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Focus on:

Large carrion beetles (Coleoptera, Silphidae) in Western Europe: a review

Jessica Dekeirsschieter [(1)], François Verheggen [(1)], Georges Lognay [(2)], Eric Haubruge [(1)]

[(1)] Univ. Liege - Gembloux Agro-Bio Tech. Department of Functional and Evolutionary Entomology. Passage des Déportés, 2. B-5030 Gembloux (Belgium). E-mail: jdekeirsschieter@ulg.ac.be, entomologie.gembloux@ulg.ac.be
[(2)] Univ. Liege - Gembloux Agro-Bio Tech. Department of Analysis Quality and Risks. Laboratory of Analytical Chemistry. Passage des Déportés, 2. B-5030 Gembloux (Belgium).

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This review focuses on carrion beetles (Coleoptera, Silphidae) of the Western Palearctic and their potential use in forensic entomology as bioindicators. Few studies have looked at Silphidae in forensic context and investigations. However, some Silphidae present the desirable characteristics of some Diptera used in postmortem estimates and thus may extend the minimum postmortem interval (PMImin). We review here the taxonomy and distribution of Western Palearctic Silphidae. The anatomical and morphological characteristics of both subfamilies are described for adults and larvae. The biology and ecology of silphids are also summarized for Silphinae and Nicrophorinae. A specific chapter gives an overview of the current uses of Silphidae in forensic entomology as postmortem indicator.
Keywords. Silphidae, burying beetles, forensic entomology, taxonomy, identification, Western Europe.

Les grands coléoptères nécrophages (Coleoptera, Silphidae) en Europe occidentale : synthèse bibliographique. Cette synthèse bibliographique fait le point sur les Silphidae du Paléarctique Ouest et leur utilisation potentielle en entomologie forensique comme bioindicateurs postmortem. Peu d'études s'intéressent aux Silphidae dans un contexte forensique. Cependant, certaines espèces de Silphidae présentent les mêmes caractéristiques que certains Diptères que l'on utilise pour calculer un intervalle postmortem (IPM) et pourraient donc servir à calculer un IPM minimum plus étendu. La classification taxonomique et la distribution géographique des Silphidae sont décrites dans cette synthèse ainsi que leurs caractéristiques morphologiques et anatomiques, et ce pour les deux sous-familles de Silphidae. La biologie et l'écologie des Silphidae ont été synthétisées afin de mieux comprendre leur éventuelle valeur en tant qu'indicateur postmortem. Un chapitre spécifique met en évidence les différentes utilisations des Silphidae en entomologie forensique à l'heure actuelle.
Mots-clés. Silphidae, coléoptère nécrophage, entomologie forensique, taxonomie, identification, Europe occidentale.

1. INTRODUCTION

Carrion beetles (Coleoptera, Silphidae) consist of a small group of Coleoptera counting less than 200 species that are worldwide spread (Sikes, 2008). Silphids perform vital ecosystem functions (Wolf et al., 2004); they promote the breakdown and recycling of organic matter into terrestrial ecosystems (Peck, 1990; Ratcliffe, 1996; Hastir et al., 2001; Kalinova et al., 2009). Most Silphids are carrion feeders (necrophagous species) but can also prey on other carrion inhabitants such as fly eggs or maggots and other small carrion beetles (necrophilous species) (Racliffe, 1996; Hastir et al., 2001; Sikes, 2005; Sikes, 2008). The "carrion" terminology is not adapted for all silphid species according to their ecological group, some species (Silphinae) are phytophagous or found in dung or fungi (Anderson et al., 1984; Sikes, 2008). Carrion beetles are also referenced as "large carrion beetles" contrary to other smaller carrion beetles such as Agyrtidae, Leiodidae ("small carrion beetles") or Cholevidae (Peck, 1990; Ratcliffe, 1996; Peck, 2001; Sikes, 2008).

Their feeding activities on carrion may also destroy some foci of infection of pathogenic bacteria (Peck, 1990). The necrophagous insects, including carrion beetles, have particular relationships with decomposing remains (vertebrate carcass) which constitute a rich ephemeral resource (Anderson et al., 1996; Grassberger et al., 2004; Carter et al., 2007). These specialized insects, including mainly Diptera and Coleoptera, are attracted to the cadaver that they colonize in a relative predictable sequence called the entomofaunal succession or insect succession

(Megnin, 1894; Putman, 1983; Schoenly et al., 1987; Marchenko, 1988; Marchenko, 2001). Their study in a medico-legal context is a part of the forensic entomology (Amendt et al., 2004; Amendt et al., 2007). Many published reports or reviews are focused on Diptera pattern colonization and neglect Coleoptera succession (Kocarek, 2003; Matuszewski et al., 2008; Midgley et al., 2009). Carrion beetles have been referenced to as being a part of the entomofaunal colonization of a dead body but very few studies have looked at them in a forensic context. However, the use of beetles in forensic entomology can be relevant (Kulshrestha et al., 2001; Watson et al., 2005; Midgley et al., 2009; Midgley et al., 2010). Carrion beetles can provide information on postmortem colonization on remains and time since death (Smith, 1986; Haskell et al., 1997; Watson et al., 2005). This review focuses on Palearctic carrion beetles (Coleoptera, Silphidae) that are carrion feeder or associated with decomposing remains.

