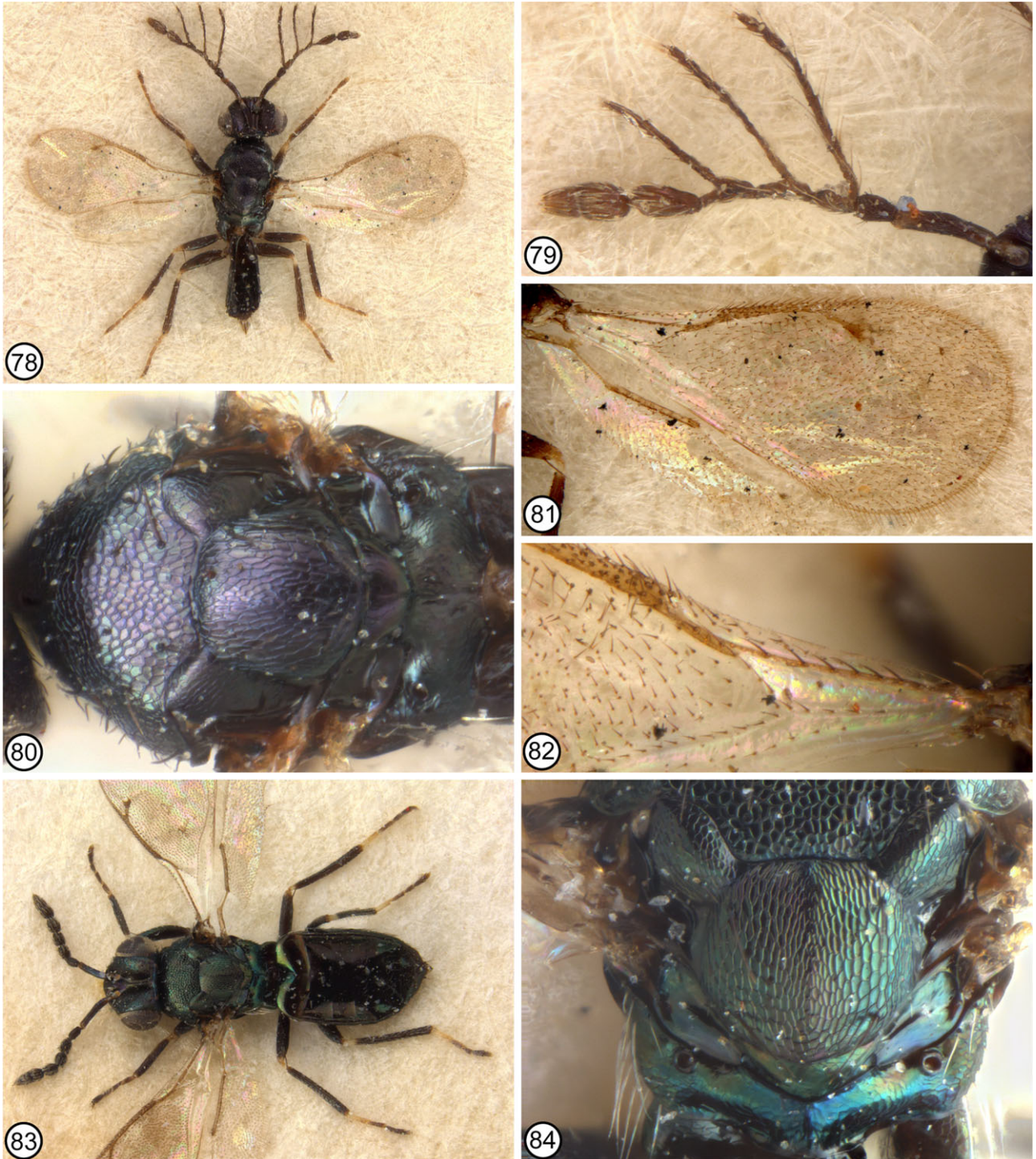
N. capitatus have the postmarginal vein only slightly longer than the stigmal vein. Females of the two species are very similar, but according to Askew (1964) *N. capitatus* females have extensively pale tibiae with the meso- and metatibiae at most infuscate only apically, and a less elongate body (gaster about $1.4 \times$ as long as wide and only about $0.77 \times$ the combined length of the head and mesosoma), but with longer funicular segments (F1 at least $3 \times$ as long as wide). The lectotype of *N. croton* has the gaster about twice as

long as wide and subequal in length to the head and mesosoma (Fig. 72). However, the gaster is strongly collapsed dorsally, which may result in a slightly greater length to width ratio, and the head is also collapsed so as to appear strongly transverse in dorsal view (Fig. 72), which probably results in a somewhat longer gaster to head plus mesosoma ratio than in fully inflated, natural specimens. Perhaps a more reliable feature is that F1 + anelli is only about $2.1 \times$ as long as wide (about $1.9 \times$ excluding anelli, Fig. 73).

Additionally, at least the metatibia is infuscate except very narrowly basally and apically. The mesotibia has a similar colour pattern except about the basal half is somewhat paler, more brownish yellow (Fig. 72).

NECREMNUS FOLIA (WALKER) (FIGS 78–84)

Eulophus folia Walker, 1839: 147. ♂ lectotype (BMNH, here designated).



Figures 78–84. *Necremnus folia*. 78–82, ♂ lectotype: 78, dorsal habitus; 79, left antenna; 80, dorsal mesosoma; 81, fore wing; 82, fore wing base. 83, ♀ dorsal habitus (2013-76). 84, scutellum-propodeum (2013-76).

Eulophus diyllus Walker, 1939: 185: ♀ (BMNH, lost); synonymy by Bouček & Askew (1968: 65).

Necremnus folia Graham, 1959: 184.

Type material

There is no indication in the original description of whether the type series of *E. folia*, collected in Ireland, consisted of more than a single individual. The BMNH has a single, card-mounted male (Fig. 78) with the following four labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular label with 'Folia' handwritten on one side and 'Quarts' on one line and 'per Dozen.' on another line printed on the other side; (3) a rectangular label with 'Eulophus Folia Walker LECTOTYPE: ♂ M. de V. Graham det. 1958' partly printed and handwritten; and (4) a square label with 'B.M. TYPE HYM. 5.2511'. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate this male as the lectotype of *E. folia*. The lectotype is entire.

In addition to the lectotype, the BMNH has a point-mounted male with the following five labels: (1) a circular label with '38/7.12/68' on three separate lines; (2) a rectangular label with 'Clermont' handwritten; (3) a rectangular label with 'Eulophus Tyrrhenus Walker' written on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (4) a rectangular label with '♂ in genus *Comedo* Ch. Ferriere det.' partly handwritten and partly printed; and (5) a rectangular label with 'Necremnus' handwritten. This male is from France (Walker, 1846a), is a *Necremnus*, and is very similar to the lectotype of *N. folia*, including lacking mps from all three rami and having the propodeal spiracle separated slightly from the metanotum. The dorsal mesosomal sculpture is stronger than for the lectotype, but this is to be expected because it is a larger individual. The scutellum has similar elongate, imbricate to very shallowly reticulate-imbricate sculpture.

Description

Male (lectotype)

Body (Fig. 78) about 1.2 mm in length. Head dark brown with very slight violaceous lustre under some angles of light. Antenna (Fig. 79) with scape about 3.4 × as long as wide; length of funiculars and clava about 1.2, 1.4, 1.5, 1.8, and 2.3 × length of pedicel, with F4 about 2.25 × and clava about 2.5 × as long as wide; rami with long, hair-like setae, elongate-slender with R1 about 2.2 × length of scape, and all rami without mps. Mesosoma dark brown with very slight violaceous lustre under some angles of light (Figs 78, 80); tegula uniformly brown. Mesonotum (Fig. 80) with mesoscutum mesh-like reticulate; scutellum longitudinally, shallowly reticulate-

imbricate to imbricate. Fore wing hyaline (Figs 78, 81); basal cell apically and speculum posteriorly delineated by complete rows of setae, and mediocubital fold basal to basal fold setose for about two-thirds of length, with four setae basal to seta marking juncture of basal and mediocubital folds (Fig. 82); speculum broadly bare dorsally; approximate ratio of cc : mv : stv : pmv = 45:34:13:16. Legs dark except with protibia longitudinally, knees and at least basal tarsomeres pale, the tarsi increasingly more distinctly brown apically. Metanotum finely mesh-like coriaceous. Propodeum (Fig. 80) without distinct median carina, mesh-like coriaceous-alutaceous to very shallowly reticulate; spiracle slightly separated from posterior margin of metanotum.

Female

Body (Fig. 83) about 1.5–1.7 mm in length. Head dark brown with variably distinct and extensive green to blue or limited coppery lustres under some angles of light. Antenna dark brown, the scape with only very slight metallic lustre; length of flagellum + pedicel subequal to about 0.9–1.0 × width of head; flagellum with length of F1 + anelli about 1.3–1.8 × as long as wide and 1.0–1.25 × length of pedicel, F2 and F3 both about 1.3–1.8 × as long as wide, and clava about 2.5–2.6 × as long as wide. Mesosoma (Fig. 83) dark with variably distinct green to coppery or violaceous-coppery lustres; tegula uniformly dark brown. Mesonotum with mesoscutum mesh-like reticulate; scutellum reticulate-imbricate with reticulations usually comparatively elongate-narrow (Fig. 84). Fore wing hyaline or at most very faintly and inconspicuously infuscate between stigmal vein and base of marginal vein; basal cell apically and speculum posteriorly delineated by complete rows of setae, and mediocubital fold setose over at most apical half of basal cell; speculum broadly bare dorsally; postmarginal vein subequal in length to stigmal vein. Legs dark except protibia at most dorsolongitudinally pale within basal half, and knees and basal tarsomeres pale. Metanotum finely mesh-like coriaceous. Propodeum (Fig. 84) with almost complete median carina, mesh-like coriaceous-alutaceous to sometimes more distinctly reticulate mesally; spiracle slightly separated from posterior margin of metanotum.

Distribution

Europe (see Noyes, 2013).

Hosts

Ceutorhynchus sp. (Gomez & Zamora, 1994) on *Hormathophylla spinosa* (L.) (Brassicaceae). This record requires confirmation of the parasitoid identification

because the parasitoids of Curculionidae on Brassicaceae usually belong to the *N. tidius* group.

Discussion

We remove *N. rhaecus* from synonymy under *N. folia* for the reasons discussed under the former name. Females that we identify as *N. folia* more closely resemble the lectotype of *N. folia* than does the lectotype of *N. rhaecus* and also more closely fit the concepts given in the keys by Bouček (1959) and Graham (1959). They differentiated females of *N. folia* from those of *N. cosconius* by the former having the fore wings hyaline or faintly, uniformly infuscate. Females of *N. cosconius* were said to nearly always have two infuscations that sometimes are joined or rarely absent. However, the couplet acknowledges the variability of fore wing infuscation and the possibility that some *N. cosconius* entirely lack infuscation. Some *N. cosconius*-group females that we have seen with entirely hyaline fore wings have a more elongate-slender, reticulate-imbricate scutellum similar to the lectotype of *N. folia* (Fig. 80), whereas others have a more uniformly mesh-like reticulate-imbricate scutellum similar to that of *N. cosconius* (Fig. 62). Females with the former scutellar sculpture are somewhat smaller than typical *N. cosconius* females, as are some with the latter scutellar sculpture and, unlike typical *N. cosconius* females, all have the protibia longitudinally pale only within about its basal half. Molecular analyses would provide valuable independent information to determine more confidently the morphological limits of the two species and the reliability of different features for species differentiation.

NECREMNUS RHAECUS (WALKER) REVISED STATUS (FIGS 85–91)

Eulophus rhaecus Walker, 1939: 182–183. ♀ lectotype (BMNH, here designated); synonymy under *Necremnus folia* by Bouček & Askew (1968: 65).

Type material

There is no indication in the original description of whether the type series of *E. rhaecus*, collected near London, consisted of more than a single individual. The BMNH has a single, card-mounted female (Fig. 85) with the following five labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular label with '*Eulophus Rhaecus* Walker' written on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (3) a rectangular label with 'in genus *Necremnus* Ch. Ferriere det.' (determination line printed); (4) a rectangular label with '*Eulophus Rhaecus* Walker LECTOTYPE: ♀ M. de V. Graham det. 1958' partly printed and handwritten on it; and (5) a square label with 'B.M. TYPE HYM. 5.2510'. As Graham did not validly designate a lectotype through

publication under ICZN rules, in order to stabilize the concept of the name we designate this female as the lectotype of *Eulophus rhaecus*. The lectotype is entire.

Description

Female (lectotype)

Body (Fig. 85) about 1.4 mm in length. Head dark brown. Antenna (Fig. 86) with scape similarly dark as flagellum; length of flagellum + pedicel about 1.1 × width of head; flagellum with length of F1 + anelli about 1.75 × as long as wide and about 1.2 × dorsal length of pedicel; F2 about 1.5 ×, F3 about 1.7 ×, and clava about 3 × as long as wide. Mesosoma brown with variably distinct green lustre under different angles of light (Figs 85, 89); tegula uniformly brownish yellow. Mesonotum (Fig. 87) with mesoscutum mesh-like reticulate; scutellum mostly mesh-like coriaceous, at most only very obscurely imbricate or reticulate-imbricate laterally under some angles of light. Fore wing (Figs 85, 88) hyaline; basal cell apically and speculum posteriorly delimited by complete rows of setae, and mediocubital fold with only two setae basal to seta marking juncture of basal and mediocubital folds (Fig. 89); speculum broadly bare dorsally (Fig. 89); approximate ratio of cc : mv : stv : pmv = 50:42:17:[?]. Legs (Fig. 85) dark except with protibia dorsolongitudinally, knees and basal tarsomeres pale. Metanotum with dorsellum very finely mesh-like coriaceous (Fig. 87). Propodeum (Fig. 87) with complete median carina, otherwise mesh-like coriaceous-alutaceous; spiracle with anterior margin slightly overlapped by posterior margin of metanotum. Gaster (Fig. 85) brown; about as 1.75 × long as wide and about 1.1 × length of mesosoma; syntergum short.

Male

Unknown.

Distribution

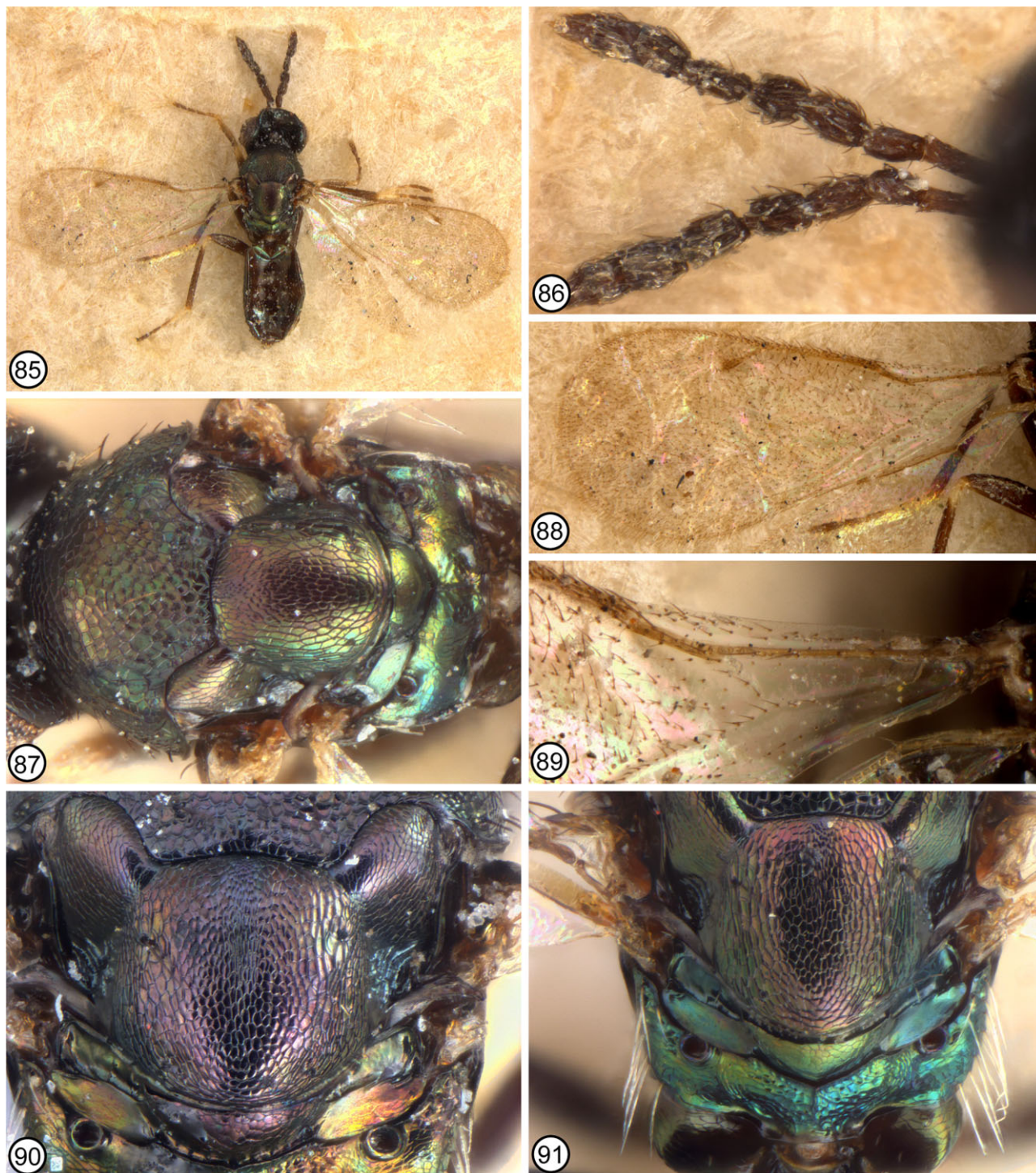
England, Sweden.

