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Back from the dead: *Thyreophora cynophila* (Panzer, 1798) (Diptera: Piophilidae) 'globally extinct' fugitive in Spain

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Abstract. We report on a sensational find in central Spain of six specimens of *Thyreophora cynophila* (Panzer, 1798), a colourful, strange-looking piophilid fly living on carcasses of big mammals in advanced stages of decay. Published data suggest that the species is known exclusively from central western Europe (Germany, Austria and France), and was observed last near Paris, France, in the late 1840s, i.e. more than 160 years ago. Accordingly, *T. cynophila* was placed in 2007 as the only dipteran on a list of recent European animals considered to be globally extinct. Collection-based data from all 16 known extant specimens found in seven European natural history museums revealed a specimen without date of *T. cynophila* from Algiers, Algeria. The status of the three thyreophorine piophilids known from Europe is summarized. For the smallest species we reinstate the name *Centrophlebomyia anthropophaga* (Robineau-Desvoidy, 1830) with *Centrophlebomyia orientalis* Hendel, 1907 as a subjective junior synonym (**syn.n.**). We speculate as to why thyreophorines, and *T. cynophila* in particular, have evaded detection for so long.

Introduction

One of the most controversial aspects in biodiversity conservation politics is the significant differences in extinction rate estimates among taxa, being two orders of magnitude higher for vertebrates than for insects (McKinney, 1999). Similar disparities among vertebrates and insects occur in the apparent percentage of threatened species (May *et al*., 1995), with little use of insects as 'flag species' for conservation biology (Kellert, 1993). Paradoxically, insects represent most of the global species richness, so the greatest number of extinctions potentially come from this group (Mawdsley & Stork, 1995).

Maybe one of the few cases in which the extinction of an insect species seemed to be well documented is the European *Thyreophora cynophila* (Panzer, 1798), a dipteran of the cheese- and bone-skipper family Piophilidae, which has acquired almost mythical status. The reasons are many: (i) its strange-looking and colourful appearance (Figs 1, 2); (ii) its attraction to big mammalian carcasses, preferably of odd-toed ungulates, in advanced stages of decay; (iii) its strange phenology, being active only during the cool season (January to March), and preferably after dark; (iv) its alleged capacity of emitting a luminous shine from its large, bright-orange head (Osten-Sacken, 1878); (v) although the species was described first in 1798, and in subsequent decades was recorded from various places in central western Europe, no further specimens have been observed or collected after 1850; (vi) only a few 160-year-old or older specimens exist today in a few of the largest natural history museums of Europe; (vii) it has long been considered as probably extinct within its former distribution area in the heart of western Europe (Germany, France and Austria); (viii) on a list of European animals considered to be globally extinct, Fontaine *et al*. (2007) placed *T. cynophila* as the only dipteran; (ix) *T. cynophila* was

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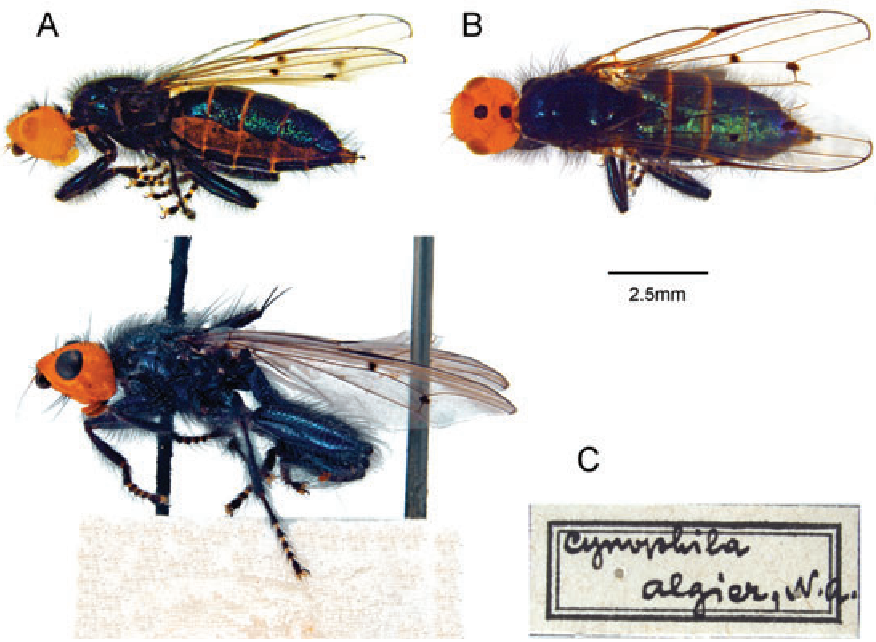

