A history of southern African research relevant to forensic entomology

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Entomological forensic evidence has been used in southern Africa for decades but explicitly forensic research began in southern Africa only 26 years ago. Although applicable local research has accumulated since 1921, it is scattered in a diverse literature or unpublished. Some overseas research has also touched on local species. This review uses a historical approach to synthesize the southern African literature and to illustrate the cross-disciplinary, opportunistic nature of forensic entomology. Distinct phases of research focused on agriculture (1921–1950), medicine (1952–1965), ecology (1968–1990) and forensics (1980–2005), but systematics spanned the entire period and tended to be *ad hoc.* Few scientists were involved, situated at geographically distant locations and with widely disparate research interests. The review concludes with an overview of southern African entomologists who have been involved in medico-legal investigations, and a critical evaluation of the past and future of the discipline locally.

Forensic entomology

Forensic entomology draws evidence applicable to civil and criminal cases from the biology of insects. It has been categorized into medico-legal forensic entomology, urban forensic entomology and stored-product forensic entomology.[1,2] Medico-legal forensic entomology is distinct in that its standards of evidence are governed by criminal law, while the others are largely judged under the less stringent evidentiary standards of civil law. Urban and stored-product forensic entomology differ primarily in whether the clients are private or corporate.

The history of forensic entomology in the northern hemisphere has been well-documented.[1–9] The discipline is still establishing itself in the southern hemisphere,[10–13] including South Africa, where it draws on a history of research on indigenous insects, little of which is explicitly forensic. Relevant South African research into carrion-associated insects and stored-product pests has accumulated since 1921, but there is a longer tradition of taxonomy. Forensic science has a strongly cross-disciplinary character, and forensic entomology draws from veterinary science, medicine, ecology, physiology, crop protection and taxonomy. Because of this diversity, literature relevant to South African forensic entomology is scattered and merits synthesis. This review adopts a historical approach to illustrate the cross-disciplinarity of forensic entomology and to review, synthesize and contextualize these published studies.

Veterinary research 1921–1950

Late in the 19th century, as it became apparent that South Africa's economic future could not depend on its finite mineral wealth, political effort turned to developing the country's agricultural resources. The history of entomology in southern Africa before 1920 was focused around this development.[14–16] By 1908, revenue from agricultural exports exceeded that from diamonds. Much of the exports was skins and hides, ostrich feathers, and wool and mohair.[16] By 1929, wool was the most important South African export after gold.[17] As the South African wool industry expanded, the threat of sheep strike or myiasis in sheep increased, which engendered the first local research that would contribute to forensic entomology.

In 1921, R.W. Thornton, principal of the Grootfontein School of Agriculture, established a committee to investigate sheep strike.[18] The work began in September 1922, when Owen Wahl, a Grootfontein entomologist, returned from Australia and the United States, where he had gathered information on sheep strike. Many Australian fly control techniques were not feasible in South Africa and it was realized that much needed to be learned about South African blowflies. In 1923, Wahl was transferred and Bernard Smit took over the work.[17–19] Smit[17,18] specifically investigated the seasonal distribution, life-history and parasitoids of South African blowflies to find methods of preventing sheep strike. He published paintings[17] of four species to assist in their identification (Fig. 1). The taxonomy of the greenbottle flies, *Lucilia sericata* (Meigen, 1826) and *Lucilia cuprina* (Wiedemann, 1830), was unclear at that stage, and Smit referred all of his material to the introduced species, *L. sericata.*