2. TAXONOMY AND DISTRIBUTION

The family of Silphidae belongs to the superfamily of the Staphylinoidea and is divided into two subfamilies: the Nicrophorinae, called burying beetles or sexton beetles, and the Silphinae (Lawrence et al., 1982; Peck et al., 1993; Ratcliffe, 1996; Dobler et al., 2000; Sikes, 2005). Some taxonomists often include a third subfamily in the silphid beetles: the Agyrtinae (Madge, 1980; Hastir et al., 2001; Debreuil, 2003a; Debreuil, 2004a). However, recent phylogenetic analyses (Hansen, 1997; Newton, 1998; Dobler et al., 2000; Caterino et al., 2005) separate the Agyrtinae of other Silphidae and consider the Agyrtidae as a valid family into itself (Lawrence et al., 1982; Peck, 1990; Ratcliffe, 1996; Newton, 1997; Dobler et al., 2000; Caterino et al., 2005). The world fauna of Silphidae is currently composed of 183 species distributed in 15 genera (Ratcliffe, 1996; Peck, 2001; Sikes, 2005; Sikes, 2008). This family has a worldwide distribution, but is predominant in Holarctic regions (temperate regions) (Peck et al., 1985; Peck, 2001; Sikes, 2005). The Palearctic region is considered as the center of their distribution (Peck et al., 1985; Dobler et al., 2000). There are the most genera and the highest number of species of Silphidae in the Palearctic (Peck et al., 1985; Dobler et al., 2000). Carrion beetles are rare or absent in tropical regions because they are out-competed by ants, flies and vertebrates (Ratcliffe, 1996). Although, there are some Australian and Latin American endemic species (*Diamesus*, *Ptomophila*, *Nicrophorus mexico*) (Ratcliffe, 1996; Scott, 1998). Nicrophorinae are less widely distributed than Silphinae, being found in the temperate northern climate (Sikes, 2005; Sikes, 2008). Silphines seem to be more tolerant to warmer climate than the nicrophorines (Sikes, 2008). The subfamily of Silphinae has a greatest generic diversity (12 genera) than the Nicrophorinae (3 genera) (Sikes, 2005). In north Western Europe, there are 28 species of Silphidae: 11 species of Nicrophorinae and 17 species of Silphinae. **Table 1** lists the species in Western Europe (Heinz, 1971; Hastir et al., 2001; Sikes et al., 2002; Debreuil, 2003a; Debreuil, 2003b; Debreuil, 2004a; Debreuil, 2004b; Debreuil, 2004c; Ružicka et al., 2004; Sikes, 2005). Among them, there are 22 species (11 *Nicrophorus* spp. and 11 Silphinae) that are carrion obligate or predacious species. There is only one genus of nicrophorine in the Western Palearctic: *Nicrophorus*. In the past, the spelling of this genus name varied from *Nicrophorus* to *Necrophorus* and back again to *Nicrophorus*, the valid genus name (Ratcliffe, 1996; Debreuil, 2004b), but it is not rare to see the wrong spelling in some publications.

3. ANATOMIC AND MORPHOLOGICAL DESCRIPTIONS

Silphid beetles are usually medium to large in size (7 to 45 mm) (Peck, 1990; Ratcliffe, 1996; Hastir et al., 2001; Debreuil, 2003a; Sikes, 2008). Although, adults and larvae vary greatly in size and shape (Byrd et al., 2009). Adults have an ovate (Silphinae) to moderately elongate shape with protuberant eyes (Sikes, 2005) (**Figure 1**). They are flattened (Silphinae) or strongly convex (Ratcliffe, 1996). Silphids are often darkened or have distinctive red-orange-yellow markings on the elytra (*Nicrophorus* spp.) that may serve as warning coloration (Ratcliffe, 1996; Hastir et al., 2001). The elytra are often short and leave several abdominal segments exposed (1 or 5 abdominal segments among the subfamily). The elytra are punctuate and truncate in Necrodes (Silphinae) and Nicrophorinae, not truncate in the remaining Silphinae (Sikes, 2005) (**Figure 2**). The scutellum is often very large and the pronotum is enlarged (Peck, 1990; Sikes, 2005; Sikes, 2008).

The antennae are constituted by eleven segments and capitate (abruptly clubbed) for Nicrophorinae or clavate (gradually clubbed) for Silphinae (Hastir et al., 2001) (**Figure 3**). The antennae are widely spread and inserted on the lateral side of head. They have often microsetae covering only apical three segments (segments 9 to 11) (Hastir et al., 2001). The abdomen with sternite 2 is not visible between hind coxae but visible laterally of metacoxae (Sikes, 2008). The tarsi or terminal portion of each leg has five segments (tarsi 5-5-5) (Peck, 1990; Hastir et al., 2001). Silphid larvae are recognizable by the possession of a combination of mandible without a molar lobe; maxilla with broad, apically cleft mala bearing setae on outer lobe; and usually a two-segmented articulated urogomphi

Table 1. List of the Western European species of "carrion" beetles (including Mediterranean species), family Silphidae LATREILLE, 1807 — *Liste des espèces de Silphidae de l'Europe de l'ouest (incluant les espèces méditerranéennes), famille Silphidae LATREILLE, 1807.*

