

The internal genitalia as a taxonomic tool: description of the relict endemic moth, *Coranarta restricta* sp. n., from the Iberian Peninsula (Lepidoptera: Noctuidae: Hadeninae)

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A comparative study of the internal genitalia and examination of ecological preferences show that the Iberian populations formerly referred to as *Coranarta cordigera* (Thunberg, 1788) should be recognised as a distinct species, *Coranarta restricta* sp. n. Because of its rarity, extremely local distribution, and endemic and relict character, it should be regarded as an endangered species and its potential as a flagship species in conservation programmes is addressed. The phylogenetic and zoogeographical relationships among the species of *Coranarta* are outlined. The utility of structural matching of internal genitalia in conspecific males and females as a taxonomic tool is discussed, together with the main hypotheses of the evolutionary significance of internal genital differentiation in allopatric species.

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1. Introduction

Berio (1985) and Beck (1991) noted differences between the type species of the hadenine noctuid genus *Anarta* Ochsenheimer, 1816 (*Noctua myrtilli* Linnaeus, 1761) and species of the *cordigera* species group, both in the adult and larval stages (see also Beck 1999). Consequently, Beck (1991) erected *Coranarta* (type species: *Noctua cordigera* Thunberg, 1788) for this latter group.

An earlier taxonomic review of this boreo-alpine group by Lafontaine *et al.* (1987) split *Coranarta cordigera*, until then considered to have a holarctic distribution, into four species: *C. cordigera* in Europe (from the Ural Mountains westwards), *C. carbonaria* (Christoph, 1893) in

Siberia and the Far East, *C. luteola* (Grote & Robinson, 1865) in North America and *C. macrostigma* (Lafontaine & Mikkola, 1987) in western North America. The main criteria for separating these species were differences in the internal genitalia (vesica in males and bursa copulatrix in females). Despite some intraspecific, apparently population-dependent, variability (Yela, in prep.), it has been shown that the three-dimensional structure of the everted and expanded vesica of a given noctuid species generally matches the three-dimensional structure of the expanded cervix bursae or posterior part of the bursa copulatrix of conspecific females (e.g. Hardwick 1958, 1970, Lafontaine 1981, 1987, Lafontaine & Mikkola 1987, Lafontaine & Poole 1991, Matthews 1991,

Table 1. Geographic and environmental descriptors of the sites where *C. restricta* has been found (all sites visited by the author). Coastal site in Calle (1983; fig. 127) is erroneous (Yela & Ortíz 1990); other sites given in Calle (1983) and Yela & Ortíz (1990) correspond with those in the Table. Province: TE = Teruel; GU = Guadalupe. Bioclimatic stage: SM = Supra-mediterranean (see definition in Rivas-Martínez 1983, 1987). 'Vegetation' refers to dominant vegetation type: P-Q = mixed forest of *Pinus nigra* and *Quercus faginea*, with scattered *Juniperus thurifera* and *J. oxycedrus*; P-Q-E = mixed forest of *Pinus halepensis*, *Quercus faginea* and *Q. rotundifolia*, with scattered *Juniperus thurifera*; J = open formation of *Juniperus thurifera*; P = *Pinus sylvestris* forest with scattered *Quercus pyraenaica*. 'Ericaceae' refers to ericaceous species found at the corresponding site: Au = *Arctostaphylos uva-ursi*, Eau = *Erica australis*, Ea = *Erica arborea*, Cv = *Calluna vulgaris*.

Specimen	Collecting site	Province	UTM coord.	Altitude	Bioclimatic stage	Vegetation	Ericaceae
Holotype	Albarracín (La Losilla)	TE	30TXK37	1250 m	SM	P-Q	Au, Eau, Ea
Paratype 1	Buenafuente del Sistol, 1	GU	30TWL61	1000 m	SM	P-Q-E	Au
Paratype 2	Buenafuente del Sistol, 2	GU	30TWL61	950 m	SM	P-Q-E	Au
Paratype 3	Albarracín (4 km W)	TE	30TXK37	1100 m	SM	J	Au
Paratype 4	Albarracín (surroundings)	TE	30TXK37	1150 m	SM	J	Au
Paratype 5	Bronchales	TE	30TXK28	1585 m	SM	P	Au, Eau, Cv
Zapater & Korb (1982)	Alcalá de la Selva	TE	30TXK97	1500 m	SM	P	Au, Eau, Cv

