

THE *Lasius* (*Chthonolasius*) *umbratus* (HYM., FORMICIDAE) SPECIES COMPLEX IN NORTH EUROPE

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Wilson (1955) took into account 42 described European forms related to *Lasius umbratus* Nylander. He was able to separate only two of these as distinct species from *L. umbratus*. These were *L. bicornis* Foerst. and *L. rabaudi* Bondroit. He considered the remainder to be more or less trivial variants of a single variable holarctic species *L. umbratus*. The more important synonyms included *L. affinis* Schenck and *L. mixtus* Nylander. Wilson's important revision has not excited the critical comment it deserved in Europe. Only Forsslund (1957) noted that *L. mixtus* and *L. umbratus* in Nylander's restricted sense appeared to him quite distinct, in Scandinavia at least. Collingwood (1957) was prepared to accept Wilson's synonymy on the information available at that time, but drew attention to features in both important synonyms that did not appear to be fully resolved in Wilson's paper. Boven (1959) ignored Wilson's work entirely in a key to Netherland ants and continued to use the names *L. mixtus* and *L. affinis*, providing keys for their separation from *L. umbratus* without further discussion. In this paper, *Lasius affinis* (Schenck) and *L. mixtus* (Nylander) are considered afresh. Evidence is given to show that *L. affinis* is distinct from *L. umbratus* even in the wide sense used by Wilson. An examination of a sufficient number of samples provides grounds also for re-establishing the separate identity of *L. mixtus*.

Lasius (*Chthonolasius*) *affinis* (Schenck)

(*Formica affinis* Schenck, 1852; *Lasius affinis* Mayr, 1861; *Lasius bicornis* var. *affinis* André, 1881; *Lasius umbratus affinis* Forel, 1915; *Formicina affinis* Bondroit, 1918; *Lasius* (*Chthonolasius*) *affinis* Stitz, 1939; *Lasius* (*Chthonolasius*) *affinis* Boven, 1955; *Lasius* (*Chthonolasius*) *umbratus* Wilson, 1955 *partim*.)

Schenck (1852) referred to this as *Formica affinis* in his original paper, but clearly included it in the *umbratus* species group as distinct from the '*Formica niger* L.' group and from what is now known as the genus *Formica* in its present restricted sense. His original types are probably no longer available, but through the courtesy of Professor E. Kessel of the University of Marburg, I have been able to examine probable syntypes labelled *Lasius*

affinis, allegedly by Schenck himself. The queen is clearly *L. affinis* according to the original careful description given by Schenck; three males are probably so, but this caste is harder to differentiate in this species group; the one worker labelled *L. affinis* however is a typical *L. umbratus*. Two other workers are labelled *L. incisus* zu *affinis* (*incisus* was Schenck's name for *L. bicornis* Foerst.), but appear to be definitely *L. affinis* and not *L. bicornis*.

The principal diagnostic features of the female castes include absence of standing hairs on scapes and tibiae, near absence of genal hairs, high, indented petiole scale, flattened antennal scape and long profuse body hairs. The flattened scape and absence of tibial hairs distinguish the species from *L. umbratus* in Nylander's restricted sense; the flattened scape and long body hairs equally distinguish it from *L. mixtus* Nylander and the combination of characters distinguish it from *L. umbratus* sensu Wilson. The species is clearly similar to *L. bicornis*, but the queen is easily distinguished by its greater size (length 7-8 mm. instead of 5-6 mm.) and less deeply indented scale. The worker is distinguished by more profuse body hairs; those on the first gaster segment are numerous and well distributed over the dorsal and basal surfaces whereas in *L. bicornis* they are more restricted to the basal face and the posterior borders of the gastric tergites. The different gaster pilosity and scale shape were clearly pointed out in Schenck's original description as also in those of subsequent authors including Mayr (1861), André (1881), Stitz (1939). More recently Boven (1955) has given a full account of *L. affinis* in Belgium, distinguishing it in a similar way both from *L. bicornis* and from Nylander's species.