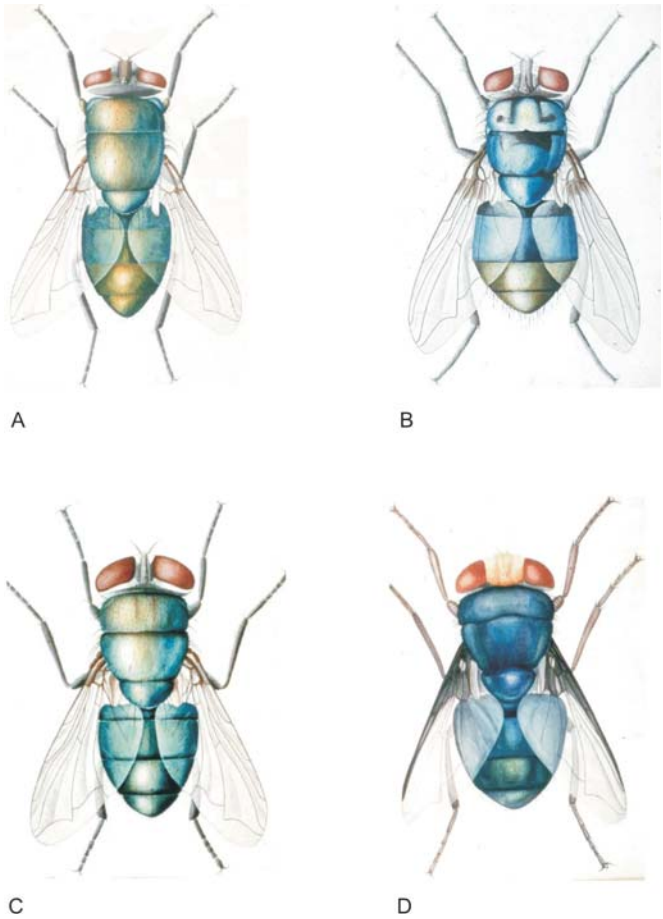

Fig. 1. Bernard Smit's[17] painted drawings of females of (**A**) *Lucilia cuprina*, (**B**) *Chrysomya chloropyga*, (**C**) *C. albiceps* and (**D**) *C. marginalis.*

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He suggested that the bluebottle fly, *Chrysomya putoria* (Wiedemann, 1830), occurred only further north in Africa;[18] and speculated that the closely related copper-tailed blowfly, *Chrysomya chloropyga* (Wiedemann, 1818), was restricted to South Africa.[18] This lack of taxonomic clarity makes some of his work difficult to interpret, but several hundred specimens from Grootfontein that are now housed in the National Collection of Insects, Pretoria, are all *C. chloropyga,* so it is likely that his research does pertain to that species. In a review of ways to destroy carcasses, Smit[17] noted that maggots of *Lucilia* species and *C. chloropyga* can burrow upwards through 1.2 m of soil.

Contemporaneously, Alexander Cuthbertson[20] began publishing observations from the Department of Agriculture in Salisbury, Southern Rhodesia (now Harare, Zimbabwe). He had a network of correspondents such as Walter Patton (Liverpool School of Tropical Medicine), Daphne Aubertin (British Museum), Charles Curran (American Museum of Natural History), John Malloch (U.S. Department of Agriculture), Albert J. Hesse (South African Museum) and George C. Arnold (Rhodesian Museum). Through such contacts, Cuthbertson[20] was able to publish or republish illustrations of several blowflies, including the larvae of *C. chloropyga, Chrysomya albiceps* (Wiedemann, 1819), *Chrysomya megacephala* (Fabricius, 1794) and *Chrysomya bezziana* Villeneuve, 1914, and the adults of five species (including three of Smit's[17,18] paintings). He included developmental and ecological details of veterinarily significant species, but made little reference to the effects of temperature on his observations. Significantly, he collaborated with Aubertin to provide good diagnostic notes for distinguishing the adults of *C. chloropyga* and *C. putoria.*[20]

A decade after Smit's work, sheep strike remained sufficiently serious that four scientists were placed under the direction of H.O. Mönnig, then head of Parasitology at Onderstepoort Veterinary Institute (OVI), to address it. G.A. Hepburn was seconded from the Division of Entomology, and the Wool Council provided a grant to employ P.A. Cilliers as a technical assistant, to study the biology of blowflies. The team worked from 1939 to 1942, and Hepburn[21] made several remarks about the effects of wartime economics on the research. These constraints resulted in experiments that were generally unreplicated[21–23] or repeated just once, resulting only in pilot studies. Hepburn[21,22] also referred all of Smit's data on *L. sericata* to the indigenous species, *L. cuprina.* The data are generally forensically useful, although it is unclear whether *C. putoria* was unmentioned because it was absent, or because it was thought synonymous with *C. chloropyga.* A provincial-scale survey was conducted to discover which flies farmers found pestilent.[22] While these data served their purpose, they are insufficiently precise for further distributional analysis.