Fig. 1. *Thyreophora cynophila* (Panzer, 1798). (A) Female, lateral view, from Pto de La Morcuera, Madrid Community, Spain, February 2007; (B) same, dorsal view; (C) male, old specimen from Algeria in the Vienna Museum.

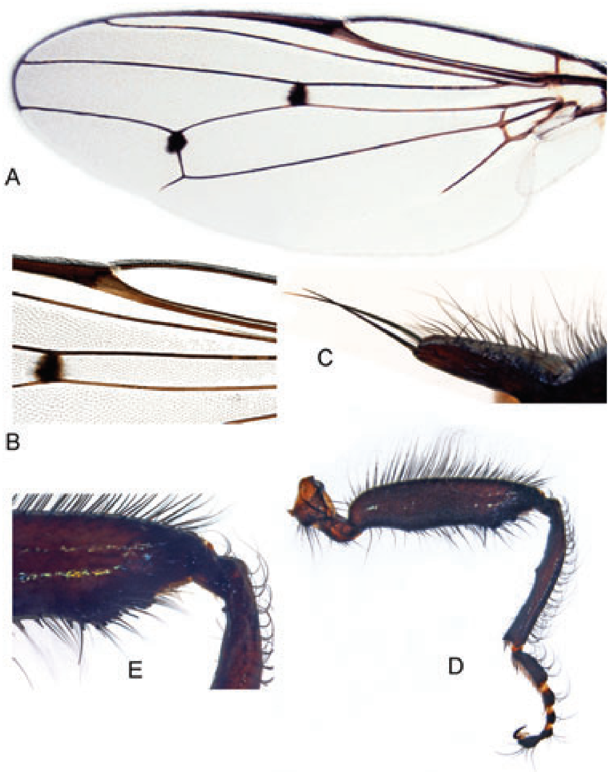

Fig. 2. *Thyreophora cynophila* (Panzer, 1798), male from Pto de La Morcuera, Madrid Community, Spain, February 2007. (A) Left wing; (B) detail of same; (C) scutellum; (D) left hind leg; (E) detail of same. Shown on different scales.

claimed as the first case of a dipteran species eradicated by humans in historical times (Courtney *et al*., 2009).

Against this background, quite unexpectedly some semi-buried, squid-baited traps, which had been operating for a week in January and February 2007 in an oak and in a holm-oak forest near Madrid (Spain), contained six metallic deep-blue flies with a big, orange head (Fig. 1A, B; 2A–E). Evidently two surviving populations of *T. cynophila* had been discovered.

Materials and methods

Sarcosaprophagous insects were studied in natural habitats in Madrid Province, central Spain from June 2006 to May 2007 using carrion-baited traps at 21 localities (Baz *et al*., 2007). Traps were baited with dead squid once a month, and were emptied 7 days later for trapped specimens and bait. Three traps were placed in each locality, so 63 traps were sampled each month, and at the end 756 samples were obtained (63 traps × 12) (Baz *et al*., 2010).

Depositories referred to as the ‘Berlin Museum’, ‘Vienna Museum’, etc. are given in full in Table S1.

