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Brachyptery and wing-polymorphism among the Coccinellidae (Coleoptera)

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ABSTRACT. Wing-reduction among the Coccinellidae occurs in less than 100 species. Wing-polymorphism in *Rhyzobius litura* (F.), *R.chrysomeloides* (Herbst) and *Subcoccinella 24-punctata* (L.) varies throughout the geographical ranges of the species. The incidence of wing-polymorphism in British *Subcoccinella* has varied markedly over the last 160 years. Wing-polymorphism in *Subcoccinella* is not sex-linked and is under complex control, influenced in some way by environmental or population stability.

Introduction

Reduction of the flight wings in such coleopterous families as Carabidae, Staphylinidae, Tenebrionidae and Curculionidae is well known and for some of these groups there is a considerable body of literature concerning its occurrence, significance, evolution and inheritance (e.g. Darlington, 1936, 1943; Jackson, 1928). Brachyptery among the Coccinellidae is relatively uncommon and it would appear that, as yet, no attempt has been made to study its manifestation in this family. In some 3500 described species, less than 100 instances are known to the author. Apart from the subfamily Tetrabrachynae (Lithophilinae) where total aptery is the rule in all of the sixty described species, wing reduction is exhibited in the Coccinellidae by a few species of *Rhyzobius* and allied genera and in the phytophagous subfamily Epilachninae by *Subcoccinella 24-punctata* (L.) and *Cynegetis impunctata* (L.). In most cases the wing reduction is constant and accompanied by diminution or total obliteration of the humeral callosities on the elytra. However, in *Subcoccinella 24-punctata, Rhyzobius litura* (F.) and *R.chrysomeloides* (Herbst) the callosities are clearly visible, though reduced, and the wing development is polymorphic. The existence of wing polymorphism in *Subcoccinella* was commented on recently by Crowson (1972). Following his note and a suggestion by Dr V. F. Eastop of the Department of Entomology, British Museum (Nat. Hist.), the author took the opportunity of studying all the material of *S.24-punctata* in the British Museum (Nat. Hist.), London, the Naturhistoriska Riksmuseet, Stockholm, and a long series from Jugoslavia, subsequently broadening the investigation to include a survey of the Coccinellidae as a whole. The results have made possible the preceding generalizations and the presentation of the following detailed accounts of wing polymorphism in *Subcoccinella 24-punctata, Rhyzobius litura* and *R.chrysomeloides.*

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Rhyzobius

Rhyzobius Stephens is a genus including more than eighty described species, most of them from Australia and New Zealand. *R.litura* and *R.chrysomeloides* are the only species known to occur in Europe. (A third species, *R.bipartitus* Fuente, 1918, described from two specimens collected at Segorbe (Castellon), eastern Spain, is almost certainly a synonym of *R.chrysomeloides*). They are very closely related, variable in appearance and difficult

to separate on external characters alone. Both are widespread on the continent, although the relative abundance of each varies from one area to another. There has been confusion in identification and much of the evidence from the literature concerning distribution and biology must be regarded as unreliable. Using Bielawski's (1955) monographic treatment of the two species to confirm the identities of specimens housed in the Museum, it is possible to state that *R.chrysomeloides* appears to be confined to continental Europe and North Africa, whereas *R.litura* has a wider distribution, including the British Isles, where it is widespread and common, and also such islands as Madeira, the Canaries and the Azores.

Of the 101 specimens of *R.chrysomeloides* examined, eighteen (18%) had fully-developed wings. In the remainder, the wings were reduced to narrow, ribbon-like structures, usually reaching to about the level of the third abdominal segment. Little variation was noted in the size and appearance of the reduced wings. Table 1 summarizes the data associated with the material, which was collected over the last 120 years.

One hundred and four examples of non-British *R.litura* included thirty-one (29.8%) with fully-developed wings. The brachypterous specimens had the wings reduced in a manner similar to that typical of *R.chrysomeloides*. Table 2 summarizes the data associated with the material. The dates of capture and general geographical coverage are similar for both species, but, as can be seen, a majority of the *litura* specimens came from Spain, Madeira, the Canaries and the Azores, whereas in the case of *chrysomeloides* the largest series was from France.

Examination of available material of *R.litura* from the British Isles produced results in sharp contrast with those obtained from continental specimens. 333 specimens included only twenty-three (7%) fully-winged individuals. The material included all the specimens from the J. F. Stephens Collection, all the material in the 'Amalgamated British collections' (see note under *S.24-punctata* below) and a few in the general collections of the Museum. They cover a wide range of localities and the dates of capture extend from about 1812 to the present year. The data associated with the fully-winged forms disclosed no clear pattern, either of locality or date. However, one point which did emerge from the analysis was that the highest proportion of fully-winged forms among the material taken by a single collector was six out of twenty-one (28.5%), a figure approaching the average rate of occurrence among all non-British examples examined. The data associated with the British material of *R.litura* is summarized in Table 3.