Hosts

Unknown.

Discussion

Eulophus rhaecus was synonymized under *N. folia* by Bouček & Askew (1968) based on the opinion of Marcus Graham, but without giving reasons for the sex association resulting in the synonymy. Furthermore, when Graham (1991) designated a lectotype from OXUM to stabilize the generic placement of *Eulophus thespius* Walker, he stated that the only Walker specimen labelled as *E. thespius* in the BMNH disagrees markedly with the original description and is a female of *N. folia*. This is true in the sense that it has a similar scutellar sculptural pattern and the anterior margin



Figures 85–91. *Necremnus rhaecus*. 85–89, ♀ lectotype: 85, dorsal habitus; 86, antennae; 87, dorsal mesosoma; 88, fore wing; 89, fore wing base. 90, ♀ scutellum and metanotum (2013-75); 91, ♀ scutellum-propodeum (2013-77).

of the propodeal spiracle slightly overlapped by the metanotum (Fig. 90), as well as the mediocubital fold mostly bare. The postmarginal vein is only slightly longer than the stigmal vein. The female is larger (about

2 mm) than the lectotype of *E. rhaecus*. Probably correlated with this is the scutellar sculpture being more distinct with more obvious, longitudinally reticulate-imbriate sculpture laterally, but mesally still quite

broadly mesh-like coriaceous with distinctly impressed lines (Fig. 90). The propodeum is also quite distinctly reticulate mesally, possibly also correlated with its larger size. We have also seen a single female from Sweden (BMNH) that is morphologically similar to the latter female (Fig. 91). By contrast, the lectotype male of *N. folia* has the propodeal spiracles slightly separated from the metanotum (Fig. 80), a more longitudinally reticulate-imbricate scutellum (Fig. 80), and a more extensively setose mediocubital fold (Fig. 82). Because of these differences and because we observed females that appear to fit Bouček's (1959) and Graham's (1959) key concept of *N. folia* (see under *N. folia*), we believe that the synonymy of *N. rhaecus* under *N. folia* is incorrect. We therefore re-establish this name as a valid species. Molecular analyses or association of the sexes through rearing would provide additional evidence of species status.

Females of *N. rhaecus* could be keyed to *N. hippia* if the length of the postmarginal vein is not apparent because of their slightly overlapped propodeal spiracles and uniformly coloured tegulae, but even the smallest *N. hippia* females have the scutellum reticulate-imbricate to slightly scalloped in appearance. Males of *N. rhaecus* presumably have a similar scutellar sculpture pattern as females and would probably also key to *N. hippia*, assuming the presence of mps on the second and third rami.

NECREMNUS TIDIUS SPECIES GROUP

Diagnosis

Both sexes: Fore wing with postmarginal vein at least $1.3 \times$ length of postmarginal vein. *Female:* tegula variable in colour pattern; propodeum variable in placement of spiracle relative to posterior margin of metanotum; fore wing hyaline; composite length of F1 + anelli at most about $1.8 \times$ (usually only $1.6 \times$) length of pedicel, and at most $2.8 \times$ as long as broad. Meso- and metatibiae with only extreme base (knees) abruptly pale, tarsi usually with only basitarsi pale. *Male:* antenna with mps on one or both of R2 and R3 but lacking from R1 and with long, hair-like setae on all three rami or, if with mps on all three rami (*N. leucarthros*), then setae very short, similar in length to mps (Fig. 150). Hosts include Coleoptera, usually Curculionidae, but possibly also insects of other orders.

NECREMNUS AENIGMATICUS GIBSON SP. NOV.

(FIGS 92–102)

Etymology

The species name is derived from the Latin *aenigma*, 'something obscure, a mystery', in reference to its molecular distinctiveness but otherwise yet question-

able morphological differentiation from other similar species as *N. duplicatus* and *N. hippia*.

Type material

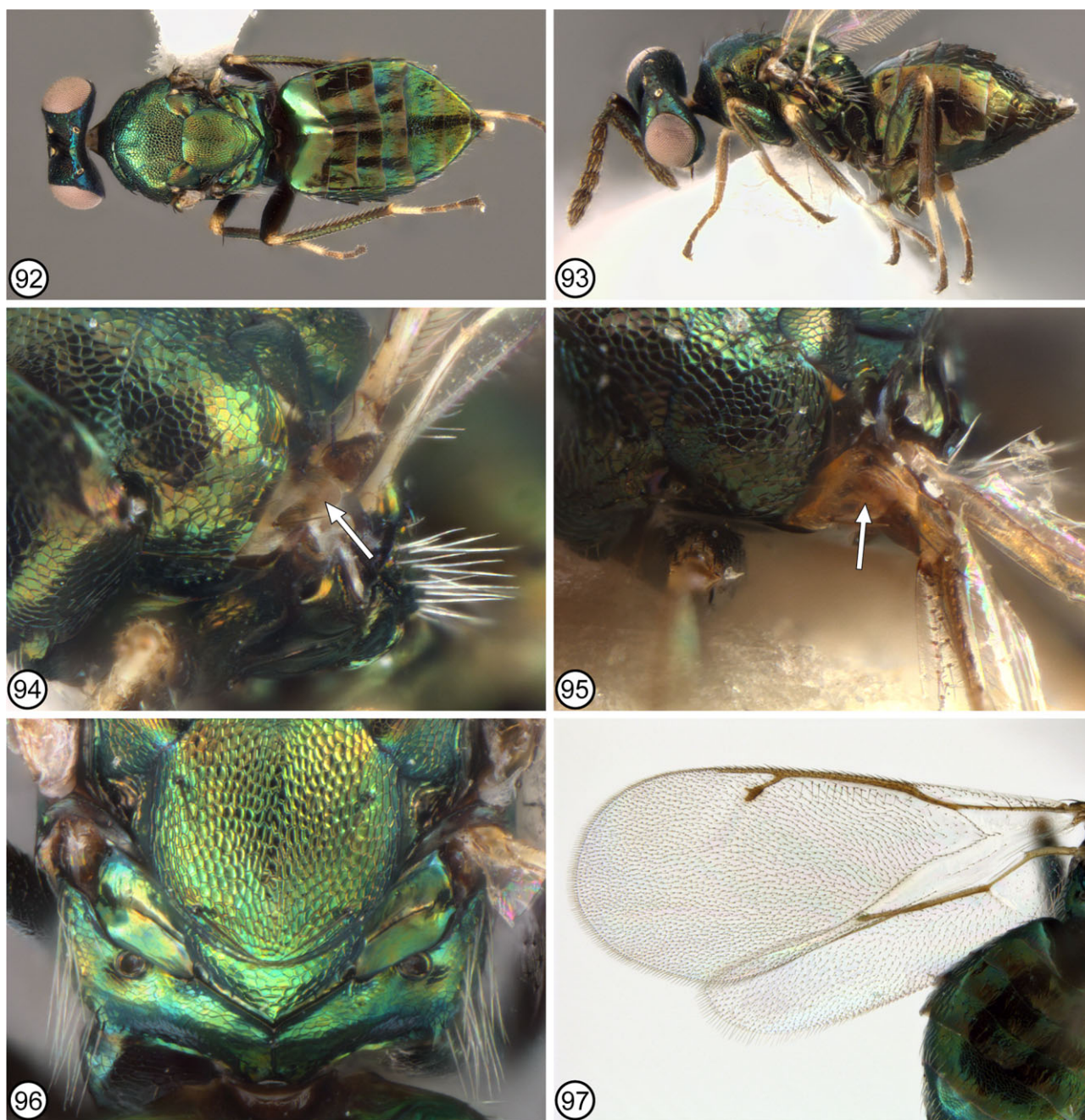
Holotype ♀ (CNC). GERMANY: Schleswig-Holstein, Bellin, 4.vii.2010, ex. *Ceutorhynchus typhae* on *Capsella bursa-pastoris* in canola field, T. Haye (point-mounted, critical-point dried, entire). *Allotype* ♂ (CNC). Same data and condition as holotype. *Paratypes* (61♀, 15♂): DENMARK: Jylland, Bov, 24/9 1955, K.-J. Hedqvist (2♀ BMNH). Jylland, Klitmølle, 22/9 1955, K.-J. Hedqvist (1♀ BMNH). ENGLAND: B. Cooke Coll. 84-52, Hippis W (1♀ BMNH). CB, Manea, A.L. Winfield, B.M. 1959-582, ex. pod of *Brassica juncea* var. Trowse, opened 24.vii.1959, pupa within em. 6.viii.1959 (1♀ BMNH). Harpenden dist., 11.IX.1943 (4♀, BMNH). FRANCE: Moulinet, sweeping herbaceous layer, NT165 (1♀). GERMANY: 21♀ (including NT90, NT92, NT93) and 14♂ (including NT67, NT91) same data as holotype. Bonn, IX.36, Weiss-Wichert, f. Turnip shoots (1♀, 1♂ BMNH). Nahkamp, Ostholstein, collected 14.VI.2000, ref. no.: #2 (1♀ NMBE), ref. no.: (1♀ NMBE), *Capsella bursa-pastoris* ex. *Ceutorhynchus floralis*. Scharnhagen nearby Kiel, S-H [or] Schleswig-Holstein, Coll: 16.06.01, Em: 28 (1♀), 29(1♀) 0.06.01, 02 (1♀), 03 (1♀), 04 (4♀), 05 (1♀), 06(1♀), 09(2♀) 0.07.01, Beate Klander, Scharnhagen/SCH, GPS latitude N54°26.972, GPS longitude E10°06.306, Ex: *Ce. uto. floralis*, In: *C. bursa-pastoris*, Leg. Klander/CABI-CH (all NMBE). SWEDEN: Sk., Gislöv, 8/9 1955, K.-J. Hedqvist (7♀ BMNH). Sk., Åhus, 3/8 1956, K.-J. Hedqvist (1♀ BMNH). Sk., Karpalund, 6/8 1967, K.-J. Hedqvist (1♀ BMNH). Sm., Visingö, 19/10 1955, K.-J. Hedqvist (4♀ BMNH). Upl., Vallentuna, 1/6 1956, K.-J. Hedqvist (1♀ BMNH). UNKNOWN LOCALITY: three handwritten labels with *Ptilius/Necremnus/Ptilius* (1♀ BMNH).

Additional material (2♀): ENGLAND: Little Cheyne, Kent, 1975, ex. *Ceutorhynchus* sp. in *B. napus* pods, leg. J. Dale (1♀, coll. R. R. Askew). SPAIN: Cabrils, Barcelona, 31.iii.2005, on *Sinapis alba* flowers, IRTA (1♀, coll. A. Ribes); Sarroca, Lleida, ex. *Diplotaxis erucoides*, col. 11.iv.2014, em. 21–30.iv.2014 (1 ♀ 2 ♂, coll. A. Ribes).

Description

Female (holotype, Fig. 93)

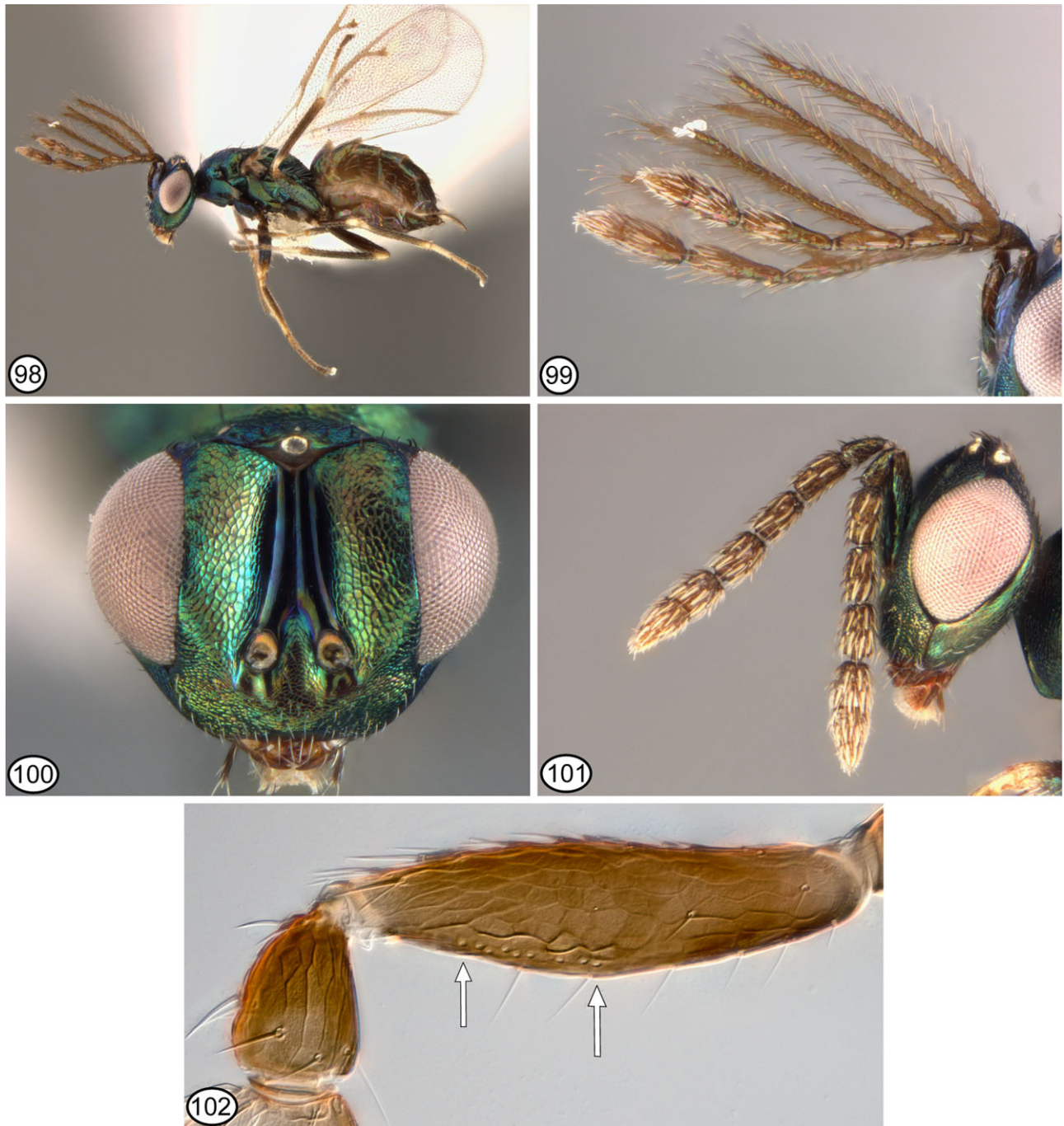
Body 1.8 mm in length. Head primarily green, but scrobal depression dark and under some angles of light parascrobal region, gena and lower face with slight coppery lustre, and vertex slightly more bluish-green (Fig. 100). Antenna (Fig. 101) with scape similarly dark as flagellum; length of flagellum + pedicel about $1.1 \times$ width of head; flagellum with length of F1 + anelli almost $2.1 \times$ as long as wide and about $1.3 \times$ length



Figures 92–97. *Necremnus aenigmaticus* sp. nov., ♀. 92, dorsal habitus; 93, holotype, lateral habitus; 94, holotype, tegula; 95, tegula (2013-48); 96, scutellum-propodeum (2013-45); 97, fore wings (2013-47). Arrow points to tegula in 94 and 95.

of pedicel; F2 about 1.9 ×, F3 about 1.8 ×, and clava about 3 × as long as wide. Mesosoma green with slight coppery lustre, most distinctly on scutellum (Figs 92, 96); tegula pale along inner margin and basally but brown apically (Fig. 94). Mesonotum with mesoscutum reticulate; scutellum longitudinally reticulate-imbricate on either side of midline (Fig. 96). Fore wing (Fig. 97) hyaline; speculum broadly bare dorsally; basal cell and

speculum posteriorly delineated by complete rows of setae, and mediocubital fold with one seta basal to basal fold; subcubital setal line composed of one row of setae along most of length; basal cell ventrally with two or three spots or minute setae mesally near submarginal vein; postmarginal vein 1.6 × length of stigmal vein. Legs (Figs 92, 93) dark except protibia dorsolongitudinally, knees narrowly, mesotibia



Figures 98–102. *Necremnus aenigmaticus* sp. nov. 98, 99, ♂ allotype: 98, lateral habitus; 99, antennae. 100, ♀ face (2013-45). 101, ♀ lateral head and antennae (holotype). 102, ♂ scape (2011-15; slide preparation, arrows point to basal- and apical-most sensillum).

narrowly apically, and basal tarsomeres of meso- and metatarsi pale, with second tarsomeres more brownish-white and apical two tarsomeres brown. Metanotum with dorsellum mesh-like coriaceous (Fig. 96). Propodeum (Fig. 96) with complete median carina; more finely mesh-like coriaceous to alutaceous than dorsellum;

spiracle obliquely oval, the rim anteriorly distinctly overlapped by metanotum. Gaster (Figs 92, 93) similarly green as mesosoma except posterior margins of basal four tergites broadly brown; about 1.5 × as long as wide (inflated) and as long as combined length of head + mesosoma; syntergum short.