Hepburn[22] trapped flies on rotting mince in one or (usually) two traps at Onderstepoort for over two years, and reported the seasonal distributions of the four most common flies. With the exception of *C. chloropyga,* these populations showed marked year-to-year variation in the size, timing and persistence of their peaks, but the peaks were generally brief, and usually occurred in summer. He also monitored the numbers of various flies emerging from two experimentally exposed sheep carcasses each month,[21] and found that these did not match the patterns from baited traps. This was ascribed to differential mortality from predation and competition in the carcasses. These results may be useful in relating events involving blowflies to a particular time of year, since there were seasonal differences in the dominance of particular flies.[21] This study illustrated differences in the preference of each species of fly for carcasses of different ages,[21] which may influence investigations. *Lucilia* species arrived within hours of exposure, followed by *Chrysomya marginalis* (Wiedemann, 1830), and later still by *C. chloropyga* and then *C. albiceps* and the fleshflies, *Sarcophaga* spp. Finally, Hepburn[21] provided anecdotal data on variation between the fly communities that established in simultaneously exposed carcasses; significantly, this variation was quite extreme in some cases.

Cilliers carried out a parallel study in the winter rainfall area encompassing Bredasdorp, Caledon and Stellenbosch.[23] Contrary to Hepburn,[21] he found almost no evidence of *L. cuprina* breeding in carcasses. Carcasses of different sizes were exposed, and those weighing less than 0.5 kg generally hosted *L. sericata, C. croceipalpis* Jaennicke, 1867, *Sarcophaga* spp. and (rarely) *L. cuprina,* whereas larger carcasses produced *C. marginalis, C. chloropyga, C. albiceps* and sometimes *L. sericata.* This contradicted results of similar experiments at Onderstepoort,[21] but sampling was inadequate to reach a firm conclusion. The topic has yet to be studied rigorously. Data for adults of the main carrion-breeding flies were presented and differed from findings made in other South African climatic regions. It is still unclear whether this represents year-to-year variation in population dynamics, or climatic differences between provinces.

The closing comment of Mönnig and Cilliers'[23] paper was that attention should be directed to the value of competition between the blowfly species as a means for their control. Contemporaneously, George C. Ullyett undertook an extensive study of competition in blowflies causing sheep strike while working in the Entomological Parasite Laboratory at the South African Department of Agriculture's Division of Entomology.[21] Ullyett focused on the potential for competition amongst maggots as a biological means to reduce blowfly populations.[24] He estimated development rates of larvae, in particular *L. sericata* and *C. chloropyga,* concluding that both intra- and interspecific competition occurred on carrion, and that *L. sericata* was the species most capable of surviving adverse conditions. These data are of fundamental significance for medico-legal forensic entomology. He also concluded that, contrary to the recommendations of the OVI team, destroying carcasses was insufficient to reduce blowfly populations and that much more information about the relationships between populations, their environment and natural controlling factors was required. Ullyett's[24] research was quantitative, experimental and encyclopaedic, and brought to an end the era of southern African veterinary studies of blowfly ecology, although sheep strike still remains a problem. Ullyett moved to the Commonwealth Bureau of Biological Control in Canada in 1949, and subsequent research at OVI focused on insecticides, in keeping with international trends in pest control.

Medical research 1950–1965

As veterinary work waned, concern arose about the health of migrant labourers, who could potentially import diseases such as poliomyelitis, tuberculosis and dysentery, which might be spread further by flies. Funded by the Department of Mining, and working at the South African Institute for Medical Research (SAIMR) in Johannesburg, Fritz Zumpt and his assistant, P.M. Patterson, reported which flies visited human faeces, rotting beef and dead guinea pigs in an urban setting.[24] The dominant species visiting these small baits were *L. sericata, Sarcophaga africa* (Wiedemann, 1824) [= *S. haemorrhoidalis* (Fallén, 1817)][25] and, at some sites, *C. albiceps* and *Sarcophaga tibialis* Macquart, 1851; with fewer muscids, *C. chloropyga* and *C. croceipalpis.* As in veterinary studies,[21] larvae reared from baits showed a different pattern of dominance from adults, which was ascribed to differential survival under interspecific competition. There was year-to-year variation in the seasonal abundance and distribution of adults that paralleled Hepburn's work.[22] Anecdotal notes were provided about the succession of visitors to specific baits and the influence of habitat on fly communities. This study provided forensic entomology with the first quantitative data on urban conditions and small carcasses.

