THE STATUS OF THE TWO SPECIES OF *LUCILIA* (DIPTERA, CALLIPHORIDAE) ATTACKING SHEEP IN AUSTRALIA

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Summary

Evidence presented demonstrates that *L. cuprina* and *L. sericata* are distinct species. A number of characters previously unrecognized are described whereby larvae and both sexes of adults of the two species may be recognized without difficulty. The geographical distribution of the two species is different, as is also their habitat preference and their degree of attraction to living sheep. Furthermore, hybridization experiments indicate that there is great difficulty in obtaining successful matings. *L. cuprina* is the principal Australian sheep blowfly, whereas *L. sericata* is comparatively rare in sheep-raising country and does little damage. There are two subspecies of *L. cuprina,* one from the Oriental and American regions (*L. cuprina cuprina*) and one from the African and Australian regions (*L. cuprina dorsalis*).

I. INTRODUCTION

It was not clearly recognized until 1930 that a species of *Lucilia* was responsible for most of the blowfly strike of sheep in Australia (Mackerras 1930) and until about 1932 the English sheep blowfly *L. sericata* was thought to be the only *Lucilia* species causing strike (Fuller 1932; Mackerras and Fuller 1937), although *L. cuprina* had been recorded from Australia several years earlier (Malloch 1927). Since the early 'thirties a considerable amount of evidence has been accumulated, which demonstrates that the most important sheep blowfly in this country is *L. cuprina* and that this species is quite different in its distribution, habits, and morphology from the economically unimportant *L. sericata.* The distinctiveness of these two species has to a large extent been assumed in most Australian publications dealing with sheep blowfly and no adequate account is available of the differences observed.

For many years in South Africa the Australian practice was followed of regarding *L. cuprina* as the principal sheep blowfly and *L. sericata* as of minor importance. In 1945, however, Ullyett reported that these two species mated in the laboratory and, using colour of fore femora and of abdomen as specific characters, he found that the F_1 hybrid had legs typical of *L. cuprina* and abdomen typical of *L. sericata.* In the F_2 generation these two colour characters segregated in a 1:4:1 ratio. Furthermore, field material always contained individuals having the appearance of hybrids and it was pointed out that, if femur coloration alone was considered, this would lead to all hybrids being considered as *L. cuprina,* resulting in far greater numbers of *Lucilia* specimens

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being recorded as *L. cuprina* than as *L. sericata.* Although it was considered for a time that this conclusion might be valid for the two "species" in South Africa, Ullyett's extension of it to cover the position in Australia was immediately recognized by Australian workers to be unsound. However, since he has recently reaffirmed his belief that the two species are identical (Ullyett 1950) it is important to consider not only the status of these two species in Australia, but also, where possible, their affinities with species bearing the same names in other parts of the world.

II. The Systematics of L. cuprina and L. sericata

(*a*) *Taxonomy*

(i) *The Significance of the Genera* Lucilia *R-D and* Phaenicia *R-D.*

Many authors have followed Robineau-Desvoidy (1830) and divided the genus *Lucilia* into two genera or subgenera, *Lucilia* and *Phaenicia,* on the basis of two characters which are illustrated by the following key:

Subcostal sclerite (at extreme base of stem vein on under side of wing) with short setulose hairs apically. Ocellar triangle reaches half way from the vertex to the lunule in females . . . . . *Lucilia* Robineau-Desvoidy

Subcostal sclerite without hairs, although soft pubescence may be present. Ocellar triangle reaches less than half way from the vertex to the lunule in females . . . . . *Phaenicia* Robineau-Desvoidy

Neither of these characters can be regarded, however, as providing adequate justification for any more than subgeneric status. Both *cuprina* and *sericata* lack hairs on the subcostal sclerite and hence belong to *Phaenicia.* In view of the recommendation of the 7th International Entomological Congress (Rosenbaum 1939) that the use of subgeneric names should be avoided, it is preferable not to use this name and to regard both species as belonging to the genus *Lucilia.*

(ii) *General Remarks on Species*

(1) *Lucilia cuprina* (Wiedemann) 1830.—Originally described as *Musca cuprina* in *Aussereurop. Zweifl. Insekten.* **2**: 654. Type locality: China. Type female in the University Zoological Museum, Copenhagen, and not, as sometimes recorded, in the Leyden Museum (Senior White *et al.* 1940).

Synonyms

Lucilia dorsalis R-D., 1830, Myodaires, p. 453. Type locality: Cape of Good Hope. Type male in Paris.

Lucilia amica R-D., 1830, loc. cit. Type locality: Timor. Type male in Paris.

Lucilia elegans R-D., 1830, loc. cit., p. 458. Type locality: Ile de France. Type female in Paris.

Lucilia argyrocephala Macq., 1846, *Mém. Soc. Roy Agric. Arts Lille,* p. 326; 1846, Dipt. Exot. Suppl. 1, p. 198. Type locality: Cape of Good Hope. Type specimen probably in Spinola's collection in Castello di Tassarola (Novi Ligure) (Horn and Kahle 1936).

Musca fucina Walk., 1849, List. Dipt. Brit. Mus. **4**: 883. Type locality: South Africa. Type in British Museum.

Musca serenissima Walk., 1852, Ins. Saunders 4: 340.
Musca temperata Walk., 1852, loc. cit.
Lucilia leucodes Frauenf., 1867, *Verh. zool.-bot. Ges. Wien* 17: 453.
Somomyia pallifrons Big., 1877, *Ann. Soc. Ent. Fr.* 7: 257.
Strongyloneura nigricornis Sen. White., 1924, *Spolia Zeylan.* 13: 115. Type locality: Cherat, North West Frontier Post, India. Type is a male.
Lucilia pallescens Shannon, 1924, *Insec. Inscit. Menst.* 12: 78. Type locality: Wilmington, North Carolina. Type male in U.S. National Museum.

The only species which requires discussion in this list of synonymy is *L. pallescens* (Shannon 1924). Although the author of this species himself later regarded it as synonymous with *L. cuprina* (Shannon 1925, 1926), Hall (1948) lists it as a valid species and gives several characters to distinguish *cuprina* from *pallescens*. These all concern the proportions of various regions of the head, but no definite measurements are given and the differences used (stated in such terms as "not so wide in comparison with . . . .", "proportionately higher in comparison with . . . ." etc.) do not appear to be valid. A comparison of a large series of *L. pallescens* from Texas, New Orleans, and Washington with Australian *L. cuprina*, using the distinguishing characters mentioned later (Section II (*b*)), failed to reveal any differences between the two forms.

The authors have come to the conclusion that, over its vast geographical range, *L. cuprina* is represented by two readily distinguishable subspecies. For these the names *L. cuprina cuprina* (Wied.) and *L. cuprina dorsalis* R-D. appear to be most appropriate. Wiedemann's type female *cuprina* has been carefully examined. The general coloration of the fly is dull olive-green (K. R. Norris, unpublished data). The typical subspecies (*L. cuprina cuprina*) occupies a very large area including China* (type locality), Japan*, Formosa*, Assam*, Malaya*, Java*, Soembawa*, Timor, Fiji*†, Hawaii, North America* (= synonym *L. pallescens* Shan.), and South America*. It is easily recognized by its dull olive-bronze body coloration. The brilliant metallic coppery green, green, or bluish green sheen of *L. cuprina dorsalis* is absent or poorly developed. The general coloration of *L. cuprina cuprina* is suggestive of a fly of the genus *Musca* rather than of the genus *Lucilia*. The type specimen of *amica* R-D. from Timor, which is housed in the Paris Museum, is dull (Séguy, personal communication) and belongs to the typical subspecies.

L. cuprina dorsalis R-D. occurs in Africa*, India, and Australia*. It is very widespread in the sheep-raising areas of Australia (see Section IV), and South Africa, it has been recorded from Kenya (Lewis 1933), and the authors have examined one specimen from Cairo. This subspecies is easily recognized by its brilliant metallic coppery green, green, or bluish green coloration, which is similar in general character to that of other well-known *Lucilia* species, such as *L. sericata* and *L. caesar*. No intermediates between this and the other subspecies of *L. cuprina* have been seen.

The name *dorsalis* R-D. has been selected for this subspecies, the type male bearing this name coming from within the geographical distribution of the

* Localities from which material was examined in this study.
† Five specimens, identified by Bezzi (1928) as *L. cuprina*, were available.

bright *cuprina* subspecies (Cape of Good Hope, South Africa, Robineau-Desvoidy 1830). This specimen is housed in the Muséum Nationale d'Histoire Naturelle, Paris. *L. dorsalis* has page priority over *L. elegans* R-D. also from the South African region (Ile de France).

(2) *Lucilia sericata* (Meigen) 1826.—Originally described as *Musca sericata* in *Syst. Beschr.* **5**: 53.

Type locality: Germany. Type apparently lost. It is not in Paris Museum (Séguy, personal communication), but may be in Halle or Vienna.

Synonyms

Musca nobilis Meig., 1826, *Syst. Beschr.* **5**: 56. Type locality: Europe. Type apparently lost, but possibly in Paris.

Musca tegularia Wied., 1830, *Aussereurop. Zweifl. Insekten* **2**: 655.