Results

Material examined. SPAIN: Madrid Prov.: Lozoya, 1121 m a.s.l. (UTM 30T 436780, 4533579), one male, February 2007; Pto de La Morcuera, 1440 m a.s.l. (UTM 30T 428653, 4525428), two males and one female, January 2007, one male and one female, February 2007 (D. Martín-Vega & A. Baz). Deposited in the Copenhagen Museum.

More than 22 000 specimens belonging to some 80 species of sarcosaprophagous Diptera came from the 756 samples. A greater number of species were present in large numbers and in many samples. As an example, over 1000 specimens of the piophilid *Prochyliza nigrimana* (Meigen, 1826) were trapped. The large necrophagous piophilid *T. cynophila* was represented by only six individuals in two localities of the 21 sampled. The first locality, near Lozoya, is a meadow at 1295 m a.s.l. in a supra-Mediterranean, deciduous holm-oak forest (*Quercus ilex* L.) on granite soil, frequented by cattle. The annual mean temperature in the sample area is 11°C, with min/max values of −11°C/24°C during sampling. The second locality, near Pto de La Morcuera (municipality of Rascafría), is a meadow at 1440 m a.s.l. in a supra-Mediterranean, deciduous oak forest (*Querqus pyrenaica* Willd.) on granite soil, with an annual mean temperature of 9°C, and with min/max values of −12°C/19°C during sampling.

Discussion

Taxonomy

***Thyreophora cynophila* (Panzer, 1798)**
(Figs 1, 2)

Musca cynophila Panzer, 1798: 22.
Thyreophora cynophila (Panzer); Meigen 1803: 276.
Thyreophora cynocephala; Becker 1905: 21. Incorrect subsequent spelling of *Thyreophora cynophila*.

The German physician, botanist and entomologist G.W.F. Panzer (1755–1829) is best known as the author from 1792 to 1810 of *Faunae insectorum germaniae initiae*, one of the finest early post-Linnean book series in systematic entomology. It appeared in a characteristic oblong octavo format, with each species treated on two opposed pages: on the left, with a hand-coloured engraving of the species prepared by one of the finest illustrators of plants and insects of the time, Jacob Sturm (1771–1848); on the right, with Panzer's text in Latin giving the name, references and a description. In this manner Panzer (1798) described the 'Hundefliege' or 'dog fly', *Musca cynophila*, as found on the carcass of a dog in Mannheim (Germany). The original illustration (Figure S1A) and the accompanying description are of a dipteran so striking in appearance that it cannot be confused with any other dipteran occurring in Europe. It was nearly 10 mm long with a bright-orange head with two mid-dorsal black marks, small eyes, body and legs metallic blue, wings clear with two black marks, scutellum very long and hind legs notably stout. The last two characters indicate that the depicted specimen was a male.

Acknowledging the remarkable appearance of *Musca cynophila*, Meigen (1803) proposed a new genus, *Thyreophora*, for it. The name means 'shield bearer' and alludes to the enlarged scutellum (Fig. 2C) of the male. Incidentally, *Thyreophora* is a name also in use for a suborder of armoured ornithischian dinosaurs.

A few additional species were assigned subsequently to or described in *Thyreophora*, but these are recognized currently in other genera that are also characterized by a prolonged and flattened scutellum, particularly in the males. This group of acalyptrate genera had been classified earlier in their own family, Thyreophoridae, but already Paramonov (1954) recommended their inclusion in the Piophilidae. This was adopted by McAlpine (1977), who argued convincingly that the family Piophilidae is paraphyletic without inclusion of the thyreophorine genera. Most subsequent authors have accepted this, and the group has been ranked either as a piophilid subtribe (Thyreophorina) or tribe (Thyreophorini). Currently it includes the following genera: *Thyreophora* Meigen, 1803 (one species, western Palaearctic), *Centrophlebomyia* Hendel, 1903 (two species, west Palaearctic, northern Oriental), *Protothyreophora* Ozerov, 1984 (one species, eastern Palaearctic), *Dasyphlebomyia* Becker, 1914 (one species, Afrotropical), *Bocainamyia* Albuquerque, 1953 (two species, Neotropical) and *Piophilosoma* Hendel, 1917 (five species, Australian). In his phylogenetic analysis, McAlpine (1977) arrived at the surprising result that *Thyreophora* is the sister group of the Australian genus *Piophilosoma*.