Together with Schenck's material, I have now had the opportunity of examining 5 queens, 8 males and 21 workers from 9 European localities. These include examples of the three castes kindly sent by Dr. J. K. A. van Boven from Belgium, a male, queen and worker from Switzerland in the Oxford University Museum, examples of the three castes and another series of workers taken by Dr. I. H. H. Yarrow in the Huesca province of Spain, two workers taken by Professor H. Franz in Pontevedra province, also in Spain, and a series of workers taken by myself in Fontainebleau Forest, France, in 1955. All examples of the female castes consistently show the diagnostic features enumerated above. The Belgian material, that of Dr. Yarrow and mine was all collected from nests in rotten stumps which conforms with recorded captures given by other authors, e.g. Stitz (1939). The nest situation of the other series is not known but it is fair to add that the species has occurred in other kinds of habitat, in particular, ground nests in grass and heather (Schenck, 1852; Kuznetsov, 1929; Sadil, 1939). The known range of *L. affinis* includes Germany, Switzerland, Belgium, France and Spain; Stitz (1939) also gives North Italy, Hungary and the Pyrenees, and there are records from Czechoslovakia (Sadil, 1939), Siberia and South

Russia (Kuznetzov, 1929). *Lasius affinis* has been keyed and, in my opinion, correctly distinguished by the older authors including Mayr (1861), Bondroit (1918), Stitz (1939) and, more recently, Boven (1955), while André (1881), Forel (1915) and Emery (1916) considered that it was related more closely to *L. bicornis* Foerst. than to *L. umbratus*.

The queen from the Schenck collection labelled '*Lasius affinis* Schenck', although rather damaged, bears out the diagnostic features given by Schenck (1852) for *Formica affinis*. These features given in general terms above, their constancy in series from a wide geographical area, the detailed comparative measurements in tables I and II and the keys to all castes provided later in this paper constitute sufficient grounds to remove *Formica affinis* formally from synonymy under *Lasius umbratus* sensu Wilson (1955) and to reinstate it here in the sense used by most European authors as the distinct and independent species *Lasius (Chthonolasius) affinis* (Schenck).

TABLE I. *Lasius affinis*—Measurements.

Key:—G—longest gaster hair on anterior face of first tergite.

H—head width across eyes.

T—maximum width of hind tibia at mid-point.

(All measurements in mm.)

Country	Locality	G	H	T		
♂ ♀	Spain	Torla (Huesca)	0.130	1.307	0.161	
			0.130	1.200	0.161	
	Ordesa (Huesca)		0.123	1.190	0.162	
			0.115	1.230	0.160	
			0.138	1.230	0.164	
			0.130	1.190	0.162	
			0.130	1.190	0.162	
	Pontevedra		0.114	1.136	0.161	
		Mondariz	0.104	1.040	0.155	
	Switzerland	Roccarano	0.138	1.196	0.165	
	Germany	Nassau		0.147	1.195	0.165
				0.136	1.227	0.163
	Belgium	Méchelen		0.130	1.270	0.162
				0.123	1.230	0.162
	France	Fontainbleau		0.130	1.153	0.164
			0.115	1.153	0.160	
			0.138	1.196	0.164	
			0.123	1.230	0.162	
			0.130	1.196	0.162	
		0.123	1.230	0.161		
♀ ♀	Spain	Torla (Huesca)	0.165	1.630	0.230	
	Belgium	Méchelen	0.177	1.730	0.235	
	Switzerland	Orchy	0.131	1.730	0.235	
	Germany	Nassau		0.178	1.691	0.237
♂ ♂	Spain	Ordesa (Huesca)	0.077	1.040		
			0.100	1.110		
			0.077	1.050		
	Belgium	Méchelen		0.085	1.080	0.120
				0.085	1.050	0.120
	Germany	Nassau		0.102	1.200	
				0.113	1.200	
				0.113	1.160	

TABLE II.

Chthonolasius spp. Mean measurements and indices.

Key:—G—Longest gaster hair on anterior face of first tergite.

H—Head width across eyes.

T—Maximum width of hind tibia at mid-point.

S—Minimum and maximum width of scape at mid-point.

(All measurements in mm.)