Zumpt also wrote a monograph on myiasis in man and animals in the Old World.[26] This extensively illustrated volume is a rich source of information on the natural history and early stages of flies that feed on live mammals, and covers most of the species that frequent carcasses. In forensic cases involving neglect of children or hospital patients, this publication is particularly germane. Mention should be made of Annie Porter, one of Zumpt's predecessors at the SAIMR, who published a short note on myiasis[27] that included an illustration of the posterior spiracle of a third-instar larva of *C. croceipalpis.*

After Zumpt retired, further work on veterinary entomology in South Africa was directed towards malaria, sleeping sickness and other diseases.

Ecological research 1968–1990

Zumpt passed on some of his knowledge to Hugh E.H. Paterson, whose doctoral thesis,[28] through the University of the Witwatersrand, involved evolutionary and population genetic studies of selected flies. Paterson conducted breeding experiments to determine whether *C. chloropyga* and *C. putoria* were separate species, concluding that they are.[28] He went on to become head of the Department of Zoology, training a number of postgraduates in evolutionary ecology.

During Paterson's tenure, theoretical ecology developed significantly, in the context of a worldwide debate over the ecological and evolutionary significance of competition. One of Paterson's postgraduates was Ivan Meskin, whose M.Sc. thesis documented the morphology, biology and ecology of the highveld blowflies breeding on small carcasses and the factors affecting their ecological co-existence in rural and suburban areas.[29] He found notable differences in adult seasonality and community composition between two simultaneously sampled sites, and differences between species in time of arrival at carcasses, preferred oviposition and pupation sites, and rates of development.[29,30] Because the experimental sites were apparently unreplicated, it is not clear whether the differences in adult seasonality should be ascribed to population dynamics, climatic differences or even the seasonally changing availability of alternative food sources at each site. Temporal patterns in community composition were consistent with previous studies. The sequence of species arriving to lay eggs was consistent and agreed with Hepburn's[21] findings. Their punctuality of arrival was also anecdotally related to the rapidity of decomposition, attributed to ambient temperatures. The tabulated differences in preferred oviposition sites may help with the identification of eggs. Meskin is now a dentist.

A contemporaneous area of growth in theoretical ecology was the movement of energy and materials through ecosystems. Research aimed at tracing the fate of dead vertebrates started overseas decades before comparable work in southern Africa. The first South African study involving insects was an M.Sc. project by Philip R.K. Richardson,[31] who monitored scavenger activity on 89 large mammal carcasses, 39 of which were examined for arthropods. Because of frequent and rapid vertebrate scavenging, only 15 of these carcasses hosted maggots, and the significance of insects in the decomposition process was not great. The blowfly species and beetle families present are listed, and graphs of their occurrence in different stages of decomposition were presented.

For his doctorate through the University of Natal, Laurence E.O. Braack studied large carcasses and their fauna to elucidate the role of decomposers in ecosystems in the Kruger National Park[32] and published much forensically useful natural history. For instance, he catalogued 224 insect species from 33 families, and some mites[33] (which provides a starting point for the identification of these animals);[34] noted the movement of small maggots upwards under the skin of the carcass (termed subcutaneous[34] or epidermal streaming[35]) and their entry to the interior of the carcass through wounds caused by predators and scavengers; and reported on the synchrony of onset of wandering phase in larvae of *C. marginalis* in contrast to *C. albiceps.*[34] He reviewed the general ecological dynamics of this community, including food webs, resource partitioning, competition, predation and parasitism, and succession.[36]

Braack was subsequently employed at Skukuza by the National Parks Board. As part of a programme on the epidemiology of anthrax, Braack and V. de Vos[37] reported on the seasonal abundance of blowflies at five sites over two years in the Kruger National Park. Although there were no replicates within each site, this work showed general concordance in the numbers of the various species between neighbouring sites within years, but disparities between years and between sites further apart. One cause of year-to-year variation within sites was the availability of carrion. The study also supported previous suggestions that *L. cuprina* was essentially a 'rural' species, while *L. sericata* was characteristically 'urban'.[30,38] They found that *C. albiceps* and *C. marginalis* fed on ^{32}P-labelled blood were later detected in traps 32.5 km and 25 km away, respectively.[40] Using flies dusted with radioactive ^{32}P-powder, Braack and P.F. Retief[39] estimated dispersal rates of *C. albiceps* and *C. marginalis* to be about 2.25 km/day, and that specimens of *C. albiceps* and *C. marginalis* were recovered 37.5 km and 63.5 km from the release site, respectively.