	Subfamily	
	Nicrophorinae KIRBY, 1837	**Silphinae LATREILLE, 1807**
Genus	*Nicrophorus* FABRICIUS, 1775	*Ablattaria* REITTER, 1885 1884
		Aclypea REITTER, 1884
		Oiceoptoma LEACH, 1815
		Phosphuga LEACH, 1817
		Silpha LINNAEUS, 1758
		Thanatophilus LEACH, 1815
		Necrodes LEACH, 1815
		Dendroxena MOTSCHULSKY, 1858
Species	* *Nicrophorus germanicus* LINNAEUS, 1758	**Necrodes littoralis* LINNAEUS, 1758
	* *Nicrophorus humator* GLEDITSCH, 1767	**Thanatophilus dispar* HERBST, 1793
	* *Nicrophorus investigator* ZETTERSTEDT, 1824	**Thanatophilus rugosus* LINNAEUS, 1758
	* *Nicrophorus interruptus* STEPHENS, 1830	**Thanatophilus sinuatus* FABRICIUS, 1775
	* *Nicrophorus sepulchralis* HEER, 1841	**Oiceoptoma thoracicum* LINNAEUS, 1758
	* *Nicrophorus sepultor* CHARPENTIER, 1825	**Silpha carinata* HERBST, 1783
	* *Nicrophorus vespillo* LINNAEUS, 1758	**Silpha obscura obscura* LINNAEUS, 1758
	* *Nicrophorus vespilloides* HERBST, 1783	**Silpha tristis* ILLIGER, 1798
	* *Nicrophorus vestigator* HERSCHEL, 1807	**Silpha olivieri* BEDEL, 1887
	* *Nicrophorus nigricornis* FALDERMANN, 1835	**Silpha puncticollis* LUCAS, 1846
	* *Nicrophorus antennatus* REITER, 1884	**Silpha tyrolensis* LAICHARTING, 1781
		Phosphuga atrata atrata LINNAEUS, 1758
		Dendroxena quadrimaculata SCOPOLI, 1772
		Ablattaria laevigata laevigata FABRICIUS, 1775
		Aclypea opaca LINNAEUS, 1758
		Aclypea undata MULLER, 1776
		Aclypea souverbiei FAIRMAIRE, 1848

* : indicates necrophagous or predaceous species — *indique des espèces nécrophages ou prédatrices* (Heinz, 1971; Hastir et al., 2001; Sikes et al., 2002; Debreuil, 2003a; Debreuil, 2003b; Debreuil, 2004a; Debreuil, 2004b; Debreuil, 2004c; Ružicka et al., 2004; Sikes, 2005)

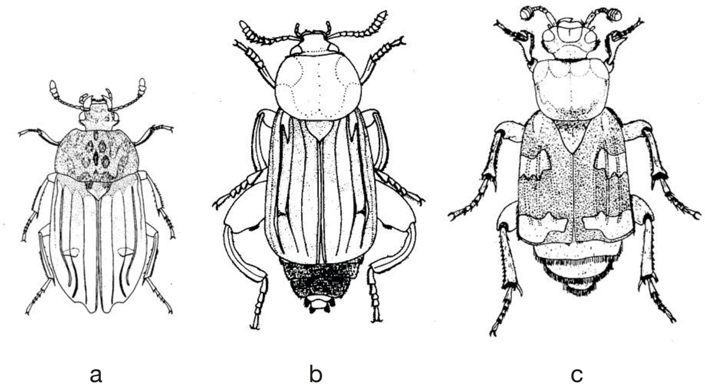

Figure 1. Habitus of Silphinae (a), (b) and Nicrophorinae (c); (a) *Thanatophilus sinuatus* ♀, (b) *Necrodes littoralis*, (c) *Nicrophorus interruptus* — *Habitus des Silphinae (a), (b) et d'un Nicrophorinae (c) ; (a)* Thanatophilus sinuatus ♀*, (b)* Necrodes littoralis*, (c)* Nicrophorus interruptus. Source: Sustek, 1981.

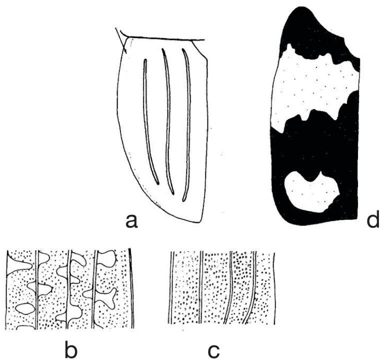

Figure 2. Left elytron of (a) Silphinae with three longitudinal costae and (d) Nicrophorinae with fasciae or maculae. Detail of the elytron of (b) *Thanatophilus rugosus* and (c) *Thanatophilus sinuatus — Élytre gauche d'un Silphinae (a) avec trois côtes longitudinales et (d) élytre d'un Nicrophorinae avec des taches ou bandes orangées aussi appelée fasciae ou maculae. Détail d'un élytre de (b)* Thanatophilus rugosus *et (c)* Thanatophilus sinuatus. Source: Sustek, 1981.

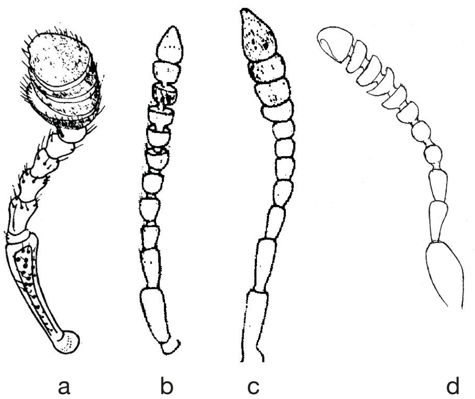

Figure 3. Antennae of (a) *Nicrophorus humator*, (b) *Aclypea undata*, (c) *Aclypea opaca* and (d) *Necrodes littoralis — Antennes de (a)* Nicrophorus humator*, (b)* Aclypea undata*, (c)* Aclypea opaca *et (d)* Necrodes littoralis. Source : a, b, c: Sustek, 1981; d: Portevin, 1926.

