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REVIEW

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Forensic entomology

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Abstract Necrophagous insects are important in the decomposition of cadavers. The close association between insects and corpses and the use of insects in medicocriminal investigations is the subject of forensic entomology. The present paper reviews the historical background of this discipline, important postmortem processes, and discusses the scientific basis underlying attempts to determine the time interval since death. Using medical techniques, such as the measurement of body temperature or analysing livor and rigor mortis, time since death can only be accurately measured for the first two or three days after death. In contrast, by calculating the age of immature insect stages feeding on a corpse and analysing the necrophagous species present, postmortem intervals from the first day to several weeks can be estimated. These entomological methods may be hampered by difficulties associated with species identification, but modern DNA techniques are contributing to the rapid and authoritative identification of necrophagous insects. Other uses of entomological data include the toxicological examination of necrophagous larvae from a corpse to identify and estimate drugs and toxicants ingested by the person when alive and the proof of possible postmortem manipulations. Forensic entomology may even help in investigations dealing with people who are alive but in need of care, by revealing information about cases of neglect.

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Introduction

With about one million described species, insects comprise the largest metazoan class (Price 1997). They are found in almost all habitats. One such habitat, providing an excellent food source for a more or less specialized insect community, is a vertebrate corpse (Anderson and Cervenka 2002). About 400 insect species have been found on a pig cadaver during its various stages of decay (Payne 1965).

In addition to their ecological importance in decomposition, such insects may represent important tools in criminal investigations (Erzinclioglu 1983; Catts and Goff 1992), allowing the time at which a dead body was colonized to be estimated (Greenberg 1991). In particular, blowflies (Calliphoridae), among the first colonizers of cadavers, may serve as a biological clock in measuring the time of death for two or more weeks. Such an entomologically-based estimate may be far more precise than the medical examiner's, which is limited to about a day or two postmortem (Greenberg and Kunich 2002). Therefore forensic entomology, defined as the use of insects and other arthropods, such as mites, in medicocriminal investigations (Hall 2001), is becoming an important field in legal medicine. The present article describes the historical development of forensic entomology, the methods, current fields of research and future trends.

Retrospective

Insects were first used in a forensic context in thirteenth-century China (McKnight 1981). A farmer had been killed in a rice field with a sharp weapon. All the suspects were called together and were told to place their sickles on the ground. No obvious evidence could be seen, but one sickle attracted numerous blowflies, apparently because of invisible traces of blood on the blade. The owner of the sickle, when confronted with this entomological evidence, confessed to the killing.

During medieval times, the correlation between maggots on a cadaver and the oviposition of adult flies was

not recognized. However, the realistic and detailed illustration of corpses containing maggots was not unusual. The idea of the spontaneous development of life emerging from pure matter prevailed; mice were believed to develop from wet sawdust, for example. By the seventeenth century, the metamorphosis of insects had become more commonly understood (Blankaart 1690).

At the beginning of the nineteenth century it was noted that flies are attracted by corpses at a very early stage of decomposition (Anonymous 1814). Mende (1829) compiled a list of necrophagous insects, including flies and beetles as well as other taxa. Orfila and Lesueur (1831) provided a more precise account, but did not link flies to the time of death. Krahmer (1857) described the opportunities and problems associated with using insects for the estimation of the postmortem interval (PMI), many of which are still relevant today.

The first application of forensic entomology in a French courtroom, in 1850, can be viewed as a breakthrough for this discipline (Bergeret 1855): skeletonized remains of a child were found behind a chimney by workmen during redecoration. Insect evidence was accepted as proof that the current occupants of the building could not have been the murderers. However, in that case, the forensic examiner was of the opinion that the development of the adult flies took about one year; clearly his results would be questionable today. At that time, forensic examiners had only a poor understanding of insect biology and their knowledge was based largely on casual observations. Although Weismann (1864) published development data for two necrophagous fly species, at the time this was not widely noted by the forensic community. Yovanovich (1888) and Mégnin (1894) were the first forensic examiners who attempted to evaluate insect succession on corpses, properly establishing the science of forensic entomology.

In the following years, side issues such as grave fauna (Reinhard 1882; Schmitz 1928), the skeletonizing of corpses (Hauser 1926; Schneider 1936), or modification of corpses caused by insects (Horoszkiewicz 1902) were explored, but data concerning the biology, ecology and succession of necrophagous insects (e.g. Fuller 1934; Bornemissza 1957) were not applied to forensic cases. Leclercq and Leclercq (1948), Leclercq (1983), Nuorteva (1959a, 1959b) and Nuorteva et al. (1967) were among the first to use forensic entomology for the determination of the postmortem interval in Europe.

This topic was revived by researchers such as Reiter and Wolleneck (1982, 1983) and Reiter (1984) in studies of the development of the common necrophagous fly *Calliphora vicina* and by several others (Marchenko 1980, 1988, 2001; Leclercq 1983; Rodriguez and Bass 1983; Vinogradova and Marchenko 1984; Greenberg 1985; Lord et al. 1986; Goff et al. 1986; Nishida et al. 1986; Introna et al. 1989). Now, at the beginning of the twenty-first century, forensic entomology has been accepted in many countries as an important forensic tool (Goff 1991; Greenberg 1991; Catts and Goff 1992; Anderson 1995; Introna et al. 1998; Bourel et al. 1999; Malgorn and Coquoz 1999; Campobasso and Introna 2001).