Species	Number of series	G	H	T	S	G × 100	
						Ratio:	H
♀	<i>affinis</i>	8 range: 0.127 (0.104-0.138)	1.199 (1.04-1.31)	0.162	0.078 × 0.118	10.6 ± 0.65	
	<i>bicornis</i>	1	1.109	0.162	0.071 × 0.12	11.6	
	<i>mixtus</i>	32 range: 0.042 (0.028-0.06)	1.027 (0.97-1.12)	0.156	0.087 × 0.112	4.1 ± 0.82	
	<i>umbratus</i>	25 range: 0.077 (0.063-0.1)	1.071 (0.93-1.15)	0.158	0.086 × 0.114	7.2 ± 1.28	
	<i>rauda</i>	25 range: 0.085 (0.046-0.107)	1.056 (0.82-1.16)	0.158	0.074 × 0.115	8.1 ± 1.04	
♀	<i>affinis</i>	3	1.69	0.235	0.095 × 0.17	9.8	
	<i>bicornis</i>	1	1.34	0.210	0.08 × 0.14	12.7	
	<i>mixtus</i>	19 range: 0.046 (0.029-0.064)	1.50 (1.32-1.68)	0.230	0.115 × 0.146	3.1 ± 0.6	
	<i>umbratus</i>	30 range: 0.106 (0.07-0.14)	1.68 (1.32-1.83)	0.246	0.12 × 0.15	6.3 ± 1.2	
	<i>rauda</i>	3 range: 0.099	1.71	0.238	0.09 × 0.15	5.7	
♂	<i>affinis</i>	4	1.02	0.12	0.08 × 0.10	9.8	
	<i>bicornis</i>	—					
	<i>mixtus</i>	3	0.99	0.11	0.08 × 0.09	4.2	
	<i>umbratus</i>	4	1.10	0.11	0.08 × 0.09	8.5	
	<i>rauda</i>	4	0.89	0.10	0.07 × 0.08	7.9	

(1-3 individuals per nest series examined)

Lasius (Chthonolasius) mixtus (Nylander)

(*Formica mixta* Nylander, 1846; *Lasius mixtus* auctt., 1870-1955; *Lasius (Chthonolasius) umbratus* Wilson, 1955 *partim*.)

Wilson (1955) found by a method of examining two or three workers from a large number of collections from America, Europe and Asia that there was no single character or combination of characters by which he could separate Nylander's *L. mixtus* from *L. umbratus* and consequently synonymised it as an intergrading variation of that species. In general the conventional character used to separate the two forms, namely appendage pilosity, appeared to increase with size in North Europe. Collingwood (1957) pointed out that there were contradictions in detail such as the existence of series of small sized workers with profuse appendage hairs. The chief stumbling block to separating the two forms from a taxonomic point of view was the apparent existence of intergrading series with sparse appendage hairs that could not safely be placed either to the one or the other. A critical examina-

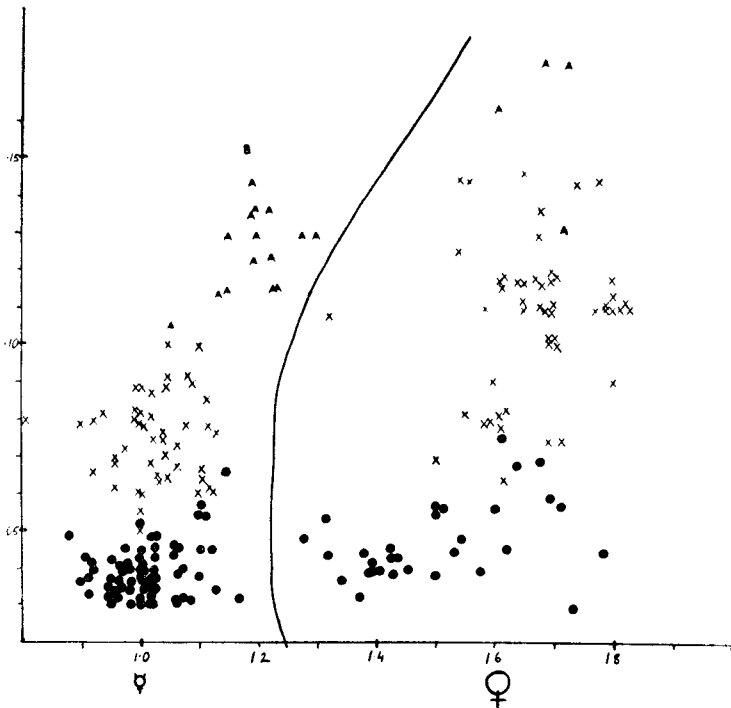


Fig. 1.—Worker gaster hair length (vertical axis) plotted against head width (basal axis).