Male (allotype, Fig. 98)

Body almost 1.5 mm in length. Similar to female except fore wings with three or five setae on mediocubital fold basal to basal fold and postmarginal vein about $1.7 \times$ as long as stigmal vein. Antenna with scape about $3 \times$ as long as wide; length of funiculars and clava about 1.0, 1.4, 1.7, 2.25, and $2.75 \times$ length of pedicel, with F4 about $3.9 \times$ and clava about $3.3 \times$ as long as wide; rami with long, hair-like setae, elongate-slender with R1 about $2.7 \times$ as long as scape, and all rami lacking mps (Fig. 99).

Variation

Female body length varies from about 1.7–2.3 mm; variably bright green and sometimes without or with only very limited, obscure coppery lustre; tegula sometimes entirely yellow (Fig. 95); mesotibia often entirely dark except basally; and gaster sometimes with up to basal four tergites entirely or almost entirely brown dorsally. Flagellum with length of first funicular + anelli about 1.3 – $1.5 \times$ length of pedicel; F2 and F3 usually comparatively shorter, and clava about 2.4 – $3.2 \times$ as long as wide. Fore wing with one or two setae beyond basal fold; basal cell often lacking minute spots mesally near submarginal vein. Metanotum and propodeum often more strongly sculptured, the dorsellum sometimes slightly reticulate-imbricate and propodeum sometimes distinctly coriaceous-alutaceous. Propodeum sometimes with anterior margin of spiracle visible under posterior margin of metanotum, but then rim sinuate or depressed. Gaster sometimes up to about $2.2 \times$ as long as wide in air-dried females.

Male body length varies from about 1.25–1.5 mm in length; otherwise similar to allotype except sometimes with only one seta on mediocubital fold basal to basal fold. A single paratype from which the antennae were slide mounted had a row of eight or nine sensory pores within the apical half of the scape (Fig. 102).

Hosts

Ceutorhynchus typhae (= *C. floralis*) (Herbst) on *Cap. bursa-pastoris*, *Ceutorhynchus* sp. on rape (*B. napus*) and probably some weevils associated with turnip (*Brassica rapa* L. var. *rapa*), Indian mustard [*B. juncea* (L.) var. *Trowse*] and white wall-rocket [*Diplotaxis eruroides* (L.)].

Discussion

We sequenced five individuals from one site in Germany and one female from France. Our inclusion of other BMNH specimens in the type series is based on the females having an entirely or partly yellow tegula (Figs 94, 95) (differentiating *N. aenigmaticus* from *N. hippia* and *N. duplicatus*), a broad fore wing speculum (Fig. 97) (differentiating *N. aenigmaticus* from *N. tidius*), and partly overlapped propodeal spiracles

(Fig. 96) (differentiating *N. aenigmaticus* from *N. leucarthros* and *N. tidius*). The reared males and the single male associated with the female from turnip also have these features as well as the complete absence of mps from all three rami. Additional sequencing of specimens from throughout Europe is advisable to more confidently establish whether a partly to entirely pale tegula is a valid differentiating feature for both sexes of *N. aenigmaticus* because this feature appears to be variable for *N. tidius*. Individuals of *N. metalarus* also have the tegula bicoloured similar to *N. aenigmaticus*, but females differ by having a much more strongly reticulate propodeum and the propodeal spiracles distinctly separated from the metanotum (Fig. 37), and males have mps on the basal ramus. The different position of the sensory pores on the scape will probably help differentiate *E. aenigmaticus* males from those *N. tidius* males lacking evident mps on the rami. Although the position of the pores within the apical half of the scape was determined for only a single male of *N. aenigmaticus* (Fig. 102), this is the same position as for *N. duplicatus* and therefore probably also characteristic for *N. aenigmaticus*. The more mesal position of the pores on the scape for *N. tidius* males (Fig. 171) was determined from numerous specimens.

Individuals of *N. aenigmaticus* were reared from *Ce. typhae* on *Cap. bursa-pastoris* in Europe and those of *N. duplicatus* from the same host in North America. We did not sequence or see any specimens of *N. aenigmaticus* from North America, but because of the host association it may be discovered there in the future. If tegular colour pattern is indeed a valid differential feature, this should be sufficient to distinguish any *N. aenigmaticus* ultimately discovered in North America.

NECREMNUS DUPLICATUS GAHAN REVISED STATUS (FIGS 103–116)

Necremnus duplicatus Gahan, 1941: 201–203. ♀ holotype (USNM, examined). Tentative synonymy under *N. tidius* by Bouček (1959: 152), and formal synonymy under *N. tidius* by Gibson *et al.* (2005: 384).

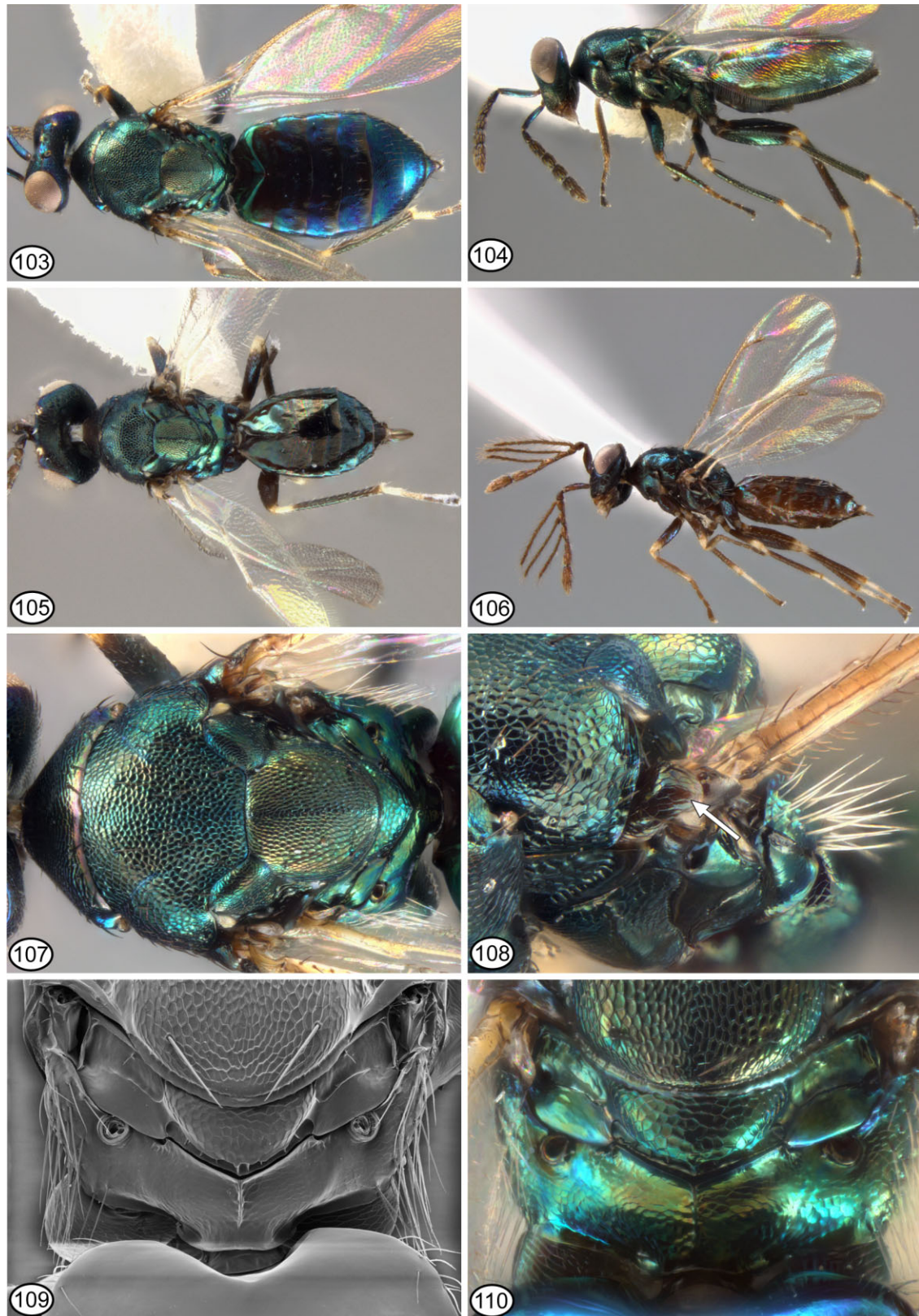
Type material

The holotype female of *N. duplicatus* is point mounted; it lacks its head but otherwise is entire (see http://www.usnmhymtypes.com/default.asp?Action=Show_Types&Single_Type=True&TypeID=7003).

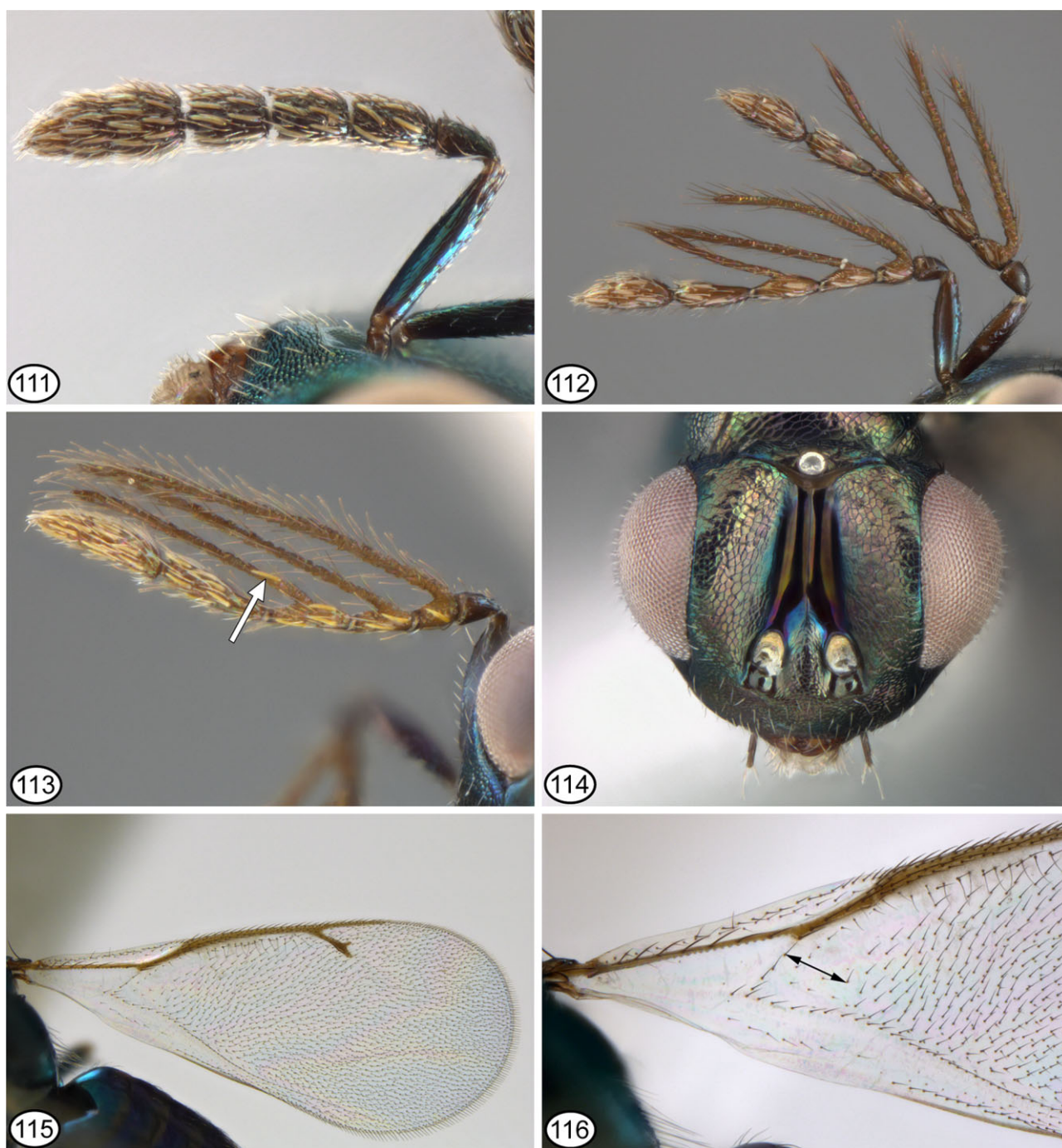
Description

Female

Body 1.4–2.3 mm in length. Head sometimes mostly brown in smaller individuals, but usually with variably distinct green to bluish-green lustres under most



Figures 103–110. *Necremnus duplicatus*. 103, 104, ♀ habitus (2012-27): 103, dorsal; 104, lateral. 105, 106, ♂ habitus: 105, dorsal (2013-36); 106, lateral (2012-17). 107, ♀ dorsal mesosoma (2012-27). 108, ♀ tegula (arrow). 109, 110, ♀ metanotum and propodeum: 109, scanning electron microscopy; 110, macrophotography (2012-27).



Figures 111–116. *Necremnus duplicatus*. 111, ♀ antenna (2012-27); 112, ♂ antennae (2012-12); 113, ♂ antenna (2013-35, arrow points to multiporous plate sensilla); 114, ♀ face (2013-37); 115, ♀ fore wing; 116, ♀ fore wing base (arrow indicates width of speculum).

angles of light except within scrobal depression and often partly blue to purple more dorsally or on vertex (Fig. 114). Antenna (Fig. 111) with scape similarly dark as flagellum; length of flagellum + pedicel about 1.0–1.1 × width of head; flagellum with length of F1 + anelli about 1.6–2.1 × as long as wide and about 1.3–1.6 ×

length of pedicel, F2 and F3 at most about 1.4 ×, and clava about 2.3–2.9 × as long as wide (Figs). Mesosoma (Figs 103, 104, 107) sometimes mostly dark brown with coppery or violaceous-coppery lustres in smaller individuals, but usually variably dark olive to bluish-green with variably distinct coppery or

violaceous-coppery lustres at least on scutellum paramedially; tegula uniformly brown (Fig. 108). Mesonotum with mesoscutum reticulate; scutellum longitudinally reticulate-imbricate on either side of midline (Fig. 107). Fore wing (Figs 115, 116) hyaline; speculum broadly bare dorsally; basal cell apically and speculum posteriorly delineated by complete rows of setae, and mediocubital row usually with less than but at most only three setae basal to basal fold; basal cell in ventral view without setae ventroapically, at most with a few inconspicuous spots or minute spicule-like setae in line adjacent to submarginal vein; speculum broadly bare dorsally; postmarginal vein 1.5–1.75 × length of stigmal vein. Legs (Fig. 104) dark except protibia dorsolongitudinally, knees narrowly, mesotibia sometimes very narrowly apically, and basal one or two tarsomeres pale. Metanotum (Figs 109, 110) with dorsellum mesh-like coriaceous to reticulate-imbricate or rarely shallowly reticulate. Propodeum (Figs 109, 110) with median carina over most of length; often somewhat more finely sculptured than dorsellum, alutaceous to mesh-like coriaceous; spiracle obliquely oval, the rim at least touching and usually slightly overlapped by metanotum. Gaster (Fig. 103) brown or dorsally under different angles of light with variably extensive and distinct, usually more blue to purple lustres than on mesosoma, except broadly brownish along posterior margins of basal four tergites and more narrowly along posterior margin of fifth tergite; up to about 1.75 × as long as wide in air-dried specimens and about as long as combined length of head + mesosoma (Fig. 103); syntergum short.

Male (Figs 105, 106)

Similar to female except for antennal structure and as follows: body often less distinctly metallic green; legs often lighter brown and tibiae sometimes more extensively to almost entirely pale. Antenna (Figs 112, 113) with flagellar rami long and slender, with long, hair-like setae, and without mps (Fig. 112) or only extremely rarely with at most one mps on R3 of one antenna (Fig. 113); scape with row of sensory pores along ventral margin within apical half (cf. Fig. 102).

Distribution

North America (see Gibson *et al.*, 2005).

Hosts

Ceutorhynchus obstrictus on *B. napus*; *Ce. neglectus* on *Erucastrum gallicum* (Wild.) O.E. Schulz and *Rorippa palustris* (L.) Besser; *Ce. omissus* on *Erysimum cheiranthoides* L.; *Ce. typhae* on *Cap. bursa-pastoris*.