Postmortem changes of the human body

After death a human or animal body undergoes many changes (Table 1) caused by autolysis of tissue, which is

Table 1 Postmortem changes in a human body (21°C ambient temperature and 30% humidity); according to Clark et al. (1997)

Time after death	Postmortem changes	Modifiers	Category
0 minutes	Circulation and breathing stop Pallor Early lividity Muscular relaxation Sphincters may relax	Temperature Humidity Outdoor location Indoor location Submerged in water	Early changes
2 hours	Vascular changes in the eyes Rigor mortis begins Algor mortis begins Lividity occurs		Late changes
4–5 hours	Coagulation of blood Fixation of lividity		
24 hours	Drying of the cornea Re-liquefication of blood		Putrid Tissue changes
48 hours	Rigor disappears Intravascular haemolysis		
72 hours	Loss of hair and nails		
96 hours	Skin slippage and bulla formation Bacterial overgrowth	Insect activity Animal activity	Bloated
Days – month	Green discoloration Bloating Release of gases Release of liquified internal organs Gradual loss of soft tissues Partial skeletonization Complete skeletonization	Mummification Adipocere formation	Destruction Skeleton

promoted by the internal chemical breakdown of cells and released enzymes as well as by the activity of bacteria and fungi, from both the intestine and the external environment (Knight 1991; Clark et al. 1997; Introna and Campobasso 2000). The body temperature decreases (algor mortis) and the skin colour reddens (livor mortis or lividity), which is generally evident at about 2 h postmortem. This is due to the gravitational pooling of blood in dependent body parts. After a few hours the colour changes from red to purple as oxygen gradually dissociates from the haemoglobin of the red blood cells. By 4–6 h after death, lividity is fixed because the fat in the dermis solidifies in the capillaries. Another sign of death is the stiffening of the muscle fibres due to the breakdown of glycogen and the accumulation of lactic acid (rigor mortis). This is first noticeable in the facial muscles 2–3 h postmortem and reaches its maximum after 24 h. The duration of rigor mortis depends on the metabolic state at death and on various factors such as body size and surrounding temperature. Later skin slippage, the loosening of the epidermis from the underlying dermis, occurs and hair and nails are easily removed. Large quantities of putrefaction gases cause the physical distortion of the body. Hydrogen sulphide (H_2S) reacts with haemoglobin and forms a green pigment which initially shows up the superficial blood vessels, but later may also be seen as a green coloration in the gastrointestinal region and those portions of the body where livor mortis was most marked. All these signs occur within the first 72–96 h after death (Henßge et al. 1995, 2000a, 2000b). However, the precise rate of postmortem decay is affected by a wide range of variables associated with the corpse itself and the surrounding environment. Moreover, after the temperature of the body has equilibrated with that of the environment and following the initial putrefaction, no reliable estimation of the postmortem interval (time since death) is possible. Subsequently, therefore, insects found on the body provide an important source of information.

Insects and death

Insects are attracted to a body immediately after death, often within minutes (Erzinclioglu 1983; Smith 1986; Anderson and VanLaerhoven 1996; Haskell et al. 1997; Anderson 2001). However, oviposition may not occur. Many taxa which appear very early at a death scene are late colonizers or even non-necrophagous species.

According to Smith (1986), four ecological categories can be identified in a carrion community:

1. Necrophagous species, feeding on the carrion.
2. Predators and parasites of necrophagous species, feeding on other insects or arthropods. This group also contains schizophagous species, which feed on the carrion at first, but may become predaceous in later larval stages.
3. Omnivorous species such as wasps, ants and some beetles feeding both on the corpse and its colonizers.
4. Other species, such as springtails and spiders, which use the corpse as an extension of their environment.

Table 2 Selection of insects of forensic importance

Order/Family	Important genera
COLEOPTERA/BEETLES	
Cleridae (Checkered beetles)	*Necrobia*
Dermestidae (Larder beetles)	*Attagenus*, *Dermestes*
Geotrupidae (Dung beetles)	*Geotrupes*
Histeridae (Clown beetles)	*Hister*, *Saprinus*
Silphidae (Carrion beetles)	*Necrodes*, *Nicrophorus*, *Silpha*
Staphylinidae (Rove beetles)	*Aleochara*, *Creophilus*
DIPTERA/FLIES	
Calliphoridae (Blowflies)	*Calliphora*, *Chrysomya*, *Cochliomyia*, *Lucilia*, *Phormia*
Drosophilidae (Fruit flies)	*Drosophila*
Ephydridae (Shore flies)	*Discomyza*
Fanniidae (Latrine flies)	*Fannia*
Heleomyzidae (Sun flies)	*Heleomyza*, *Neoleria*
Muscidae (House flies)	*Hydrotaea*, *Musca*, *Muscina*, *Ophyra*
Phoridae (Scuttle flies)	*Conicera*, *Megaselia*
Piophilidae (Skipper flies)	*Piophila*, *Stearibia*
Sarcophagidae (Flesh flies)	*Liopygia*, *Sarcophaga*
Sepsidae (Black scavenger flies)	*Nemopoda*, *Themira*
Sphaeroceridae (Small dung flies)	*Leptocera*
Stratiomyidae (Soldier flies)	*Hermetia*, *Sargus*
Trichoceridae (Winter gnats)	*Trichocera*
LEPIDOPTERA/BUTTERFLIES	
Tineidae (Clothes moths)	*Tineola*
HYMENOPTERA/WASPS	
Ichneumonidae (Ichneumon wasps)	*Alysia*
Pteromalidae (Fly wasps)	*Nasonia*, *Muscidifurax*

For the purposes of forensic entomology, the first two groups are the most important. They include mainly species from the orders Diptera (flies) and Coleoptera (beetles) (see Table 2). The succession on corpses can be divided into different waves over the various stages of decay, although this has been debated (Schoenly and Reid 1987). Nevertheless, since the attractiveness of a decaying body differs between necrophilous insects, changes over time and the colonization of the corpse will occur in a predictable sequence (see Fig. 1).