In 1991, Braack[41] reported that he had misidentified *C. megacephala* as *C. bezziana* in his earlier studies. *C. megacephala* was common in the Kruger National Park by 1980, and had reached the Karoo National Park, near Beaufort West, by May 1991. It is unclear how *C. megacephala* spread across South Africa, since it was first discovered near Cape Town in 1978.[42]

Braack also identified insects collected during a brief study by George Ellison of the effects of scavenger activity on the insect community of two suspended impala carcasses, one culled in July and the other in August.[43] The explicit conclusion of this work was that the composition of the insect community was a poor estimator of post-mortem interval in the case of mutilated bodies, which gives it particular forensic relevance. Unfortunately, the degree of mutilation is unreplicated, and the experiment is uncontrolled and confounded by seasonal effects. This paper also contains a species list and some quantitative natural history that are useful to forensic entomology.

Forensic research 1980–2005

The first mention of forensic entomology in a specifically southern African context was probably made in a textbook of medical jurisprudence,[44] which mentioned the scientific names of a few flies, including some non-African species. These details were absent from a previous edition of the book,[45] and were apparently based on a British textbook.[46] All three works briefly illustrated the forensic potential of maggots by referring to the Ruxton case, which is recounted in detail by Smith.[1]

The first explicitly forensic research in South Africa was conducted by André Prins at the South African Museum. He was approached by the South African Police (SAP) and the State Health Department regarding cases of murder and cattle theft,[47] and pursued doctoral studies[48] on decomposition. He published details of the life cycle of six South African blowflies and a key to their larvae, illustrated morphology, commented on ecology, and indicated developmental rates.[49] This was followed by a series of notes on arthropods associated with decaying matter.[47,50,51] He discovered the Asian *C. megacephala*,[42] confirmed by Zumpt, in South Africa in March 1978, in a seagull carcass at Ysterfontein in the Western Cape. Prins retired to Velddrif in 1989.

In 1992, at the University of the Free State in Bloemfontein, discussions between the Department of Forensic Medicine and Theunis C. van der Linde, a medical entomologist in the Department of Zoology and Entomology, culminated in the founding of the Forensic Entomology Investigation Team of the Universiteit van die Oranje Vry Staat (FEITUOVS).[52] An initial survey of 17 human corpses[52] provided the best inventory of carrion insects occurring in the province. In subsequent conference abstracts, van der Linde and his students reported on development rates of maggots;[53,54] the use of maggots as toxicological indicators;[55] maggot anatomy;[56] and carrion succession on pigs that were wrapped or clothed,[57–59] burned or frozen,[60–62] in shade or sun,[63] suspended[64,65] or stabbed.[66] They collaborate with Gail S. Anderson, of Simon Fraser University in Canada.

In 1993, Martin H. Villet (who had studied under Paterson) initiated student projects at Rhodes University that focused on ecological succession in dead cats. This work soon turned to the systematics and thermo-ecology of carrion insects. Subsequent students have studied forensic toxicology[67] and designed an electronic key (IdentiFly) to southern African carrion-breeding blowflies and fleshflies.[68] Work has also been conducted on the identification of blowflies using DNA sequencing[13,69,70] on the development rates of maggots,[69] and on the distribution of blowflies in South Africa.[71] This centre of research has become known as the Southern African Forensic Entomology Research (SAFER) laboratory.[72] Eunice Musvasva[67] is now studying toxicology in Boston, Angela Bownes[68] is employed in biological control research, Nicola Lunt[69] is pursuing postgraduate studies in mammal ecology, and Kirstin Williams[71] is curator of entomology at the Durban Natural Science Museum, specializing in forensic entomology. Collaborators include Mervyn Mansell, Jeff Wells (U.S.A.), Michelle Harvey (Australia) and Iain Dadour (Australia).