The genus *Thyreophora* (and only included species *T. cynophila*) differs from other thyreophorine genera by the following combination of characters: head brightly orange, contrasting with metallic bluish to greenish black body and legs (Fig. 1); anepisternum with long, dense setulae, but without a strong hind marginal seta; disc of scutellum with long, dense setulae (Fig. 2C); wing (Fig. 2A) with two rounded, black marks on cross-vein r–m and on anterior part of cross-vein dm–cu; vein C (Fig. 2B) bare except for anterior and anteroventral rows of fine, close-set setulae.

Existing information on T. cynophila

From the literature. The published information on the occurrence and habits of *T. cynophila* is summarized below in chronological order.

1. The original description by Panzer (1798) was based on a single specimen according to Meigen (1826) and von Röder (1882), which was a male found in Mannheim on the carcass of a dog. The holotype (Figure S1A) has been considered lost, but see below under point 8.
2. The next record is by Meigen (1826), who found specimens originating from France in the large insect collection of M. Baumhauer. Meigen even illustrated both sexes in colour (Figure S1B), but regrettably the numerous colour plates of European Diptera were not published until long after his death, by Morge (1976).
3. Robineau-Desvoidy (1830) stated that *T. cynophila* was extremely rare in France. He knew of two or three observations, all from the Paris area, on strongly decomposed carcasses of various big mammals. He was also told that a specimen in the possession of A.L.M. Le Peletier had been caught at night in a cavalry stable, allegedly given away

by its luminous head! He received a further specimen for his collection from L.-A. Bosc d'Antic.

4. Macquart (1835) provided a dramatic description of the nocturnal habits of *T. cynophila* that in translation says, 'In the dark shine from their luminous heads they jump upon partly skeletonized carcasses to feed on the last animal remains'. It is unlikely that this alleged case of bioluminescence was based on personal observations. Rather, he was told so by Le Peletier, or merely elaborated on what Robineau-Desvoidy (1830) wrote about this species. Macquart's sketchy but unmistakable illustration of the male fly (Figure S1C) indicates that he had access to authentic material.
5. Robineau-Desvoidy (1842) noted briefly that on 26 January 1836, soon after the snow had melted, he found several specimens of *T. cynophila* on carcasses of horse and donkey.
6. Robineau-Desvoidy (1849) reported some new observations of *T. cynophila* made by himself in January and February on carcasses of horse, donkey and mule. He concluded that the fly had a preference for carcasses of odd-toed ungulates, and further stated that he could not verify the claimed luminosity of this fly's head by his own observations. Apparently these were the last published field observations of *T. cynophila*.
7. All post-1850 reports on *T. cynophila* were made by authors who knew the species only from pinned specimens preserved in the insect collections of a few European natural history museums. Thus, Schiner (1862) recorded the species for the first time from Austria, based on specimens he had seen in the Vienna Museum.
8. During the present study we noticed that von Röder (1882) in a footnote stated that he possessed the original specimen of *Musca cynophila* Panzer, 1798. Actually, Röder's Diptera collection at the Zoological Institute in Halle (Saale) contains two old male specimens of *T. cynophila*. One bears an old identification label, possibly in J.W. Meigen's hand, and therefore we consider this male as the holotype of *M. cynophila*.
9. Mégnin (1894), in his celebrated 'La faune des cadavres', placed '*Tyreophora* [sic] *cynophila*' and other 'tyreophores' in the 'fifth squad' of arthropods taking over in the decomposition of carrion. However, he probably based this on evidence from existing literature rather than his own observations.
10. Becker (1902) stated that he knew about specimens of *T. cynophila* in the collections of the Vienna and Paris Museums.
11. Séguy (1932, 1934) summarized the existing records and observations of *T. cynophila* in France and Germany, and presented a fine colour illustration of the male (Figure S1D).
12. Sack (1939), in a revision of Palaearctic Thyreophoridae, stated that *T. cynophila* was a rare central and southern European species, but apparently was more common to the south. Unfortunately, no evidence for this range extention was given, and has thus been widely ignored by subsequent authors.
13. Lindner (1949) published an illustration (Figure S1E) of a female *T. cynophila* from the collections of the Vienna Museum.
14. Séguy (1950) noted that *T. cynophila* had not been observed or collected in the field during the last 100 years.