Blowflies, are typically the first colonizers, attracted to the carrion by the odour produced during decomposition (Wall and Warnes 1994; Fisher et al. 1998; Anderson 2001), even over large distances (Braack 1981; Erzincli-oglu 1996). Besides olfactory stimuli, vision, colour and the presence of other conspecific insects on the dead body all play a role (Hall 1995; Hall et al 1995; Wall and Fisher 2001). The presence of ammonia-rich compounds and hydrogen sulphide are important stimulants for oviposition, as well as moisture, some pheromones, and tactile stimulants (Ashworth and Wall 1994; Fisher et al. 1998; Anderson 2001). Female Diptera do not oviposit in dehydrated or mummified tissue, as eggs and larvae need moisture for successful development (Introna and Cam-

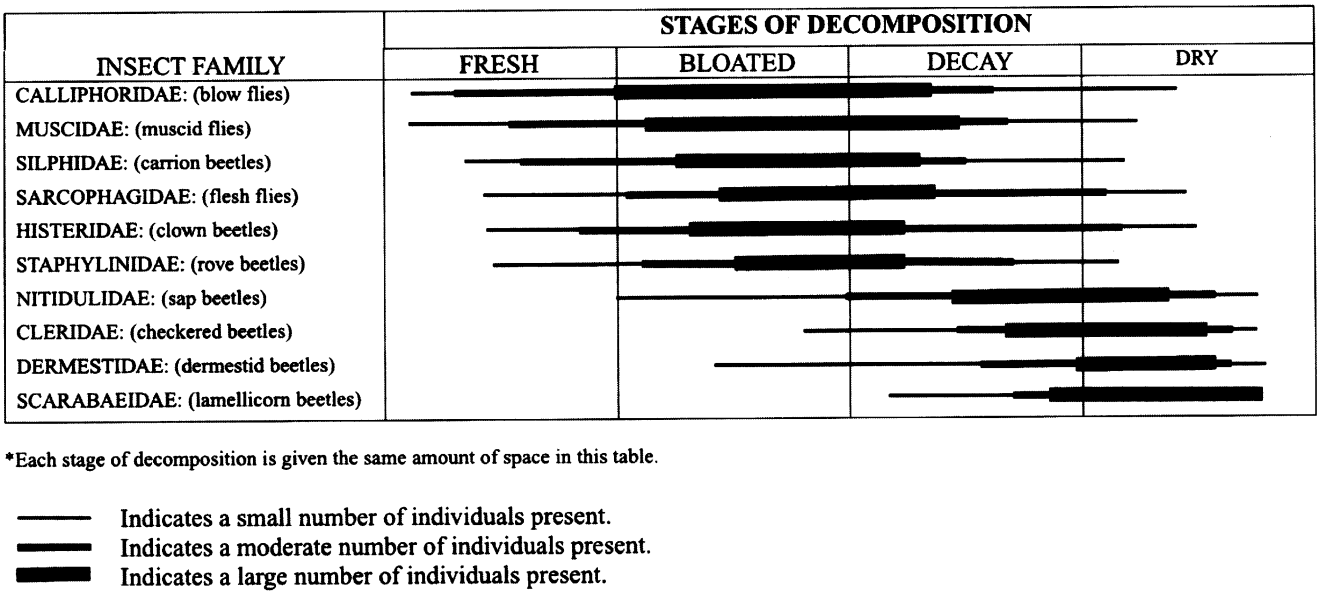

Fig. 1 Succession of adult arthropods on human cadavers in east Tennessee (during spring and summer); adapted from Rodriguez and Bass (1983) and Hall (2001)

pobasso 2000). Oviposition first occurs at the orifices or wounds of the corpse. The size of the carcass seems to affect its attractiveness, at least to species of the fly families Calliphoridae and Sarcophagidae (Nuorteva 1959b; Davies 1990; Erzinclioglu 1996; Povolný and Verves 1997). However, not all necrophagous insects prefer larger carcasses; some species oviposit preferentially on smaller animals such as rodents or even snails. Several factors restrict the colonization of a corpse, such as its burial (Mann et al. 1990). Most Diptera are not able to colonize bodies buried deeper than 30 cm (Introna and Campobasso 2000; Campobasso et al. 2001); however, exceptionally, groups such as the Phoridae may be found in buried coffins (Schmitz 1928; Stafford 1971; Smith 1986; Anderson 2001). Burial, therefore, will influence the time required for insects to reach the carcass as well as the species composition of the necrophagous fauna (Payne et al. 1968; Rodriguez and Bass 1985; VanLaerhoven and Anderson 1999; Campobasso et al. 2001; Bourel et al. 2004). Such a delay may not only occur in buried corpses, but also in those that are covered or wrapped (Goff 1991) or in cadavers found at indoor scenarios (authors' unpublished data).

Studies on animal carcasses (Fig. 2) have demonstrated that species composition and insect succession on a cadaver vary with respect to the geographical region and the season (Bornemissza 1957; Reed 1958; Payne 1965; Goddard and Lago 1985; Introna et al. 1991; Anderson and VanLaerhoven 1996; Richards and Goff 1997; Anderson 2001; Arnaldos et al. 2001; Carvalho and Linhares 2001; Grassberger and Frank 2003a; Watson and Carlton 2003). Data collected for a particular region or area should be used with caution when determining time of death in another region. Even local characteristics of the death scene, like the ecology of the area or the degree of sun exposure, can alter the pattern of insect colonization (Smith 1986; Shean et al. 1993; Erzinclioglu 1996). Some insect species are found in both urban and rural areas, while others are very specific to a certain habitat (Catts and Haskell 1990). Since species commonly considered as rural species have also been collected in urban regions, care must be used in determining whether remains have been moved based on entomological evidence alone (Anderson 2001; Grassberger and Frank 2003a). For example, the blowfly *Calliphora vomitoria*, usually considered to be a rural species, has also been found in residential apartments (C. Reiter, personal communication; authors' unpublished data).