Mikkola 1992, Yela 1992, Lafontaine 1998). There is a causal, functional explanation for this fact, because the success of sperm transfer from the spermatophore(s) to the ductus seminalis depends on the ability of the male to place the spermatophore tip just in front of the opening of ductus seminalis. This has the evolutionary consequence of structural matching of the internal genitalia of both sexes (Callahan & Chapin 1960, Byers & Hincks 1978, Lafontaine 1981, Mikkola 1993), brought about by strong stabilizing selection and intersexual coevolution (Mikkola 1993) (cohesion *sensu* Templeton 1989). Slight differences in the orientation of either structure may make sperm transfer difficult or impossible, even in closely related species (Byers & Hincks 1978, Lafontaine 1981, Byers & Lafontaine 1982, Mikkola 1993). The four currently recognised species of *Coranarta* show differences of this nature, which are thought to be indicative of reproductive isolation (Lafontaine *et al.* 1987).

During the course of my studies on Ibero-balearic Noctuidae, I found evidence that individuals from Spain referred to as *C. cordigera* show remarkable differences in both male ($n = 1$) and female internal genitalia ($n = 5$) from the remaining European populations (see also Yela & Ortíz 1990, Yela 1998). In addition, the Iberian populations are not restricted to true bogs and peatlands, as is usual in the other species (Mikkola & Spitzer 1983, Lafontaine *et al.* 1987), but are instead associated with sites that are seasonally dry and hot in summer and very cold in winter. This led to the question addressed in this paper: are the internal genital differences found in the Iberian populations of a similar degree to those between other congeneric species of *Coranarta*? If so, the Iberian populations would have to be treated, and described, as a new species.

2. Material and methods

2.1. Field work

Moths of all species of *Coranarta* fly in sunshine, so the adults of Iberian *Coranarta* were collected using a butterfly net. No explicit collecting programme was employed by any of the collectors. I visited all collecting sites to identify their ecological and physiographic characteristics (Table 1) and plant species composition, as well as to search for larvae and their putative host plants.

2.2. Genitalia manipulation

Abdomina were dissected and genitalia mounted using standard techniques. Vesicas and bursas were carefully everted and/or expanded with isopropanol prior to the final mounting in Euparal (e.g. Hardwick 1950, Lafontaine 1981, Lafontaine & Mikkola 1987, Yela 1992, Fibiger & Goater in Fibiger 1997). Although Siloprene (Magro 1994) is probably a better mountant, allowing not only full expansion of internal structures and their measurement, but also three-dimensional comparisons from all angles, it was not used here because of the irreversibility of the process. Measurements were made using a micrometer incorporated into a standard binocular microscope. Drawings were made using a Bianchi projector, prior to the final mounting (to avoid possible distortion by the cover glass). Spermatophore counts were made using a microscope with 100× magnification to minimize errors.

2.3. Statistics

Basic statistics were calculated using STATISTICA 5.5 (StatSoft 1999).

2.4. Terminology

Abbreviations: MNCN = Museo Nacional de Ciencias Naturales, Madrid (Spain); JLY = José Luis Yela.

3. Results

Preliminary doubts about the taxonomic identity of Iberian *Coranarta* arose from its habitat preferences, which are strikingly different from those of all other European populations (see Yela & Ortíz 1990, and below). Examination of the genitalia of several individuals ($n = 6$) reinforced this concern. As shown below, the internal genital differences are sufficient to presume reproductive isolation, and thus specific status, until experimental data are available.

3.1. Diagnosis

Coranarta restricta Yela, sp. n. (Figs. 1a–d, 2a, 3a–b)

Externally, similar to the Eurasiatic species, *C. cordigera* (Europe) and *C. carbonaria* (Siberia