B=*Lasius bicornis* Foerst.

A=*Lasius affinis* Sch.

X=*Lasius umbratus* Nyl.

●=*Lasius mixtus* Nyl.

tion of numbers of queens and workers in the present study has shown that there are indeed a few such anomalies but they are in the great minority with about 95% of all series falling into one of two definite groups.

I have been able to examine some 80 nest series of workers and/or queens of *L. umbratus/mixtus* from Britain and about 20 from Europe including Finland, Norway, Spain, France, Jugoslavia and the Alps. Fig. 1 shows the results of individual measurements of 1, 2 or 3 individuals per nest series with respect

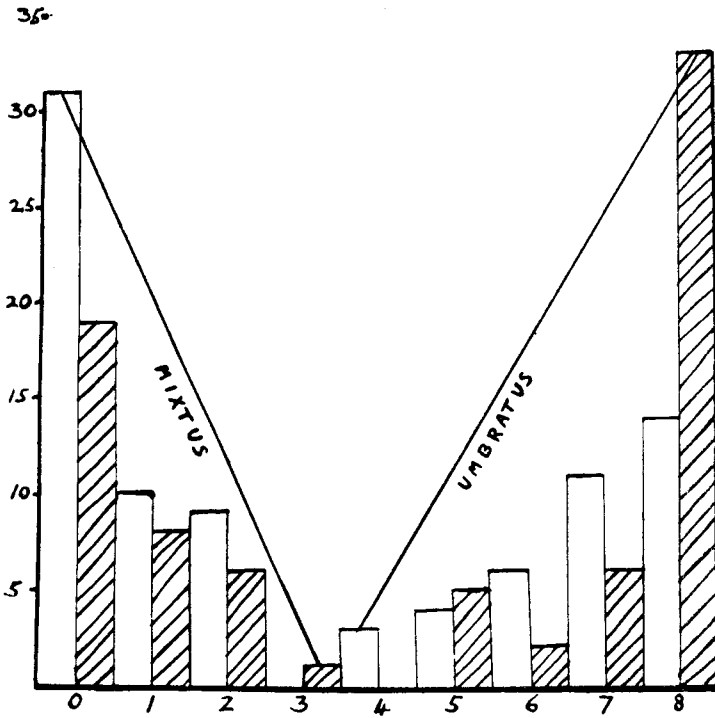


Fig. 2.—Compound character diagram: shaded columns, ♀♀; white columns, ♂♂.

Scoring:—	0	1	2
funiculus segment 8:	wider than long =0	as wide as long=1	longer than wide=2
gaster hair length:	shorter than 0.055 mm.	0.055-0.06 mm.	longer than 0.06 mm.
genal hairs one side:	less than 6	6-9	10 or more
hind tibial hairs:	nil	1-3	4 or more

to gaster hair length relative to head width across the eyes for *L. mixtus*, *L. umbratus* and *L. affinis*. Fig. 3 shows this ratio expressed in histograms. These diagrams show a clear division into three groups with a relatively small area of overlap between *L. umbratus* and the others and none between *L. mixtus* and *L. affinis*. For the purposes of this study I have taken *L. mixtus* as workers and queens with a seta count in Wilson's method and terminology of no more than two (with an average of much less than 1) while *L. umbratus* is taken as having more than 5. Fig. 2 shows a compound character index diagram for *L. umbratus/mixtus* with the criteria tibial hairs, genal hairs, funiculus segment proportions and gaster hair length as shown in the key to the diagram. While the method of scoring separates the species in