From the collections. A request was sent to collection managers at 16 natural history museums housing major insect collections to assess the total holdings of *T. cynophila* in terms of sex and depository for all extant specimens, along with their label data. The results are provided in Table S1.

A total of 16 specimens (eight males, seven females and one unknown sex) were found in the museums of Paris (four), Vienna (four), Halle (Saale) (two), Stockholm (two), Berlin (two), Copenhagen (one) and London (one). Most specimens originate from France ('Gallia'), some specifically from Paris or Lyon, but the holotype of Panzer's *M. cynophila* from Germany (Mannheim) has evidently survived in the Röder Collection of Diptera in Halle (Saale). Schiner (1862) recorded *T. cynophila* from Austria based on material in the Vienna Museum. Unless he had access to more material than the four specimens present there today, the only specimen of possible Austrian origin is a female labelled 'cynocephala/Alte Sammlung'.

The most interesting specimen, also in the Vienna Museum, is a male from F. Hendel's collection (Fig. 1C). It bears a label 'Cynophila/Algier N.A.' probably in Hendel's handwriting. It is in German and says that the specimen comes from the city or province of Algiers (Algeria). The 'N.A.' could be the initials of the collector, or simply stand for 'Nord-Afrika'. The specimen in question suggests a substantial extension of the previously documented distribution of *T. cynophila* in central western Europe. Furthermore, the slender original pin suggests that the specimen is probably from the second half of the 19th century. Subsequently, probably when Hendel got the specimen for his collection, it was re-staged in a block of pith kept on a thicker pin, and provided with the label discussed above. It may seem strange that Hendel never made this new information public, but perhaps he did not fully rely on the label data.

European thyreophorines: an overview

Three species of thyreophorines are known with certainty from Europe: *Thyreophora cynophila* (Panzer, 1798), *Centhrophlebomyia furcata* (Fabricius, 1794) and *Centhrophlebomyia anthropophaga* (Robineau-Desvoidy, 1830) (or *Centhrophlebomyia orientalis* Hendel, 1907). As explained below, these three species have all at times been declared as probably extinct in Europe or globally.

1. In respect to *T. cynophila*, the literature documents its occurrence only in continental western Europe (southern Germany, France and Austria), but it has not been found there since 1850. However, new collection-based evidence

suggests that a male specimen from F. Hendel's collection in the Vienna Museum originates from Algiers (Algeria, North Africa). The specimen is without a collecting date, but might well be from after 1850. The new find, from January and February 2007, of six individuals in carrion-baited traps a little north of Madrid indicates that, even if *T. cynophila* may have become extinct within its former distribution area, evidently it has been overlooked in other parts of Europe up to the present day. The declared global extinction of *T. cynophila* is obviously no longer valid.