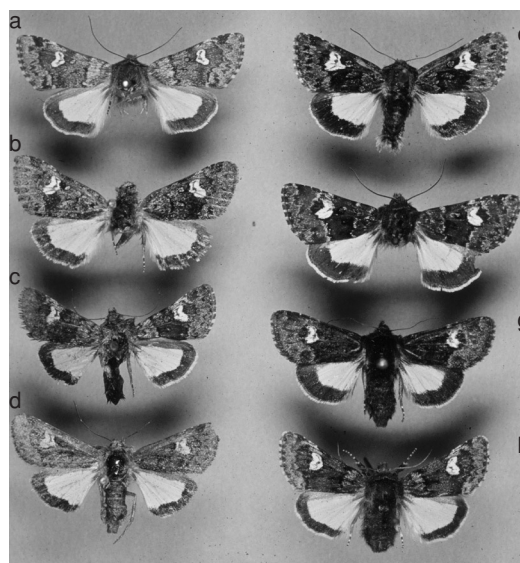


Fig. 1. Adults of *Coranarta*. — a. *C. restricta*, holotype male, Spain, Teruel, Albarracín. — b. *C. restricta*, paratype female, Spain, Guadalajara, Buenafuente del Sistol. — c. *C. restricta*, paratype female, Spain, Teruel, Bronchales. — d. *C. restricta*, paratype female, Spain, Teruel, Albarracín. — e. *C. cordigera*, male, Poland, Nowe Bagienice k. Muocgova. — f. *C. cordigera*, male, Germany, Kammerwald. — g. *C. cordigera*, dark form, female, N. Russia, Arctic Ural, Polarnyi village. — h. *C. carbonaria*, female, without data.

and the Far East), particularly the former, but easily distinguishable by the width of the terminal band of the hindwing, which is relatively narrower in *C. restricta*. The terminal band is rather broad in *C. cordigera* (Figs. 1e–g) and very narrow in *C. carbonaria* (Fig. 1h). In the male genitalia, the vesica of *C. restricta* is closest to that of *C. cordigera*, i.e. it lacks the additional subbasal diverticulum of *C. carbonaria*, but the two main diverticula are longer and the median one is directed toward the anterior part of the aedeagus, reaching its central zone. In the female genitalia, the ductus bursae is more rounded than in *C. cordigera* and *C. carbonaria*. Also, the bulge in the right side of the ductus bursae is smoother, the pouch in the right wall of the corpus bursae is absent or only very slightly developed and the ductus seminalis has a small pouch at its base, pointing in a more inner direction than in *C. cordigera* (similar to *C. carbonaria*).

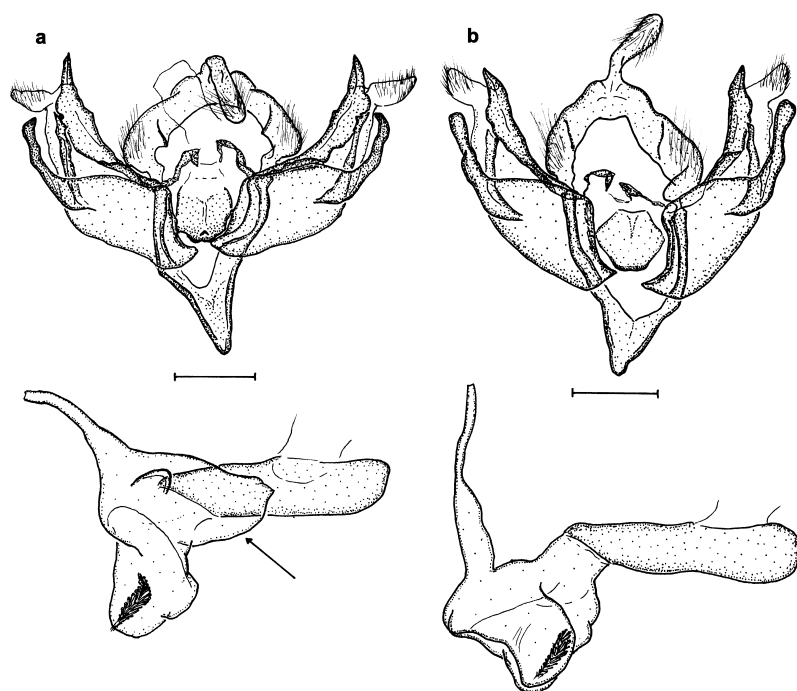


Fig. 2. Male genitalia of *Coranarta*. — a. *C. restricta* Yela, sp. n., holotype male, Spain, Teruel, Albarracín (median diverticulum indicated by an arrow) — b. *C. cordigera*, male, Germany, Kammerwald. Scale bars 1 mm.