Subcoccinella

Subcoccinella Agassiz is a monobasic genus. *S.24-punctata* (L.) is widespread in Europe

TABLE 1. *Rhyzobius chrysomeloides*, all specimens

Country of origin	No. of specimens	Fully winged	Brachypterous
France	51	10	41
Switzerland	6	0	6
Spain (incl. Gibraltar)	2	1	1
Portugal	1	0	1
Czechoslovakia	1	0	1
'Europe' (?France)	14	2	12
Europe (no further data)	5	1	4
'N. Africa' (no further data)	7	0	7
Tunis	1	1	0
Algeria	7	1	6
Syria	1	0	1
Sardinia	4	2	2
Jersey	1	0	1
Totals	101	18	83

TABLE 2. *Rhyzobius litura*, non-British specimens

Country of origin	No. of specimens	Fully-winged	Brachypterous
France	8	1	7
Spain (incl. Gibraltar)	21	11	10
Germany	2	0	2
Italy	1	1	0
Hungary	2	0	2
Greece	1	0	1
'Europe' (?France)	7	6	1
Egypt	2	0	2
Tangier	2	1	1
Tunis	1	0	1
Guernsey	2	0	2
Malta	8	4	4
Sardinia	1	0	1
Sicily	1	0	1
Corfu	1	0	1
Canary Is.	16	0	16
Madeira	14	1	13
Azores	14	6	8
Totals	104	31	73

TABLE 3. *Rhyzobius litura*, British specimens

Source of material	No. of specimens	Fully-winged	Brachypterous
J. F. Stephens coll. (1812–35)	26	6	20
J. A. Power coll. (1861–73)	19	0	19
D. Sharp coll. (1863–1916)	51	3	48
G. C. Champion coll. (undated)	21	6	15
H. Donisthorpe coll. (1892–1923)	11	2	9
C. J. Saunders coll. (1923–33)	11	1	10
C. E. Tottenham coll. (1917–67)	81	4	77
Various small colls. (*c.* 1880–1974)	10	1	9
V. F. Eastop coll. (1965–76)	103	0	103
Totals	333	23	310

from Scandinavia (recorded from as far north as southern Nordland in Norway (66°N)) to the Mediterranean and generally distributed in the British Isles from the south coast as far north as Jura and the river Tweed in Scotland. There are records for a number of Welsh counties, both in the north and south, but in Ireland the species appears to be restricted to county Antrim in Ulster. Very recently (first recorded in 1972), *S.24-punctata* has been discovered as an established immigrant in the U.S.A. (Gordon, 1975, p. 206).

The wing structure seen in brachypterous examples differs from that developed by the two species of *Rhyzobius*. In *Subcoccinella* the appendages are usually oval, or elongate-oval, often barely reaching the hind border of the metasternum. In a few specimens, one from Hungary, one of the more northerly Swedish specimens, three from Jugoslavia, and

TABLE 4. *Subcoccinella 24-punctata*, non-British specimens

Country of origin	No. of specimens	Fully-winged	Brachypterous	Remarks
France	46	7	39	Localities of fully-winged forms scattered
Spain (incl. Gibraltar)	34	14	20	Localities of fully-winged forms scattered
Germany	12	9	3	Fully-winged forms restricted to S. and E. Germany
Austria	11	2	9	Both fully-winged examples from east Austria
Switzerland	12	0	12	
Italy (incl. Sicily)	18	0	18	Localities mostly N. and N.E., mainly alpine
Sweden	91	29	62	Most fully-winged forms from extreme south
Denmark	1	1	0	
Poland	4	2	2	All specimens from southern Poland
Czechoslovakia	23	15	8	Most specimens from near Prague
Hungary	10	6	4	One brachypterous specimen showing intermediate wing-development
Jugoslavia	428	424	4	
Albania	1	1	0	
Greece	14	12	2	
Corfu	3	1	2	
Crete	2	2	0	
Turkey	14	14	0	
Syria	2	0	2	
W. Iran	3	0	3	All specimens show intermediate wing-development
Morocco	1	1	0	
Guernsey	13	0	13	
Totals	743	540	203	

three from western Iran, much longer, but still obviously reduced and non-functional wings were found.

A larger sample of material, together with better documentation in the literature, has allowed a more detailed analysis of the data than was justifiable with the two species of *Rhyzobius*. There has been no confusion over identification and in parts of southeastern Europe the species is of economic interest. Data from 400 British specimens and 743 from continental Europe are summarized in Tables 4 and 5. Fig. 1 shows how the incidence of fully-winged forms was found to vary geographically. The picture seems quite clear: in Europe, fully-winged individuals predominate in the southeast, Greece, Turkey, Crete, Jugoslavia and Albania so far yielding minimal evidence for the existence of brachyptery among their populations of *Subcoccinella*. The fact that fully-winged forms appear to be distinctly commoner in the Iberian peninsula than in France prevents the European distribution being regarded as a simple northwest/southeast cline, but it is perhaps significant that the figure for the peninsula includes a single series of six fully-winged specimens from Gibraltar. The situation in the U.S.A. has been investigated by means of a series of eighteen specimens, collected in various states during 1974 and kindly supplied by Dr R. Gordon of the United States Department of Agriculture. As with the material from Greece and Turkey,