Discussion

Morphologically, females of *N. duplicatus* and *N. hippia* cannot yet be differentiated reliably. However, based

on our molecular results, *N. duplicatus* appears to be restricted to North America and *N. hippia* to Europe. Males of the two species are easily differentiated by the absence compared with presence of mps on R2 and R3 in *N. duplicatus* vs. *N. hippia*. Males and females of *N. duplicatus* are also similar to those of *N. aenigmaticus*, which is also known only from Europe but may eventually be found in North America (see Discussion under latter species). Individuals share a comparatively broad speculum and the propodeal spiracles at least touching if not slightly overlapped by the posterior margin of the metanotum (cf. Figs 96, 110). However, individuals of *N. duplicatus* have a uniformly dark tegula (Fig. 108), whereas those of *N. aenigmaticus* have an entirely to partly pale tegula (Figs 94, 95). Males of the two species are additionally similar in lacking mps from all three rami. However, one male from British Columbia (Abbotsford) that we identify as *N. duplicatus* has a single mps on the outer surface of R3 of the left antenna (Fig. 113), the right antenna lacking mps from all rami. This is similar, if not the identical pattern as the lectotype male of *N. tidius* (Fig. 155) (see Discussion under latter species). Our identification of the British Columbia male as *N. duplicatus* rather than *N. tidius* is based on the propodeal spiracle being slightly overlapped by the metanotum and the individual being reared from canola along with several other females and males typical for the species. Owing to the condition of the antennae of some males it was not always possible to be completely certain that the R2 and R3 ramus completely lacked mps, but presence of at most a single mps is at least very rare for *N. duplicatus* males. When Gibson *et al.* (2005) synonymized *N. duplicatus* under *N. tidius*, the complete absence of mps from the rami of North American males was noted and illustrated (Gibson *et al.*, 2005: fig. 3). The lectotype male of *N. tidius* had been examined, but presence of the single mps on R3 was not observed. The presence of mps on the apical two rami of some European specimens was also discussed, but was assumed to represent intraspecific variation within the very few males then seen from Europe.

In North America, females of *N. duplicatus* key to couplet 8 and males to couplet 13 using Gahan (1941), who differentiated females of *N. leucarthros* from those of *N. duplicatus* by the former having a comparatively longer gaster and a darker marginal vein. The noted gastral difference does appear to be valid (cf. Figs 103, 140). Females of *N. leucarthros* have a more elongate-lanceolate gaster, except rarely at least 1.8 × as long as wide. Females of *N. duplicatus* have a more ovate-lanceolate gaster that is at most about 1.75 × as long as wide. However, this feature is not always sufficient to distinguish females because of artefacts of differential drying (cf. Figs 140, 145). Furthermore, Gahan

(1941) did not key *N. tidius*. Both sexes of *N. duplicatus* are usually readily differentiated from those of *N. leucarthros* and *N. tidius* by placement of the propodeal spiracles. These are slightly separated from the metanotum in *N. leucarthros* (Figs 143, 147) and *N. tidius* (Figs 172, 173). However, it is sometimes difficult to be certain whether or not the spiracles are slightly overlapped by the metanotum vs. touch the metanotum or touch the metanotum vs. being slightly separated from it. Some of the variation in spiracular position is probably explained by the metanotum being slightly moveable relative to the propodeum, but it is also affected by the exact angle at which the mesosoma is viewed (cf. Figs 131, 132). Males are additionally distinguished by flagellar features. Males of *N. leucarthros* are readily identified by uniquely having mps on all three rami and very short (Fig. 150) rather than long, hair-like setae (Figs 112, 113). Except for the rare exception discussed above, males of *N. duplicatus* lack mps from all three rami whereas those of *N. tidius* typically have at least one mps on at least R2 and often R3 (see Discussion under *N. tidius*). Furthermore, *N. duplicatus* males have the sensory pores within the apical half of the scape (cf. Fig. 102) whereas they are essentially mesal in position for *N. tidius* males (Fig. 171), the distance between the basal-most pore and the basal margin at most only slightly greater than that between the apical-most pore and apical margin. Females of *N. tidius* are additionally distinguished from those of the other two species by the fore wings being more densely or at least more extensively setose so that dorsally the speculum is comparatively narrow (Fig. 168), and they usually also have at least three and typically more setae on the mediocubital fold basal to the basal fold (Fig. 168). However, so do most *N. leucarthros* females. Females of *N. duplicatus* have fewer than three setae (Fig. 116) except very rarely. Female *N. tidius* usually also have distinctively more elongate-slender funiculars (Fig. 167) than the funiculars of females of the other two species (Figs 111, 149). In addition to their more elongate-lanceolate gaster and typically more numerous setae on the mediocubital fold, female *N. leucarthros* often also have quite distinct although short setae ventroapically within the basal cell when viewed ventrally. They are also typically somewhat brighter green to bluish-green with at most limited, inconspicuous coppery lustre compared with *N. duplicatus* females (cf. Figs 103, 145 and 104, 146), although this difference is not always obvious.

NECREMNUS HIPPIA (WALKER) REVISED STATUS
(FIGS 117–138)

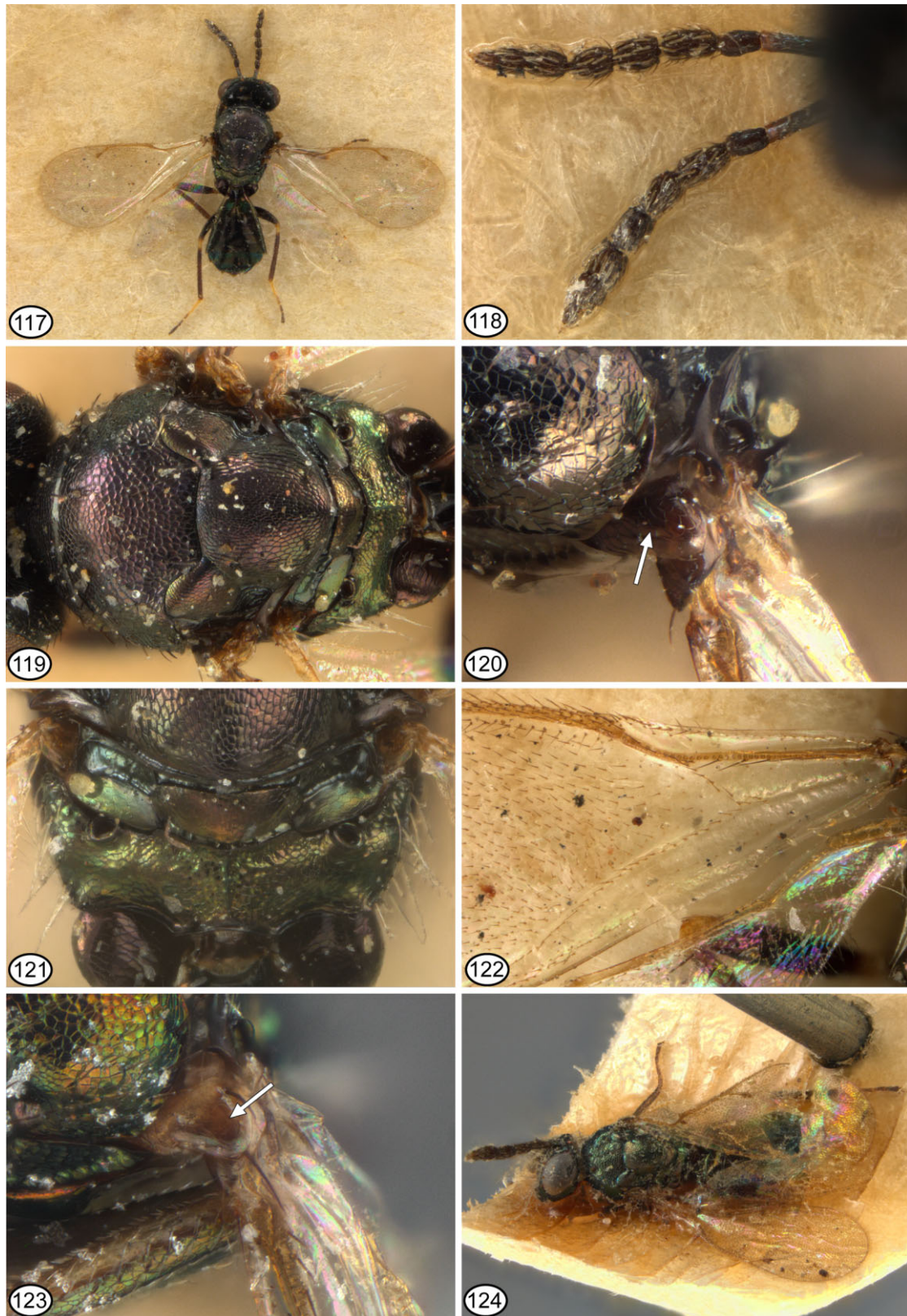
Eulophus Hippiia Walker, 1839: 185–186. ♀ lectotype (BMNH, here designated). Synonymy under *N. leucarthros* by Gahan (1941: 201) and Bouček (1959:

151), and under *N. tidius* by Graham in Bouček & Askew (1968: 67).

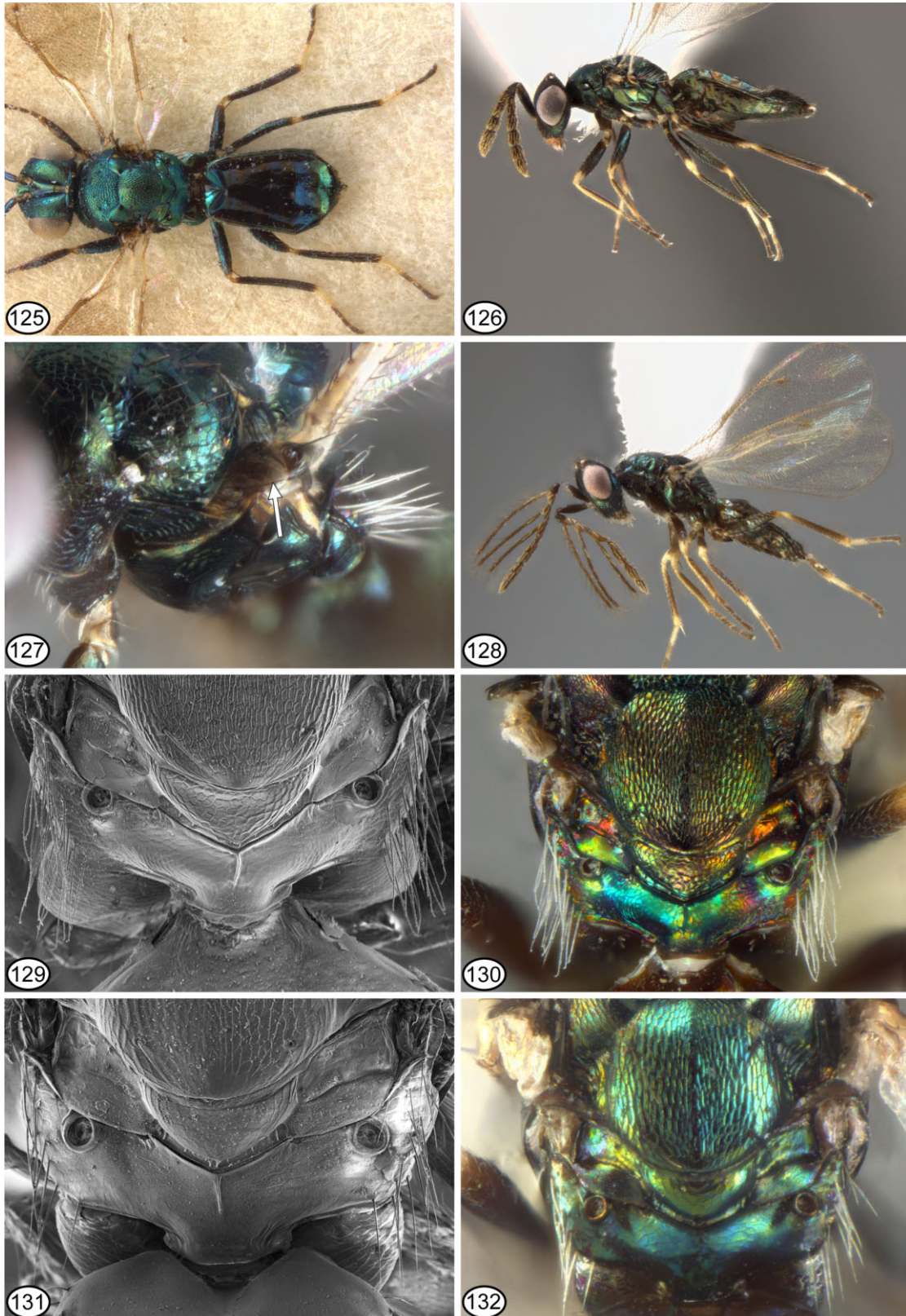
Entedon cyrinus Goureau, 1851: 147, pl. 6, no. VIII, figures 7–9. ♀ syntype (OXUM, examined). Synonymy under *N. tidius* by Graham, 1963: 190. syn. nov.

Type material

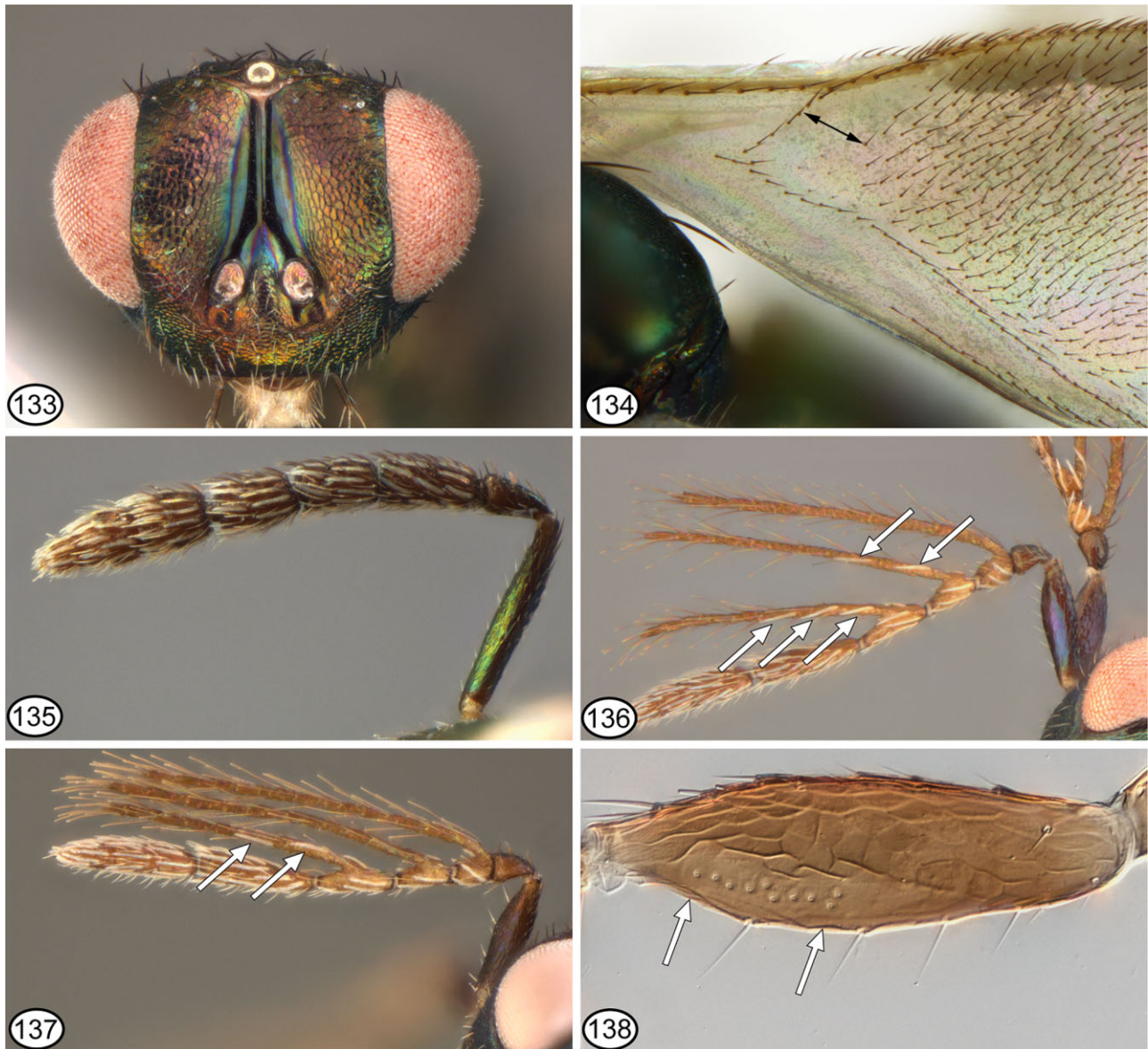
Walker (1839) described *Eulophus hippia* based on at least three females, the description also including two variants. The BMNH has five specimens indicated to form part of the type series. One point-mounted female has the following seven labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a circular label with '38/7.12/53' on three separate lines; (3) a small, rectangular, handwritten label with 'Britain'; (4) a rectangular label with '*Eulophus Hippiia* Walker' handwritten on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (5) a rectangular, handwritten label with 'Type M. de V. G.'; (6) a rectangular label with '*Eulophus hippia* Walker LECTOTYPE: ♀ M. de V. Graham det. 1958' partly printed and handwritten; and (7) a square label with 'B.M. TYPE HYM. 5.2507'. This female lacks its gaster and most of its middle and hind legs including the tibiae and tarsi except for the right metatibia. The tegula is extensively yellow, only the apex being partly brown (Fig. 123). The head and mesosoma are also much brighter green, with only limited coppery lustre on the mesonotum under some angles of light, than a second female labelled as 'type'. This latter female is card mounted (Fig. 117) and has five labels: (1) a circular, red-bordered label with 'Type'; (2) a handwritten label with '*Hippiia*'; (3) a printed label with 'Walker coll. 1901–120'; (4) a handwritten label with 'in BM. under *Eulophus hippia* Walk.'; and (5) a handwritten label with 'this is prob. not type of hippia & is a Necremnus, MG. 1952.'. This female has entirely dark tegulae (Fig. 120) and is dark with very slight violaceous lustres under some angles of light (Figs 117, 119). The three other BMNH specimens are point mounted and have circular, blue-bordered 'PARALECTOTYPE' labels. One of these, a female, has the same double-sided label as for the specimen with Graham's lectotype labels, whereas another female and one male have printed labels with 'Standing over *Eulophus hippia* in BMNH collection viii.2012'. The mesonotum of the former female is variably green to coppery under some angles of light and the tegula is partly yellowish along the inner margin and narrowly basally, whereas the latter female and male are very similar to the female labelled as 'type'. All the specimens have the propodeal spiracles slightly overlapped by the metanotum (Fig. 121) and at least the females have similar fore wing setal patterns with a comparatively broad speculum (Fig. 122) and similar antennae (Fig. 118). The male lacks both antennae. As



Figures 117–124. *Necremnus hippia*. 117–122, ♀ lectotype: 117, dorsal habitus; 118, antennae; 119, dorsal mesosoma; 120, tegula (arrow); 121, scutellum-propodeum; 122, fore wing base. 123, *N. hippia*, ♀ paralectotype (= *Necremnus aenigmaticus*), tegula (arrow). 124, *Eulophus cyrinus*, ♀ syntype.