Estimating time since death

When human remains are found days, weeks, or even longer after death, body temperature, and conditions such as rigor mortis or livor mortis are no longer appropriate for estimating time since death. In such cases, insects may provide important indications of the postmortem interval (PMI). The ages of insect immature stages found on a dead body can provide evidence for the estimation of a *minimum* PMI ranging from 1 day up to more than 1 month, depending on the insect species involved and the climatic conditions at the death scene. However, this period will not always match the exact PMI. Moreover, the infestation of live vertebrates by flies, called myiasis (Zumpt 1965), is not only a veterinary problem but has been reported in humans (see, e.g., Greenberg 1984; Erzinclioglu 1996; Sherman 2000), and should be kept in

Fig. 2A–D Decomposition of a pig carcass in a forest in Germany during a period of 42 days (mid-June until end of July); mean temperature 19.5°C (minimum 10.3°C, maximum 32.9°C); **A** postmortem interval of 2 days, **B** PMI of 14 days, **C** PMI of 32 days, **D** PMI of 42 days

Table 3 Development data for *Calliphora vicina* (from Anderson 2000)

	15.8 ± 0.004°C Time to reach stage (h)		20.6 ± 0.03°C Time to reach stage (h)		23.3 ± 0.02°C Time to reach stage (h)	
Stage	Min	Max	Min	Max	Min	Max
1st instar	41.4±1.2	46.7±0.6	22.5±0.2	36.0±4.0	21±0	29.5±5.2
2nd instar	83.0±10.0	88.3±12.7	57.0±6.0	57.0±6.0	45.0±0	52.0±0
3rd instar (feeding stage)	128.0±9.0	146.0±15.6	84.0±10.0	93.5±0.5	77.0±0	85.0±8.0
Prepupal	228.0±3.3	257.0±9.6	155.5±4.2	162.5±1.1	146.0±0	173.0±0
Pupal stage	294.0±4.7	440.3±42.1	213.0±4.5	233.0±0.9	202.8±5.8	279.0±22.5
Adult	719.7±6.0	874.6±20.7	514.8±3.7	572.0±10.0	454.0±6.0	499.5±7.5

mind when using entomological evidence in a death scene investigation.

Exact species identification of insect samples is the first essential step in estimating the age of the larvae found. Insect larvae differ in growth rates and biology. Larvae of *Lucilia sericata*, for instance, grow faster at 25°C than larvae of *Calliphora vicina*; blowflies usually deposit eggs on a corpse (but see below) while fleshflies are larviparous. These examples demonstrate that the same stage of development of larvae found on a corpse do not necessarily indicate the same age or the same time of colonization. For estimating the minimum PMI, the age of the immature larval stages must be determined. Various procedures for estimating their age exist, but all are based on the fact that the rate of development depends on the ambient temperature (see Table 3, Fig. 3). Measuring the length or the dry weight of the oldest larva may reveal its age by comparing it with reference data (e.g. Reiter 1984; Nishida et al. 1986; Davies and Ratcliffe 1994; Wells and LaMotte 1995; Grassberger and Reiter 2001, 2002a, 2002b). Another approach, known as thermal summation (Wigglesworth 1972), is the accumulation of degree hours (ADH) or degree days (ADD). According to Greenberg and Kunich (2002) it is assumed that the relation between the rate of development and temperature is linear in the mid-range of a sigmoidal curve, with an upper and a lower threshold below which development ceases. The total amount of heat required, between the lower and upper thresholds, for an insect to develop from the time of oviposition to the time of hatching is calculated in units

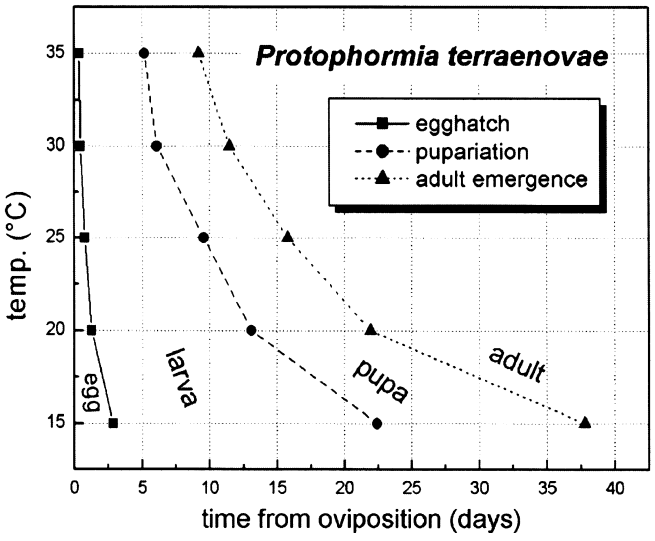

Fig. 3 Growth curves for the blowfly *Protophormia terraenovae*, showing the time required to reach the larval, pupal and adult stages at 15, 20, 25, 30 and 35°C; areas between lines represent identical morphological stages, e.g. pupa (Grassberger and Reiter 2002a)

called degree days or degree hours (Baskerville and Emin 1969; Allen 1976). Laboratory data are obtained by summing the number of hours from egg to adult and then multiplying by the temperature, after subtracting the temperature of the lower developmental threshold. Hence, degree-days or -hours are the accumulated product of time and temperature between the developmental thresholds for each day. Each developmental stage has its own total developmental requirement and each species requires a defined number of degree-days to complete its development. This fact helps us to predict the time when a certain developmental stage will be reached. Numerous papers describe ADH/ADD values and thresholds for forensically important insects, mainly blowflies and fleshflies (e.g. Kamal 1958; Greenberg 1991; Byrd and Butler 1998; Anderson 2000; Marchenko 2001; but see Ames and Turner 2003; Kaneshrajah and Turner 2004). The usefulness of these methods depends on the thermal history of the immature stages and, to be used, they therefore require the evaluation of temperature data at the death scene before the body was found. Hence, multiple temperature measurements have to be taken at the crime scene, at the body as well in the maggot masses on the cadaver. These data should be compared with data obtained from the nearest weather station. If these data sets are reasonably similar, the weather station data can simply be used to extrapolate temperatures at the crime scene (Greenberg and Kunich 2002). Alternatively, if more substantive differences exist, the weather station temperature data have to be corrected for the average difference using mathematical methods such as linear regression, prior to extrapolation of the expected temperatures at the crime scene. However, when using estimates of ambient temperature to calculate development rates, it should be noted that these data are not necessarily representative of the temperatures experienced by the insects in the corpse. Large numbers of maggots may create a so-called "maggot mass effect" which, according to the metabolic and feeding rate of these immature insects, can generate a temperature substantially higher than ambient (Wells and LaMotte 1995). Moreover, development data obtained in different geographical regions may not be comparable (Greenberg 1991; Grassberger and Reiter 2001). Populations of *Lucilia sericata* in Russia, for example, may have different minimum threshold temperatures than populations in the UK, and may therefore develop at different rates under the same temperature conditions.