Taxonomic research 1900–2005

Unlike the disciplines already discussed, taxonomy has never occupied a discrete historical phase, and contributions to forensic entomology were often made incidentally. Most early descriptions of carrion insects were done in Europe, and included most of the common species, especially those of economic significance.[14]

Cuthbertson[20] summarized his contemporaries' understanding of blowfly taxonomy, but did not make any original contribution. Zumpt published landmark monographs of the systematics of African blowflies[73] and fleshflies.[74] These works contain descriptions, illustrations and keys for identifying many carcass-associated flies. However, perhaps his most valuable contribution to forensic entomology is his monograph on myiasis in man and animals in the Old World,[26] which has a much broader taxonomic scope and application to veterinary and medical cases where the victim is still alive. Zumpt did not recognize *C. putoria* as a separate species, and because *C. megacephala* and *C. vicina* were not known from Africa until later,[41,42,75] specimens of these species will be misidentified when using Zumpt's keys. *Chrysomya putoria* has recently been raised from synonymy with *C. chloropyga*,[76] a decision implicit in previous local work.[20,37,70,77] The nomenclature in Zumpt's work on fleshflies has been superseded by Pape's worldwide catalogue,[25] which contains valuable information about synonyms, for interpreting published studies on the biology of these flies, but Zumpt remains a primary resource for identification.

Amongst the incidental taxonomic contributions to southern African forensic entomology, Ullyett[78] cast doubt on the distinctness of *L. sericata* and *L. cuprina* in South Africa. His breeding experiments suggested that these species readily interbred and that these hybrids were fertile, but it was not clear whether this happens in the field. As by-products of their ecological studies, Prins[42] and Braack[41] discovered alien species, while Prins[42,49] and Meskin[30,79] described eggs and larvae of southern African blowflies. At the University of the Witwatersrand, Beatrice R. Aspoas described third-instar larvae of four local fleshflies.[80]

Beetles received less protracted and concerted attention. Clarke H. Scholtz at the University of Pretoria monographed the African Trogidae,[81–84] while the African Silphidae were discussed by Prins[50] and monographed by Wolfgang Schawaller.[85] Two naturalized species of *Dermestes* occur in South Africa, although other species are occasionally intercepted in imported goods.[86] Apart from Prins's[50,51] notes, Braack's[36] species list for the Kruger National Park, and Harney's[86] book on stored-product pests, there is no systematic synthesis of the southern African carrion-associated beetles.

Early descriptive studies have recently been complemented by collaborative research using molecular systematics to identify African blowflies.[13,70] The results of these studies have been used to construct phylogenetic trees to predict these flies' developmental parameters.[69]

Forensic entomology in investigations

Several entomologists have been consulted by the South African police on entomological matters, and have often undertaken unpublished research.

In the late 1950s, M.J. Oosthuizen (Department of Entomology, University of Natal, Pietermaritzburg) gave informal lectures on forensic entomology. He occasionally received samples of insects collected at murder scenes by the police, bred them under laboratory conditions and advised on time-frames, but did not attend crime scenes, and had no formal working relationship with the SAP (C. Brammage, pers. comm.). He retired in 1971.

Albert J. Hesse was an entomologist in the South African Museum from 1924 until 1974, and undertook forensic consultations (Gess, pers. comm.). He trained Fredrik W. Gess, assistant entomologist at the museum from 1959–1968, who was on several occasions asked to assist the local state pathologist with identification of maggots and estimation of a post-mortem interval. Gess never testified in court but provided evidence in written reports (Gess, pers. comm.). In 1968 he joined the Albany Museum to work on wasps, and Prins took over from him. Prins's subsequent involvement in forensic entomology is discussed above.

Between 1966 and 2001, the British South Africa Police (BSAP) Forensic Laboratory in Salisbury and its successor, the Zimbabwe Republic Police Laboratory in Harare, consulted Barry Blair (Department of Research and Specialist Services, Plant Protection Research Institute), mainly to estimate time of death. A case involving Scotland Yard concerned three British medical students visiting Zimbabwe whose bodies were found near Nyanga during winter. Fly larvae helped to estimate the post-mortem interval to within half a day (Blair, pers. comm.). Occasionally, cases involved nangas, or traditional healers, who had administered fatal concoctions of herbs and blister beetles (mainly *Mylabris* spp., *Cyanolytta* spp. and *Decaptoma* spp., Coleoptera, Meloidae) to their patients. These concoctions were examined for insect parts that were then identified. Where blister beetles were present, post-mortem examination revealed extensive internal bleeding resulting from damage to the oesophageal and gastric mucosa. In one prosecution, a nanga cross-examined Blair in court, asking whether the quantity of blister beetles that he had quoted as causing internal trauma referred to Europeans or to Africans; he maintained that Africans were 'tougher' and able to tolerate larger doses. The magistrate passed a judgment of manslaughter (Blair, pers. comm.). Some of Blair's practical experience of forensic entomology was summarized in an article in the BSAP newsletter, *The Outpost*.[87] He retired in 2002.