2. *Centrophlebomyia furcata* was described from France in 1774, and was subsequently found in Denmark, the Czech Republic, Austria, Germany, Great Britain and Algeria. However, from 1906 onwards to 2004 no records were made of this fly in Europe, and several countries have declared it extinct. However, Freidberg (1981) reported that in Israel *C. furcata* could be found regularly on carcasses of goat, sheep and cow from November to January. Furthermore, he established that the male holotype from Palestine, upon which Sack (1939) based his description of a new genus and species, *Thyreolepida cinerea*, is actually a female of *C. furcata*. More recents finds of this fly are from Cyprus shortly before 2001, Spain in 2004 and Turkey in 2008, see Gómez-Gómez *et al*. (2009) for details. The website http://www.diptera.info contains an image uploaded by 'Gordon' that documents the occurrence of a male on a dead dog at 'Strymon river bank, far northern Greece, 24 November 2009' (http://www.diptera.info/forum/viewthread.php?thread_id=26429). Evidence is thus accumulating that *C. furcata* is not particularly rare or threatened, at least in the eastern part of the Mediterranean subregion.
3. Robineau-Desvoidy (1830) described *Thyreophora anthropophaga* based solely on his memory of specimens he had observed in large numbers destroying preparations of human muscles, ligaments and bones in the Paris School of Medicine in August 1821. Like *T. cynophila* and *C. furcata*, it had a lengthy scutellum with a pair of coarse apical bristles, but it was only one-third their size and of reddish and brown colour. No specimens matching that description could be found in the collections, and usually earlier dipterists listed it as an unrecognized, possibly extinct species. Paramonov (1954) thought it might be a species of the genus *Centrophlebomyia*, and Freidberg (1981) even suggested it might be a synonym of *C. furcata*. Papp (1984) dismissed *Thyreophora anthropophaga* Robineau-Desvoidy, 1830 as an 'invalid name' (apparently in the sense that it would be nomenclaturally unavailable under the provisions of the International Code of Zoological Nomenclature, ICZN). Papp argued that the original description, as based on a memorized image of specimens never preserved, is against the legislation of the ICZN code. However, it seems to us that no provisions of the ICZN code make a name proposed before 1931 unavailable under these circumstances.

Michelsen (1983) collected in Kashmir (India), on the remains of a horse, some specimens of *Centrophlebomyia* matching Robineau-Desvoidy's description of *T. anthropophaga*. Accordingly, he made the rather bold assumption that they were conspecific, and recorded the Kashmir material as *Centrophlebomyia anthropophaga* (Robineau-Desvoidy, 1830). This assumption was supported by Contini & Rivosecchi (1993), who recorded the same species from Sardinia (Italy), i.e. much closer to Paris, based on 51 specimens found in 1980 on a bait of dead snails. Apparently accepting Papp's rejection of the name *anthropophaga*, Ozerov (2000) applied a younger name to the same species, viz. *Centrophlebomyia orientalis* Hendel, 1907. This name appeared almost forgotten, and was inadvertently omitted from the catalogue of Oriental Diptera by Delfinado & Hardy (1977). The brief description by Hendel (1907), in a key to the thyreophorine genera and species known at that time, was based on material from Darjeeling (West Bengal, India) held in the Vienna Museum. However, in the absence of evidence to the contrary, we propose that *C. anthropophaga* is resurrected as the valid name for the present species, with *C. orientalis* as a subjective junior synonym (**syn.n.**).

European thyreophorines: species facing extinction?

Why are the European species of thyreophorine Piophilidae so rare in the collections? Several dipterists have speculated on possible reasons: improved hygiene in Europe might have led to rarity and extinction (Lindner, 1949); the fact that entomologists limit their collecting efforts during winter, and are generally reluctant to collect from carcasses, might also be important (McAlpine, 1977), supporting Paramonov's (1954) experience that Australian thyreophorines were rarely collected, but were found in numbers on carrion in the cool season. Menier (2003) explained the possible extinction of *T. cynophila* in western Europe as follows: the larvae preferably feed on marrow from within the long bones of large carcasses but, with the disappearence of wolves and other large predators capable of crushing these bones, this food source became largely inaccessible.