Knowing the chronology of insects colonizing carrion in a certain area (see also the section titled *Insects and death*), analysis of the fauna on a carcass can be used to estimate the time elapsed since death (Goff and Flynn 1991; Anderson 2001). A simple succession model can be used when estimating both the age of a larva and the time interval between death and the insect's arrival on the body (Wells et al. 2001b). Succession data have been used to calculate a PMI up to 52 days (Schoenly et al. 1996) and, if there are adequate data, may be applied to a much longer time interval (authors' unpublished data).

DNA analysis in forensic entomology

In forensic entomology, information is essential not only on the development stages of the insects found on the body, but also on their identity. Morphological methods are usually used (Schumann 1971; Smith 1986; Povolný and Verves 1997). However, these techniques require specialized taxonomic knowledge. Although identification keys are available, only a few experts are able to identify the larvae of forensically relevant insects to species level. Furthermore, for some groups of insects (e.g. Sarcophagidae) differentiation at the larval stages using morphological criteria is still not possible. Time-consuming rearing of the larvae to adults for identification may delay the criminal investigation or cause significant problems when rearing fails. Under these circumstances, species identification based on genetic examination is an option. PCR amplification of suitable regions of the genome, sequence analysis of the amplicons obtained, and alignment of the data with reference sequences is the usual and recommended method.

For sequence analysis, DNA has to be isolated from the specimen. This can be done by various established methods including phenol/chloroform extraction (Sambrook and Russel 2001), CTAB extraction (Stevens and Wall 1996), Chelex extraction (Junqueira et al. 2002), or using commercial extraction kits, such as the QiAmpTissue Kit (Qiagen, Hilden, Germany; Wells et al. 2001a) or DNAzol (Molecular Research Center, Cincinnati, Ohio, USA; Wallman and Donellan 2001). DNA extraction from specimens collected at a crime scene is usually successful. However, with museum specimens, which may represent reference species, an extraction of typable

DNA is not always successful due to damage of the DNA during storage (Pääbo 1989; Pääbo et al. 1989) or to the influence of the ethyl esters used for killing the insects (Dillon et al. 1996).

After DNA extraction, PCR and subsequent sequence analysis can be performed, either as described by the authors cited above or by evaluating new primers for specific gene regions of interest. Frequently investigated genes are the subunits I and II of the cytochrome oxidase, ND5, ND1, 12S and 16S DNA (mitochondrial encoded) as well as 28S, ITSI and II DNA (nuclear encoded). For an overview, see Simon et al. (1994), Loxdale and Lushai (1998) and Caterino et al. (2000). To date, mitochondrial genes in particular have been analysed; sequence information of the complete mitochondrial genome is available for about 400 species (deposited at GOBASE, http://megasun.bch.umontreal.ca/gobase/; Shimko et al. 2001).

Flies are the most important insects in forensic entomology and therefore genetic research has focused on Diptera (Sperling et al. 1994; Wells and Sperling 1999; Malgorn and Coquoz 1999; Wells and Sperling 2000, 2001; Wells et al. 2001a, 2001b; Stevens and Wall 2001; Wallman and Donellan 2001, Harvey et al. 2003). In most of these investigations the use of the genes of subunit I and/or II of the mitochondrial encoded gene for cytochrome oxidase, a part of the respiratory chain within the mitochondrial membrane, has been examined.

When a sequence of an unknown insect matches a reference sequence, it can be concluded that these two taxa are identical or at least belong to the same species complex. If not, different species can be assumed because, in most cases, considerable differences between species can be observed (Table 4). However, where differences occur, information about the intraspecific vs the interspecific variation is necessary in order to evaluate these differences. Wells and Sperling (1999, 2001) demonstrated, by examining COI and COII sequences, that the blowflies *Chrysomya rufifacies* and *Chrysomya albiceps* exhibit less than 1% intraspecific and about 3% interspecific differences. However, the authors also state that these data have to be seen as preliminary because an overlap of intraspecific and interspecific sequence variation cannot be excluded based on the data currently available. Similar observations have been reported for the fleshflies *Sarcophaga argyrostoma* and *S. crassipalpis* [intraspecific variation 1%, interspecific variation about 3%, respectively (Wells et al. 2001a)] and the blowflies *Calliphora vicina* and *C. vomitoria* [intraspecific variability of less than 1%, interspecific variability of about 5% in the COI (Vincent et al. 2000) and COII subunits (authors' unpublished data)].

Since intraspecific variation will mostly be smaller than interspecific variation, unambiguous identification at the species level may be possible. However, careful interpretation should be employed until more data are available. The need for caution is also demonstrated by the following observations: Stevens and Wall (1996) examined the mitochondrial encoded 12S rRNA, COI and COII sequences of the two blowflies *Lucilia cuprina* and *L. sericata* originating from different geographical regions throughout the world. *Lucilia cuprina* specimens from Hawaii, which exhibit a clear affiliation to this species on the basis of morphological characters, were assigned to *L. sericata* rather than to *L. cuprina* on the basis of the mitochondrial sequence data. This may reflect hybridization between *L. sericata* and *L. cuprina* in Hawaii and this is supported by analysis of the nuclear encoded 28S rDNA sequence, which was identical to that of *L. cuprina* from various other locations outside Hawaii (Stevens et al. 2002)

In addition, unexpected variability between two specimens of *C. vomitoria* from different geographical origins (the USA and the UK) was found within the D1–D7 region of the nuclear encoded 28 s rRNA sequences (Stevens and Wall 2001), although the 28S gene is known to be quite conservative. These differences between two individuals exhibited the same values as between those of *C. vicina* and *C. vomitoria* (both from the UK).