Figures 125–132. *Necremnus hippia*. 125, 126, ♀ habitus: 125, dorsal; 126, lateral. 127 ♀ tegula (arrow); 128, ♂ lateral habitus. 129, 130, ♀ scutellum-propodeum (Nec-126/NT136): 129, scanning electron microscopy (SEM); 130, macrophotography. 131, 132, ♂ scutellum-propodeum (Nec-108/NT130): 131, SEM; 132, macrophotography.



Figures 133–138. *Necremnus hippia*. 133, ♀ face (2013-40); 134, ♀ fore wing base (Nec-126/NT136); 135, ♀ antenna (Nec-126/NT136); 136, ♂ antennae (2013-39); 137, ♂ antenna (2013-38); 138, ♂ scape (2012-46; slide preparation). Arrows denote width of speculum in 134, multiporous plate sensilla in 136 and 137, and basal- and apical-most sensillum in 138.

Graham did not validly designate a lectotype through publication under ICZN rules, all of the specimens remain available for designation. In order to stabilize the concept of the name, we designate as the lectotype of *E. hippia* the card-mounted female originally labelled as ‘Type’ because the original description specifically states that the tegulae were pitch black (*squamulae piceae*), it has a handwritten label with ‘*Hippia*’ similar to most other specimens selected as Walker *Necremnus* lectotypes, it is entire, and it is more likely to remain complete because of its card mount-

ing. A rectangular red lectotype label has been added to the specimen. We designate the incomplete, point-mounted female bearing Graham’s lectotype label as a paralectotype of *E. hippia*, as we do the other two females and one male previously bearing paralectotype labels.

There is no indication in the original publication of the number of females from which Goureaux (1851) described *Entedon cyrinus*. A single female remains in OXUM labelled as ‘Type’. It has the following five labels: (1) a card cut into an L-shape with ‘ex mined leaves

of Ranunculaceae- [?], Paras of *Phytomyza flava*? Meig' handwritten; (2) a small, diamond-shaped, blue label with a 'W' that is underscored and overscored with a dark line; (3) a circular, red-bordered printed label with '-TYPE O.U.M.'; (4) a rectangular, handwritten label with 'beetle - room drawer 5 left bottom'; and (5) a rectangular, handwritten label with '*Entedon cyrinus* Goureau, 1851, OX. UNI. MUS. NAT. HIST. (OUMNH)'. The female is entire but is in poor condition because it is encased in glue on a curved piece of paper (Fig. 124). However, the anterior rims of the propodeal spiracles appear to be slightly overlapped by the metanotum and the fore wings appear to have a comparatively broad speculum. The tegulae also appear to be entirely dark. For these reasons we newly synonymize *Entedon cyrinus* Goureau under *Necremnus hippia* (Walker), but do not designate the female as the lectotype in case another, better preserved specimen is found in the future.

Description

Female

Body 1.1–2.1 mm in length. Head primarily brown in smallest individuals, but usually green with slight coppery lustre to extensively coppery except for scrobal depression (Fig. 133), and vertex often slightly more bluish to purple. Antenna (Figs 118, 135) with scape similarly dark as flagellum; length of flagellum + pedicel about 1.0–1.2 × width of head; flagellum with length of F1 + anelli 1.4–2.1 × as long as wide and 1.0–1.5 × length of pedicel; F2 and F3 at most about 1.7 ×, and clava 2.7–3.3 × as long as wide. Mesosoma usually green to bluish-green with slight coppery lustre, most distinctly on scutellum (Figs 125, 130), although sometimes darker with more extensive coppery lustre; tegula uniformly dark brown (Figs 120, 127). Mesonotum with mesoscutum reticulate (Fig. 119); scutellum longitudinally reticulate-imbricate on either side of midline (Fig. 130). Fore wing hyaline; speculum broadly bare dorsally (Fig. 134); basal cell and speculum posteriorly delineated by complete rows of setae, and mediocubital fold with one to three seta basal to basal fold (Fig. 134); subcubital setal line composed of one row of setae along at least about basal half (Fig. 134); basal cell ventrally usually entirely bare, only rarely with one to three spots or minute setae near submarginal vein; postmarginal vein 1.6–1.9 × length of stigmal vein. Legs (Figs 125, 126) dark except protibia dorsolongitudinally, knees narrowly, mesotibia narrowly apically, and basal tarsomeres of meso- and metatarsi pale. Metanotum with dorsellum mesh-like coriaceous to often reticulate-imbricate (Figs 129, 130) or sometimes quite distinctly reticulate posteriorly. Propodeum (Fig. 121) with median carina over most of length; more finely mesh-like coriaceous to alutaceous than dorsellum; spiracle oblique-

ly oval, the rim usually variably distinctly overlapped by metanotum (Figs 129, 130), but if anterior margin visible (Fig. 132) then rim sinuate or slightly depressed. Gaster (Fig. 125) variably extensively green to sometimes more blue or purple dorsally, although posterior margins of basal four tergites at least broadly brownish along posterior margins and sometimes up to basal five tergites mostly to entirely brown or coppery-brown; about 1.5–1.9 × as long as wide and as long as combined length of head + mesosoma; syntergum short.

Male (Fig. 128)

Similar to female except for antennal structure and as follows: basal cell ventrally with at least three and usually more spots or minute setae in line along most of length of submarginal vein; mediocubital fold with up to four setae basal to basal fold. Antenna (Figs 136, 137) with flagellar rami long and slender, with long, hair-like seta, and with variably numerous and conspicuous mps on second and third rami, usually with two or more mps on both rami and rarely with up to five mps on at least third ramus; scape with line of sensory pores along ventral margin obviously more within apical half, the distance between basal-most pore and basal margin much greater than distance between apical-most pore and apical margin, the basal separation more similar to length of sensory row (Fig. 138).

Distribution

Europe (Italy, Romania, Switzerland).

Hosts

Ceutorhynchus cardariae on *Car. draba*; *Ce. typhae* on *Cap. bursa-pastoris*.

Discussion

Based on tegular colour pattern, the type series of *N. hippia* appears to consist of *N. hippia* in the present sense (those with dark tegulae, Fig. 120) as well as *N. aenigmaticus* (the two females with partly yellowish tegulae, Fig. 123). Colour of the tegula is the only feature that we found to reliably differentiate females of *N. hippia* from those of *N. aenigmaticus*, although based on observed material *N. aenigmaticus* females apparently more commonly have minute spots within the basal cell near the submarginal vein. Males of the two species are differentiated both by colour of the tegulae and by presence in *N. hippia* (Figs 136, 137) or absence in *N. aenigmaticus* (Fig. 99) of mps on R2 and R3. Owing to their broad fore wing speculum (Fig. 134) and uniformly brown tegula, females of *N. hippia* are not reliably distinguished from those of *N. duplicatus* and can also be mistaken for smaller *N. leucarthros* females. Females of *N. leucarthros* usually have the propodeal spiracles slightly separated from

the metanotum (Figs 143, 147), although this differential feature is not always obvious, as discussed under *N. duplicatus*. Female *N. leucarthros* typically also have a somewhat more elongate-lanceolate gaster and more numerous spots along the submarginal vein in the basal cell that often in ventral view appear as very short but quite distinct setae, at least apically toward the basal fold.

NECREMNUS LEUCARTHROS (NEES) (FIGS 139–150)

Eulophus leucarthros Nees ab Esenbeck, 1834: 172. Described ♀ (type status and location unknown).

Eulophus cornu copiae Förster, 1841: 44. ♂ syntypes (Vienna, Munich). Synonymy by Bouček (1959: 151).

Eulophus anaxippus Walker, 1846b: 182. ♀ lectotype (BMNH, here designated). Synonymy by Graham in Bouček & Askew (1968: 65).

Eulophus teratocerus Förster, 1861: 37. ♀ and ♂ syntypes (location unknown). Synonymy by Bouček & Askew (1968: 65).

Necremnus leucarthros; Thomson, 1878: 234.

Eulophus cornucopiae Förster; justified emendation by Bouček (1959: 152).

Necremnus arthos Yefremova, 2007: 31. *Lapsus calami* for *N. leucarthros*.

Type material

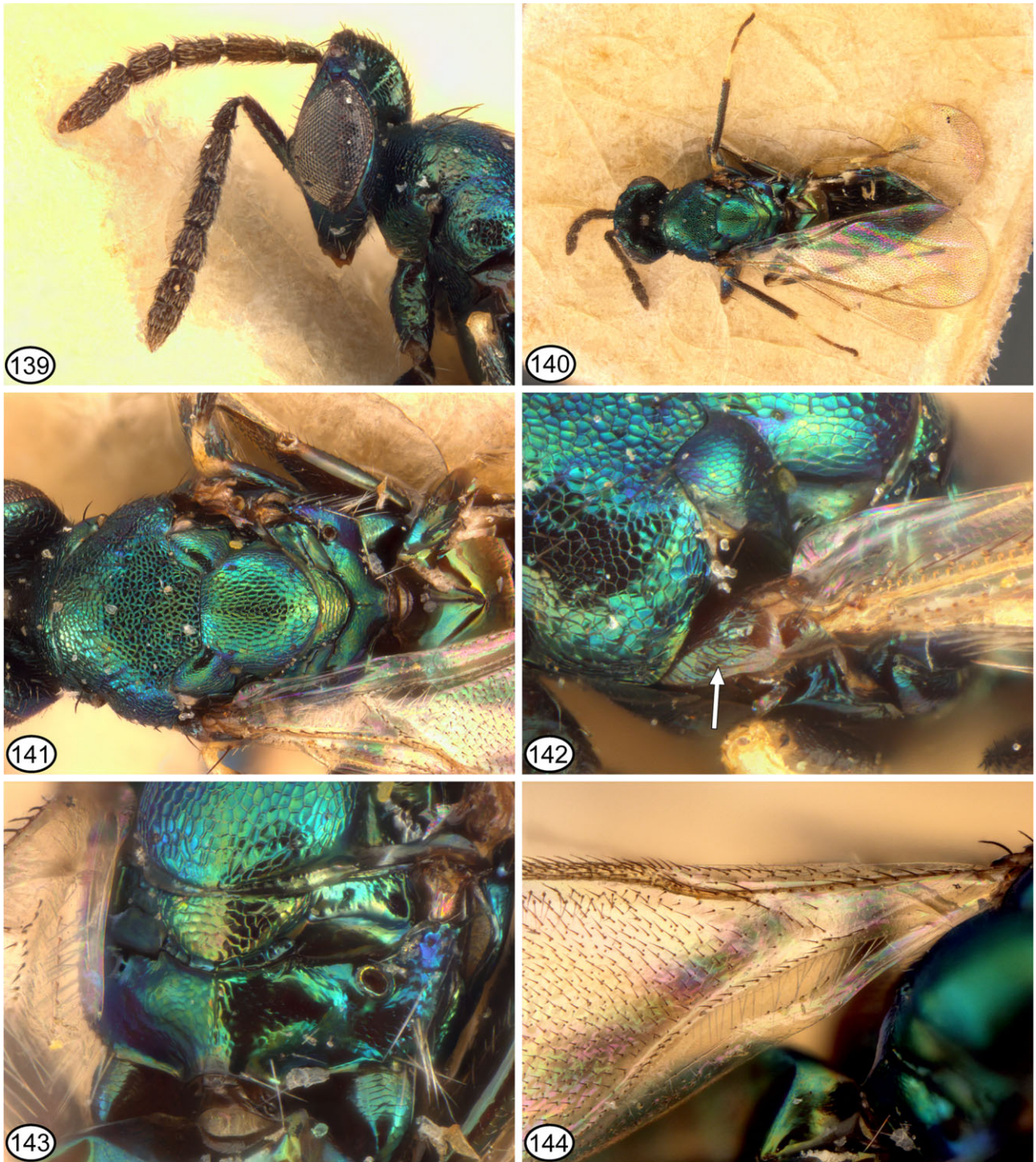
We did not examine type material of *N. leucarthros*, which apparently is lost. Gahan (1941: 201) formed his concept of *N. leucarthros* in North America based on ‘specimens identified by Thomson, Ruschka, and Schmiedeknecht’, although he incorrectly recognized *N. hippia* as a junior synonym of *N. leucarthros*. Bouček (1959) stated that he saw several syntypes of *Eulophus cornucopiae* in Vienna and Munich and confirmed their synonymy with *N. leucarthros*. Bouček & Askew (1968) synonymized *Eulophus teratocerus* under *N. leucarthros*, but did not provide any reason or information about type material. The type material of *E. anaxippus* consists of a single, card-mounted female (Fig. 140) in the BMNH that has the following four rectangular labels: (1) a handwritten label with ‘*Anaxippus*’; (2) a ‘Ch. Ferriere det.’ label with ‘= *Necremnus leucarthros* Ths.’ handwritten; (3) a label with ‘*Eulophus anaxippus* Walker LECTOTYPE: ♂ [sic] M. de V. Graham det. 1958’ partly printed and handwritten; and (4) a label with ‘B.M. TYPE HYM. 5.2505’. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate this female as the lectotype of *E. anaxippus*. The lectotype is entire except for lacking its right set of wings and having a small portion of the right hand side of the gaster missing within its basal half (Fig. 140). It fits our concept of *N. leucarthros*, including having the combined length of F1 + anelli

about 1.7 × length of the pedicel (Fig. 139), the propodeal spiracles slightly separated from the posterior margin of the metanotum (Fig. 143), a comparatively broad fore wing speculum (Fig. 144), and a line of six minute setae ventrally in the basal cell near the submarginal vein.