(Newton, 1991). Each subfamily has a very distinctive habitus (Newton, 1991) (**Figure 4**).

3.1. Silphinae

Adults. Silphine species have often a darkened color and are dorsoventrally flattened (**Figure 5**). Their size is ranging from 8 to 25 mm (Debreuil, 2003a).The elytra have apices rounded or acute, not truncate or shortened (Peck, 1990; Ratcliffe, 1996). The elytra are usually costate or carinate (0-3 per elytron with 0 for the genus *Ablattaria*) (Peck, 1990; Debreuil, 2003a) but never striate (**Figure 2a**, **2b**, **2c**). The frontoclypeal suture is absent (**Figure 6b**) and the gular sutures are

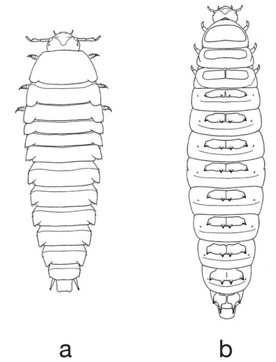

Figure 4. Larval habitus of (a) Silphinae and (b) Nicrophorinae — *Habitus d'une larve (a) de Silphinae et (b) d'un Nicrophorinae*. Source: Ratcliffe, 1996.

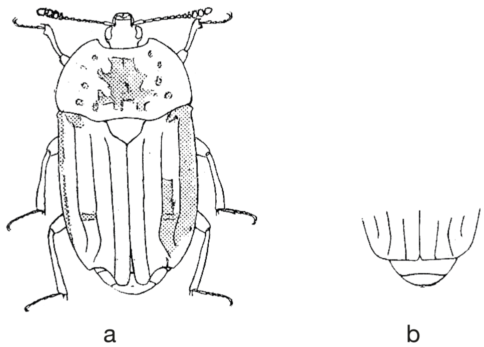

Figure 5. (a) *Thanatophilus sinuatus* ♀, (b) apex of *Thanatophilus sinuatus* ♂ — (a) Thanatophilus sinuatus ♀, (b) *détail de l'apex de l'élytre* ♂ Thanatophilus sinuatus. Source: Portevin, 1926.

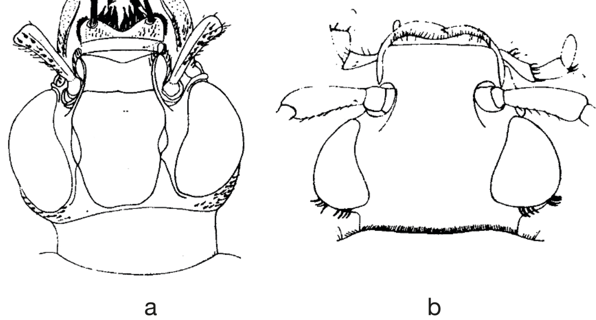

Figure 6. (a) Head of *Nicrophorus* species with clypeal membrane and (b) head of silphine species without frontoclypeal suture. Pictures from Sustek (Sustek, 1981) — (a) *Tête d'un* Nicrophorus *sp. avec la suture frontoclypéale et (b) tête d'une espèce de Silphinae sans suture frontoclypéale*. Source: Sustek, 1981.

clearly separate, but strongly constricted medially (Peck, 1990; Sikes, 2005). The antennae have eleven well differentiated segments broaden gradually; particularly the last three or four segments (**Figure 3b**, **3c**, **3d**).

Larvae. Silphine larvae are campodeiform with body surfaces heavily pigmented and sclerotized (Newton, 1991; Sikes, 2005; Sikes, 2008) (**Figure 4a**). The body length of mature larvae is ranging from 12 to 40 mm (Newton, 1991). On each side of the head, there are 6 pigmented stemmata (ocelli). The anal lobes bear numerous fine teeth (Sikes, 2005). The tergites are large, laterally produced; each tergite is usually with posterior angles attenuated (Anderson et al., 1985; Ratcliffe, 1996).

3.2. Nicrophorinae

Adults. Nicrophorina species are darkened with red-orange markings (bands or spots), called fasciae or maculae, on elytra extending to the epipleura (**Figure 1c**), except for the species *Nicrophorus humator* and *Nicrophorus germanicus* which are completely darkened (black or brown) (Ratcliffe, 1996; Hastir et al., 2001; Sikes, 2008). Elytra have apices truncate (always smooth) and shortened exposing 3 or 4 abdominal segments (Peck, 1990; Ratcliffe, 1996) (**Figures 1c** and **2d**). The frontoclypeal suture is present as a fine line (Peck, 1990; Sikes, 2005) (**Figure 6a**); the gular sutures are confluent posteriorly and reduce gula to a small triangular piece (Peck, 1990; Sikes, 2005). On the fifth dorsal segment, there is a pair of stridulatory files in both sexes which is used for communication (Lane et al., 1965; Peck, 1990; Ratcliffe, 1996; Sikes, 2008). The antennae are clubbed, the second antennal segment (pedicel) is often reduced and fewer differentiated than the scape (appearing 10-segmented) (Peck, 1990) (**Figure 3a**). The compact club is constituted by the last four antennal segments (Peck, 1990; Ratcliffe, 1996; Hastir et al., 2001). In most *Nicrophorus* species, there is a sexual dimorphism in tarsomeres. The nicrophorine males possess expanded segments of the protarsus (foretarsus) (Peck, 1990; Ratcliffe, 1996).