Nevertheless, species analysis based on DNA sequence data appears to be promising. Examining the intraspecific variability of individuals of the same species collected from distant locations showed a relatively low variability compared with interspecific differences (Stevens and Wall 1996, 2001). However, studies on the intraspecific

Table 4 Pairwise percent sequence differences for a 386 bp region of COI of selected Sarcophagids compared to *Drosophila yakuba* (from Zehner et al. 2004b)

		1	2	3	4	5	6	7	8	9	10	11	12
1	*Sarcophaga carnaria*	–											
2	*Sarcophaga subvicina*	4.7	–										
3	*Sarcophaga variegata*	2.7	4.1	–									
4	*Parasarcophaga albiceps*	8.4	8.1	8.1	–								
5	*Bercaea africa*	9.5	9.1	8.4	9.8	–							
6	*Liopygia argyrostoma*	6.8	6.1	7.1	7.8	7.4	–						
7	*Liopygia crassipalpis*	8.4	8.1	7.8	8.1	6.1	6.1	–					
8	*Liosarcophaga teretirostris*	8.4	7.8	8.8	7.8	8.8	8.1	7.8	–				
9	*Liosarcophaga tibialis*	9.1	8.1	8.8	6.4	9.1	7.1	8.8	7.1	–			
10	*Pandelleana protuberans*	9.8	8.8	8.8	7.8	10.1	9.5	9.5	8.8	9.1	–		
11	*Thyrsocnema incisilobata*	8.4	7.1	7.8	8.8	9.5	7.4	8.8	9.5	8.4	10.5	–	
12	*Helicophagella melanura*	9.5	8.4	8.4	8.1	8.8	6.8	7.4	8.4	8.1	8.4	7.1	–
13	*Drosophila yakuba*	13.5	14.2	13.5	14.5	12.2	11.8	12.5	13.9	15.2	15.2	14.5	14.2

variability of a much larger number of individuals are necessary in order to provide a more solid basis for species identification.

In general, with sequence analysis, such as for COI, the maximum molecular data are obtained. By applying other techniques such as PCR-RFLP, where specific restriction patterns are produced due to different restriction sites in the sequences (Sperling et al. 1994; Malgorn and Coquoz 1999; Vincent et al. 2001; Schröder et al. 2003), only limited information about a small region within the sequence, such as the restriction site within the amplicon, is achieved. In cases of intraspecific variation at a certain restriction site, this may lead to false exclusions because an unknown restriction pattern may occur, although the other parts of the sequence are identical. In addition, the technique of random amplified polymorphic DNA fingerprinting (RAPD, Williams et al. 1990; Benecke 1998) or single strand conformation polymorphism (SSCP, Gasser and Chilton 2001; Rath and Ansorg 2000) can only be used in direct site-to-site comparisons, because it is not possible to generate data which are comparable from one laboratory to another. Although these techniques offers fast results they cannot be used for direct and unambiguous species determination.

The technique of sequence analysis, in particular, has become very popular in recent years. Analysis kits, computer-based sequencers and software-aided analysis of the sequences generated make sequence analysis relatively easy. Moreover, many companies now offer sequence analysis for a relatively small charge. Sequence analysis may be the method of choice for species determination.

The analysis of human DNA extracted from maggots is another important application of molecular tools (Wells et al. 2001b; Clery 2001). This kind of analysis may become important in cases where the source of the maggot's food is disputed, when only maggots but no corpse is found at the scene of possible murder, or where an alternative food source is present at the scene. By detecting human DNA in the digestive tract of the maggots, it may be demonstrated that they have fed on a human cadaver. By analysis of individual-specific DNA (mitochondrial d-loop, STR) a maggot can be assigned to a specific corpse (Zehner et al. 2004a).

Entomotoxicology

Larvae which feed on corpses may sequester drugs and toxicants which had been ingested by the deceased person. Analysis of carrion-feeding insects, to detect toxic substances and to investigate the effects on insect development, is known as entomotoxicology (Goff and Lord 2001). Bodies in a state of advanced decomposition or that are skeletonized may be difficult to examine for toxicologically relevant substances due to the lack of appropriate sources such as tissue, blood or urine. Instead, analysis of the insects encountered may enable toxicological assessment of the cause of death (Nolte et al. 1992; Goff and Lord 1994, 2001; Introna et al. 2001; Campobasso et al. 2004; but see Tracqui et al. 2004). After maceration of the larvae, analyses such as thin-layer chromatography (TLC), radioimmunoassay (RIA), gas chromatography (GC), gas chromatography/mass spectrometry (GC/MS), or high-performance liquid chromatography/mass spectrometry (HPLC/MS) may be performed (Gagliano-Candela and Aventaggiato 2001; Goff and Lord 2001). This can also be applied to adult insects or even remnants of larval and puparial shells, which are often found at the death scene, even after several years (Miller et al. 1994; Bourel et al. 2001a, 2001b).

The detection of mercury in the larvae of various species of blowfly reared on tissues containing known concentrations of this metal was described by Nuorteva and Nuorteva (1982). Their study was based on a case of an unidentified female corpse found in an advanced stage of decomposition in a rural area of Finland (Nuorteva 1977). Fly larvae were collected from the corpse, allowed to complete their development and the emerged adults analysed for mercury. The low concentration of mercury detected in the flies indicated that the victim was from an area relatively free of mercury pollution and not from the area where her body was found. These findings drew the attention of the police to a certain area, enabling the successful identification of the victim and resolution of the case. Kintz et al. (1990) demonstrated that toxicological data from Diptera larvae seem to be more reliable than those from cadaver tissues. Benzodiazepines, barbiturates and tricyclic antidepressants were detected in calliphorid larvae collected from a corpse 67 days postmortem. Goff et al. (1997) analysed antidepressant drugs from maggots and empty puparia of Diptera; Miller et al. (1994) showed the presence of these drugs in empty Diptera puparia (Phoridae), cast beetle exuviae (Dermestidae) and even in faecal material of beetles (Dermestidae). The usefulness of entomotoxicological methods has been demonstrated in experimental (e.g. Introna et al. 1990; Sadler et al. 1997a; Goff et al. 1997; Hedouin et al. 2001; Pien et al 2004) as well as miscellaneous case studies (e.g. Beyer et al. 1980; Kintz et al. 1994; Sadler et al. 1995).