Chrysomyia capensis R-D., 1830, Myodaires, p. 451. Type locality: Africa. Type in Paris.

Musca pruinosa Meig., 1830, *Syst. Beschr.* **7**: 294. Type locality: not stated. Type female in Paris.

Lucilia chloris Halid., 1833, *Ent. Mag.* **1**: 165.

Lucilia flavipennis Macq., 1842 (*nec Kram.*) *Mém. Soc. Roy. Agric. Arts Lille,* p. 296; 1842, *Dipt. Exot.* **2** (3): 139. Type locality: Ceylon. Type male in Paris.

Lucilia basalis Macq., 1842, *Mém. Soc. Roy. Agric. Arts Lille,* p. 305; 1842, Dipt. Exot. **2** (3): 148. Type locality: America. Supposed type in Paris, but bears Mogador as locality.

Musca lagyra Walk., 1849, List. Dipt. Brit. Mus. **4**: 885. Type locality: Fayal. Type in British Museum.

Lucilia latifrons Schin., 1862, *Fauna Austriaca* **1**: 590.

Lucilia sayi Jaenn., 1867, *Abh. senckenb. naturf. Ges.* **6**: 375. Type locality: Illinois. Type in British Museum.

Lucilia frontalis Br. and von B., 1891, *Zweiflügler des Kaiserlichen Museums zu Wien* **5**: 116, *nomen nudum.* Type locality: Egypt. Type in Vienna.

Lucilia giraulti Towns., 1908, *Smiths. Misc. Coll.* **51**: 121. Type locality: Paris, U.S.A. Type male in U.S. National Museum.

Lucilia barberi Towns., 1908, loc. cit. **51**: 121. Type locality: Williams, Arizona. Type male in U.S. National Museum.

The only additions to synonyms previously published are "species A" and "species B" of Miller (1939). Through the courtesy of Dr. Miller 31 specimens of *Lucilia* "species A" were made available for examination. Most of these were bred specimens of about half normal size, probably caused by inadequate food in the larval stage. Except for coloration, the characters of "species A" are the same as those of *L. sericata.* The lighter coloration of "species A" may be partly due to the fact that the specimens were pinned shortly after emergence and before hardening and darkening had been completed. This is suggested not only by their colour but also by the fact that their relatively light-coloured legs are collapsed and twisted, as often happens when unhardened flies are killed.

"Species B"* is also typical morphologically of *L. sericata,* although its coloration is somewhat lighter. This again may have resulted from the specimen having been pinned before it had hardened and darkened. In Dr. Miller's

* The single "type" specimen was available for examination. This specimen has no locality label and Miller says that it may have been collected in Europe, Australia, or New Zealand. It cannot, therefore, be referred to New Zealand.

collection there are two additional males labelled "species B" which were not mentioned in his 1939 paper. These are two typical male *L. sericata* having normal *sericata* coloration. An examination of many specimens of *L. sericata*

TABLE 1

SUMMARY OF SPECIFIC DIFFERENCES BETWEEN *L. CUPRINA* AND *L. SERICATA* ADULTS (SEE TEXT FOR MORE PRECISE DATA ON CHARACTERS)

Characters	*L. cuprina*	*L. sericata*
Head		
1. Occipital bristles (Figs. 1 and 2)	1 on each side	6 to 8 on each side
2. Clypeus (Figs. 3 and 4)	Black	Light amber
3. Frontal stripe (Figs. 3 and 4)	About as wide as a parafrontal	About twice as wide as a parafrontal
Thorax		
4. (i) Humeral calli (Figs. 5, 6, and 7)	2 to 4 hairs	6 to 8 hairs
4. (ii) Notopleura (Figs. 5, 6, and 7)	3 to 5 hairs	8 to 16 hairs
5. Second pair of presutural acrostichals (Fig. 5)	Do not extend to first pair of postsutural acrostichals	Extend at least as far as insertions of first pair of postsutural acrostichals
6. Scutellar bristles (Fig. 5)	Dorsal bristles slightly smaller than, or equal to, lateral hairs	Dorsal bristles distinctly smaller than lateral hairs
7. Colour of fore femora	Metallic green	Dark metallic blue to black
Abdomen		
8. Hairiness of 2nd, 3rd, and 4th abdominal sternites (only for males)	Hairs longer than on hind femora and tibiae	Hairs about the same length as on hind femora and tibiae
9. Contour of last abdominal tergite	Generally smooth	Collapsed
10. Male genitalia (Figs. 8 and 9)		
(i) Terminal claspers	Long and slender, outer margins of apical third parallel	Broader, tapering regularly, outer margins converge and are not parallel
(ii) Subterminal claspers	Slender, similar and parallel to terminal claspers	Semicircular and much broader than *cuprina*, particularly at basal half. Widely separated at tip

from New Zealand indicates that they normally have the metallic bluish green coloration typical of this species from other parts of the world and not the "peculiar coppery colour" recorded by Aubertin (1933).

(*b*) *Distinguishing Features of* L. cuprina *and* L. sericata

(i) *Adults*

In the past, *L. cuprina* and *L. sericata* have generally been separated by differences in coloration of the fore femora (Hardy 1940; Joint Blowfly Committee 1933). Although this is a valuable character, it is not always reliable if the specimens have been killed before they have hardened and darkened properly or if they have been exposed to high temperatures or become fouled by animal or plant juices. The only additional characters available are the differences in male genitalia, readily visible only after dissection, and differences in the hairiness of the male abdomen (Aubertin 1933; Hardy 1940; Malloch 1927).

Ullyett (1945) states that, in *L. cuprina,* the abdomen is green with a bronze sheen, whereas in *L. sericata* it is a distinct blue-green. Although the distinction holds in a general fashion, exceptions are far too numerous for it to be at all reliable both for Australian *L. cuprina* and *L. sericata* and for South African specimens of these species seen by the authors.

As a result of examining many hundreds of well-preserved *L. cuprina* and *L. sericata* the following distinguishing features can be listed (Table 1):

Characters on the head

(1) *Hairiness of Central Region of Occiput.*—The occipital region consists of a central area (the cerebrale) and on either side a lateral area separated from the cerebrale by a distinct suture (Figs. 1 and 2). Whereas the lateral areas carry many hairs, the cerebrale is nearly bare, although on its upper part there are some hairs which provide a means of distinguishing *L. cuprina* from *L. sericata.*

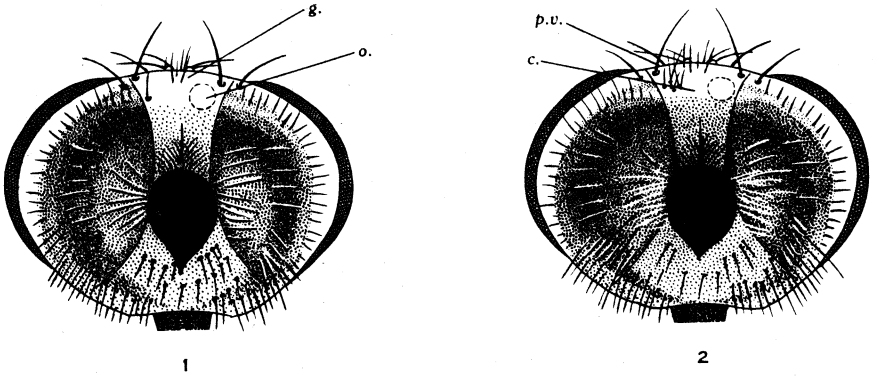


Fig. 1.—Posterior view of head of *L. cuprina.*
Fig. 2.—Posterior view of head of *L. sericata.*
c., cerebrale; *g.*, guide hairs; *o.*, area of cerebrale bearing occipital hairs useful in distinguishing *L. cuprina* and *L. sericata; p.v.*, postvertical bristles.

In both *L. cuprina* and *L. sericata* there is a single pair of "guide hairs" on the upper part of the cerebrale directly behind the ocellar triangle*, the

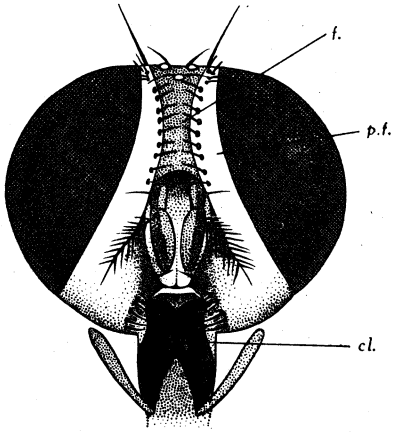
* Occasionally one or more additional, but smaller, hairs may be present in this region.

distance between these hairs being nearly equal to that between the posterior ocelli. In *L. cuprina* there is, a little lower down the cerebrale, a second pair of hairs separated by a space several times as great as that between the first pair. At times (less than 20 per cent. of individuals) one or both of the hairs of the second pair is accompanied by a second hair which is, however, often smaller than the first.

In *L. sericata* the second pair of hairs is replaced on each side by a group, each group normally consisting of six to eight hairs, although as few as three and as many as fourteen may be present. The number is, however, frequently different on either side of the same insect. Very occasionally the number of hairs is reduced to two on one or on both sides.