Larvae. Nicrophorinae larvae are campodeiform or eruciform and body surfaces are lightly pigmented and unsclerotized with the exception of the head and legs (Newton, 1991; Ružicka, 1992; Sikes, 2005) (**Figure 6b**). The body length of mature larvae is ranging from 12 to 40 mm (Newton, 1991). The ventral surface is soft and creamy white (Anderson et al., 1985; Ružicka, 1992; Ratcliffe, 1996). On each side of the head, there is only one unpigmented stemma (Ratcliffe, 1996; Sikes, 2005). Contrary to Silphinae larvae, the anal lobes are without teeth (Newton, 1991; Sikes, 2005). The tergites are small; those on abdomen have 4 small spines (Anderson et al., 1985; Ratcliffe, 1996). For more detailed information about the morphology of larvae of *Nicrophorus*, Ružicka (1992) describes the immature stages of the following European species: *N. vespillo*, *N. vespilloides*, *N. humator*, *N. investigator*, *N.* (*fossor*) *interruptus*.

4. ECOLOGY AND BIOLOGY

Carrion beetles (Coleoptera, Silphidae) perform vital ecosystem functions (Wolf et al., 2004); they promote the breakdown and recycling of organic matter into terrestrial ecosystems (Ratcliffe, 1996; Hastir et al., 2001; Kalinova et al., 2009). **Tables 2** and **3** list the different ecological characteristics of Nicrophorinae and Silphinae Western European species based on the relevant literature (Portevin, 1926; Heinz, 1971; Anderson et al., 1984; Ružicka, 1994; Scott, 1998; Kocarek, 2001; Hastir et al., 2001; Gueorguiev et al., 2002; Kocarek, 2002; Ružicka, 2002; Sikes et al., 2002; Kocarek, 2003; Debreuil, 2003a; Debreuil, 2003b; Debreuil, 2004a; Debreuil, 2004b; Debreuil, 2004c; Ružicka et al., 2004; Aleksandrowicz et al., 2005; Chauvet et al., 2008). Silphidae are mainly carrion feeder (necrophagous species) or prey on other carrion inhabitants such as fly eggs or maggots and other carrion beetles (necrophilous species) (Racliffe, 1996; Hastir et al., 2001; Sikes, 2005; Sikes, 2008). There are some species of Silphinae that feed on soil invertebrates (snails, caterpillars or slugs predators: *Silpha* spp., *Dendroxena* spp.) or are phytophagous species (*e.g. Aclypea* spp.) (Sikes, 2005; Ikeda et al., 2007; Ikeda et al., 2008). Some Silphidae may be attracted by decaying fungi (*e.g. Phallus impudicus*), dung or rotten plant (Ratcliffe, 1996; Hastir et al., 2001; Sikes, 2005). Silphidae have reduced interspecific competition in partitioning species (niche differentiation) (Anderson, 1982; Peck, 1990; Ohkawara et al., 1998; Hocking et al., 2007): they have different temporal activities; some species are more active during spring whereas other species are active in summer, few species are active during autumn (Ružicka, 1994; Scott, 1998; Kocarek, 2001). In carrion beetles communities, niche differentiation can occur along dimensions of season, habitat (biotope) and carcass size (Scott, 1998; Hocking et al., 2007). The daily activity is also different, Silphidae are primarily nocturnal insect but some species are diurnal (*e.g. Thanatophilus* spp.) or crepuscular (Ohkawara et al., 1998; Scott, 1998; Kocarek, 2001). Habitat preferences are also different; some species are subservient to forest biotope (*e.g. O. thoracica*, *N. vespilloides*), whereas other species prefer open habitats (field/meadow species) (Scott,

Table 2. Ecological and body size of Nicrophorinae of Western Europe (trophic group: necrophagous predaceous) — *Caractéristiques écologiques et morphologiques des Nicrophorinae de l'Europe de l'ouest (groupe trophique : prédateur nécrophage).*

Species	Distribution	Abundance	Body size (in mm)	Temporal activity	Habitat preference &/or location	Daily activity
Nicrophorus germanicus	BE-FR-GE-LU-NL-DE-GB-IT-SZ	rare	20-35	May-September	field, large cadaver, dung	nocturnal
Nicrophorus humator	BE-FR-GE-LU-NL-DE-GB-IT-PT-SP-SZ	very common	14-33	April-September	forest (hardwood), cadaver, rotten mushrooms	nocturnal
Nicrophorus investigator	BE-FR-GE-LU-NL-DE-GB-IT-SP-SZ	common	11-22	April-September	forest, open areas, cadaver	crepuscular
Nicrophorus interruptus	BE-FR-GE-LU-NL-DE-GB-IT-PT-SP-SZ	rare	10-22	April-October	field, sometimes in forest, cadaver	crepuscular
Nicrophorus sepulchralis	FR-IT-SZ	rare	19-21	N.A.	cadaver, European mountain species (Alps)	N.A.
Nicrophorus sepultor	DE-FR-GE-IT-NL-SP-SZ	very rare	11-22	April-September	forest, open areas, cadaver, rotten mushrooms	N.A.
Nicrophorus vespillo	BE-FR-GE-LU-NL-DE-GB-IT-PT-SP-SZ	common	10-23	May-September	field, open areas, sometimes in forest, cadaver	crepuscular, nocturnal
Nicrophorus vespilloides	BE-FR-GE-LU-NL-DE-GB-IT-SP-SZ	very common	9-19	April-September	forest, cadaver, rotten mushrooms	diurnal
Nicrophorus vestigator	BE-FR-GE-LU-NL-DE-GB-IT-PT-SP-SZ	common	9-23	April-October	field, open areas, cadaver	N.A.
Nicrophorus nigricornis	FR	rare	12-20	N.A.	cadaver, mountain species (Caucasius)	N.A.
Nicrophorus antennatus	FR-IT-NL	rare	N.A.	N.A.	cadaver	N.A.