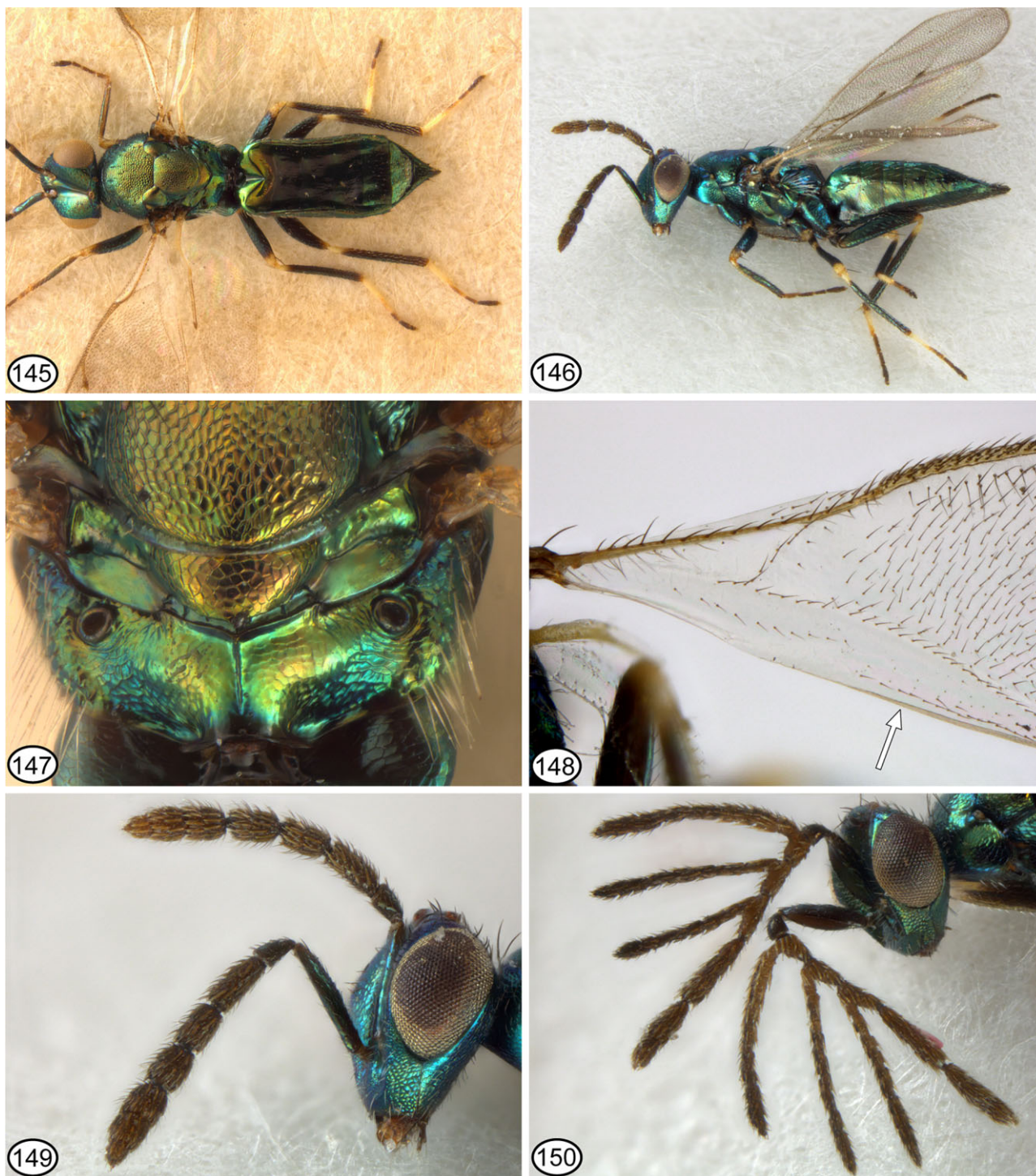
Description

Female

Body length 1.7–2.5 mm. Head comparatively bright green (Fig. 145) to bluish-green (Fig. 149) or more blue to purple dorsally, usually without coppery lustre. Antenna (Figs 139, 149) with scape similarly dark as flagellum; length of flagellum + pedicel about 1.1 × width of head; flagellum with length of F1 + anelli about 1.9–2.5 × as long as wide and about 1.3–1.8 × length of pedicel, second at most 1.8 ×, third funicular at most 1.5 ×, and clava about 2.6–2.9 × as long as wide. Mesosoma comparatively bright green to blue, usually without but at most with only very limited, inconspicuous coppery lustre (Figs 140, 141, 145, 146); tegula uniformly dark brown or with slight metallic lustre (Fig. 142). Mesonotum with scutellum reticulate; scutellum longitudinally reticulate-imbricate on either side of midline (Figs 141, 147). Fore wing hyaline; speculum usually quite obviously broadly bare dorsally (Fig. 148); basal cell apically and speculum posteriorly delineated by complete rows of setae, and mediocubital fold with two to seven setae basal to basal fold, often over at least about apical half of basal cell; subcubital line of setae, except very rarely, consisting of only one row of setae over at least its basal half (Fig. 148); basal cell with at least three and often five or more spots in line adjacent to submarginal vein, including in ventral view usually short but quite distinct setae, particularly apically toward basal fold, and rarely with single seta dorsally; postmarginal vein 1.5–1.6 × length of stigmal vein. Legs (Figs 140, 145, 146) dark except protibia dorsolongitudinally, knees narrowly, and basal tarsomeres of meso- and metatarsi pale, although rarely second tarsomeres brownish to white. Metanotum (Figs 143, 147) with dorsellum mesh-like coriaceous to reticulate-imbricate or rarely shallowly reticulate. Propodeum (Figs 143, 147) with median carina over most of length; often somewhat more finely sculptured than dorsellum, alutaceous to mesh-like coriaceous; spiracle obliquely oval, usually slightly separated from metanotum but if touching then with uniformly developed rim. Gaster (Figs 140, 145) variably extensively green to blue or purple dorsally with posterior margins of basal four tergites at least broadly brownish along posterior margins and tergites 2–4 sometimes entirely brown to coppery-brown; about 1.8–2.3 × as long as wide and subequal in length to combined length of head + mesosoma; syntergum short.



Figures 139–144. *Necremnus leucarthros* (*Eulophusanaxippus*, ♀ lectotype). 139, head and antennae; 140, dorsal habitus; 141, dorsal mesosoma; 142, tegula (arrow); 143, scutellum-propodeum; 144, fore wing base.



Figures 145–150. *Necremnus leucarthros*. 145, ♀ dorsal habitus (2013-72); 146, ♀ lateral habitus (2012-2); 147, ♀ scutellum-propodeum (2012-72); 148, ♀ fore wing base (2013-73) (arrow points to subcubital setal line); 149, ♀ head and antennae (2012-2); 150, ♂ head and antenna (2012-3).

Male

Similar to female. Antenna with dense mps on all rami and short setae at most about as long as width of rami (Fig. 150); position of sensory pores on scape not determined.

Distribution

Palearctic and Nearctic (see Noyes, 2013); we sequenced specimens from France and Switzerland.

Hosts

See Noyes (2013). Some of the hosts listed require confirmation of the parasitoid identification, especially those from Lepidoptera, as the species in *N. tidius* group are associated with Coleoptera.

Discussion

Males of *N. leucarthros* are easily identified by their antennal structure, all three rami being covered with very short setae and dense mps (Fig. 150). Males of other species all have long, hair-like setae regardless of whether all or some of the rami have mps. Females can be more difficult to distinguish. Recognition of *N. leucarthros* females in North America is discussed under *N. duplicatus*. In Europe, females of *N. hippia* and *N. aenigmaticus* have the propodeal spiracles slightly overlapped by the metanotum or if touching the metanotum then the anterior rim of the spiracle is somewhat depressed or sinuate. Females of *N. leucarthros* usually have the propodeal spiracle slightly separated from the metanotum (Figs 143, 147), but at least the rim is uniformly developed as in *N. tidius*. Both Bouček (1959) and Graham (1959) separated females of *N. leucarthros* from *N. tidius* by the former having a dark green body and the latter a bronze or greenish-bronze body. Askew (1968) separated them also by the extension of the speculum, and length of gaster. Although *N. leucarthros* females are typically a brighter green there sometimes is very little difference in colour of individuals of the two species. Females usually are much more readily distinguished by the fore wing disc being more extensively setose in *N. tidius* than in *N. leucarthros*. As a result, the speculum is narrower in *N. tidius* and the subcubital setal line consists of two or more rows of setae over most of its length (Fig. 168). The subcubital setal line usually consists of only one row of setae over about its basal half (Fig. 148) in *N. leucarthros*, although rarely there are two rows. Furthermore, some *N. tidius* females have the tegulae yellowish along the inner margin adjacent to, although sometimes concealed by, the mesoscutum, and often have noticeably more oblong funiculars, although this latter feature is quite variable and not always distinctive. If the length of the postmarginal vein relative to the stigmal vein is not observable, females could also be confused with those

of *N. cosconius* except for an often subtle difference in fore wing colour pattern (see Discussion under latter species).

***NECREMNUS TIDIUS* (WALKER) (FIGS 151–175)**

Eulophus Tidius Walker, 1839: 146–147. ♂ lectotype (BMNH, here designated).

? *Eulophus Zeugma* Walker, 1839: 183. ♂ syntypes (BMNH, lost); synonymy under *N. tidius* by Graham in Bouček & Askew (1968: 67).

Eulophus Metanira Walker, 1839: 183–184. ♀ lectotype (OXUM, examined) designated by Graham (1991: 8); synonymy under *N. tidius* by Graham (1991: 8).

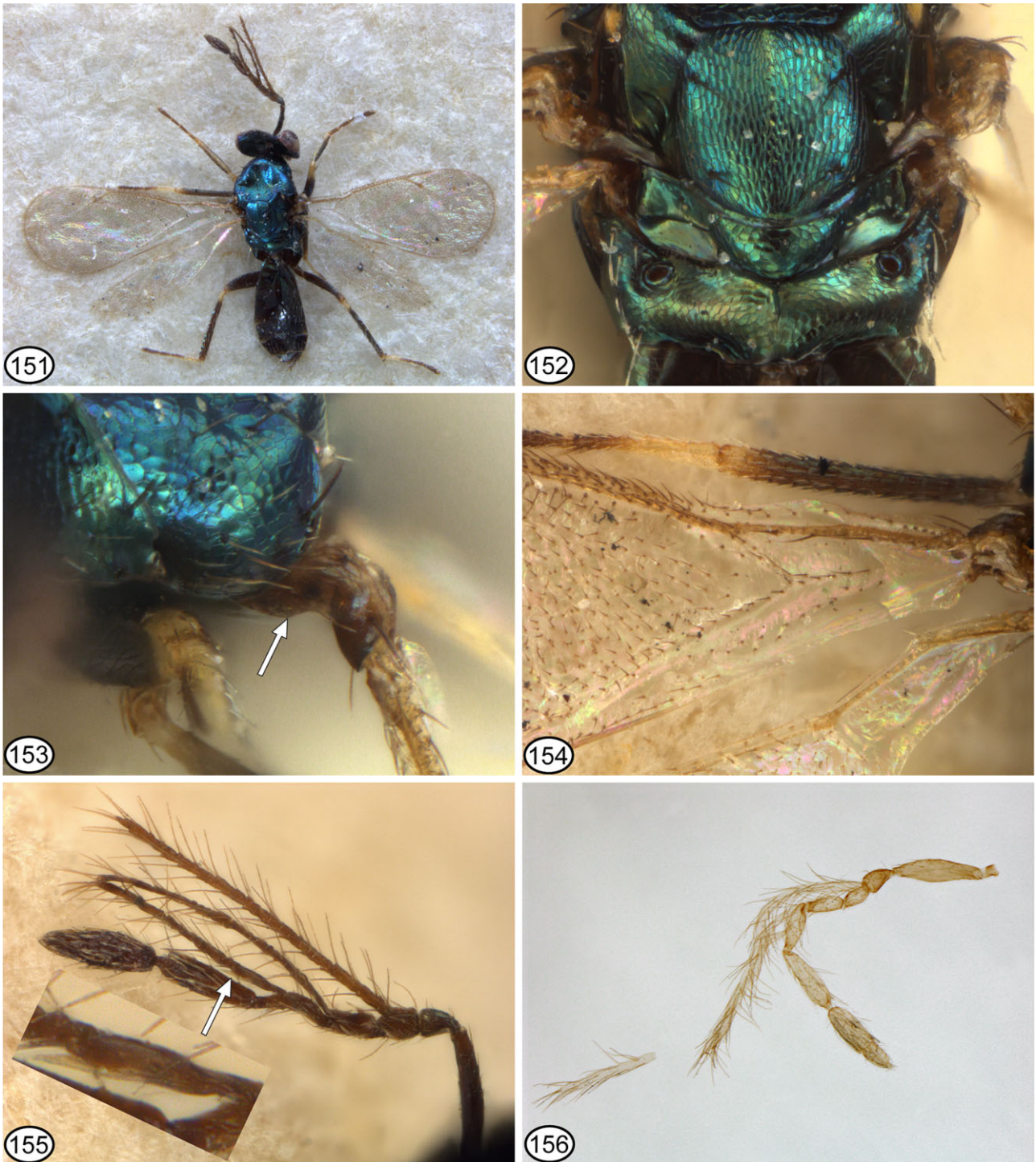
Eulophus Mamurius Walker, 1848: 232. ♂ lectotype (BMNH, here designated); synonymy under *N. tidius* by Graham in Bouček & Askew (1968: 67).

Necremnus tidius; Graham, 1959: 184.

Type material

Walker (1839) described *E. tidius* from at least two males, describing also a 'Var. β' from material collected near London. A single card-mounted male (Fig. 151) remains in the BMNH with the following six labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular, handwritten label with '*Tidius*'; (3) a 'Ch. Ferriere det.' label with '♂ prob. in *Necremnus*? handwritten; (4) a rectangular label with "*Eulophus Tidius* Walker, LECTOTYPE: ♂, M. de V. Graham det. 1958' partly printed and handwritten; (5) a square label with 'B.M. TYPE HYM. 5.2508'; and (6) a rectangular, handwritten label with 'right antenna on slide'. The lectotype is entire except for the right antenna, which was dissected and slide mounted (Fig. 156) by J. Noyes. The slide has two labels with '♂ *Eulophus tidius* Walker LECTOTYPE right antenna LT 5.2508' and '25Jan2012'. We did not observe any mps on the rami of the slide-mounted antenna, but cannot be certain of absence because of the condition of the antenna. The left antenna has at least a single mps on the outer surface of the third ramus (Fig. 155). The tegulae appear mostly brown (Fig. 153), but are linearly yellowish along the inner margin basally. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate this male as the lectotype of *E.anaxippus*.

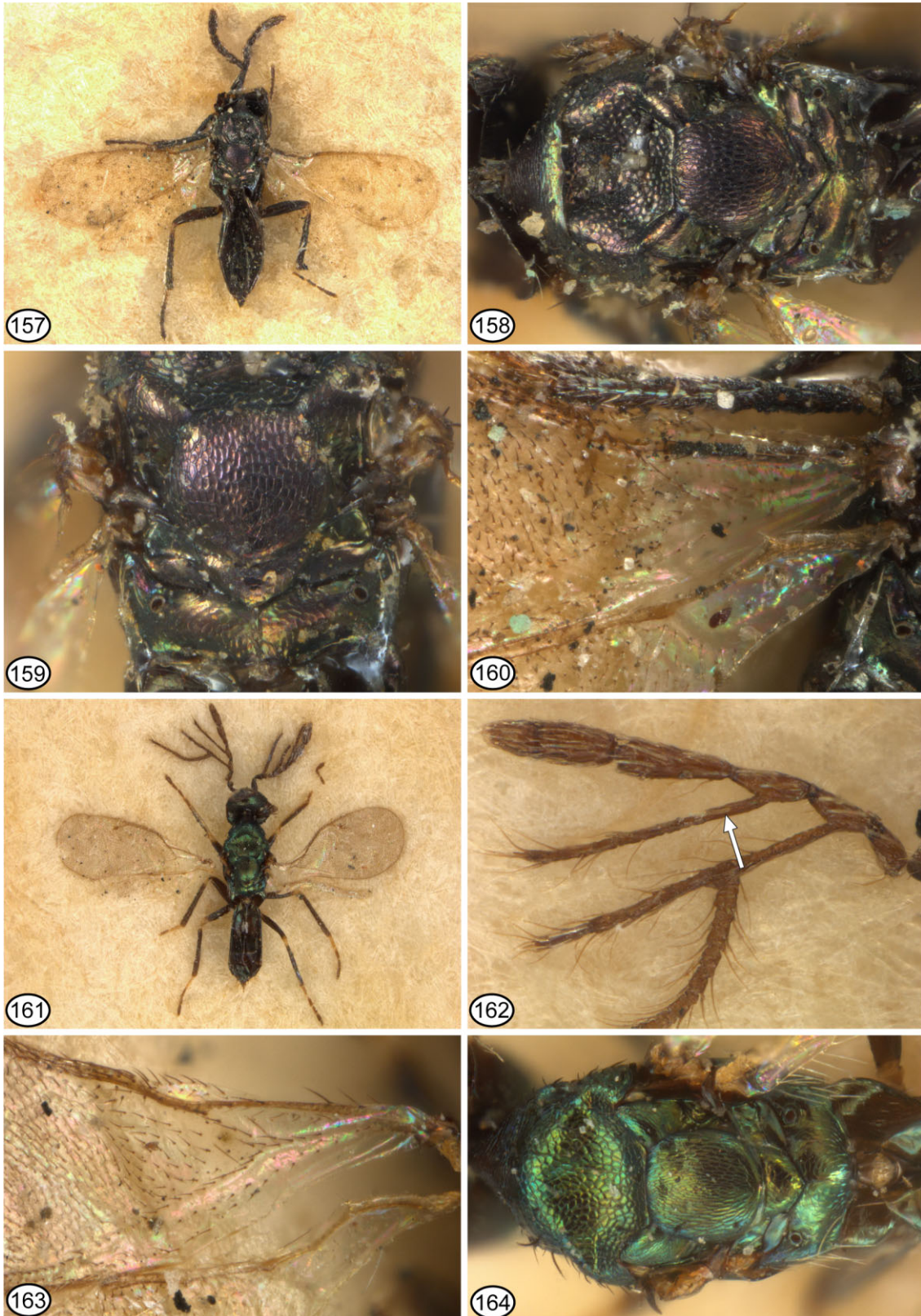
There is no indication in the original publication that Walker (1839) described *E. metanira* from more than one female, but Graham (1991) selected the single remaining female in OXUM as the lectotype. It is card mounted and entire (Fig. 157). Synonymy under *N. tidius* is indicated by the fore wing being comparatively extensively setose without a distinct speculum (Fig. 160) and the propodeal spiracle being well separated from the metanotum (Fig. 159). The tegulae are uniformly dark brown.