A magnification of 20x to 40x is required for the accurate determination of these occipital hairs. They are seen most readily if the head is viewed from above and to one side and only very rarely and in badly damaged specimens are they broken. This character is extremely reliable.

(2) *Degree of Sclerotization of Clypeus.*—On its dorsal surface the proboscis is flexed between the clypeus and the frons, and the clypeus being bounded laterally by the rostrum (Figs. 3 and 4). It is difficult to see the whole of the clypeus unless the proboscis is extended, which is not often the case in pinned specimens. However, if the insect is turned in such a way that the upper part of the mouth cavity is visible, sufficient of the frontal margin of the clypeus can almost always be seen to enable determination of the character described below.



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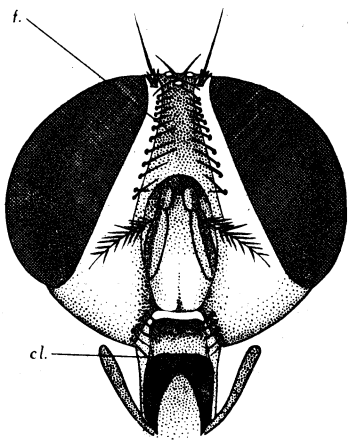

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Fig. 3.—Anterior view of head of male *L. cuprina*.
Fig. 4.—Anterior view of head of male *L. sericata*.
cl., clypeus; *f.*, frontal stripe; *p.f.*, parafrontal.

In *L. cuprina* the clypeus, which is slightly bifurcated at its frontal margin, is jet black or a very dark brown, in contrast with the light amber coloration of the rostrum. In *L. sericata* the clypeus is not as distinctly bifurcated anteriorly and is often a light amber colour. However, in a high proportion

of individuals (particularly in males), there are all degrees of sclerotization between amber and dark brown. When the clypeus exhibits its darker shades it is noticeable that its upper half (adjoining the frons) is generally lighter in colour than the lower half.

In spite of the variability of this character it is useful for the rapid initial separation of the two species because it can be employed at low magnifications (10x to 20x). When the sclerotization of the clypeus is such that the specimen cannot be assigned immediately either to *L. cuprina* or *L. sericata,* one or more of the other characters must be used.

(3) *Width of Frontal Stripe.*—The region between the antennae and the ocelli is divided into three areas, namely a median frontal stripe, on either side of which lie the parafrontals (Figs. 3 and 4). The feature distinguishing the two species is the relative widths of the frontal stripe and parafrontals at a level midway between the base of the antennae and the anterior ocellus.

In *L. cuprina* the frontal stripe at this level is equal to, or a little broader than, the width of a parafrontal. In *L. sericata* the frontal stripe is considerably broader (generally at least twice as broad) than either of the parafrontals. Confusion sometimes arises in female *L. cuprina* which occasionally may have the frontal stripe almost twice as wide as a parafrontal. It is, however, a reliable character for males.

Characters on the thorax

(4) *Hairiness of the Lateral Areas of the Mesonotum* (Figs. 5, 6, and 7).—The mesonotum consists of a middle region, on each side of which are two lateral areas. The anterior, somewhat semicircular, areas are sometimes known as the "humeral calli" and the posterior triangular areas as the "notopleura."

Humeral calli.—Arranged transversely across the humeral calli (Figs. 6 and 7) there are three or four large bristles. On the area posterior to these there are, in *L. cuprina,* two or four (rarely up to eight) hairs, whereas in *L. sericata* there are typically six to eight hairs, although all numbers between four and thirteen may be found. Although these hairs can be seen very easily in well-preserved specimens (magnification 30x to 40x), this portion of the body is often rubbed and the bristles and hairs broken off.

Notopleura.—Near the posterior edge of each notopleuron (Figs. 6 and 7) there is a large bristle which can be used to demarcate a narrow region lying between it and the posterior border of this sclerite. In *L. cuprina* there are three to five hairs on this area, whereas in *L. sericata* there are not only eight to sixteen hairs, but these are longer than those of *L. cuprina.* Furthermore, the remaining area of the notopleuron is more sparsely clothed with hairs of shorter length in *L. cuprina* than in *L. sericata.* It is convenient, however, to restrict the area examined to that demarcated above, since this area is less frequently damaged than the remainder of the notopleuron. A magnification of about 40x is required for examination of this character.

(5) *Length of the Second Pair of Presutural Acrostichal Bristles on Mesonotum.*—In *L. cuprina* the second pair of acrostichal bristles (not the dorsocentrals) is much shorter than in *L. sericata.* As a ready means of assessing this, they are, for instance, distinctly shorter than the postvertical bristles (situated lateral to the posterior ocelli (Fig. 2)) and also distinctly shorter than the distance between their point of insertion and the point of insertion of the first pair of postsutural acrostichal bristles (Fig. 5*A*). In *L. sericata,* the second pair of acrostichal bristles is about the same length as the postvertical bristles and they extend back at least as far as the first postsutural acrostichals (Fig. 5*B*). This character is very easy to use in well-preserved specimens, but suffers from the disadvantage that the bristles are often broken.

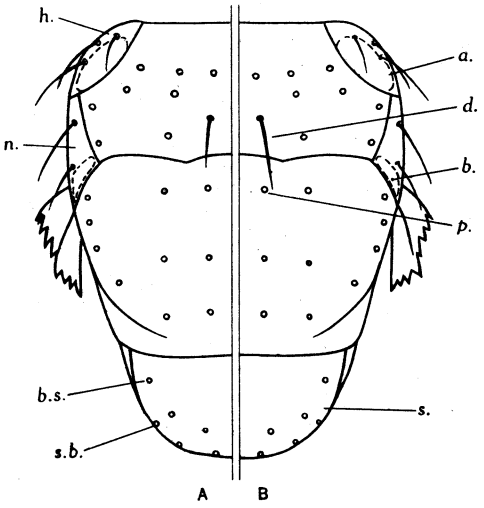


Fig. 5.—Diagram of dorsal aspect of thorax of *L. cuprina* (*A*) and *L. sericata* (*B*).

a., area of humeral calli bearing hairs useful in distinguishing *L. cuprina* and *L. sericata; b.*, area of notopleuron bearing hairs useful in distinguishing *L. cuprina* and *L. sericata; b.s.*, basal bristle; *d.*, second pair of presutural acrostichal bristles; *h.*, humeral calli; *n.*, notopleura; *p.*, first pair of postsutural acrostichal bristles; *s.*, scutellum; *s.b.*, sub-basal bristle.

(6) *Length of Bristles on the Scutellum.*—On the lateral margin of the scutellum there are a series of stout bristles. Between the two anterior bristles (basal and sub-basal) on either side (see Fig. 5) there are a number of hairs. The feature distinguishing the two species is the relative lengths of these hairs and of those on the dorsal surface of the scutellum. In *L. cuprina* the latter hairs are slightly smaller than, or about equal in length to, the lateral hairs. In *L. sericata* the lateral hairs are considerably longer than the dorsal hairs.

(7) *Colour of Fore Femora.*—In *L. cuprina* the exterior surface of the femora of the forelegs is characteristically a very distinct metallic green. This is sometimes modified by a coppery or bronzy sheen and less frequently by a bluish sheen. In *L. sericata* the fore femora are dull, with rarely a dark blue metallic sheen.

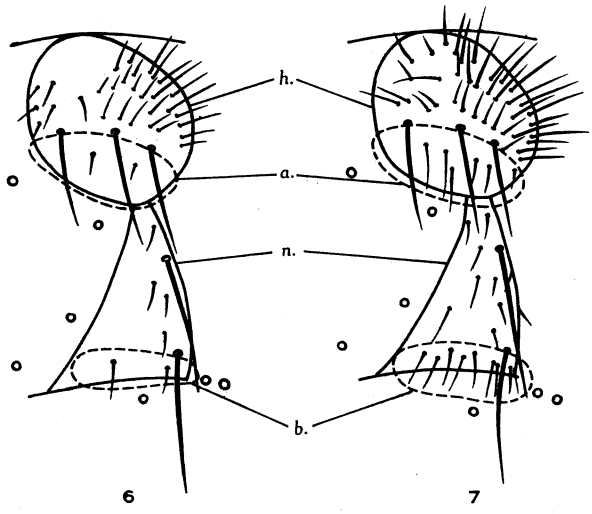


Fig. 6.—Diagram of right lateral area of thorax of *L. cuprina.*

Fig. 7.—Diagram of right lateral area of thorax of *L. sericata.*

a., area of humeral calli bearing hairs useful in distinguishing *L. cuprina* and *L. sericata; b.*, area of notopleuron bearing hairs useful in distinguishing *L. cuprina* and *L. sericata; h.*, humeral calli; *n.*, notopleura.