BE: Belgium — *Belgique*; FR: France — *France*; Ge: Germany — *Allemagne*; Lu: Luxembourg — *Luxembourg*; NL: The Netherlands — *Pays-Bas*; DE: Denmark — *Danemark*; GB: Great Britain — *Grande-Bretagne*; IT: Italy — *Italie*; PT: Portugal — *Portugal*; SP: Spain — *Espagne*; SZ: Switzerland — *Suisse*. N.A.: not available data in the specific literature — *données indisponibles dans la littérature spécialisée* (Portevin, 1926; Heinz, 1971; Anderson et al., 1984; Ružicka, 1994; Scott, 1998; Kocarek, 2001; Hastir et al., 2001; Gueorguiev et al., 2002; Kocarek, 2002; Ružicka, 2002; Sikes et al., 2002; Kocarek, 2003; Debreuil, 2003a; Debreuil, 2003b; Debreuil, 2004a; Debreuil, 2004b; Debreuil, 2004c; Ružicka et al., 2004; Aleksandrowicz et al., 2005; Chauvet et al., 2008).

Table 3. Ecological and body size of Silphinae of Western Europe — *Caractéristiques écologiques et morphologiques des Silphinae de l'Europe de l'Ouest*.

Species	Distribution	Abundance	Body size (in mm)	Temporal activity	Habitat preference &/ or location	Daily activity	Trophic group
Necrodes littoralis	BE-FR-LU-GE-NL-SP-DE-GB-IT-PT-SZ	common	15-25	April-September	forest or open areas, cadaver (large carcass), below seaweeds	N.A.	necrophagous predaceous
Thanatophilus dispar	BE-FR-GE-NL-DE-GB-IT-SZ	rare	8-11	May-July	field, cadaver	diurnal	necrophagous
Thanatophilus rugosus	BE-FR-LU-GE-NL-DE-GB-IT-PT-SP-SZ	common	9-12	April-September	field, open areas, cadaver	diurnal	necrophagous predaceous
Thanatophilus sinuatus	BE-FR-LU-GE-NL-DE-GB-IT-PT-SP-SZ	very common	9-12	April-September	field, open areas, cadaver	diurnal	necrophagous predaceous
Oiceoptoma thoracicum	BE-FR-LU-GE-NL-DE-GB-IT-SP-SZ	common	11-16	April-September	forest, cadaver, dung, mushrooms (*e.g. Phallus* sp.)	diurnal	necrophagous predaceous
Silpha carinata	BE-FR-LU-GE-NL-DE-GB-IT-SZ	common	13-20	April-September (imago hibernates under barks of trees)	forest, cadaver, crushed slugs and snails, mushrooms	N.A.	necrophagous predaceous
Silpha obscura obscura	BE-FR-LU-GE-NL-DE-GB-IT-SP-SZ	common	11.5-17	May-September (imago hibernates in litter & soil)	field, open areas	N.A.	predaceous necrophagous
Silpha tristis	BE-FR-LU-GE-NL-DE-GB-IT-PT-SP-SZ	rare	13-15	May-September (imago hibernates in litter & soil)	field	N.A.	predaceous necrophagous
Silpha olivieri	FR-IT-PT-SP	rare	15-19	Mid March-Mid September	Mediterranean species	N.A.	predaceous
Silpha puncticollis	FR-IT-PT-SP	rare	14-17	Mid March-Mid September	Mediterranean species	N.A.	predaceous
Silpha tyrolensis	FR-GB-IT-PT-SP	rare	13-14	Mid March-Mid September	mountain species	N.A.	predaceous
Phosphuga atrata atrata	BE-FR-KU-GE-NL-DE-GB-IT-PT-SP-SZ	very common	9-16	May-October (imago hibernates under a bark, moss or litter)	forest	N.A.	predaceous (snails)
Dendroxena quadrimaculata	BE-FR-KU-GE-NL-DE-GB-IT -SP-SZ	common	11-14	May-July	forest (deciduous forest)	N.A.	predaceous (caterpillars)
Ablattaria laevigata laevigata	BE-FR-LU-GE-NL-GB-IT-SP-SZ	rare	11-16	May-October	field, gardens	N.A.	predaceous (snails)
Aclypea opaca	BE-FR-LU-GE-NL-DE-GB-IT-SP-SZ	common	9-12	April-September	field	N.A.	phytophagous (Chenopodiaceae, pest of sugar beets)
Aclypea undata	BE-FR-LU-GE-NL-DE-GB-IT-PT-SP-SZ	rare	11-16	April-September	field	N.A.	phytophagous (Chenopodiaceae)
Aclypea souverbiei	FR-GE-SP	rare	10-12	N.A.	N.A.	N.A.	phytophagous

legend — *légende*: see **table 2** - *voir* ***tableau 2***.