Ingested drugs or toxicants may influence the development of the necrophagous insects (O'Brien and Turner 2004). Goff et al. studied the effects of cocaine (Goff et al. 1989) and heroin (Goff et al. 1991) on the rate of development in Sarcophagidae and demonstrated that maggots of *Boetterisca peregrina* develop more rapidly if reared on the liver or spleen of rabbits which had been killed by a lethal dose of cocaine or heroin. This illustrates the potential impact of drugs when estimating postmortem intervals by calculating the rate of development. Bourel et al. (1999) showed that an underestimation of the postmortem interval up to 24 h is possible if the presence of morphine in tissue is not considered when calculating the development time of *Lucilia sericata*. In a suicide case where the pesticide malathion had been used,

the development stages of two blowflies, *Chrysomya megacephala* and *C. rufifacies*, found on the dead body, indicated a minimum postmortem interval of 5 days, although the victim had last been seen alive 8 days prior to the discovery of his body (Gunatilake and Goff 1989). The authors concluded that malathion in the tissues delayed the colonization by insects for several days.

The absence of a drug in larvae may not indicate that the drug was not present in the food source (Sadler et al. 1997a, 1997b, 1997c). The toxicological analysis of *Calliphora vicina* larvae reared on a substrate containing four benzodiazepines yielded a negative result for the rapidly eliminated loprazolam, although bromazepam and diazepam were detected (Sadler et al 1997b). Larval drug and food source concentrations differed in an unpredictable ways and were found not to be useful for quantitative calculations.

These examples demonstrate that insects found on corpses can be used in toxicological analyses, but also illustrate the risk of calculating an incorrect postmortem interval because of a modified rate of development of the immature stages. Further research should focus on the bioaccumulation and metabolism of drugs in necrophagous insects and their effects on the rate of development.

Future trends in forensic entomology

The precise estimation of PMI is the most important goal of forensic entomology by refining the techniques used. Developmental and succession data, consideration of a greater number of geographical regions and a range of death scene scenarios are essential. Moreover there are several parameters which need further attention.

It is important to consider factors that might alter the time of oviposition, such as covering corpses with branches or tight wrapping with blankets, carpets or plastic bags, and indoor placement, because these factors may delay initial oviposition (Higley and Haskell 2001). Seasonal influences, such as cold and rainy weather, may inhibit or even prevent fly activity and delay oviposition (Erzinclioglu 1996). However, Faucherre et al. (1999) observed flying as well as ovipositing *Calliphora vicina* under extreme conditions in the Swiss Alps, colonizing a corpse in a 10-m deep cave at a temperature of about 5°C. The generally accepted assumption that activity of necrophagous flies ceases below an air temperature of 10°C (Williams 1984) or even 12°C (Smith 1986; Erzinclioglu 1996) may be questionable (see also Deonier 1940; Nuorteva 1965). However, the case described by Faucherre et al. (1999) occurred at an altitude of 1,260 m and therefore a cold-adapted population of *C. vicina* may have been involved.

Blowflies usually show peaks of oviposition activity in the early afternoon (Nuorteva 1959a; Baumgartner and Greeenberg 1984, 1985; Greenberg 1990). These insects are not active at night and generally do not lay eggs during nighttime (Greenberg 1985). A postmortem interval estimation based on that assumption has to consider the possibility that a corpse which was found about noon and was infested by recently hatched maggots, could have been deposited there in the late evening of the previous day. Hence, fly eggs detected on a corpse during the night would lead to the conclusion that death occurred during the previous day or earlier (Nuorteva 1977). Greenberg (1990) presented the first experimental evidence of nocturnal oviposition by three forensically important blow flies, *Calliphora vicina*, *Phormia regina* and *Lucilia* (*Phaenicia*) *sericata*. On the other hand, Tessmer et al. (1995) reported that blowflies fail to lay eggs at night both in urban (with lighting) and rural dark habitats. However, Singh and Bharti (2001) supported the findings of Greenberg (1990). Hence nocturnal oviposition is a possibility and should be taken into consideration.

Diapause, the period during which growth and development of insects is suspended, is still a challenge for the forensic entomologist (see also Ames and Turner 2003). Depending on the insect taxa, the major influences on larvae or pupae are photoperiod and temperature. Declining day length and/or decreasing temperatures indicate approaching winter and induce diapause, preventing development under unfavourable environmental conditions. In many forensically important blowflies, diapause is under maternal control and exposure of females to short day lengths induces diapause in the offspring (Vinogradova 1991). Species with a large geographical range have to face changes in day length throughout the year. The critical day length which induces diapause will be longer in populations from a northern range than in southern populations (McWatters and Saunders 1998). The forensic entomologist working in a temperate region investigating a sample of dead maggots collected from a corpse during late September has to consider the possibility that these maggots had already entered diapause. Besides day length, temperature may also influence the incidence of diapause (Vinogradova and Zinovjeva 1972). Unlike photoperiod, temperature is not a noise-free signal, as it is subject to considerable variation both within and between years (McWatters and Saunders 1998). Increasing constant temperature is known to reduce the incidence of diapause in forensically important Dipteran species, such as *Liopygia argyrostoma* (Saunders 1975), *Protophormia terraenovae* (Vinogradova 1986) and *Calliphora vicina* (McWatters and Saunders 1998).

The duration of diapause is another important parameter. McWatters and Saunders (1998) showed that in *C. vicina* kept at temperatures of 15°C and 20°C, respectively, diapause was terminated in most larvae within 30 days. However, the diapause ended earlier in larvae whose parents had been kept at 20°C than those whose parents had been kept at 15°C. These observations should be a caveat for the forensic entomologist and points to the need for further studies on other species.