3.2. Description

3.2.1. Adult

Wingspan 21.8–26.0 mm ($\bar{x} \pm \sigma = 24.6 \pm 1.7$; $n = 5$). Male basal coremata absent (as in other *Coranarta*). Male and female antenna filiform, finely and shortly ciliate ventrally to tip; cilia more dense in male antenna. Eye reduced, elliptoid (corresponding to diurnal activity of adults). Ground colour of head, thorax and forewing above dark grey. Median field of forewing slightly darker than basal and terminal fields. Antemedian line black, straight, clearly marked in most individuals. Postmedian line less marked, relatively straight, slightly toothed on veins, not excurved around basal part of the reniform stigma (as in *C. cordigera*). Subterminal line visible as row of blackish spots in the single known male; barely visible in females. Orbicular stigma very small, dark grey, very faint. Reniform stigma large but relatively narrow, whitish, with a black longitudinal, slightly angled strip towards the centre (in *C. cordigera* strip is located toward inner part of reniform). Claviform stigma absent. Fringe dark grey with whitish spots at veins. Forewing under-

side blackish with yellowish patch at position of reniform stigma, slightly larger than in *C. cordigera* but clearly smaller than in *C. carbonaria* (see figures 4 and 8 in Lafontaine *et al.* 1987). Hindwing above and below yellow in approximately basal 4/5 with grey on costa and blackish grey band on approximately the marginal 1/5 of wing. On the right hindwing, the blackish band excluding fringe at vein M1 is 0.9–1.2 mm wide (1.1 ± 0.1 ; $n = 6$), at vein Cu1a 0.7–1.1 mm wide (0.9 ± 0.1 ; $n = 6$). Discal spot absent.

Male genitalia (Fig. 2a). External armature very close to that of *C. cordigera*. In the single known male, the costal extensions of valva and vinculum comparatively longer. Aedeagus also very similar to that of *C. cordigera*. Vesica consisting of relatively long and narrow subbasal diverticulum, with subapical patch of short spines and, at right, long median diverticulum directed toward anterior part of aedeagus and reaching its central zone. Median diverticulum with smooth subbasal conical elevation. Ductus ejaculatorius widened basally.

Female genitalia (Figs. 3a–b). Ovipositor short. Ductus bursae almost circular, with very smooth bulge in right side; ratio of width of duc-

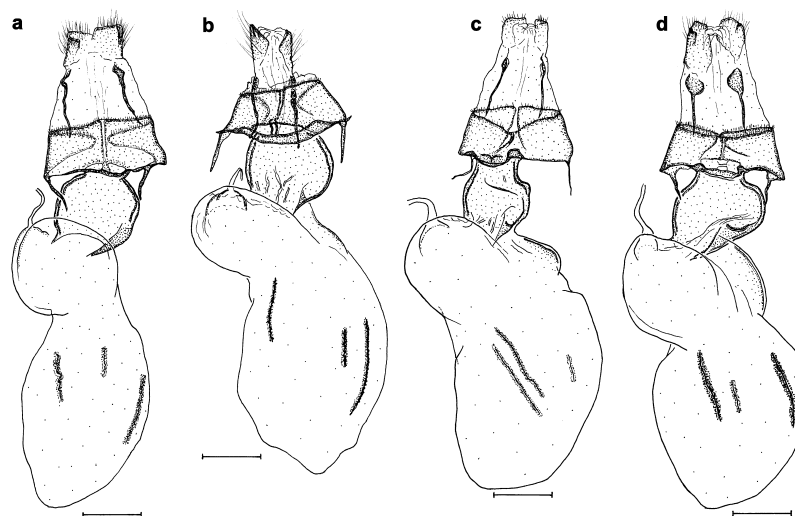


Fig. 3. Female genitalia of *Coranarta*, ventral view. — a. *C. restricta* Yela, sp. n., paratype female, Spain, Guadalajara, Buenafuente del Sistol. — b. *C. restricta* Yela, sp. n., paratype female, Spain, Teruel, Albarracín. — c. *C. cordigera*, female, Finland, Koski. — d. *C. cordigera*, female, without data. Genitalia shown in slightly different positions to allow better comparisons. Scale bars 1 mm.

tus bursae (at widest segment) to that of length (at longest segment) is 1.10–1.19 (1.13 ± 0.04 ; $n = 5$), in *C. cordigera* it is 0.90–0.99 (0.94 ± 0.04 ; $n = 5$). Right wall of the corpus bursae lacking pouch (Fig. 3a) or, when present (Fig. 3b), very shallow. Corpus bursae relatively large, ellipsoidal with three longitudinal signa. Cervix bursae comparatively long and rounded. Ductus seminalis directed toward ductus bursae, with small basal pouch.