This is generally a useful and highly reliable character except when specimens of *L. cuprina* have been killed too soon after emergence (when full coloration has not been attained). It is also difficult to use when specimens have been wet with plant or animal juices, or have been exposed to high temperatures. Under these circumstances the colour of the fore femora is duller and darker than in typical specimens and less easy to distinguish from *L. sericata.*

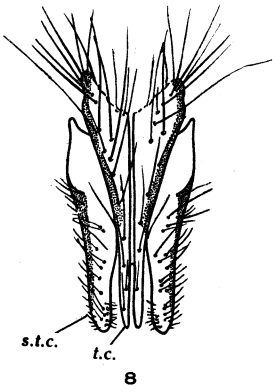
Characters on the abdomen

(8) *Hairiness of Abdominal Sternites.*—This character is of value in separating the males only of the two species. The region involved in this distinguishing character consists of the second, third, and fourth sternites, together with the adjoining margins of the second, third, and fourth tergites. When viewed laterally it can be seen that this region bears a number of stout bristles.

In *L. cuprina* these bristles are much longer than those on the hind femora and tibiae, whereas in *L. sericata* the bristles are about the same length as those

on the hind legs. This character is noteworthy in that it is the only one observed in which there is greater bristle development in *L. cuprina* than in *L. sericata*, but it is not an easy one to use without experience.

(9) *Contour of the Last Abdominal Tergite.*—In dried specimens of *L. cuprina* the contour of the last abdominal tergite is smooth without depressions, whereas in *L. sericata* this tergite frequently has one or more irregular depressions or dints. This character, which is applicable to dried specimens only, apparently depends on the hardness of the tergite and its resistance to distortion after death of the fly. It is unreliable, therefore, in flies which have been killed too soon after emergence and before hardening has been completed.



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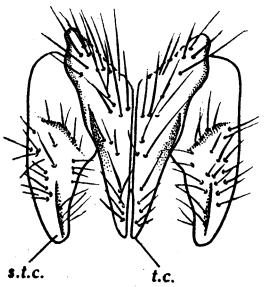

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Fig. 8.—Posterior (exterior) view of male genitalia of *L. cuprina*.
Fig. 9.—Posterior (exterior) view of male genitalia of *L. sericata*.
s.t.c., sub-terminal clasper; *t.c.*, terminal clasper.

(10) *Male Genitalia* (Figs. 8 and 9).—Three differences can be seen between the two species in the terminal and subterminal claspers when the dorsal surfaces of these structures are compared:

(i) In *L. cuprina* the terminal claspers are long and slender, the outer margins of the apical third being parallel. In *L. sericata* the terminal claspers are broader and they taper regularly, so that the outer margins of the apical third converge and are not parallel.

(ii) In *L. cuprina* the subterminal claspers are slender and similar in shape to the terminal claspers. In *L. sericata* the subterminal claspers are very much broader than in *L. cuprina*, particularly at their basal half.

(iii) In *L. cuprina* the subterminal claspers are nearly parallel to the terminal claspers, whereas in *L. sericata* the subterminal claspers are nearly semicircular.

(11) *General Appearance.*—In general appearance *L. cuprina dorsalis* is typically a metallic coppery-green, *L. sericata* a bluish green without any coppery sheen. However, there are too many exceptions for this to be a reliable

character. For instance, *L. cuprina* specimens exposed after death to high temperatures (e.g. strong sunlight) often become bluish green and, at times, specimens of *L. sericata*, particularly when freshly killed, have a coppery appearance.

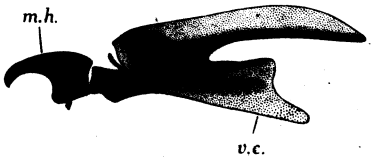
In general, *L. cuprina* is a smaller and more slender fly than *L. sericata*. However, size alone may be deceptive since, due to limitation of larval food, small adults of both species are not uncommon.

Characters of type of L. cuprina cuprina

Except for general coloration (see earlier) Wiedemann's type female of *L. cuprina* agrees with Australian *cuprina* in all the above characters which can be used (K. R. Norris, personal communication). Thus, the hairiness of the central region of the occiput is typical; the clypeus is black; the frontal stripe is about 1½ times the width of a parafrontal; there are two hairs behind the bristles on the humeral calli; the notopleural hairs are typical; and the right fore femur is green. The left fore femur, the presutural acrostichals, and the dorsal hairs on the scutellum are missing.

(ii) *Larvae*

Fuller (1932) has described several features whereby *L. cuprina* and *L. sericata* larvae may be distinguished from one another. Although some of these are useful, others do not appear to be valid. For example, the anterior spiracles of *L. cuprina* were stated to have seven or eight finger-like processes and *L. sericata* ten. In larvae available to us, *L. cuprina* has an average of seven processes (range five to nine) and *L. sericata* has an averge of eight (range six to ten). Although this feature can be used to distinguish two populations, it is



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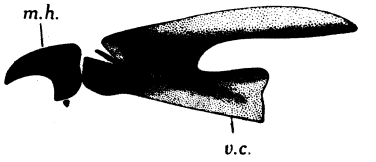

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Fig. 10.—Lateral view of buccopharyngeal armature of *L. cuprina*.

Fig. 11.—Lateral view of buccopharyngeal armature of *L. sericata*.

m.h., mouth hooks; *v.c.*, ventral cornua.

clearly of limited value in assigning a single larva to a given species. A number of differences were described in the mouth hooks of the two species, but the only constant difference appears to be that the hooks are slightly more curved in *L. cuprina* than in *L. sericata* (Figs. 10 and 11). An apparently constant difference, which was not recorded, but is readily seen, is in the shape of the posterior edges of the ventral cornua. In *L. cuprina* the ventral border is prolonged posteriorly. In *L. sericata* this edge is relatively straight (Figs. 10 and 11). The shape and degree of sclerotization of the posterior spiracles

of the two species (Table 2) is as described by Fuller (1932) but the differences are apparent only to the practised observer. It is clear, however, from Table 2 that there are recognizable differences between the larvae of the two species.

Patton (1920) records six to eight processes in the anterior spiracles of *L. cuprina* from the Orient, whereas Knipling (1936) states that there are four to six in *Phaenicia pallescens* (*L. cuprina*) from North America.

L. sericata is said to have ten to eleven processes in England (Patton and Evans 1929) and five to ten in North America (Knipling 1936).

TABLE 2

SPECIFIC DIFFERENCES BETWEEN AUSTRALIAN *L. CUPRINA* AND *L. SERICATA* LARVAE

Character	*L. cuprina*	*L. sericata*
Length (fully grown)	12 mm.	14 mm.
Mouth hooks	Distinctly curved	Rather less curved
Ventral cornua	Posterior edge prolonged ventrally	Posterior edge relatively straight
Posterior spiracles	Roughly oval in shape, peritreme wide and dark	Somewhat pear-shaped, peritreme narrow and not heavily sclerotized
Anterior spiracles	Composed of 7 finger-like processes (av.)	Composed of 8 finger-like processes (av.)

III. GEOGRAPHICAL DISTRIBUTION OF L. SERICATA AND L. CUPRINA

L. sericata is almost cosmopolitan, having been recorded from all the temperate countries of the world (British Isles, Europe, Africa, Asia, Japan, Australia, New Zealand, North and South America). Hall (1948), however, states that no specimens were collected in Central or South America in 1942 and 1943, nor on any of the islands of the central or south-west Pacific in 1944 and 1945, although over 100,000 flies were collected in these areas. This may be because the regions concerned are unfavourable for *L. sericata* or because this species has not been introduced. It is interesting to note, for example, that Miller (1939) concluded that *L. sericata* has become common in New Zealand only since the closing years of last century. Exprience in Australia (see later) suggests that this species occurs principally in the vicinity of homes, which evidently provide suitable requirements often absent elsewhere.

L. cuprina occurs in North and South Africa, Madagascar, Mauritius, India, Assam, Malaya, Indo-China, Laos, China, Java, Soembawa, Timor, Australia, Fiji, Hawaii, North and South America (Brazil). It has not been recorded from the British Isles, Europe, or New Zealand. In 1949 some thousands of blowflies were trapped by B. A. O'Connor in the vicinity of Suva, Fiji, but not a single *Lucilia* was taken. In general, *L. cuprina* appears to be restricted to the warmer sub-equatorial regions, whereas *L. sericata* not only

occurs in these regions, but extends also into the cooler regions of the world. *L. cuprina* appears to tolerate semi-arid conditions better than *L. sericata*, which is typically found in habitats of high humidity.