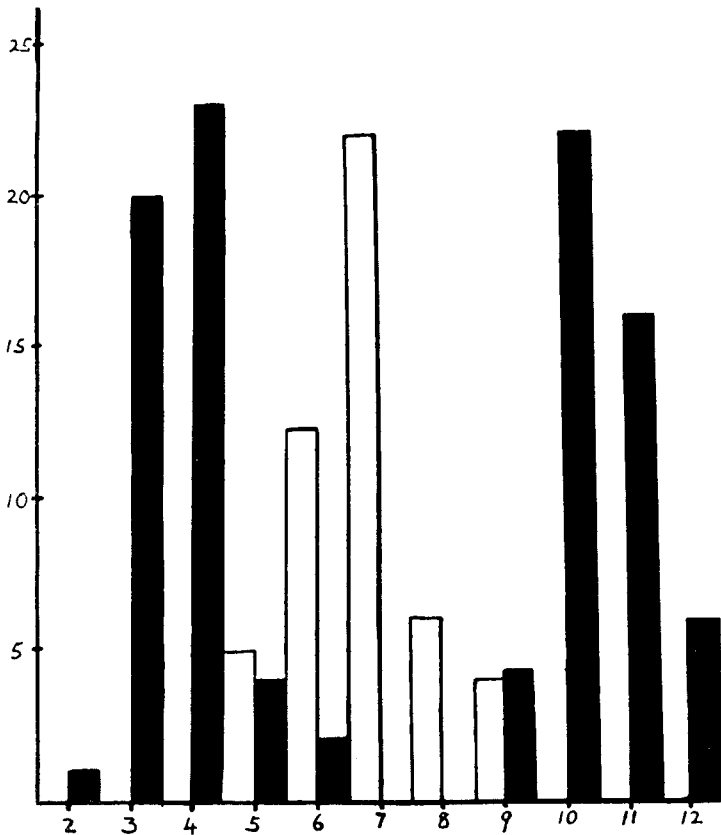


Fig. 3.—Ratio worker gaster hair length: head width $\times 100$ (basal axis).
 Black column to left—*Lasius mixtus* Nyl. (means of 50 nest series).
 Black column to right—*Lasius affinis* Sch. (25 individuals $\times 2$).
 White column—*Lasius umbratus* Nyl. (means of 50 nest series).

what appears to be a fairly well defined way, the characters necessarily chosen are probably interdependant manifestations that may be related to total body size as Wilson suggested. In this respect fig. 1 is the more reliable in that it shows that when the three species are segregated according to appendage pilosity and other characters, gaster hair length is clearly not related to body size, i.e. head width, and can be used as a true guide to separating the species.

Wasmann is quoted in Donisthorpe (1927) as stating that intermediates between *L. umbratus* and *L. mixtus* are as common as the types. Donisthorpe himself, however, gave remarkably few examples for this intermediate category. I have had the opportunity of examining some of his doubtful specimens in the British Museum, the Leicester City Museum, the National Museum of Wales and the Oxford University Museum. These include typical *L. mixtus* queens with no appendage hairs from Bletchington and Woodeaton labelled *L. umbratus*, a typical *L. mixtus* worker from Snave Bridge, S.W. Ireland, labelled *mixto-umbratus*; a queen from Seaton labelled *mixto-umbratus*, which I would have named *L. umbratus*—the specimen has long subdecumbent appendage hairs—and several queens, males and workers from Porthcawl and Weybridge labelled *mixto-umbratus* which are in fact *L. rabaudi* Bondroit, a species not then recognised by Donisthorpe. I myself recorded '*mixto-umbratus*' from Worcestershire, but these were males and queens flying to light on successive evenings. They divide straight-forwardly into *L. mixtus* and *L. umbratus* and there was no reason to suppose that they came from the same colony. It will be seen, therefore, that some of the early captures were misidentified and some at least of the few intermediates so recorded by Donisthorpe were another species.