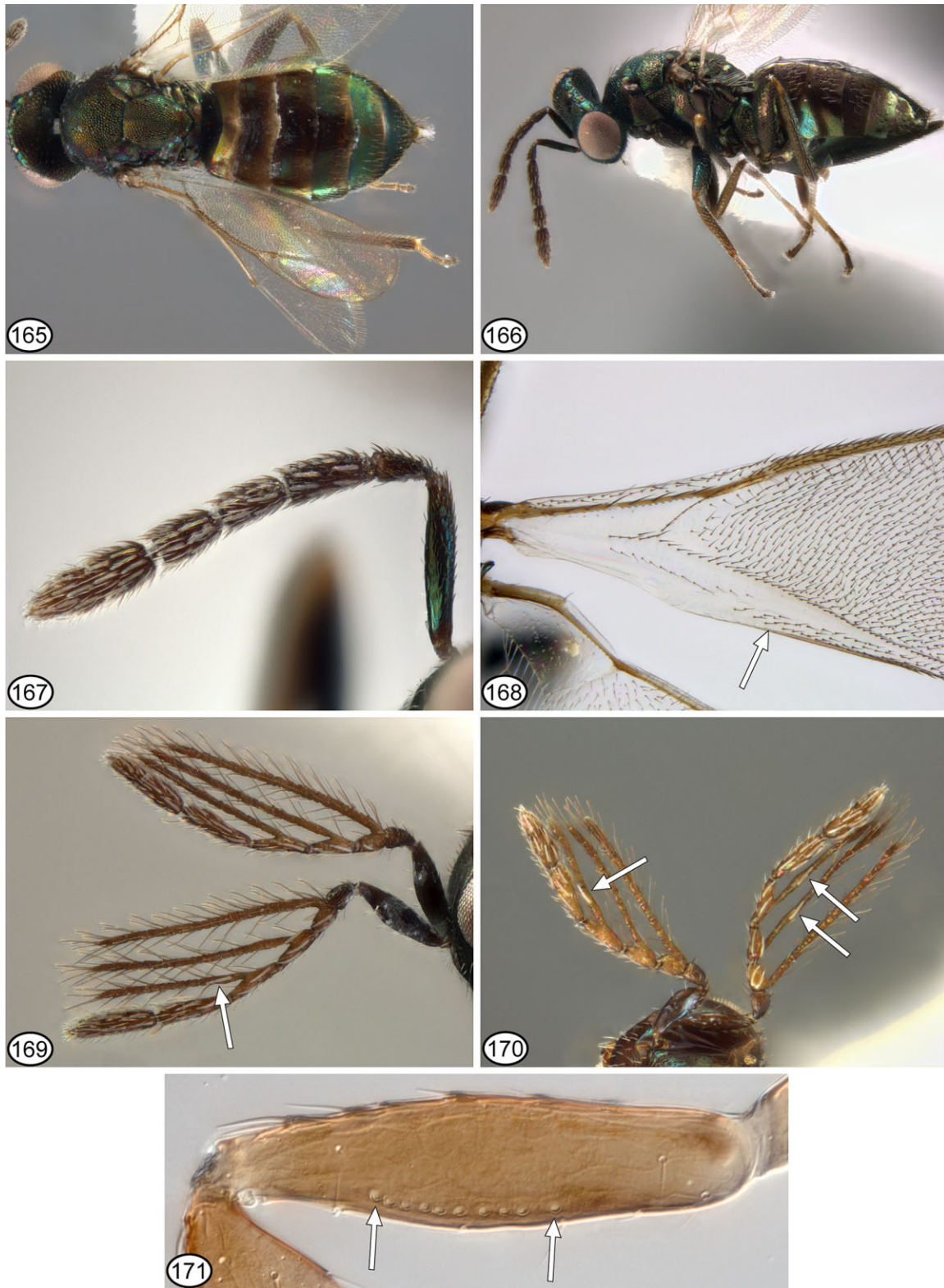
Figures 151–156. *Necremnus tidius*, ♂ lectotype. 151, dorsal habitus; 152, scutellum-propodeum; 153, tegula (arrow); 154, fore wing base; 155, left antenna (arrow points to multiporous plate sensilla, enlarged below); 156, right antenna (slide preparation).

There is no indication in the original publication that Walker (1839) described *E. mamurius* from more than one male. A single BMNH male (Fig. 161) bears the following four labels: (1) a circular, purple-bordered label

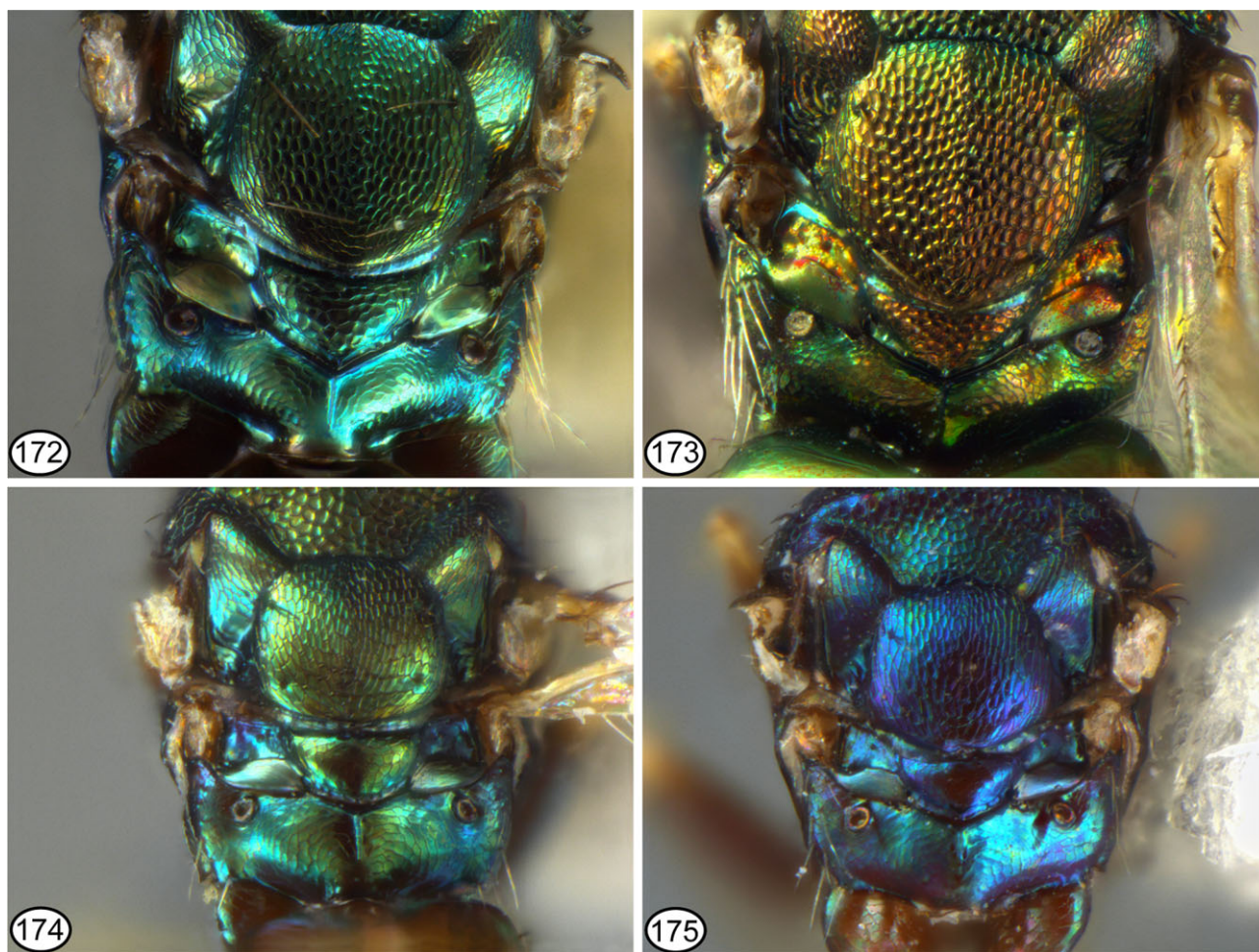
with 'LECTOTYPE'; (2) a rectangular, handwritten label with 'Mamurius'; (3) a rectangular label with '*Eulophus Mamurius* Walker, LECTOTYPE: ♂, M. de V. Graham det. 1958' partly printed and handwritten; and (4) a



Figures 157–164. *Necremnus tidius*. 157–160, *Eulophus metanira*, ♀ lectotype: 157, dorsal habitus; 158, dorsal mesosoma; 159, scutellum-propodeum; 160, fore wing base. 161–164, *Eulophus mamurius*, ♂ lectotype: 161, dorsal habitus; 162, left antenna (arrow points to multiporous plate sensilla); 163, fore wing base; 164, dorsal mesosoma.



Figures 165–171. *Necremnus tidius*. 165, 166, ♀ habitus: 165, dorsal (2012-25); 166, lateral (2012-26). 167, ♀ antenna (2012-25). 168, ♀ fore wing base (arrow points to subcubital setal line). 169, ♂ antennae (Nec-125/NT135). 170, ♂ antennae (2012-22). 171, ♂ scape (arrows point to basal- and apical-most sensillum). Arrows point to multiporous plate sensilla in 169 and 170.



Figures 172–175. *Necremnus tidius*, scutellum-propodeum. 172, ♀ (Nec-23/NT123); 173, ♀ (Nec 113/NT131); 174, ♂ (Nec-31/NT124); 175, ♂ (Nec-115/NT132).

square label with 'B.M. TYPE HYM. 5.2513'. As Graham did not validly designate a lectotype through publication under ICZN rules, in order to stabilize the concept of the name we designate this male as the lectotype of *E. mamurius*. Synonymy under *N. tidius* is indicated by the propodeal spiracles being separated from the metanotum (Fig. 164) and the fore wing being comparatively extensively setose with only a narrow speculum (Fig. 163). Although the antennae are covered in glue on the card at least the third ramus appears to have at least one mps (Fig. 162). The tegulae are uniformly dark brown.

Walker (1839) described *E. zeugma* from at least two males, from near London and North Wales. Neither male could be found in the BMNH and both syntypes are presumed lost. The original description is insufficient to confidently establish synonymy of *N. zeugma* under *N. tidius* or *N. hippia*, but we tentatively retain the prior synonymy of Graham in Bouček & Askew (1968) for the sake of stability.

Description

Female

Body 1.3–2.1 mm in length. Head usually variably dark or green to bluish-green except usually for at least slight coppery to bronze lustres under some angles of light (smaller individuals often with less distinct metallic lustre). Antenna (Fig. 167) with scape similarly dark as flagellum; length of flagellum + pedicel about 1.1–1.2 × width of head; flagellum with length of first funicular + anelli about 2.1–2.8 × as long as wide and about 1.25–1.6 × length of pedicel; second and third funicular often quite distinctly oblong, but second about 1.7–2.0 × and third about 1.6–2.0 × as long as wide, and clava about 2.8–3.5 × as long as broad. Mesosoma rarely mostly dark brown with violaceous-coppery lustres, but usually green (Figs 165, 172) to somewhat bluish-green except often for variably distinct and extensive coppery or reddish-coppery lustres (Fig. 173) under some angles of light; tegula uniformly brown or variably distinctly and extensively yellowish along inner

margin or basally, but brown apically or apicolaterally. Mesonotum with mesoscutum reticulate; scutellum longitudinally reticulate-imbricate on either side of midline. Fore wing hyaline; speculum comparatively narrowly bare dorsally (Fig. 168); basal cell apically and speculum posteriorly delineated by complete rows of setae, and mediocubital fold with two to seven setae basal to basal fold often over at least apical half of basal cell; subcubital line of setae with two or more rows of setae along most of its length (Fig. 168); basal cell sometimes with one dorsal setae but in ventral view usually with at most line of spots or minute spicules adjacent to submarginal vein; postmarginal vein 1.6–1.75 × length of stigmal vein. Legs (Fig. 166) dark except protibia dorsolongitudinally, knees narrowly, and basal tarsomeres of meso- and metatarsi pale, although rarely second tarsomeres brownish to white. Metanotum with dorsellum coriaceous, alutaceous or more distinctly mesh-like reticulate. Propodeum with median carina over most of length; often somewhat more finely sculptured, alutaceous to mesh-like coriaceous than dorsellum; spiracle obliquely oval, usually at least very slightly separated from metanotum (Fig. 172) although sometimes uniformly developed rim touching metanotum (Fig. 173). Gaster (Fig. 165) mostly brown in smaller individuals to variably extensively green to blue or purple dorsally, although posterior margins of basal four tergites at least broadly brownish along posterior margins and sometimes up to basal five tergites entirely brown to coppery-brown; about 1.6–2.4 × as long as wide (smaller ratio typical of critical point-dried, inflated specimens, and larger ratio of air-dried specimens with gaster strongly collapsed), and subequal in length to combined length of head + mesosoma; syntergum short.

Male (Figs 151, 161)

Similar to female except for antennal structure and as follows: body sometimes much more distinctly blue to purple (Figs 151, 175); speculum sometimes not as distinctively narrow; propodeal spiracle more commonly obviously separated from metanotum (Figs 174, 175). Antenna with flagellar rami long and slender, with long, hair-like seta, but with at most comparatively sparse and inconspicuous mps, rarely without but usually with at least one mps basally on R3 of at least one antenna, often with one or two mps on one or both of R2 and R3, and rarely with up to three mps on R3 of one antennae, the two antennae usually being asymmetric in mps pattern (Figs 155, 162, 169, 170); scape with row of closely spaced sensory pores along ventral margin mesally, the distance between basal-most pore and basal margin similar to or only slightly greater than distance between apical-most pore and apical margin, and much less than length of row of pores (Fig. 171).

Distribution

North America (British Columbia, Ontario) and Europe (England, France, Romania, Sweden).

Hosts

Ceutorhynchus cardariae on *Car. draba*; *Ceutorhynchus erysimi* (Fabricius) and *Ce. typhae* on *Cap. bursapastoris*. Other hosts listed (Noyes, 2013) require confirmation of the parasitoid identification, especially those from Lepidoptera, as the species in the *N. tidius* group are associated with Coleoptera. A further confirmed plant host record based on a specimen in R. R. Askew's collection (England, Yorkshire, 23.vii.1963) is *Cakile maritima* Scop. (Brassicaceae).

Discussion

Recognition of *N. tidius* in North America is discussed under *N. duplicatus* and in Europe under *N. leucarthros*. Variation in position of the propodeal spiracles relative to the metanotum (see Discussion under *N. duplicatus*) makes keying *N. tidius* females more difficult, but a comparatively narrow speculum in combination with a more extensively setose subcubital setal line (Fig. 168) and often more distinctively oblong funiculars (Fig. 167) will help identify those females in which the spiracles appear to touch the metanotum (Fig. 173). Males are also variable in the number and arrangement of mps on R2 and R3, rarely being entirely absent but usually with at least one mps and rarely up to three mps on R3 of one antenna (Figs 169, 170). This mps pattern is intermediate between that of *N. duplicatus* and *N. aenigmaticus*, which typically lack mps, and *N. hippia*, which normally has a greater number and therefore more conspicuous mps. As discussed under *N. duplicatus*, males of *N. duplicatus* very rarely have a single mps on R3 of one antenna (Fig. 113) whereas rare *N. tidius* males apparently lack mps from all rami. The absence of mps can be difficult to establish confidently because the presence of just a single mps on one ramus can be very difficult to observe even in well-preserved males. However, males that we identify as *N. tidius* without any mps have the propodeal spiracles obviously separated from the metanotum (Figs 174, 175). Furthermore, amongst *N. tidius* complex species (*N. duplicatus*, *N. aenigmaticus*, *N. hippia*, and *N. tidius*), males of *N. tidius* uniquely have the sensory pores of the scape occupying a mesal position (Fig. 171) rather than within the apical half of the scape (Figs 102, 138).