IV. Distribution of the Two Species According to Habitat

Mackerras and Fuller (1937) record that *L. cuprina* is very widespread in Australia. It occurs in all mainland States (Fig. 12), but has not yet been recorded from Tasmania. It reaches its greatest abundance in the subtropical and semi-arid regions of northern New South Wales and southern Queensland, particularly during spring and autumn. However, it is abundant also on the

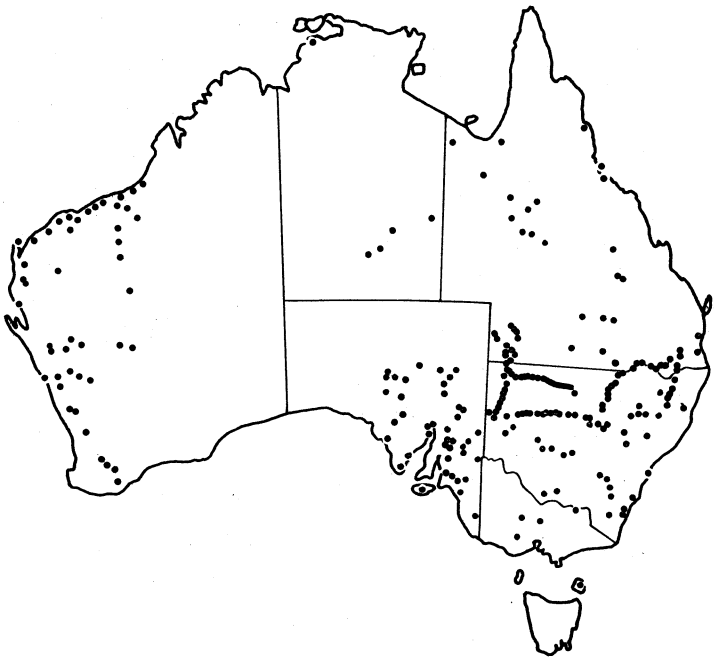

Fig. 12.—Map showing known distribution of *L. cuprina*. The rows of dots in eastern Australia trace the path of a collecting trip on which a blowfly trap was exposed at each stop. They indicate a continuous distribution of *L. cuprina* in the area traversed.

cooler southern New South Wales tablelands, and in mountainous as well as low-lying districts. One of the most important factors limiting its distribution appears to be the presence of susceptible sheep on which to breed (Waterhouse 1947). On the other hand, although *L. sericata* has been recorded from all States, including Tasmania (Fig. 13), it is usually an uncommon fly, except in limited areas, and its distribution has no relation to the distribution of sheep. It is known principally from closely settled districts in the cooler parts of Australia, conditions provided by domestic gardens and associated refuse apparently favouring the maintenance of quite dense populations.

However, it has also occasionally been taken many miles from the nearest permanent habitation.

L. sericata occurs commonly in Canberra gardens and *L. cuprina* in the open savannah woodland, characteristic of much sheep-grazing country, which surrounds Canberra. An examination was made, therefore, of the preferences of the two species for these habitats. The method employed was to count the numbers of the two species caught in similarly constructed and baited traps exposed simultaneously in a garden, in open country, and in intermediate situations.

Fig. 13.—Map showing known distribution of *L. sericata*.

In the first experiment the catch from a trap exposed in a well-watered garden with luxuriant green vegetation was compared with catches from traps placed in an unwatered orchard on the outskirts of Canberra, and in three traps placed in open grazing country (Table 3). In the garden, *L. cuprina* formed less than 1 per cent. of the *Lucilia* specimens trapped, in the orchard only 11 per cent., whereas in open country 82-94 per cent. of the *Lucilia* specimens were *L. cuprina*. This suggested a definite preference of *L. cuprina* for open country and of *L. sericata* for more humid, vegetated situation.

To obtain further data, a second experiment was carried out in which the catch from the garden was compared with that from a trap situated 85 yards away in a dry, open, conifer plantation and with other traps extending 760 yards in roughly a straight line into open country (Plate 1). Three traps were also exposed five miles from the city on a sheep-grazing property. It can be seen (Table 4) that, whereas only about 1 per cent. of *Lucilia* specimens

caught in the garden were *L. cuprina*, the proportion rose to about 40 per cent. less than quarter of a mile away in open country and to 97 per cent. five miles from the city on a sheep property. This general trend was followed closely

TABLE 3

RESULTS OF TRAPPING *LUCILIA* IN DIFFERENT HABITATS (23.xi.48 TO 25.xi.48)

Type of Locality		*L. cuprina* (%)	Number of *Lucilia*	
			L. cuprina	*L. sericata*
Humid garden	No sheep in vicinity	0.7	7	1025
Unwatered orchard adjoining a garden	No sheep in vicinity	11	22	173
Open grassland near irrigated plots	Sheep near trap	82	74	16
Lucerne paddock near irrigated plots	Sheep near trap	88	170	24
Open dry grassland	Sheep near trap	94	98	6

during each of the three trapping periods (Table 4). The numbers of *L. cuprina* caught in traps 1 to 6 were not greatly different and the variation in the percentages of this species in the catches was principally due to the fact

TABLE 4

RESULTS OF TRAPPING *LUCILIA* IN DIFFERENT HABITATS

Trap No.	Type of Locality	Distance from Garden (yds.)	Percentage *L. cuprina* of total *Lucilia*			Number of *Lucilia* caught					
			Period 1	Period 2	Period 3	Period 1		Period 2		Period 3	
			14-17.xii.48 21-23.xii.48 25-28.i.49	21-23.xii.48 25-28.i.49	25-28.i.49	*L. cuprina*	*L. sericata*	*L. cuprina*	*L. sericata*	*L. cuprina*	*L. sericata*
1	Humid garden	0	1.5	1.2	1.6	48	3246	23	1912	21	1256
2	Unwatered plantation	85	8	5	17	35	390	26	300	19	94
3	Grassland within plantation	150	34	27	42	40	79	11	29	7	10
4	Open grassland	390		37	55	—	—	10	17	6	5
5	Open grassland	610	42	42	40	32	45	21	30	4	6
6	Open grassland	760		44	47	—	—	17	22	7	8
7	Sheep-grazing property	5 miles			96					24	1
8					98					42	1
9					97					34	1

that far larger numbers of *L. sericata* were caught in the garden and the plantation (traps 1 and 2) than elsewhere. It appears, therefore, that *L. sericata* has a very definite preference for the conditions prevailing in the garden. *L.*

cuprina, on the other hand, does not exhibit such a clear preference for any of the situations examined.

This is in accord with the work of Gilmour, Waterhouse, and McIntyre (1946) who found that, in the Canberra district at least, the *L. cuprina* population ranged widely and at random over the countryside, individual flies being capable of covering up to about five miles in less than 30 hours. The larger numbers of *L. cuprina* trapped five miles from Canberra than elsewhere (Table 4) are probably due to the presence of sheep in the immediate vicinity of these traps, whereas no sheep were near traps 1 to 6 during, or for some time before, the experimental period. A similar explanation probably holds for the comparatively high catches of *L. cuprina* in the three traps of the first experiment (Table 3) which were exposed in the vicinity of sheep. Because sheep are specifically attractive to *L. cuprina* and particularly to the gravid female of this species (Mackerras and Mackerras 1944), one would expect a somewhat higher density of these flies near sheep than elsewhere. Furthermore, any struck sheep would result, at least temporarily, in a considerable local increase in the numbers of *L. cuprina*.

Cragg (unpublished data) found that, in North Wales, *L. caesar* is present in highest density along hedgerows and that the rate of dispersal of a population is comparatively slow. It may be inferred from the present experiments that in Australia *L. sericata* behaves similarly. In Canada and U.S.A., *L. sericata* frequents urban districts, where it is common on almost any kind of garbage, especially when this contains meats or damaged fruit. It frequently rests on leaves of vegetables and shrubs and is attracted to honeydew (Hall 1948). Its observed behaviour in Australia is similar to that recorded from America.

V. Hybridization Experiments

Successful crosses between *L. cuprina* and *L. sericata* were made by Mackerras (1933), but no details are given except that a F_1 male and a F_1 female from a male *L. cuprina* × female *L. sericata* mating were both indistinguishable from typical *L. cuprina*. These F_1 hybrids were used in a fertility experiment, one particular female laying 3171 eggs. Since this was considerably more than usually obtained either from pure *L. cuprina* or pure *L. sericata* it was suggested that hybrid vigour might be responsible. The results were not published in any further detail because, by the criteria then available (coloration of fore femora and structure of male genitalia) all flies of F_1 and F_2 generations of this and the reciprocal cross exhibited only *L. cuprina* characters, a result which could not be explained on the basis of any known behaviour of genes. The only other information available on these experiments is that the original species crosses produced few eggs, which seemed to support the idea that this was an unusual cross (M. J. Mackerras, personal communication).

Some of the flies from these crosses are still available for study. These were examined using the characters described earlier. All the flies (Table 5) of the F_1 and F_2 generations are typical *L. cuprina*.

In an endeavour to check these extraordinary results, pupae from pure *L. cuprina* and *L. sericata* cultures were separated into individual tubes a day or two before emergence and the adults subsequently sexed and set up in cages

TABLE 5

FLIES AVAILABLE FOR EXAMINATION FROM MACKERRAS'S (1933) *L. CUPRINA* × *L. SERICATA* CROSSES

Parents		F_1		F_2	
Male	Female	Male	Female	Male	Female
L. cuprina	*L. sericata*	1	1	124	142
L. sericata	*L. cuprina*	1	1	5	5
L. sericata	*L. cuprina*	1	1	—	—
L. sericata	*L. cuprina*	—	11	—	—
L. sericata	*L. cuprina*	9	1	71	26

as shown in Table 6. Fresh liver was provided daily and each cage was supplied continuously with sugar and water. The cultures were kept at about 25°C. and 30 per cent. relative humidity, conditions under which both species breed readily.