There are, however, series that are sufficiently intermediate that it becomes a matter of opinion as to which species they belong. Thus some queens, in the Oxford Museum from Shotover, are labelled *umbratus*, but recorded as *mixtus* by Donisthorpe. These have a rectangular scale, many genal hairs, scattered appendage hairs and are dark in colour. That is, they are darker in colour and have fewer appendage hairs than normal *L. umbratus* while the petiole scale, but no other feature, is reminiscent of *L. rabaudi*. Similar series of queens from Heston and Osterley are present in the British Museum collection. I have also seen the odd queens in the Copenhagen Universitets Zoologisk Museum, through the courtesy of Mg. C. Bisgaard, that have relatively long gaster hairs but very few appendage hairs and are somewhat intermediate between the two. In my own collection, I have what I regard as *L. mixtus* with occasional suberect tibial hairs and *L. umbratus* with a reduced number of such hairs. However, these with the Shotover queens include only 5 series out of the 100 that I have been able to study. Wilson included the North American '*aphidicola*' in his conception of *L. umbratus*. This entirely lacks appendage hairs and in this respect shows no variation whatever

towards conventional *L. umbratus*. A small series of workers, queens and a male labelled *L. umbratus* by Wilson was very kindly sent among other American ants by Dr Marion Smith. I cannot distinguish the workers from European *L. mixtus*, the queens however are distinctively lighter in colour than ours which, in North Europe at least, are always dark, while the single male sent has long genal hairs which do not occur in any specimens of our species that I have seen.

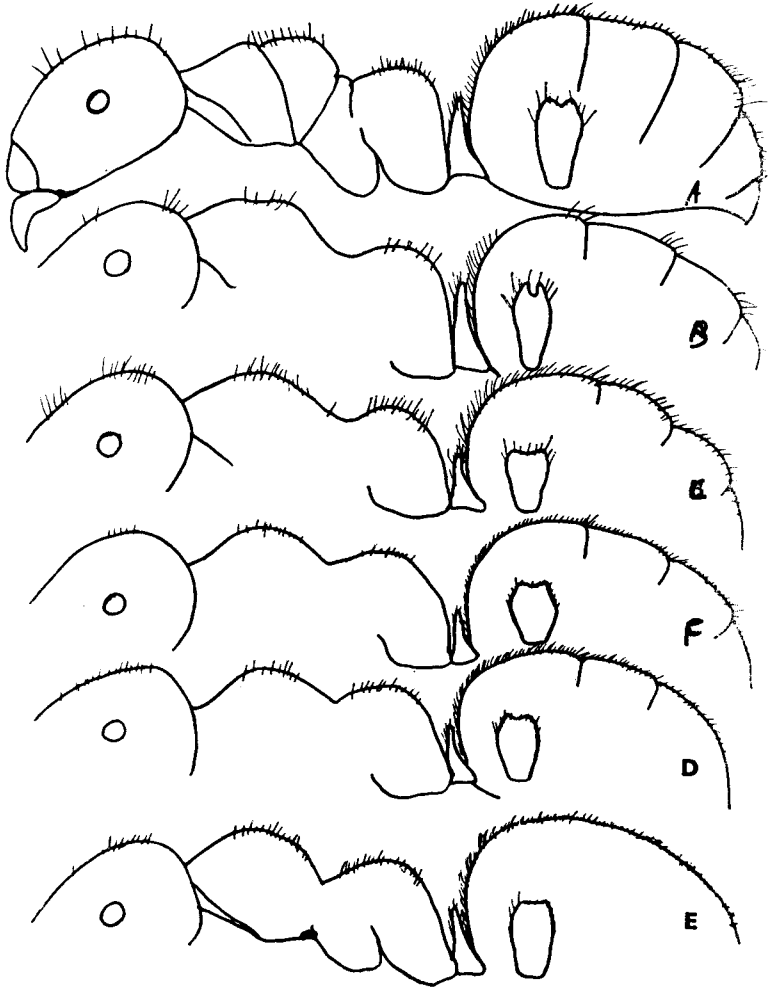


Fig. 4.—Worker profile + scale front view of: A, *Lasius affinis* Sch.; B, *Lasius bicornis* Foerst.; C, *Lasius flavus* Fab.; D, *Lasius umbratus* Nyl.; E, *Lasius rabaudi* Bon.
F. *L. mixtus* Nyl.