Type material. Holotype male, Spain, Teruel, Albarracín, slide 90.Y.38 (JLY), coll. T. Seebold in coll. MNCN, Madrid (type number 8987). Paratypes: 2 females, Spain, Guadalajara, Buenafuente del Sistol, 950–1000 m, 10.V.1987 and 19.IV.1993, slides 90.1591 and 90.1868 (JLY), leg. M. Ortíz in coll. JLY, Spain, Toledo; 2 females, Spain, Teruel, Albarracín, 1100–1150 m, 13.V.1929 and 21.V.1988, slides 90.Y.53 and 90.Y.49 (JLY), leg. B. H. H. Cooke (in coll. M. Fibiger, ex coll. B. H. H. Cooke; det. M. Fibiger) and leg. et coll. V. Redondo, Spain, Zaragoza; 1 female, Spain, Teruel, Bronchales, 1585 m, V.1978, slide 90.Y.48 (JLY), leg. et coll. F. Blat, Spain, Teruel, Bronchales.

Etymology. The name *restricta* refers both to the restricted blackish band of the hindwings and the restricted distribution area.

3.2.2. Early stages

Unknown. A single last instar larva, apparently matching that of *C. cordigera*, was found on *Arctostaphylos uva-ursi* (Ericaceae) in the Tagus valley on 20.VI.1998 by a Spanish amateur colleague, some 10 km further SW of Buenafuente del Sistol, Guadalajara Province. The larva had dried up by the time I examined it and no morphological comparative data with the well-known larva of *C. cordigera* could be ascertained.

3.3. Life cycle

The moths are on the wing from mid-April to early June, with most observations and collections in May. The moths fly rapidly in bright sunshine. The males are much more active and difficult to observe and collect. Sometimes they visit flowers of *Arctostaphylos* and other low plants, or are found resting on the leaves of *Arctostaphylos*. On one single occasion (May 1987), they were observed in relatively high numbers, 10 individuals in two hours, but usually they are very scarce (all these data M. Ortíz, Guadalajara, pers. comm.). Multiple mating is common, and thus sperm

competition is possible. The number of spermatophores found inside the bursae varies from 1 to 4 (1, 1, 2, 3, 4). From the form and length of the ovipositor, the eggs are probably laid on the leaves of the foodplant. The only known larval foodplant (if the examined larva was actually referable to *C. restricta*) is *Arctostaphylos uva-ursi*, which is also a foodplant of *C. cordigera* (e.g. Allan 1941, Mikkola & Jalas 1977, Lorimer 1979, Koch 1984). This is the sole Ericaceae growing in all sites where *C. restricta* has been found (Table 1). Nevertheless, other Ericaceae, such as *Erica australis* var. *aragonensis*, *Erica arborea* and *Calluna vulgaris*, are present in certain sites and may also serve as larval food. I have sought larvae intensively on several occasions (late July to early September, 1997 to 2000, potential months for finding larvae of the related *C. cordigera*; e.g. Koch 1984), with negative results. The sampling effort includes hundreds of individuals of the putative hostplants, in every location where they grow. The larval period should last from May to late June or early July. Larvae are expected to prefer tender and young, structurally less defended leaves of the hostplant, as is usually the case with woody plant feeding noctuids. These, like *C. restricta* and the other *Coranarta* species, are generally univoltine (Yela & Herrera 1993). Bud burst of *Arctostaphylos uva-ursi* occurs in late April and early May in Central Iberia, and relatively young leaves can be found until early-mid July. Although no pupae were found either, the pupa is expected to be subterranean and remain in the ground from June/July until the following spring. This strategy of long aestivo-hibernation in the pupal stage is well documented both for temperate and boreal Eurasian woody plant feeding noctuids (data on single species in e.g. Forster & Wohlfahrt 1971, Mikkola & Jalas 1977, 1979, Lorimer 1979, 1983, Goater 1983) and for Mediterranean species (Templado 1990, Yela & Herrera 1993; data on single species in Ronkay *et al.* 2001).