TABLE 6

DETAILS OF *L. CUPRINA* AND *L. SERICATA* CROSSES

Parents		Type of Experiment	No. of Tests	No. of *L. cuprina* per Experiment	No. of *L. sericata* per Experiment	Result
Male	Female					
L. cuprina	*L. sericata*	Single pairs	29	1	1	No larvae
		Communal cages	1	6	6	No larvae
		Communal cages	1	35	3	No larvae
		Communal cages	1	5	1	No larvae
		Communal cages	1	10	9	No larvae
		Communal cages	1	14	10	No larvae
		Communal cages	1	21	32	No larvae
		Communal cages	1	7	14	No larvae
L. sericata	*L. cuprina*	Single pairs	8	1	1	No larvae
		Communal cages	1	9	8	No larvae
		Communal cages	1	9	9	No larvae
		Communal cages	1	16	16	
		Communal cages	1	50	25	290 F_1 adults

Eggs were laid in a number of these negative experiments, but failed to hatch. The amount of oviposition was no greater, however, than would have been expected from unfertilized females.

In the only successful cross 25 male *L. sericata* and 50 female *L. cuprina* were kept in a 12 × 12 × 12 in. cage. Although 10 egg masses were laid

over a period of about a month, larvae were produced on only seven occasions, resulting in 151 male and 139 female F_1 hybrids. Since the number of offspring per female from an intra-species cross generally lies between 300 and 500 the small number of progeny (290) obtained indicates that the cross was not a very successful one. Perhaps only one of the 50 females was responsible for laying the fertile eggs.

The reciprocal cross (21 male *L. cuprina* × 32 female *L. sericata*) carried out at the same time under identical conditions produced eggs on many occasions, but none hatched.

The 75 parents and 290 F_1 hybrids from the successful cross were examined individually for all characters except male genitalia. All the parents were typical of the particular species to which they belonged (Table 6). The results of the examination of hybrids may be summarized as follows:

Characters in which *L. cuprina* was usually dominant:

(*a*) Sclerotization of clypeus (generally black or dark brown).
(*b*) Coloration of fore femora (about 5 per cent. of individuals had legs which were duller than typical *L. cuprina*).
(*c*) Length of ventral abdominal bristles in the male.
(*d*) Length of bristles on the scutellum.

Characters in which *L. sericata* was sometimes dominant:

(*a*) Length of second pair of presutural acrostichal bristles (often nearly as long as in *L. sericata*, but many intermediates occurred).
(*b*) Width of frontal stripe in male.
(*c*) Width of frontal stripe in female (although there were many intermediates).
(*d*) Contour of the last abdominal tergite.

Characters generally intermediate between the two species (see Table 7):

(*a*) Occipital bristles (about 10 per cent. indistinguishable from *L. cuprina*, but less than 1 per cent. indistinguishable from *L. sericata*).
(*b*) Hairiness of humeral calli.
(*c*) Hairiness of notopleura.

About 80 per cent. of the F_1 hybrids had characters or combinations of characters which clearly placed them as intermediates between *L. cuprina* and *L. sericata* but generally closer to *L. cuprina*. About 10 per cent. were indistinguishable from *L. cuprina* and the remaining 10 per cent. distinguishable only with varying degrees of difficulty. No F_1 hybrids were found that could be confused with *L. sericata*. Although the "dominant" characters of *L. cuprina* and *L. sericata* generally appeared together in the progeny, there did not appear to be any close linkage between any of the characters examined, since any character at times varied independently of any other.

F_2 progeny were obtained from three of the seven batches of F_1 hybrids. One hundred and forty-eight F_2 males and 117 F_2 females from three separate ovipositions of one of these three F_1 batches were examined and all were found

to be indistinguishable from typical *L. cuprina*. On the other hand, of 25 F_2 males and 31 F_2 females from the other two batches of F_1 hybrids that laid eggs, one male and six females were indistinguishable from *L. cuprina*, three males and one female were indistinguishable from typical *L. sericata*, and the remainder were intermediates, although many of the latter only differed from one or other species by a single character.

TABLE 7

AVERAGE NUMBER OF HAIRS (AND UPPER AND LOWER LIMITS) ON THREE REGIONS OF *L. CUPRINA*, *L. SERICATA*, AND F_1 HYBRIDS

Species	Sex	Occipital Hairs	Humeral Calli	Notopleura
L. cuprina	Male	1 (0-2) (5% with 2 on one side)	2 (0-8)	3 (2-5)
L. cuprina (parents)	Female	1 (1-3) (20% with 2 on at least one side); (1 with 3 on one side)	2 (0-7)	3 (1-5)
L. sericata (parents)	Male	6 (4-9)	8 (6-13)	11 (9-16)
L. sericata	Female	8 (5-14)	6 (4-12)	11 (9-15)
F_1	Male	2 (1-5)	5 (1-11)	7 (2-11)
F_1	Female	2 (1-6)	3 (1-7)	5 (4-9)

Summing up, it is clear that there is considerable difficulty in obtaining successful matings between *L. cuprina* and *L. sericata*. Most of the F_1 hybrids exhibited characters of both species, although some could not be distinguished from *L. cuprina*. The picture in the F_2 generation is very complicated. Some entire F_2 batches are typical of *L. cuprina*, whereas others are mainly intermediates. Further work is required before an explanation can be advanced for this result and for the results of Mackerras.

General confirmation of our findings comes from some material* of Ullyett's crossing experiments, which have been outlined earlier (Ullyett 1945). The specimens comprised 12 male *L. cuprina*, 9 female *L. sericata*, which were used as parents, and 7 male and 6 female F_1 hybrids. The male *L. cuprina* were typical, except that the frontal stripe was rather more divergent ventrally than usual (i.e. they tended slightly towards *L. sericata* in this respect). The abdominal coloration was indistinguishable from that of Australian male *L. cuprina* and *L. sericata* and varied from coppery to green. Six of the female *L. sericata* were typical; the wings of the remaining three were crumpled and the ptilinum had not been properly retracted. There was no blue coloration whatever of the abdomen. The hybrids were typical of *L. cuprina* in all our characters except the degree of sclerotization of the clypeus, which was typical of *L.*

* Made available by courtesy of the Division of Entomology, Pretoria.

sericata. All must therefore be regarded as intermediates. The abdominal coloration of these hybrids was a deeper bluish green than that of their parents and the first visible segment had a bluish sheen in most specimens, but not all. This may be due to different conditions of drying (they were pinned 11 days after their parents), since the authors have found that specimens tend to become bluish if they are dried at higher temperatures than usual. No support whatever could be found from these specimens for Ullyett's contention that abdominal coloration is useful for distinguishing between *L. cuprina* and *L. sericata.*

VI. Relation of the Two Species to Blowfly Strike

(*a*) *Attractiveness of Sheep to the Two Species*

There is good evidence from insectary experiments that *L. sericata* does not lay its eggs on sheep as readily as does *L. cuprina* (Mackerras and Mackerras 1944). In one experiment eight sheep were exposed for a week in an insectary to gravid *L. sericata,* eggs being laid on two of the sheep. Some *L. cuprina* were then added to the insectary, and, within four hours, all eight sheep had eggs laid on them, indicating that the sheep were more attractive to *L. cuprina* than to *L. sericata.* Some of the freshly laid eggs were collected from each sheep and allowed to develop. From seven of the eight sheep these eggs produced both *L. cuprina* and *L. sericata* and from the eighth sheep only *L. cuprina.* It is clear, therefore, that oviposition by *L. cuprina* stimulated *L. sericata* to lay eggs on sheep which they had previously ignored.

In another experiment three sheep were exposed in turn in a small cubicle to a high density of mature *L. sericata.* After about five hours, when no eggs had been laid, each was transferred to a similar density of *L. cuprina* in another cubicle, eggs being laid on each sheep within two hours. When similar sheep were exposed first to *L. cuprina,* oviposition followed in the first few hours (Mackerras and Mackerras 1944).

Cragg (1950*a*) has also obtained results with *L. sericata* in Great Britain under field conditions which indicate that this species and Australian *L. cuprina* show marked differences in behaviour.

(*b*) *Importance of the Two Species in Causing Strike*

Records of the occurrence of the two species in field strikes in Australia (Table 8) show quite clearly that *L. cuprina* is far more important than *L. sericata* in producing strike wounds. In the Australian Capital Territory, from which the most strikes were examined, 58.3 per cent. of the *L. cuprina* strikes contained no other species, while only 3.8 per cent. of the *L. sericata* strikes contained this species alone. *L. sericata* was present in significant numbers in one year only. The relatively small number of *L. sericata* strikes and the small percentage in which this species alone occurs is doubtless due to two factors. One is the comparatively low population density of this species in open country and the second is the fact that it is not as powerfully attracted as *L. cuprina*

to lay its eggs on sheep. Its presence in strikes principally from around Canberra may be a result of the fact that sheep are grazed closer to gardens here than is common in other parts of Australia.

L. cuprina is the principal cause of blowfly strike in South Africa (Hepburn 1943; Monnig and Cilliers 1944) and it has also been recorded as attacking sheep in Kenya (Lewis 1933). It is apparently of no economic importance in North America as far as sheep are concerned (Hall 1948), nor is it a serious sheep pest in the Orient, possibly owing to the presence of relatively few susceptible sheep.