1998; Kocarek, 2001). The type of carrion (age and carcass size) that they use is an important parameter (Anderson, 1982; Peck, 1990; Scott, 1998). Silphinae tend to use preferentially large vertebrate carcasses whereas Nicrophorinae prefer small carcasses (Anderson, 1982; Peck, 1990; Eggert et al., 1992). Both subfamilies have different reproductive strategy. Nicrophorinae have a surprising behavior for insects: the biparental care of their offspring (Pukowski, 1933; Anderson, 1982; Scott, 1998; Smiseth et al., 2006). This is the highest level of sociability attained in the Coleoptera (Milne et al., 1976; Ratcliffe, 1996). At contrary, Silphinae show no parental care (Ratcliffe, 1996). Silphidae have particular relationships with nematodes and mites (phoresy) (Springett, 1968; Richter, 1993; Ratcliffe, 1996; Sikes, 2008). These relationships, poorly known, could be mutualism, commensalism or parasitism (Sikes, 2008).

4.1. Silphinae

Contrary to the Nicrophorinae, little is known about the biology and ecology of the Silphinae (Ratcliffe, 1996; Hoback et al., 2004; Ikeda et al., 2007). Concerning necrophagous silphine species, females are semelparous and lay their eggs in or on the soil around large vertebrate carcasses and provide no care of their offspring (Sikes, 2005; Ikeda et al., 2008). Silphine appear usually on large carcasses (> 300 g) (Peck, 1990; Sikes, 2005) because these provide sufficient food resource for the great number of beetles that may be present (Anderson, 1982; Watson et al., 2005). Eggs hatch in 4-5 days and silphine larvae feed on carrion remains (Anderson, 1982). They may also compete with nicrophorine species for small vertebrate carcasses that they use for feed but not for reproduction and larval development (Bishop, 2001; Hoback et al., 2004). Silphinae colonize a carcass during the early or mid-stage of decay and thus compete with flies (Diptera) for the food resource (Payne, 1965; Anderson, 1982). Contrary to Nicrophorinae, there are some flightless silphine species or some flight-dimorphic species (Ikeda et al., 2007; Ikeda et al., 2008).

4.2. Nicrophorinae

Many studies on burying beetles behavior have been published since the pioneer work of Pukowski (Pukowski, 1933; Milne et al., 1976; Sikes, 2005). More than 150 behavioral ecology studies on the *Nicrophorus* spp. were conducted in the past 25 years (Sikes, 2008). The reviews of Milne et al. (1976), Ratcliffe (1996), Scott (1998) or Sikes (2005; 2008) provide detailed information about the nicrophorine (or Silphidae) ecology. Burying beetles specialized on carrion (necrophagous and necrophilous species) are subsocial (Pukowski, 1933; Milne et al., 1976; Trumbo et al., 1993; Ohkawara et al., 1998; Scott, 1998). *Nicrophorus* species use small vertebrate carcasses (< 300 g, usually < 100 g) such as rodents or birds that they bury and prepare for rearing offspring (Pukowski, 1933; Milne et al., 1976; Trumbo, 1990b; Scott, 1998; Smith et al., 2001; Sikes, 2005; Sikes, 2008). When the carcass is found by a single pair of male and female, they search a suitable spot for burial that is usually completed in 5 to 8 hours during the night (Ratcliffe, 1996; Scott, 1998). Carcasses are often located by several individuals of both sexes (Pukowski, 1933; Müller et al., 1998; Steiger et al., 2009). In this case, fighting occurs between individuals for the ownership of the carcass by a single male-female pair (Pukowski, 1933; Müller et al., 1998; Steiger et al., 2009). Searching behavior is guided by olfaction; burying beetles have sensitive chemosensors located on their antennae adapted to detect the smell of a recently dead animal (Shubeck, 1975; Bartlett, 1987; Peck, 1990; Ratcliffe, 1996; Kalinova et al., 2009; Steiger et al., 2009). If a male discovers a suitable carcass for reproduction, it emits a sexual pheromone to attract the female (Eggert et al., 1989; Eggert, 1992; Ohkawara et al., 1998). After the burial [10-20 cm depth (Hastir et al., 2001)], Nicrophorine removes the skin (fur or feathers) and the remains are fashioned into a compact ball. Then, they inoculate the carrion ball with oral and anal secretions that have antimicrobial properties to delay the decomposition process (Ratcliffe, 1996; Eggert et al., 1997; Scott, 1998; Hoback et al., 2004; Rozen et al., 2008; Cotter et al., 2010) and remove also fungi (Scott, 1998). The female makes a chamber above the carrion ball in which it lays 10-50 eggs. Both parents regurgitate food in this crypt for feeding their larvae. Larvae may also feed directly on the surface of the carrion ball (Ratcliffe, 1996; Ohkawara et al., 1998; Sikes, 2008). The larvae receive parental care during their entire development (Ratcliffe, 1996; Scott, 1998). Parents provide extensive care: they feed their offspring, they protect them from predators and intruding burying beetles (inter- and intraspecific competitions) and they maintain a pathogen free nest with preservative secretions (Ratcliffe, 1996; Scott, 1998; Smiseth et al., 2006). Female stays on the crypt until complete larval development (1-4 weeks), whereas the male abandons the brood a few days earlier (Trumbo, 1991; Müller et al., 1998). If the brood is too large for a successful development, adults may regulate brood size by selective cannibalism. They kill smaller larvae during the first 24 h after hatching (Trumbo, 1990a; Ratcliffe, 1996). After one week, the larvae have consumed the entire carrion ball and pupate in the nearby soil during two weeks (Ratcliffe, 1996; Ohkawara et al., 1998). Then, adults emerge and the overwintering occurs in the adult stage or in the pre-pupal stage for some species (Ratcliffe, 1996; Ohkawara et al., 1998). Sometimes, nicrophorine may colonize large carcass (too large to bury) and several male-female pairs breed communally their larvae in a subsocial fashion: cooperative breeding (Pukowski, 1933; Eggert et al., 1992; Ratcliffle, 1996; Scott, 1998).