3.4. Habitat associations

A generalisation of the ecological preferences of *C. restricta* can be derived from Table 1. The spe-

cies has been found in 7 sites only, two of them (Buena fuente del Sistol 1 and 2) relatively close to one another. The sites are located between 950–1585 m altitude, in the Supra-mediterranean bioclimatic stage (Rivas-Martínez 1983, 1987), which is characterised by cold to very cold winters (as indicated by the presence of *Juniperus thurifera*) and warm to relatively hot and dry summers (as indicated by many xerophytic plants). There are no true bogs or peatlands in any of these sites. The ground becomes completely dry in early-mid July and remains so until mid or late August. Only in Bronchales (1585 m) and Alcalá de la Selva (1500 m) are some soil patches covered by bryophytes that could retain some humidity during summer, especially during rainy years. These patches are not proper peat bogs, but are to some extent their Mediterranean (wet in winter, dry in summer) counterparts. Wet patches throughout the year (true peat bogs, including *Sphagnum* and *Drosera* species), called ‘tremedales’ by local people, do exist in the southern Teruel province, but are scarce and no populations of *C. restricta* have yet been found in or near them. In the Bronchales and Alcalá de la Selva sites the soil is acid, favouring a slight podsolization and allowing the presence of *Calluna vulgaris* and *Quercus pyraenaica*. In the remaining sites, the soil is basic. Five sites (Albarracín -La Losilla, Buena fuente del Sistol 1 and 2, Bronchales and Alcalá de la Selva) are covered by relatively dense Mediterranean woodland with clearings (Fig. 4) and the remaining two (surroundings of Albarracín) by markedly xerophytic, open bushy-treelet formations. Common to all of them is the presence of *Arctostaphylos uva-ursi* as a creeping shrub. In contrast, the central and north European species, *C. cordigera*, is a strict typhobiont (e.g., Mikkola & Spitzer 1983).

3.5. Distribution

C. restricta is known from a few sites in central Spain (Guadalajara and Teruel provinces). A map showing all the confirmed Iberian sites can be found in Yela & Ortíz (1990). Fig. 5 shows the known distribution of both *C. restricta* and *C. cordigera*.



Fig. 4. Collecting site of *Coranarta restricta* Yela, sp. n. at Bronchales (1585 m a.s.l.): *Pinus sylvestris* forest with scattered *Quercus pyraenaica* and *Cistus laurifolius*, and *Arctostaphylos uva-ursi* covering the ground.

4. Discussion

4.1. Population and conservation biology

No formal studies have yet been carried out to evaluate population sizes of *C. restricta* nor its spatio-temporal dynamics or functionality in the ecosystem processes. Apparently, it is a scarce species. A twenty-five and a half hour observation yielded 24 individuals at Buenafuente del Sistol (about one individual per hour; M. Ortíz pers. comm.). Due to its apparent rarity, extremely local distribution and endemic character, it is a strong candidate for inclusion in the Red Lists as an endangered, or at least vulnerable, species (categories and definitions in IUCN 2000).

Carroll *et al.* (1996), seeking scientific criteria for the listing process, recorded the 'inclusive

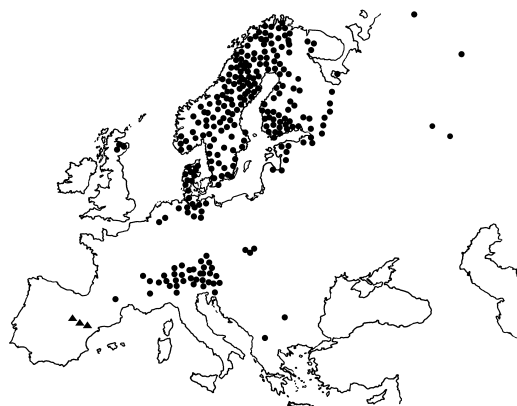


Fig. 5. Geographical distributions of *Coranarta restricta* Yela, sp. n. (▲) and *Coranarta cordigera* (Thunberg, 1788) (●, according to Lafontaine *et al.* 1987, Nowacki & Fibiger 1996, Beshkov 2000, Mikkola pers. comm. and unpubl. data).

benefits' that a species may produce on the whole environment. The distribution area of *C. restricta* encompasses most of the extraordinarily rich and diverse Upper Tagus Valley (data in Junta de Comunidades de Castilla-La Mancha 2001). Actions for conserving all known populations of this species and their habitats may serve as surrogates to preserve the entire region. The Upper Tagus Valley is already classed as a Natural Park (Junta de Comunidades de Castilla-La Mancha 2001). However, many floristically and faunistically unique sites located in the Upper Tagus Natural Park have already been degraded or simply ravaged by massive tourist or industrial usage during the last two decades (Yela 1992). Furthermore, a project exists to construct a golf course in the Bronchales area (a seasonally water-poor district). Thus, any sensible effort towards both the conservation of this region and its flora and fauna, and its reasonable, sustainable use would be welcome, be it based on a single-species or a multi-species approach (e.g. Simberloff 1998).