TABLE 8

DETAILS OF STRIKES IN WHICH *LUCILIA* LARVAE WERE PRESENT (FROM MACKERRAS AND FULLER 1937; MACKERRAS AND MACKERRAS 1944)

State	Number of Strikes	
	L. cuprina	*L. sericata*
Queensland	197	0
New South Wales	242	5
Australian Capital Territory	696	79
South Australia	196	0
Western Australia	175	0
Total	1506	84

L. sericata is the principal sheep blowfly of the British Isles (Davies 1934; Macleod 1943; Ratcliffe 1934) and is one of the two important sheep blowflies of New Zealand (Miller 1939). Blowfly strike of sheep by *L. sericata* occurs also in South Africa (Hepburn 1943) and in U.S.A. (Bishopp 1915), but this species is not a serious pest in either country. *L. sericata* does not appear to attack sheep at all commonly in eastern Europe (Cragg 1950*b*) or in the Ukraine or in Northern Caucasus (Paramonov 1937), although it is not an uncommon fly in these regions.

VII. DISCUSSION

It is abundantly clear from the evidence presented that the flies known in Australia as *L. cuprina* and *L. sericata* are distinct species. Not only are there many constant morphological differences between the adults, but the larvae can also be distinguished; hybridization experiments suggest that there is often considerable difficulty in obtaining successful matings; examination of several thousand wild *Lucilia* failed to reveal any intermediates; ecological studies show that the two species have different habitat preferences and that their geographical distribution is not alike; their degree of attraction to living sheep is very different; and finally there are physiological differences.

One result of these physiological differences is the larger size of both larvae and adults of *L. sericata* when this species and *L. cuprina* are bred in an identical fashion and provided with adequate food. Further, the duration of the developmental period from egg to adult is significantly longer in *L. sericata* (14-15 days at 25°C.) than in *L. cuprina* (12-13 days).

Many interesting problems have arisen in the course of this survey of the two species. What, for example, are the factors which restrict the spread of *L. sericata* from the vicinity of dwellings into the surrounding country, and where do they breed? When one or two hundred *L. sericata* were trapped on each of several consecutive days in the Canberra garden (Tables 2 and 3) there was no apparent fall in the numbers of wild *L. sericata* remaining. In this area there could scarcely have been sufficient dead vertebrates (none were known to exist at all) to maintain a relatively steady population, apparently equivalent to between 500 and 1000 *L. sericata* per acre. It would be interesting to determine whether this species can maintain a high population density by breeding in vertebrate excrement, particularly since it has been recorded in small numbers from pig manure (Thomsen 1938) and both it and *L. cuprina* from fowl manure (Illingworth 1923; Tanada, Holdaway, and Quisenberry 1950). Other possible breeding grounds are small invertebrates (e.g. dead snails or fleshy insects) and vegetable material. *L. cuprina* is thought not to be able to maintain a high population density in the absence of sheep (Waterhouse 1947), and even in typical sheep country near Canberra its population density is comparatively low, densities of 0.3 to 5.7 per acre being recorded at different times of the active sheep blowfly season (Gilmour, Waterhouse, and McIntyre 1946).

Another question which arises is whether or not *L. cuprina cuprina* and *L. cuprina dorsalis* are really quite distinct in spite of the fact that there do not appear to be any constant morphological differences which would enable a taxonomist to assign specific status to them. The most striking differences are in general coloration and in the fact that, in North and South America, which are the only important sheep-raising countries falling within its distribution, *L. cuprina cuprina* is not an important sheep pest. The latter might be due to the fact that American sheep are relatively insusceptible to blowfly strike, although this is improbable in view of the common occurrence in some regions of the wrinkly Vermont breed.

From South Africa the bulk of the evidence on habits and behaviour of *L. cuprina* and *L. sericata* and also a morphological comparison of specimens from that country and from Australia suggest that the respective *Lucilia* species are very similar, perhaps even identical, in the two countries. There is as yet insufficient evidence to decide whether or not *L. sericata* from England and Australia are similar in physiology and behaviour as well as in morphology.

Finally, the hybridization experiments indicate a most unusual state of affairs, which does not appear to be at all clear on the basis of simple Mendelian laws. Although the early results of Mackerras could not be substantiated in detail because of difficulties of securing successful crosses, our one fertile mating demonstrated that it was possible to obtain at least some F_1 hybrids which were apparently typical *L. cuprina* and also that the entire F_2 progeny from some (but not all) F_1 hybrids appeared to be typical *L. cuprina*. Mackerras (1933) found that *L. cuprina* characters were dominant even if the original male parent was *L. cuprina* and the female *L. sericata*, a cross which

the authors could not repeat. A comparable result does not appear to have been recorded before, although it is known from mosquitoes that the characters of the female may appear in all offspring. For example, when *Aedes albopictus* males are mated with *A. aegypti* females, the F_1 and F_2 progeny have *A. aegypti* characters (7 features examined) (Downs and Baker 1949; Toumanoff 1937), but if male *A. aegypti* are crossed with female *A. albopictus* the F_1 and F_2 progeny are typical of *A. albopictus* (Hoang-Tich-Try 1939; Toumanoff 1937, 1939). Crosses between *L. cuprina* and *L. sericata* appear to be well worthy of further attention by the geneticist.

It has been suggested that *L. cuprina* was introduced into Australia, and the history of the spread of blowfly strike supports this view (Joint Blowfly Committee 1933). More recent evidence lends further support. For instance, the gradual spread of this species up the coast of Western Australia, which was recorded by Mackerras (1936) and Mackerras and Fuller (1937) is apparently still continuing (Jenkins 1945). Thus strike, believed to be due to *L. cuprina*, was first recorded at Mt. Anderson (near Derby) in 1942, although at that time properties further east in the Fitzroy basin had experienced no trouble. Furthermore, there are other corroborative reports, such as from Nappamerrie station (extreme south-western Queensland), where sheep were run from 1900 to the late 'twenties with no blowfly trouble. In the late 'twenties, successive severe waves of strike caused sheep-raising to be abandoned in this district. However, as recently as November 1949, *L. cuprina* was taken at Nappamerrie, so that it is evidently able to maintain a population for 20 years or more in the absence of sheep. It is most unlikely that there would have been some 30 successive strike-free years if *L. cuprina* had always occurred in this region, as would be expected if it were a native species.

There is now no support for the view (Joint Blowfly Committee 1933) that *L. cuprina dorsalis* was introduced into Australia from the East (i.e. Eastern Asia, or the islands to the north of Australia), since it is not known to occur in this region. It now appears more probable that it was introduced from South Africa or India during the last century. The fact that there are no records of strike in Australia before 1883 (Joint Blowfly Committee 1933) does not necessarily mean that *L. cuprina dorsalis* was introduced about that time, since the first strikes were recorded in South Africa about 1900 (Smit 1931), although *dorsalis* (Robineau-Desvoidy 1830) and *argyrocephala* (Macquart 1846) had been present for at least 70 years before that time. If *L. cuprina cuprina* is found to occur in Northern Australia (and this possibility cannot be ruled out without further collections from this region) it would be circumstantial evidence in support of the view that *L. cuprina dorsalis* is an introduced species.

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IX. References

Aubertin, D. (1933).—Revision of the genus *Lucilia* R-D. (Diptera, Calliphoridae) *J. Linn. Soc. (Zool.)* **38**: 389-436.

Bezzi, M. (1928).—Diptera Brachycera and Athericera of the Fiji Islands. British Mus. Nat. Hist., London.

Bishopp, F. C. (1915).—Flies which cause myiasis in man and animals—some aspects of the problem. *J. Econ. Ent.* **8**: 317-29.

Cragg, J. B. (1950*a*)—The reactions of *Lucilia sericata* (Mg.) to various substances placed on sheep. *Parasitology* **40**: 179-86.

Cragg, J. B. (1950*b*).—Studies on *Lucilia* species (Diptera) under Danish conditions. *Ann. Appl. Biol.* **37**: 66-79.

Davies, W. M. (1934).—The sheep blowfly problem in North Wales. *Ann. Appl. Biol.* **21**: 267-82.

Downs, W. G., and Baker, R. H. (1949).—Experiments in crossing *Aedes* (*Stegomyia*) *aegypti* Linnaeus and *Aedes* (*Stegomyia*) *albopictus* Skuse. *Science* **109**: 200-1.

Fuller, M. E. (1932).—The larvae of the Australian sheep blowflies. *Proc. Linn. Soc. N.S.W.* **57**: 77-91.

Gilmour, D., Waterhouse, D. F., and McIntyre, G. A. (1946).—An account of experiments undertaken to determine the natural population density of the sheep blowfly, *Lucilia cuprina* Wied. Coun. Sci. Industr. Res. Aust. Bull. No. 195.

Hall, D. G. (1948).—"The Blowflies of North America." (Thomas Say Foundation: U.S.A.)

Hardy, G. H. (1940).—Notes on Australian Muscoidea. V. Calliphoridae. *Proc. Roy. Soc. Qd.* **51**: 133-46.

Hepburn, G. A. (1943).—Sheep blowfly research. I. A survey of maggot collections from live sheep and a note on the trapping of blowflies. *Onderstepoort J. Vet. Sci.* **18**: 13-7.

Hoang-Tich-Try (1939).—Essai de croisement de *St. albopicta* ♀ et de *St. fasciata* ♂ en espace restreint. *Bull. Soc. Path. Exot.* **32**: 511-3.