Sadly but undeniably the world's biological diversity is threatened everywhere by an ever-increasing human population. Loss and fragmentation of wilderness areas, pollution, climate change and the spread of invasive species exert devastating pressures on countless species, both locally and globally. Mass extinctions seem inevitable, but documentation of species extinctions, especially in insects and other small organisms, is difficult. Dunn (2005) emphasized this in estimating that there have been 44 000 insect species extinctions over the last 600 years, whereas the observed number was just 40! One of the main problems regarding this is that much of the existing theoretical framework for investigating species extinctions is based on studies of large vertebrates and plants, but the basic distributions of invertebrates are very different (Mawdsley & Stork, 1995). Moreover, in the case of rediscoveries of 'extinct' species it is essential to know the self-sustainability of the populations to plan effective conservation measures (Ladle *et al*., 2009). However, there is a lack of knowledge about the minimum size of a self-sustaining population in insects: the rediscovery of the Lord Howe Island stick-insect [*Dryococelus australis* (Montrouzier, 1885)] showed that a large invertebrate can persist at very low population numbers, in very localised microhabitats, for a very long time (Priddel *et al*., 2003).

The rediscovery of *T. cynophila* raises some concerns about the future conservation of their populations, making it necessary to take measures to ensure the population viability by removing their major threats. In this sense, it is a priority to include this species in the national catalogue of protected species in order to regulate or ban, if necessary, the indiscriminate capture by insect collectors, which is a problem regarding rediscovered insect species (Priddel *et al*., 2003). The protection of habitat is also essential (Priddel *et al*., 2003), although in this case it is lucky that the known populations are within the limits of the future Guadarrama National Park. Finally, taking into account the particular trophic spectrum of this species, it is essential to guarantee an adequate and continuous supply of food. This involves the maintenance of traditional livestock in the area and preventing the removal of corpses from the field, a common practice since the crisis of bovine spongiform encephalopathy (BSE) in Europe, which has already caused a severe reduction in populations of scavenging birds in Spain (Tella, 2001), and could potentially affect other scavengers that maintain small population sizes and very strict trophic requirements, as occurs with *T. cynophila*.

On the other hand, it is true that some insect species are more extinction prone than others, at both local or global scales. Many studies suggest that vulnerable and acutely threatened insect species belong to one of the following categories: (i) species that have a small total range size, as seen in endemic species and species swarms on islands or isolated mountains; (ii) species with a narrow habitat or microhabitat dependency; (iii) parasitic species (in a broad sense, including parasitoids and phytophages) with a narrow host-choice dependency. Species belonging to the first two categories are vulnerable because their total population is small or disjointed, and because they occupy small areas or narrow habitats susceptible to disturbance. Species in category 3 – perhaps a subset of category 2 – are vulnerable because their existence depends on the well-being of their host species.

European thyreophorine species, for obvious reasons, belong to neither category 1 nor 3 listed above, but are they so specialized in their microhabitat requirement (crushed bones?) that this makes them category-2 candidates? We find this very unlikely, although big carcasses of horse, donkey and mule, supposedly the favoured microhabitat for *T. cynophila*, are rarely found exposed in the field these days. What strikes us, however, is that the expected increase in thyreophorine populations during the frequent European wars of the 20th century totally escaped the notice of Diptera collectors. The only likely explanation seems to be that of Paramonov (1954): that thyreophorines are not particularly rare in nature, but are collected only rarely. Who thinks of collecting flies on large carcasses in winter after dark?

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-3113.2010.00541.x

Figure S1. *Thyreophora cynophila* (Panzer, 1798). Colour illustrations of specimens collected before 1850. A, male holotype of *Musca cynophila*, from Panzer (1798); B, male, female and male body parts, from early 19th century colour plate by Meigen published in Morge (1976); C, male, from Macquart (1835); D, male, from Séguy (1932); E, female, from Lindner (1949). The illustrations are all given on different scales.

Table S1. Results from an inquiry regarding the holdings of extant specimens of *Thyreophora cynophila* (Panzer, 1798) in 16 major natural history museums.

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