That being said, *C. restricta* is not a stereotypic dull and inconspicuous noctuid, but a splendid and colourful insect. Beautiful, attractive and lively animals, for example butterflies, are frequently used in conservation to attract the attention of the public opinion (so-called flagship or charismatic species; e.g. Blab & Kudrna 1982, Collins & Thomas 1991, New *et al.* 1995). Public opinion is more

sensitive to the decline or loss of flagship species, and is thus more likely to invest in conservation programmes or to create political support for the protection of these species and their ecosystems (e.g. Meffe & Carroll 1997, Simberloff 1998). The flagship status of *C. restricta* should be made evident and developed to conserve both the species and its habitats.

4.2. Phylogeny and zoogeography

The five known species of *Coranarta* are externally strikingly similar (see Lafontaine *et al.* 1987). The sclerotised parts of their genitalia are also very uniform. The most apparent differences are found in the membranous, inner parts of their genitalia. Morphological similarity suggests a relatively recent origin for the genus. In the context of Cenozoic historical events (progressive splitting and reorganisation of continents, and progressive cooling and xerophication of the Holarctic climate, e.g. de Lattin 1967, Olson 1988, Webb & Bartlein 1992, Hewitt 1996), the distribution patterns (for details, see Lafontaine *et al.* 1987 and Introduction) and association with boreal/cold-montane habitats also point towards a relatively recent origin for *Coranarta*.

C. restricta and *C. cordigera* are morphologically very closely related. The origin of *C. restricta* is plausibly related with Pleistocene contingencies (e.g. de Lattin 1959, Mikkola 1987). It is very likely a result of the well-documented north-south Pleistocene faunal migrations (Huntley & Webb 1989, Blondel & Aronson 1999) and concomitant isolation in the mountain ranges of the Iberian refuge, which are situated across the main migration dynamics (de Lattin 1967, Blondel & Aronson 1999). In this context, *C. restricta* is a relict of Pleistocene times. Although a formal cladistic analysis is still not possible due to lack of sufficient material, the sister pair, *C. restricta* and *C. cordigera*, probably form the sister group of *C. carbonaria*, based on internal genital features. The separation of *C. cordigera* (or the ancestor of *cordigera* and *restricta*) from the Eastern Palaeartic *C. carbonaria* is plausibly related to long isolation caused by the West-Siberian wide ice-melt lake that formed between Western and Eastern Palaeartic populations in the early

Pleistocene. The Nearctic species *C. luteola* is also close to the group comprising *C. restricta*, *C. cordigera* and *C. carbonaria*, supporting past connections via Beringia (see Mikkola *et al.* 1991 for a general discussion on the Beringian refuge). The ancestral species of these four is likely to have inhabited the northern strip of the arboreal zone, with which peatlands are associated. This arboreal zone was continuous between the present Palaeartic and Nearctic during the Miocene but broke up about 6.5 million years ago (at the early Pliocene), leading to speciation between the Palaeartic and Nearctic regions (Mikkola 1987). Finally, *C. macrostigma*, also of the Nearctic, is probably the most phylogenetically basal species of *Coranarta*.

4.3. Evolutionary mechanisms of genital differentiation and isolation

Coranarta consists of five known species, four of them allopatric, which show remarkable differences in internal genitalia. In noctuids, internal genital differences are frequently found in congeneric, allopatric species (see Mikkola *et al.* 1991 for discussion on Palaeartic-Nearctic sister species, and Yela 1992 for data on European-Iberian sister species). The mechanism responsible for constant differences in the configuration of the internal genitalia between allopatric noctuid species that evolved through vicariance, that is, the driving force leading closely related noctuid species to differentiate complicated internal genitalia even in allopatry, remains in dispute (e.g. Mikkola 1993, but see Arnqvist 1998). The allopatric speciation model, as first proposed by Dobzhansky (1937, 1940), proposes that populations differentiate genetically in allopatry and that divergences in mating systems then occur at a later stage, during secondary contact. Evolution of isolation mechanisms to prevent hybridisation is called reinforcement. However, Dobzhansky's model has been challenged, because genital divergence does occur in allopatry. Thus, secondary sympatry is not necessary for the evolution of specific mating systems (Paterson 1980, 1985, Templeton 1989). Why, then, do internal genitalia differ in the absence of secondary sympatry and concomitant reinforcement? There are two

possible explanations.