Horn, W., and Kahle, I. (1936).—Uber entomologische Sammlungen (Ein Beitrag zur Geschichte der Entomo-Museologie). Entomologische Beihefte aus Berlin-Dahlem **3**: 264.

Illingworth, J. F. (1923).—Insect fauna of hen manure. *Proc. Hawaii Ent. Soc.* **5**: 270-3.

JENKINS, C. F. H. (1945).—Entomological problems of the Ord River irrigation area. *J. Agric. W. Aust.* **22**: 131-45.

JOINT BLOWFLY COMMITTEE (1933).—The sheep blowfly problem in Australia. Report No. 1. Coun. Sci. Industr. Res. Aust. Pamph. No. 37.

KNIPLING, E. F. (1936).—Some specific taxonomic characters of common *Lucilia* larvae, Calliphoridae, Diptera. *Iowa St. Coll. J. Sci.* **10**: 275-94.

LEWIS, E. A. (1933).—Observations on some Diptera and myiasis in Kenya Colony. *Bull. Ent. Res.* **24**: 263-7.

MACKERRAS, I. M. (1930).—Recent developments in blowfly research. *J. Coun. Sci. Industr. Res. Aust.* **3**: 212-9.

MACKERRAS, I. M. (1936).—The sheep blowfly problem in Australia. Results of some recent investigations. Coun. Sci. Industr. Res. Aust. Pamph. No. 66.

MACKERRAS, I. M., and FULLER, M. E. (1937).—A survey of the Australian sheep blowflies. *J. Coun. Sci. Industr. Res. Aust.* **110**: 261-70.

MACKERRAS, I. M., and MACKERRAS, M. J. (1944).—Sheep blowfly investigations. The attractiveness of sheep for *Lucilia cuprina*. Coun. Sci. Industr. Res. Aust. Bull. No. 181.

MACKERRAS, M. J. (1933).—Observations on the life-histories, nutritional requirements and fecundity of blowflies. *Bull. Ent. Res.* **24**: 353-62.

MACLEOD, J. (1943).—A survey of British sheep blowflies. *Bull. Ent. Res.* **34**: 65-88.

MACQUART, P. J. M. (1846).—Diptères exotiques nouveaux ou peu connus. Supplement 1. Paris.

MALLOCH, J. R. (1927).—Notes on Australian Diptera. XI. *Proc. Linn. Soc. N.S.W.* **52**: 299-335.

MEIGEN J. W. (1826).—Systematische Beschreibung der europäischen zweiflügeligen Insekten **5**:

MILLER, D. (1939).—Blowflies (Calliphoridae) and their associates in New Zealand. Cawthron Institute Monographs No. 2.

MONNIG, H. O., and CILLIERS, P. A. (1944).—Sheep blowfly research. VII. Investigations in the Cape winter-rainfall areas. *Onderstepoort J. Vet. Sci.* **19**: 71-7.

PARAMONOV, S. J. (1937).—Das Rätsel der Fliege *Lucilia sericata*. *Mg. Trav. Mus. Zool. Acadm. Sci. Ukr.* **19**: 183-96.

PATTON, W. S. (1920).—Some notes on Indian Calliphoridae. Part 2. *Ind. J. Med. Res.* **9**: 548-54.

PATTON, W. S., and EVANS, A. M. (1929).—"Insects, ticks, mites and venomous animals of veterinary and medical importance. Part 1. Medical." (Liverpool School of Tropical Medicine: Croydon.)

RATCLIFFE, F. N. (1934).—Observations on the sheep blowfly (*Lucilia sericata* Meig.) in Scotland. *Ann. Appl. Biol.* **22**: 742-53.

ROBINEAU-DESVOIDY, J. B. (1830).—Essais sur les Myodaires: 452-62.

ROSENBAUM, W. (1939).—Anträge für die Nomenklatur – Sektion des VII Internationalen Kongresses für Entomologie in Berlin 1938. Verhandlungen VII Internationalen Kongresses für Entomologie. I: 591-8.

SENIOR WHITE, R., AUBERTIN, D., and SMART, F. (1940).—The fauna of British India, Diptera, **6**: 1-288.

SHANNON, R. C. (1924).—Nearctic Calliphoridae, Luciliini (Diptera). *Insec. Inscit. Menst.* **12**: 67-81.

SHANNON, R. C. (1925).—A note on the distribution and synonomy of a myiasis producing fly. *Proc. Ent. Soc. Wash.* **27**: 196.

SHANNON, R. C. (1926).—Synopsis of the American Calliphoridae (Diptera). *Proc. Ent. Soc. Wash.* **28**: 115-39.

SMIT, B. (1931).—A study of the sheep blowflies of South Africa. Union of S. Afr. Dep. Agric. 17 Rept. Dir. Vet. Services An. Indust. Part 1: 299-421.

TANADA Y., HOLDAWAY, F. G., and QUISENBERRY, J. H. (1950).—D.D.T. to control flies breeding in poultry manure. *J. Econ. Ent.* **43**: 30-6.

THOMSEN, M. (1938).—Stuenfluen og Stikfluen. 176 *de Beretn. Forsöglaboratoriet Kbh.* p. 352.

TOUMANOFF, C. (1937).—Essais préliminaires d'intercroisement de *St. albopicta* Skuse avec *St. argentea* Poiret. *S. fasciata* Theob. *Bull. Soc. Med. Chir. Indochine* **15**: 964-70.

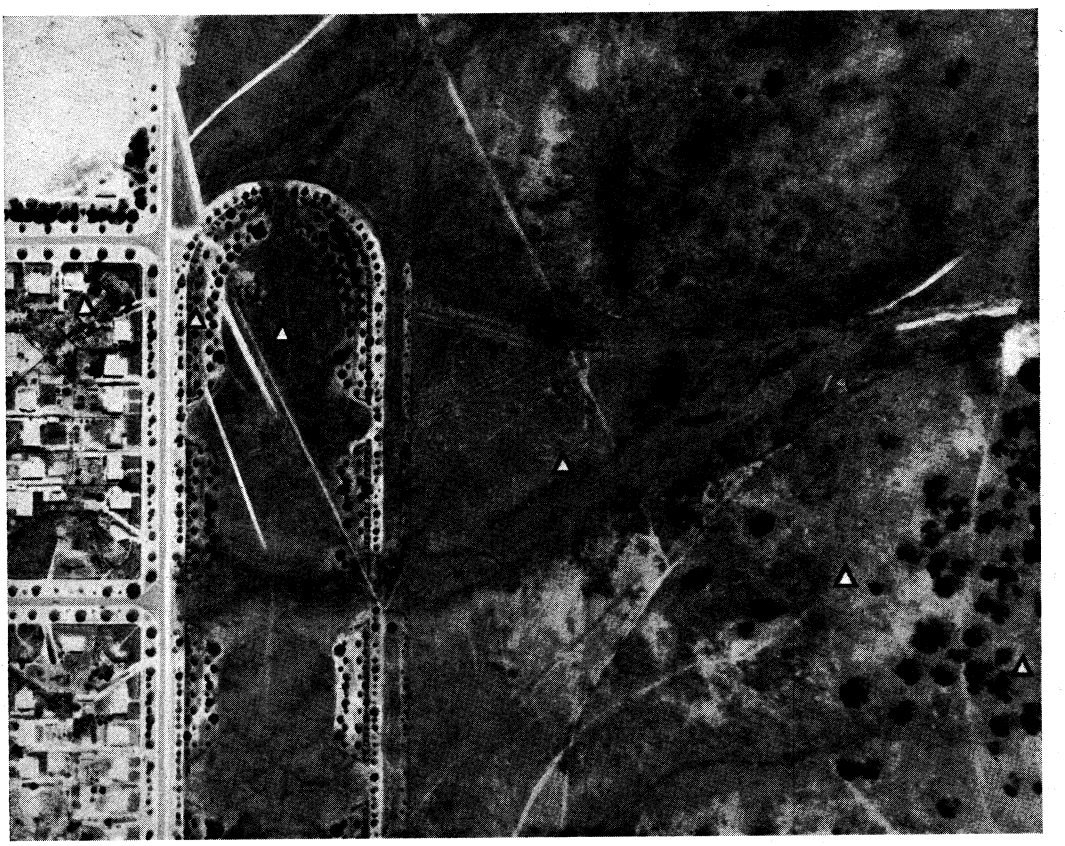
TOUMANOFF, C. (1939).—Les races géographiques de *St. fasciata* et *St. albopicta* et leur intercroisement. *Bull. Soc. Path. Exot.* **32**: 505-9.

ULLYETT, G. C. (1945).—Species of *Lucilia* attacking sheep in South Africa. *Nature* **155**: 636-7.

ULLYETT, G. C. (1950).—Competition for food and allied phenomena in sheep blowfly populations. *Philos. Trans.* B **234**: 77-174.

WATERHOUSE, D. F. (1947).—The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina*. Coun. Sci. Industr. Res. Aust. Bull. No. 217.

WIEDEMANN, C. R. W. (1830).—Aussereuropäische zweiflügelige Insekten, **2**: 1-684.



Aerial photograph showing the distribution of traps (indicated by white triangles) in the habitat preference experiment.