5. THE UTILITY OF CARRION BEETLES IN FORENSIC ENTOMOLOGY

Most forensic researches have focused on flies while beetles have been neglected (Midgley et al., 2009; Midgley et al., 2010). When a corpse colonized by insects is found, two situations could be considered (Amendt et al., 2007; Lefebvre et al., 2009). In the first situation, which is the most frequent case in forensic investigations, insects are pioneer species and the minimum postmortem interval (PMI) is estimated with the age of the oldest specimens found on the death scene, principally blowflies (Amendt et al., 2007; Lefebvre et al., 2009). In the second situation, later necrophagous species colonize the corpse with a delay, often after the departure of pioneer species. The estimation of the PMI is only possible by analyzing the chronological succession (Amendt et al., 2007; Lefebvre et al., 2009). A frequent objection against the use of Coleoptera in forensic investigations is the fact that flies (pioneer species) locate corpses faster than beetles (later necrophagous species). Thus, the minimum postmortem interval estimates are more accurate with Diptera, especially with the families of Calliphoridae and Sarcophagidae (Smith, 1986; Midgley et al., 2010). However, recent researches have shown that some Silphidae (*e.g. Thanatophilus micans* FABRICIUS) can locate a corpse within 24 h and their larvae have been observed soon after death, during the early stage of decomposition (Midgley et al., 2009; Midgley et al., 2010). This implies that some carrion beetles have the same forensic interesting characteristics than carrion flies and can be considered as pioneer species. In this case, some species of Coleoptera can be used as reliable forensic indicators such as blowflies (Midgley et al., 2009; Midgley et al., 2010). However, there are no available information about early postmortem colonization by European carrion beetles such as in South Africa with *T. micans*. Some recent publications (Matuszewski et al., 2008; Matuszewski et al., 2010) associate the silphid activity on carcasses during the active decay stage, primarily for Silphinae (*N. littoralis*, *Thanatophilus* spp.). The most important application of insects in forensic investigations is the estimation of the minimum PMI (Greenberg, 1991; Amendt et al., 2004; Amendt et al., 2007). These minimum PMI estimates are primarily based on the duration of immature stages of Diptera (development models) (Amendt et al., 2007). Contrary to flies, there are few studies on the rates of development of Coleoptera with forensic interest (Midgley et al., 2009; Midgley et al., 2010). For example, Midgley et al. (2009) studied the development of *T. micans* at ten constant temperatures. They established a robust statistical model of development for this common African species. Currently, there is no development model ("size-at-age data") for forensically relevant European silphids. However, research on development of Coleoptera with a forensic interest can be a useful tool for medico-legal entomologists (Midgley et al., 2010). In addition, carrion beetles have generally a longer life cycle than forensic Diptera (Midgley et al., 2009; Midgley et al., 2010). They can colonize a corpse during later decay stages when many maggots have already left the corpses (Kocarek, 2003; Matuszewski et al., 2008; Midgley et al., 2010). The PMI estimates can be established by analyzing the arthropod community present on a corpse including many Coleoptera during the later stage of decomposition (Smith, 1986). However, the biology and ecology of most forensically relevant species of Coleoptera are unknown (Midgley et al., 2010). To increase the accuracy and the validity of the PMI estimates based on ecological successions, there is a necessity to generate data on insect succession and insect seasonal activity on carrion in specific geographic regions and various biotopes within these regions (Catts et al., 1992; Amendt et al., 2004; Sharanowski et al., 2008; Lefebvre et al., 2009). All carrion beetles do not have the same forensic interest; species of Silphinae seem to have a more important value as forensic bioindicators (Watson et al., 2005; Matuszewski et al., 2010). Indeed they have ecological preferences for small vertebrate carcasses, while Nicrophorinae present less interest in forensic entomology (Watson et al., 2005). However, *Nicrophorus* spp. could be frequently found on human corpses, including in houses (Chauvet et al., 2008). This is an inventory extracted from 700 real forensic cases that occurred during 15 years in France. Midgley et al. (2010) suggest to focus on the biology of both Silphinae (*Silpha* and *Thanatophilus*). While Matuszewski et al. (2010) highlight the forensic usefulness of the following silphine species: *Necrodes littoralis* (larvae and adults), *Thanatophilus* spp. (larvae and adults) and *O. thoracica* (larvae). In some cases, necrophagous beetles can also provide information on the presence of drugs or poisons by bioaccumulation (entomotoxicology) (Bourel et al., 2001; Introna et al., 2001; Carvalho, 2010). Adults, larvae or beetle remain such as exuviae, puparial cases or fecal material of Coleopterans may be used for toxicological analysis when conventional toxicological samples (blood, urine, internal organs) are not available (Miller et al., 1994;

Bourel et al., 2001; Introna et al., 2001; Carvalho, 2010).

6. CONCLUSION

The potential uses of European carrion beetles as bioindicators in forensic entomology are obvious. Silphids and principally burying beetles (*Nicrophorus* spp.) are widely studied in various contexts including biology and ecology (Ratcliffe, 1996; Scott, 1998). Indeed, carrion beetles are poorly studied in a forensic context (Midgley et al., 2010). Nevertheless, their use in forensic investigations can be relevant (Watson et al., 2005; Midgley et al., 2009; Midgley et al., 2010). Are there some European carrion beetles with forensically interesting characteristics? Before creating development model for Paleartic Silphidae of forensic value, forensic entomologists need to increase data on carrion beetle's ecology and insect succession.

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