First, differences are the result of past secondary sympatry events plus reinforcement, and subsequent allopatry. Although theoretically possible, this scenario is unrealistic as a general case. Second, differences are due to steady character displacement promoted by post-mating sexual selection (e.g. sperm competition and sperm choice *sensu* Birkhead 2000, or e.g. sperm competition and cryptic female choice; Thornhill & Alcock 1983, Eberhard 1985, 1996) in initially peripheral (in either an ecological or geographic sense), then later fully separated populations. There is increasing experimental evidence of sexual selection acting on genital characters in insects (Thornhill & Alcock 1983, Shapiro & Porter 1989, Eberhard 1985, 1990, 1993, 1996, Arnqvist 1998 and references therein; see also <http://darwin.ekzool.umu.se/gaq/genital.html>).

Lepidopterists studying noctuids have generally neglected or at least underestimated the role of post-mating sexual selection on genital traits. This is probably due to acceptance of the interpretation that structural matching between the internal genitalia of both sexes serves as a mechanical isolation mechanism and promotes speciation, revitalising the lock-and-key hypothesis (Lafontaine & Mikkola 1987, Mikkola 1992, 1993). Mechanical (i.e. internal genital) isolation would play the role of a postcopulatory but prezygotic isolation mechanism. But despite the acknowledged value of the data gathered, the ultimate significance of the structural matching between the internal genitalia of both sexes in noctuids, and in ditrysian Lepidoptera in general, remains in doubt. Genital differentiation among closely related species may be merely a consequence (not necessarily of pleiotropic nature) of genetic isolation promoted by geographic separation or prezygotic isolation mechanisms (e.g. pheromonal recognition), maintained by sexual selection (e.g. Eberhard 1996, Arnqvist 1998), as described above, and not the cause of isolation and further differentiation. The general morphological similarity but divergent internal genitalia in *Coranarta* suggest that internal genitalia in noctuids may be subject to stronger selective pressures than other morphological structures. In fact, selective pressures tend to be stronger on reproductive traits contributing to (though not neces-

sarily responsible for) reproductive isolation (e.g. Mayr 1969, O'Donald 1980). Under this scenario, post-mating sexual selection would be a plausible explanation for the differentiation of internal genitalia in allopatric noctuid sister species, an explanation that has been sought by noctuid taxonomists in recent years (e.g. Mikkola 1993). If observational and experimental data corroborate this assumption (Arnqvist 1998), structural matching in internal genitalia in noctuids would lose any significance as a mechanism of internal, mechanical isolation, and the lock-and-key hypothesis would again be shown to be unsupported.

4.4. Internal genitalia as taxonomic tools

Regardless of the causes and mechanisms, structural matching between the internal genitalia of both sexes has become a common α -taxonomic tool for lepidopterists studying noctuids in recent decades (Lafontaine 1981, 1987, 1998, Lafontaine & Poole 1991, Matthews 1991, Yela 1992, Mikkola 1992, 1993, Fibiger 1997). Even in the absence of experimental evidence with living material, this tool can still be used by morphologists. However, a fundamental question remains. Some taxa, regarded either as specific or subspecific, show very subtle differences in internal genitalia from other species or subspecies (see examples in Lafontaine 1987 and Fibiger 1997). This would appear to be evolution in progress, but it leads to the question (Ronkay *et al.* 2001): When are vesicas or bursas that are apparently only slightly or subtly different, sufficiently different to allow us to infer lack of sperm transfer and, consequently, lack of interbreeding and therefore specific status? This pitfall must be tackled by noctuid-taxonomists, preferably using experimental and molecular (genetic) tools. In the present case of *Coranarta*, such differences, together with ecological arguments, appear strong enough to imply the specific status for *C. restricta*.

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