Competition may affect development and growth of the larvae. Smith and Wall (1997a, 1997b) presented data which indicate that the larvae of *Lucilia sericata* in carcasses experience significant levels of competition and that the intensity of this competition may be sufficient to

reduce the numbers of adult *L. sericata* able to emerge successfully.

Reiter (1984), Smith (1986) and Erzinclioglu (1990) pointed to another factor which could complicate the estimation of the postmortem interval—precocious egg development in flies. In some female flies, eggs may be retained in the oviduct, having been fertilized as they pass the spermathecal ducts in advance of the act of oviposition (Wells and King 2001). In cases where a suitable oviposition site is not available, the eggs may remain inside the fly until they have completed embryonic development. It has been reported for several species of the tribe Calliphorini, including the forensically important *Calliphora vicina*, that the larva hatches from such eggs immediately following oviposition (Erzinclioglu 1990; Wells and King 2001). Precocious eggs are more likely to be found in bluebottles (*Calliphora* spp.) than in other lineages of carrion-feeding blowflies and the proportion of wild flies carrying an egg that is about to hatch can be quite high (Wells and King 2001).

Parasitoid larvae feed exclusively on other arthropods, mainly insects, resulting in the death of the parasitoid's host (Godfray 1994). The majority of parasitoids are either members of the order Hymenoptera or Diptera, representing an extremely diverse group and constituting about 8.5% of all described insects (LaSalle and Gauld 1991; Godfray 1994). They also attack necrophagous taxa and therefore could appear on carrion. Fabritius and Klunker (1991) listed 83 parasitoid species, mainly wasps, which attack the larval and pupal stages of synanthropic Diptera in Europe. There are few reports on the use of parasitoids in forensic entomology (Smith 1986; Haskell et al. 1997; Amendt et al. 2000; Anderson and Cervenka 2002; Grassberger and Frank 2003b). The life-cycles of the common parasitoid species are known (e.g. Geden 1997) and, even if the adults have already emerged and left the host, the pupal exuviae of the parasitic wasps can be identified for a long time afterwards (Geden et al. 1998; Carlson et al. 1999). The parasitoid developmental times can then be calculated and added to the time of development of the blowfly host. Pupal parasitoids of blowflies may play an especially important role in the estimation of the postmortem period because their time of attack is often restricted to a small, well-defined window of time at the beginning of the pupal development of the host insect (Anderson and Cervenka 2002). An example of the practical application of these wasps involved a case where the early colonizers, individuals of the blowfly *Protophormia terraenovae*, had finished their development and already left the scene but adults of the parasitoid *Nasonia vitripennis* (Hymenoptera: Pteromalidae) were just about to emerge. These wasps need, at a constant temperature of 25°C, 350 accumulated degree days, equating to about 14 days, to reach adulthood (Whiting 1967; Grassberger and Frank 2003b). By contrast the host *P. terraenovae* needs about 9 days at this temperature to reach the stage appropriate for the parasitoid's oviposition (Marchenko 2001; Grassberger and Reiter 2002a). It can therefore be assumed that the flies had access to the body for at least about 23 days before the corpse was found. The calculation of developmental times for the host and the parasitoid allowed the estimation of a greater minimum postmortem interval than the estimated development time of *Protophormia terraenovae* alone. This enabled the criminal investigators to disprove the testimony of a witness who claimed that he had seen the victim alive 20 days before the corpse was found. However, when thinking about the potential influence, especially of larval parasitoids, it is important to remember that this specialized group might also create significant problems for forensic entomology. Holdaway and Evans (1930) described, for example, the change in developmental times for *Lucilia sericata* after the attack of its parasitoid *Alysia manducator*, which resulted in premature pupariation.

The role of freshwater and marine fauna in forensic investigations has received very little attention (Payne and King 1972; Nuorteva et al. 1974; Goff and Odom 1987; Haskell et al 1989; Catts and Goff 1992; Vance et al. 1995; Sorg et al. 1997; Davis and Goff 2000). Knowledge about the role of aquatic arthropods during decomposition is still scanty (Keiper et al. 1997; Tomberlin and Adler 1998; Hobischak and Anderson 1999, 2002; Anderson 2001; Merrit and Wallace 2001; Anderson and Hobischak 2004). Compared with terrestrial habitats, decomposition in an aquatic environment is completely different. It occurs at a rate roughly half that of decomposition on land, mainly due to the prevention of insect activity and cooler temperatures (Knight 1991). Merrit and Wallace (2001) have distinguished six decompositional stages ranging from submerged fresh, floating decay to sunken remains. Aquatic insects of forensic importance belong to the Ephemeroptera (mayflies), Trichoptera (caddis flies) and Diptera (true flies); the latter are mainly represented by Chironomidae (midges) and Simuliidae (black flies). However, these insects, unlike their terrestrial counterparts, are not obligatory saprophages, but instead use the submerged carrion both as a food source and a breeding site. The use of these insects for estimating the time of death is therefore more difficult and depends on the season and on other conditions of the aquatic systems. No successional insect model exists which describes the different waves of colonization of a corpse in aquatic habitats (Merrit and Wallace 2001).

Finally, forensic entomology may help in investigations dealing with living, but ill, people by revealing neglect. The occurrence of maggots in the wounds or natural orifices of living persons may indicate such a neglect. Estimating the age of these maggots can reveal how long the neglect has been happening (Benecke 2003).

Conclusions

Despite 150 years of use, forensic entomology is still a young discipline. One of the most important challenges for the future is to combine experimental data and

practical case work. Due to the wide variations in biotic and abiotic factors which occur at death scenes, a improvement of the existing understanding can only be established through an increased number of detailed and quantified observations. Forensic entomologists are always presented with the task of reconstructing the death scene conditions as closely as possible. A model for the calculation and handling of the data is crucial for the credibility of this discipline.

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