Within the *N. tidius* group, the colour pattern of the tegulae appears to be uniquely variable in *N. tidius*. Some individuals appear to have an entirely dark tegula, whereas in others it is only very narrowly yellow along the inner margin to obviously yellow except apically or apicolaterally similar to *N. aenigmaticus* and *N. metalarus*. Individuals of *N. tidius* that we

sequenced included females with the tegulae entirely or virtually entirely dark (e.g. NT31, NT33) and ones with the tegulae quite obviously partly pale (e.g. NT20, NT33, NBT95). Careful observation is required and a bicoloured pattern may not be apparent in some instances in which the wings are held over the body and the tegula is aligned longitudinally with its inner, lighter coloured margin slightly overlapped by the mesoscutal margin. All the individuals that we identify as *N. aenigmaticus* have a partly to entirely yellowish tegula (Figs 94, 95), whereas individuals of the other *N. tidius* group species have an entirely dark tegula. Individuals of *N. metalarus* within the *N. artynes* group also have a bicoloured tegula (Fig. 28), but amongst other features females are readily distinguished by their more strongly sculptured, reticulate propodeum (Fig. 37), and a broad speculum (Fig. 36), and males by having mps on the basal ramus.

The BMNH has a single female of *N. tidius* from England labelled as 'ex. *Helianthemum* leaf miner'

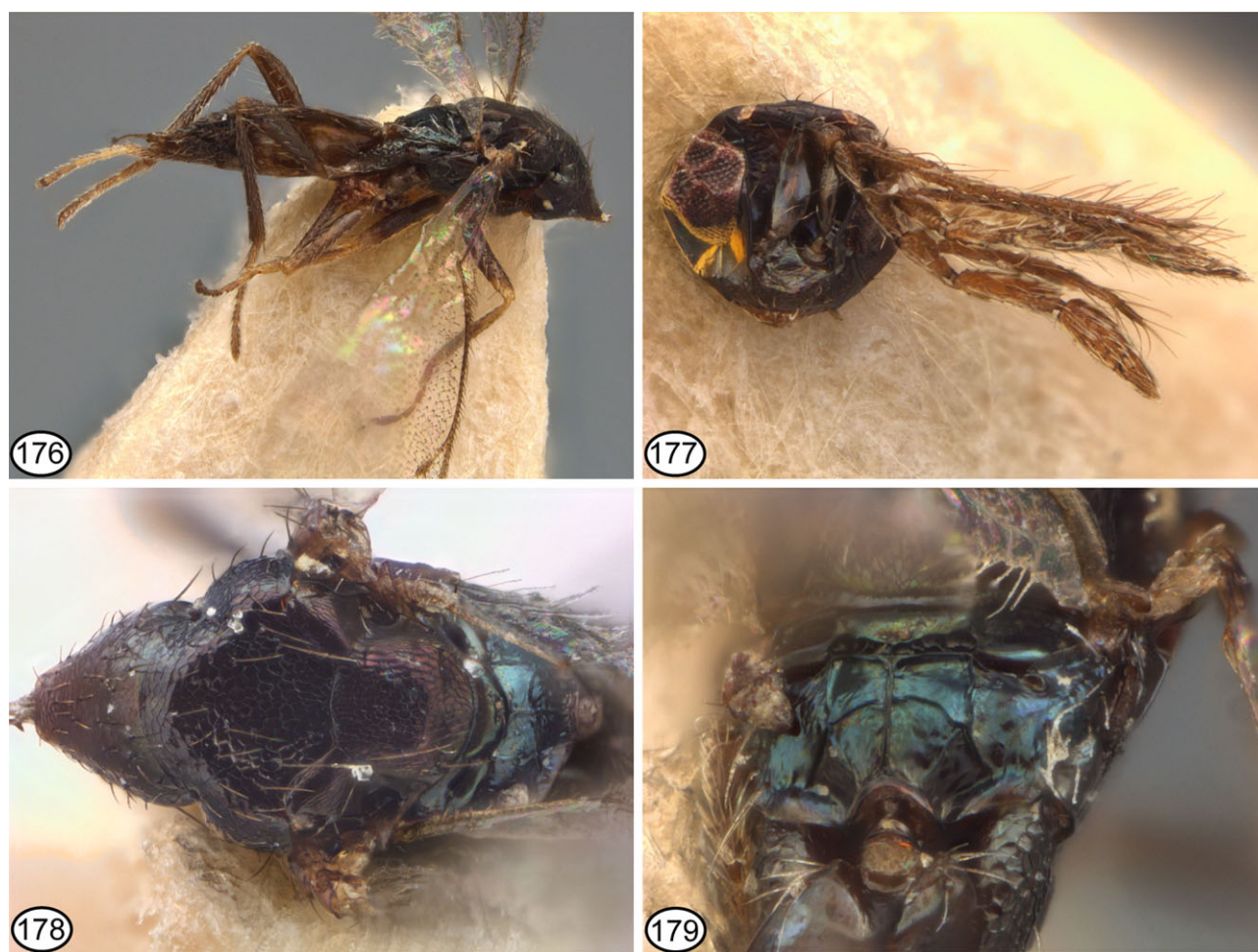
(Cistaceae) and a male and female from an unstated locality, although probably England, labelled as reared from clover heads. The clover host might have been the clover head weevil, *Hypera meles* (Fab.) (Curculionidae), but regardless, the clover and *Helianthemum* hosts probably were not *Ceutorhynchus* species. We did not sequence material of *N. tidius* from England, the type locality of *N. tidius*, and this should be carried out, particularly from specimens reared from such plants as clover, to determine whether their genotypes are the same as what we here identify as *N. tidius* or belong to yet another cryptic species.

SPECIES REMOVED FROM *NECREMNUS*

PNIGALIO TYRRHENUS (WALKER) COMB. NOV.

(FIGS 176–179)

Eulophus Tyrrhenus Walker, 1839: 147–148. ♂ lectotype (BMNH, here designated).



Figures 176–179. *Pnigalio tyrrhenus*, ♂ lectotype. 176, lateral habitus without head; 177, head and antennae; 178, dorsal mesosoma; 179, propodeum.

Eulophus tyrrhenus Bouček & Askew, 1968: 150 (possible synonym of *Pnigalio pectinicornis* L.).

Type material

There is no indication in the original publication that Walker (1839) described *E. Tyrrhenus* from more than one male, collected near London. The BMNH has a single point-mounted male with the following six labels: (1) a circular, purple-bordered label with 'LECTOTYPE'; (2) a rectangular label with '*Eulophus Tyrrhenus* Walker' handwritten on one side and 'Stood under this name in old B.M. Coll. C. Waterhouse.' printed on the other side; (3) a rectangular, handwritten label with '*tyrrhenus* Lectotype M. de V. Graham'; (4) a rectangular, handwritten label with '♂ +'; (5) a rectangular label with '*Pnigalio*' [apparently in handwriting of Zdenek Bouček (N. Dale-Skey, pers. comm.)]; and (6) a square label with 'B.M. TYPE HYM. 5.2516'. The specimen is mounted by its left side to the tip of the point (Fig. 176) and the head is detached and glued on the point (Fig. 177).

Discussion

We examined type material of *E. Tyrrhenus* because Noyes (2013) included the name in *Necremnus*, the species was described by Walker (1839) immediately following *N. folia*, and a male from Clermont, France, identified as *E. Tyrrhenus* in Walker (1846a) is probably a male of *N. folia* (see under Type material for the latter species). However, Bouček & Askew (1968) had suggested that *E. Tyrrhenus* was synonymous with *Pnigalio pectinicornis* L., crediting 'Graham (*in litt.*)' for this proposal. Although the original Latin description of *E. Tyrrhenus* follows that of *E. folia* and differs little from it other than in a few relative features, it does state '*pedes nigri*' (legs black) and '*tarsi picei*' (tarsi pitch), which fits the male labelled as the lectotype, but not males of *N. folia*. In order to stabilize the name, we formally designate the Graham-labelled male as the lectotype of *Eulophus tyrrhenus* Walker and transfer the species to *Pnigalio* Schrank as *Pnigalio tyrrhenus* (Walker) comb. nov. The generic transfer is based in part on the antennae having three rami (Fig. 177) similar to males of *Necremnus*, but the propodeum having a complete median carina, plicae, and costulae (Fig. 179), and the mesoscutum having numerous conspicuous, bristle-like setae (Fig. 178). The proposed synonymy of *P. tyrrhenus* and *P. pectinicornis* by Bouček & Askew (1968) remains questionable based on the colour habitus drawing of a male of the latter species by Thuróczy (1999: fig. 2). This shows the tibiae and tarsi to be mostly pale and the propodeal costulae intersecting the median carina quite close to the anterior margin of the propodeum. The propodeal sculptural pattern of the lectotype (Fig. 179) of *P. tyrrhenus* is more

similar to that illustrated by Miller (1970: fig. 126), with the costulae intersecting the median carina closer to its midlength.

DISCUSSION

Phylogenetic analyses performed using DNA sequence data from a mitochondrial gene and two ribosomal regions revealed complexes of genetic lineages in both of what previously had been identified as *N. tidius* and *N. artynes* based on morphology. Re-examining morphology under the light of molecular evidence enabled subsequent partitioning of morphological features initially thought to be continuous into different character combinations that enabled both sexes of the genetic lineages to be distinguished. Sequencing new individuals identified using the revised morphological concepts in an iterative fashion supported the newly discovered differential features for lineage recognition and, hence, the strong support of discrete species based on both molecular and morphological evidence. This study provides a straightforward example of an iterative integrative taxonomy process that can be stopped at the level of integrating molecular and morphological data without the need to consider other independent lines of evidence. However, although we do not anticipate it at this moment, it is not to be excluded that the relatively high intraspecific *COI* variation found here within some species could hide as yet undetected cryptic morphological variation.

One of the most important features for differentiating the sexes of *Necremnus* species is antennal structure, including pattern of the mps on the rami and position of the sensory pores of the scape for males. Cryptic speciation in parasitic Hymenoptera is particularly interesting because host finding in parasitoids involves both host volatiles and volatiles from the plant associated to the herbivore host (Vet & Dicke, 1992). Furthermore, males react to conspecific females by courtship displays that induce sexual receptivity (Van den Assem *et al.*, 1980). Hence, it is likely that antennal features are subjected to strong selective pressures and that this explains at least in part why different species differ in their sensory apparatus. The same rationale might help explain differences in body or wing colour patterns that are important for sexual receptivity. However, there is less obvious evolutionary rationale for the differences in most of the other differential features found for the *N. artynes* and *N. tidius* complexes, such as relative position of the propodeal spiracles and setal patterns of the fore wings. More detailed study of the different sensory structures of slide-mounted antennae or through scanning electron microphotography for both females and males is warranted in any future, more comprehensive revision of *Necremnus*. A gross difference in relative position of

the sensory pores on the scape was found for males in both the *N. tidius* and *N. artynes* complexes, but this character has not been studied for males of all *Necremnus* species.

The present study, through reversing the synonymy of *N. duplicatus* under *N. tidius*, explains previously noticed variation that Gibson *et al.* (2005) interpreted as possibly representing host-induced variation or evidence of sibling species. The presence of more than one species under the name *N. tidius* also explains the apparent anomaly of this 'species' commonly being a major parasitoid of the cabbage seedpod weevil in North America, but not in Europe. It has further implications for the host range recorded in the literature for *N. tidius*, which includes not only ceutorhynchine weevils but also beetles of other families as well as Diptera, Lepidoptera, and Hymenoptera (Noyes, 2013). Our results suggest that at least some of these recorded hosts result from misidentifications of the parasitoid, and possibly the presence of additional cryptic species within Europe. It must be noted that all of the previously existing names used for both the *N. tidius* and *N. artynes* complexes are based on specimens described from Britain, but we only sequenced individuals from mainland Europe. Collection and sequencing of fresh specimens from Great Britain is necessary to prove that our application of nomenclature is correct. Further sequencing, particularly for individuals reared from other hosts throughout Europe, is necessary to further resolve the true extent of sibling species and establish accurate host ranges.

Necremnus duplicatus appears to be most closely related to *N. aenigmaticus* based both on our molecular results (Fig. 1) and morphology. Numerous rearings in North America indicate that *N. duplicatus* is the only species that attacks *Ce. obstrictus* on canola, although both species have been reared from *Ce. typhae* on *Cap. bursa-pastoris*. Different genotypes of this latter weed are thought to have been introduced into North America by the earliest colonizers from Europe: to the southern and western parts of North America by the Spaniards and to the eastern parts of North America by the French and English (Neuffer & Hurka, 1999). Although closely related, the genetic differences between *N. duplicatus* and *N. aenigmaticus* make it unlikely that the former species was introduced along with *Ce. typhae* on one of the genotypes of *Cap. bursa-pastoris* from Europe. Hence, *N. duplicatus* is mostly likely a North American species that expanded its host range to include *Ce. obstrictus* as a host once it had been introduced. The question of the identity of the *Necremnus* species reported in the literature to parasitize *Ce. obstrictus* in Europe (Gibson *et al.*, 2005 and references therein) remains. In this study, in spite of a large sampling effort, no *Necremnus* was reared from the cabbage seedpod

weevil, not even in fields heavily infested by hoary cress or shepherd's purse where *N. hippia* and *N. tidius* have been collected (Tim Haye, CABI, Delémont, pers. comm.). However, we suggest that the species might indeed be *N. aenigmaticus* based on the morphological similarity between *N. duplicatus* and *N. aenigmaticus* and because museum specimens suggest that hosts of *N. aenigmaticus* include weevils on other species of *Brassica*. By contrast, the present study suggests that *N. tidius* was introduced along with *Ce. typhae* on *Cap. bursa-pastoris* from Europe. The comparatively limited genetic variation of North American samples is compatible with a genetic bottleneck consequence of a small founder population introduced by the early settlers.

Contrary to other recent studies that have shown that polyphagous species are indeed complexes of more or less host-specific cryptic species (Gebiola *et al.*, 2012; Deng *et al.*, 2013), the species identified here seem not to be restricted to a single host, especially for the *N. tidius* complex. This is probably because of the homogeneity, abundance, and closeness of the host plants, which all belong to the family Brassicaceae. An exception in this study is represented by *N. tutae*. In this case the only host yet recorded is invasive to Europe and to date there is no evidence of a *Necremnus* native to South America that might have been introduced to Europe along with the pest. Consequently, it is very likely that the native host of *N. tutae* has eluded our sampling effort.

Our findings also explain the synchrony between the invasion of canola fields by *N. duplicatus* and *Ce. obstrictus*, because its two native hosts, *Ce. neglectus* and *Ce. omissus*, have larval development that occur earlier in the season than that of *Ce. obstrictus*. However, this does not solve the problem that its early parasitization coincides with the time of recommended insecticidal treatment.

Two species of *Necremnus* that we can now identify as *N. cosmopterix* and *N. tutae* were initially reared and commercialized by an Italian insectary (Bioplanet, Cesena, Italy) (Ferracini *et al.*, 2012). At some point, Bioplanet decided to commercialize only *N. tutae* owing to its better sex ratio, a shorter life cycle, and more effective parasitization rates (Ferracini *et al.*, 2012). Hitherto, *N. tutae* has shown promising control activity in the lab (Ferracini *et al.*, 2012), and in Tunisia it is reported to parasitize up to 25.5% of populations of *T. absoluta* in the field (Abbes *et al.*, 2014). Similarly, at IRTA (Spain), both *N. tutae* and *N. artynes* were initially reared, but *N. artynes* was dismissed because it is not as effective as *N. tutae* (Rosa Gabarra, pers. comm.). The studies of Ferracini *et al.* (2012), Calvo *et al.* (2013), and Chailleux *et al.* (2013) revealed behavioural and biological differences in terms of host larval stage preferences. As the species used was the

same (Rosa Gabarra, pers. comm.), the differences might be explained by different experimental procedures, environmental conditions, or different populations. Although we are now able to correct misidentifications and assign proper names to species of the *N. artynes* complex [for example, the species used by Balzan & Wäckers, (2013) is most likely to be *N. tutae* and not *N. artynes*], it is not always easy to a posteriori link biological data accumulated prior to the cryptic species here characterized. Indeed, it cannot be excluded that more than one species was used in any one study because of the difficulty in distinguishing them. However, within the *N. artynes* group, it is now clear that the most abundant species in the field, the most geographically widespread, the one that is performing better in the lab, and that is being commercially distributed is not *N. artynes* but *N. tutae*. The discovery that three out of four species of the *N. artynes* complex are able to parasitize *T. absoluta* is very encouraging for the medium–long term control of this invasive pest. However, nothing is known about potentially deleterious competition amongst species in the field; the present paper may indeed provide a framework for such studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Bayesian majority rule consensus tree based on the cytochrome oxidase subunit I (*COI*) data set. Posterior probabilities > 0.95 above branches.

Figure S2. Maximum likelihood tree based on the cytochrome oxidase subunit I (*COI*) data set. Bootstrap values > 70% above branches.

Figure S3. Bayesian majority rule consensus tree based on the ribosomal data set. Posterior probabilities > 0.95 and bootstrap values > 70% relative to similar splits in the maximum likelihood (ML) tree are indicated above branches.

Table S1. Uncorrected p-distances based on *COI*: a) infraspecific; b) interspecific. S.E. = standard error (above diagonal in square brackets in b).