In North Europe as a whole, *L. mixtus* and *L. umbratus* occupy the same geographic range although in the British Isles *L. umbratus* becomes relatively scarce in the north (Table III). Populations of *L. mixtus* from the mountains of north Spain, Pyrenees, Alps and Scandinavia, as well as a single queen I have seen from east Siberia, are morphologically consistent throughout this range and show no clinal trends, but a single isolated queen, taken by Dr I. H. H. Yarrow in Huesca province, North Spain, may represent the category *L. distinguenda* Emery (1916). This includes series of large individuals taken in south Europe with numerous body hairs but no appendage hairs. The Spanish specimen has a flat scape, a high angularly emarginate scale and hairless scapes and tibiae as in *L. affinis*, but profuse genal and body hairs in number and length within the *L. umbratus* range. *L. distinguenda* may well be a good species but I have seen no other material from south Europe to justify an opinion. Only Staercke (1937) of recent authors appears to have studied this form, but neither he nor Emery described or distinguished the male. Series of workers that I collected in south France in 1955 have hairy tibiae and scapes and appear to be mostly *L. rabaudi*, a much more abundant species in Europe than was realised before Wilson (1955). In England there are now authenticated records for this species from Kent, Surrey, Berkshire, Hampshire, Glamorgan, Pembroke, Suffolk and Norfolk.

TABLE III.

Distribution of members of the *Lasius umbratus* complex in Britain from all available records.

	<i>umbratus</i>	<i>mixtus</i>	<i>rabaudi</i>	Number of Vice- counties	Records per Vice-county
Scotland	5 (31%)	9 (64%)	0	41	0.34
Ireland	3 (14%)	18 (86%)	0	40	0.53
N. Wales, N. England	15 (58%)	11 (42%)	0	25	1.04
S. Wales, S. England	148 (63%)	48 (24%)	26 (13%)	46	4.39
	142 (57%)	83 (33%)	25 (10%)		

I have recorded habitats for my own captures of the three species and the percentage of nests in each of three types of site are given in Table IV. In my experience *L. mixtus* is rather a species of subalpine pasture in Europe whereas *L. umbratus* is associated more definitely with woodland or hedgerow trees. *L. rabaudi* is a characteristic inhabitant of heath and sandy pasture in South England and Scandinavia but seems to occur as frequently in scrub and woodland in France and Spain. The three species obviously overlap in habitat distribution but the table does suggest a trend difference which supports the morphological differences.

TABLE IV.
Habitat trends in North Europe
(total site records in brackets).

Nature of site	<i>umbratus</i> (20)	<i>mixtus</i> (25)	<i>rabaudi</i> (20)
Woodland including old trees, stumps and wooded banks	55%	12%	5%
Open sites including stony pasture, open scrub, quarries and sea coast	40%	88%	30%
Sandy heath	5%	0	65%

To sum up, the evidence for the specific separation of *L. mixtus* Nyl. from *L. umbratus* Nyl. is less clearcut than that for the separation of *L. affinis* Sch. from either. The majority of series however are easily distinguished and only about 5 out of more than 100 series of workers and/or queens examined show intergrading characters which are open to a variety of explanations. While final judgment must be deferred until cytogenetical studies or interbreeding experiments provide additional evidence, it appears to me sounder at the present time to assume that, in addition to *L. rabaudi* Bond., there are at least two other species in North Europe which should continue to be named *L. umbratus* Nyl. and *L. mixtus* Nyl. according to the presence or absence of scape and tibial hairs and other criteria given in the keys at the end of this paper. The American population should, in my view, be excluded from identification with either on the grounds that the male at least appears to be distinctively different. The male caste of all members of this species group has been given insufficient attention and should repay further study. It will be noted that in the keys, I have endeavoured to separate all castes of *L. rabaudi* from *L. umbratus* which are very similar in the worker caste, but I am confident that this can easily be done with a little experience. If the single queen from north Spain alluded to earlier is representative of the south *L. distinguenda* Em., it may be separated from *L. mixtus* by the flat scape and abundant body hairs and from *L. affinis* by the abundant genal hairs and shorter body hairs.