South African courts lagged slightly in their use of entomological evidence, but in 2000 the Johannesburg Supreme Court convicted Albert du Preez Myburgh of indecent assault and murder, partly based on entomological evidence provided by Mervyn W. Mansell (Biosystematics Division, Plant Protection Research Institute [PPRI], Agricultural Research Council). This appears to have been the first South African case where insect-related evidence aided in conviction.[88] The South African Police Service (SAPS) first involved Mansell in 1995, in the Moses Sithole serial murders, leading to a productive association that included the cases known as the Phoenix serial murders, the Pretoria Highwayman serial murders, and the Pretoria Koppies serial murders. Other high-profile murder cases included those of Jacqueline Carter, Michael Bottril, Marlene Konings and Leigh Matthews (Mansell, pers. comm.). Working with van der Linde, Mansell has now been involved in more than 150 investigations,[88–93] and has lectured to the SAPS's Serious and Violent Crime Units and at Investigative Psychology Units on entomological evidence. He currently works for the U.S. Department of Agriculture's Animal and Plant Inspection Service in Pretoria and still consults for the SAPS.

In 2005, entomological evidence was also provided in court in the Leigh Matthews case by Police Forensic Science Laboratory biologist Sergeant André Massyn and PPRI specialist scientist Ansie Dippenaar-Schoeman.[94,95]

Conclusion

Although much of the research conducted on southern African carrion insects was not undertaken in a forensic context, it yielded useful results if evaluated carefully. The standards for scientific evidence are different from those for legal cases.[96,97] For instance, scientific results are re-evaluated in the light of new research, while legal cases need to be judged and closed.

Historically, southern African taxonomic studies have shown an increasing ability to identify all life stages of the principal insects found on bodies and stored products, and have attained high standards in relation to forensic entomology. Molecular phylogenetics has kept the field at the forefront of systematic research. However, globalization of trade has brought an increasing number of exotic species (e.g. *L. sericata*, *C. megacephala* and *Calliphora vicina* Robineau-Desvoidy 1830)[75] to the region, posing fresh challenges to forensic entomologists.

Early ecological studies were essentially natural history, but the level of quantification has steadily increased. Ullyett's[24] studies were somewhat ahead of their time in this respect. Individually, many of the quantitative studies are unreplicated and therefore open to legal (and scientific) challenges on the grounds of confounding variables. However, the accumulated evidence of these studies has gone some way to resolving some of these shortcomings, which are faced by forensic entomologists throughout the world. The other remaining challenge facing ecological research is the need to improve and quatify the degree of precision that it can deliver.

Southern African forensic entomology is perhaps weakest in physiological studies such as development and toxicology. Relevant data have been assembled, and until direct measurements of development are published, Lunt's[69] phylogenetic studies provide a predictive model that can fill the gaps for blowflies. Again, the issue of precision remains to be addressed globally.

The bulk of this review has focused on insects that regularly have prominence in medico-legal cases. Southern African research that has been directed at species relevant to urban or stored-product forensic entomology has been collated by Harney.[86] In the case of stored-product insects and household pests, most species are cosmopolitan,[86] and information can also be found in the overseas literature.

This review has shown that the application of entomological evidence in southern African law has a longer history than that of explicitly forensic research in the region. The successful use of entomological evidence in this situation can be ascribed to the cross-disciplinary nature of forensic science in general, which allows many allied disciplines to fill the needs of the legal system. The types of entomological evidence relevant to a particular case may be unpredictable, as Blair's story of love potions illustrates. In this sense, the boundaries of forensic entomology are ill-defined, and the subject is not distinct from entomology in general. This accounts for the scarcity of professional forensic entomologists throughout the world, and explains why many people filling this role are academics. As with any area of enquiry, however, now that it receives specific attention, forensic entomology is becoming a consolidated discipline worldwide. Collaborations with overseas practitioners are helping to ensure that South Africa is part of this trend.

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