Keys to *Chthonolasius* species in Europe

Males

- Mandibles with single apical tooth *Lasius*, *Dendrolasius*,
Cautolasius
- Mandibles with five more or less distinct teeth *Chthonolasius*
1. Petiole in side view thick and convex; length 3-3.4 mm.
carniolicus Mayr
 - Petiole in side view thin and tapered above; length
3.6-4.8 mm. 2
 2. Hind tibiae and scapes with suberect hairs 3
 - Hind tibiae with one or two occasional hairs at most, scapes
without suberect hairs 4

3. Frontal furrow deep and distinct; frontal triangle smooth and well defined; appendages thickly haired *rabaudi* Bond.
Frontal furrow shallow and poorly defined; frontal triangle rugose; appendage pilosity variable *umbratus* Nyl.
4. Hairs on gaster less than 0.4 maximum hind tibial width
mixtus Nyl.
Hairs on gaster more than 0.7 maximum hind tibial width 5
5. Petiole high, tapered and deeply indented; dorsal gaster hairs sparse *bicornis* Foerst.
Petiole widely emarginate at most; dorsal gaster hairs numerous *affinis* Schenck

Queens

Colour shining black with scutum occupying entire anterior thoracic convexity *Dendrolasius*
Colour yellow, brown or dull black; pronotum not completely overhung by scutum

Head width across eyes less than maximum width of thorax *Cautolasius*, *Lasius*

Head width across eyes as wide or wider than thorax
Chthonolasius

1. Length less than 5.5 mm. 2
Length at least 6.5 mm. 3
2. Petiole convex thick and low in profile *carniolicus* Mayr
Petiole high, tapered and deeply indented above
bicornis Foerst.
3. Scapes and tibiae with suberect hairs 4
Scapes and tibiae without erect hairs; one or two on hind tibiae at most 5
4. Scape flattened with thin front edge when viewed in horizontal plane; funiculus segments distinctly longer than broad; petiole scale rectangular in front view; body colour dark
rabaudi Bond.
Scape subcylindrical; funiculus segments slightly longer than broad, more cup-shaped; petiole more hexagonal in outline with more or less rounded sides; body colour ochrous to dark brown *umbratus* Nyl.
5. Scape flattened; hairs on dorsum of gaster more than 0.7 maximum hind tibial width *affinis* Schenck
Scape subcylindrical; gaster hairs less than 0.3 maximum hind tibial width *mixtus* Nyl.

Workers

Eye length at least 0.2 × head width; colour brown, black or bicoloured *Lasius*

Eye length 0.16 × head width or less;

colour jet black *Dendrolasius*

colour yellow *Cautolasius*, *Chthonolasius*

1. Petiole scale low and thick in side view, convex in front view; genal margins curving inward strongly towards mandibular insertions *carniolicus* Mayr
Petiole scale thin in side view with flat to emarginate dorsal border 2
2. Scapes and tibiae with numerous suberect hairs 3
Scapes without hairs; hind tibiae occasionally with one or two at most 4
3. Scape flattened with a distinct thin edge viewed from in front; petiole with flattened dorsal crest and straight to feebly curved sides *rabaudi* Bond.
(Fig. 4, f.)
Scape subcylindrical; petiole variable but usually emarginate above and sides distinctly sloped inwards in front view *umbratus* Nyl.
(Fig. 4, e.)
4. Dorsum of gaster with short hairs less than $0.4 \times$ maximum hind tibial width *mixtus* Nyl.
(Fig. 4, d.)
Dorsum of gaster with long hairs exceeding $0.7 \times$ maximum hind tibial width 5
5. Petiole broad and low, not tapered above when seen in front view; size very variable, length 2.4-5 mm.
Cautolasius flavus Fab.
(Fig. 4, c.)
Petiole high, distinctly tapered above when seen in front view; monomorphic; length 4.3-4.8 mm. 6
6. Petiole bicornute with deep semicircular emargination; dorsal gastric hairs sparse, mainly restricted to basal face and hind edges of gastric tergites *bicornis* Foerst.
(Fig. 4, b.)
Petiole with angular emargination; dorsal gastric hairs numerous and evenly distributed over surface
affinis Schenck
(Fig. 4, a.)

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