TABLE 5. *Subcoccinella 24-punctata*, British specimens

Source of material and dates	No. of specimens	Fully-winged	Brachypterous
J. F. Stephens coll. (1812–35)	67	16	51
J. A. Power coll. (1857–66)	26	3	23
D. Sharp coll. (1862–68+ undated material)	72	0	72
G. C. Champion coll. (undated)	23	0	23
H. Donisthorpe coll. (1893–1945)	29	1	28
C. J. Saunders coll. (1923–36)	21	0	21
C. E. Tottenham coll. (1919–59)	97	0	97
Various small colls. (*c.* 1880–1973)	32	0	32
P. M. Hammond, London, 1974	19*	2	17
P. M. Hammond, Essex, 1975	1	0	1
V. F. Eastop, Kew, Surrey, 1975	1	0	1
V. F. Eastop, Kew, Surrey (1975–76)	12	4	8
Totals	400	26	374

* A female and eighteen reared offspring, see text.

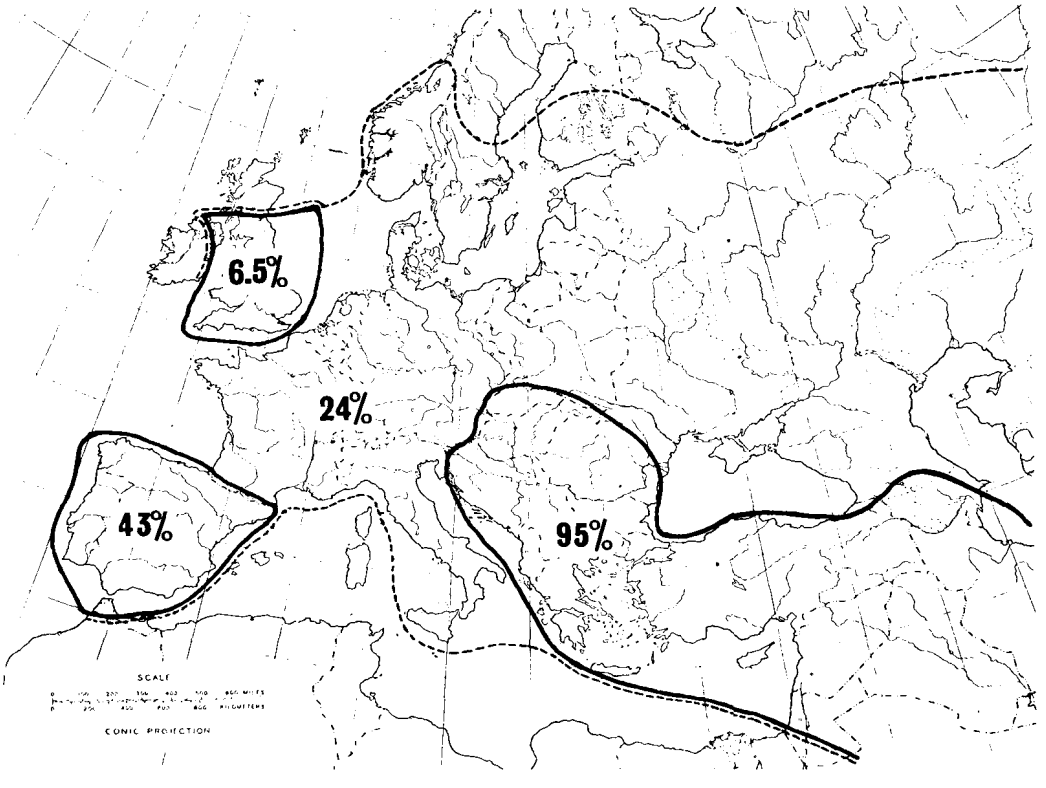

FIG. 1. *Subcoccinella 24-punctata.* Regional variation of fully-winged individuals. The dotted lines represent the recorded northern and southern limits of the species.

every specimen had fully-developed wings.

The frequency of fully-winged forms among the British material (6.5%) is much lower than the average figure for northern and central Europe (24%), a situation reminiscent of that found in the case of *Rhyzobius litura*. However, a detailed investigation of the dates and places of capture relating to fully-winged British specimens yielded some remarkable results. The collections of J. F. Stephens, mainly based on London and largely assembled between 1812 and 1835, include sixty-seven examples of *S.24-punctata*, sixteen of them (24%) being fully-winged. The 'Amalgamated British collections' of Coleoptera, including those of Power, Sharp, Donisthorpe, Champion, Saunders, Tottenham and others were made between about 1845 and 1969. They contain material collected in many parts of the British Isles and their total for *Subcoccinella* is 300 specimens. Of these, four (1.3%) were found to have fully-developed wings. Two were taken at Henley, Oxon., in 1858, one at Mickleham, Surrey, in 1861 and one at Streatley, Berks., in 1924. A further contrast was discovered among the most recently collected material available. A single male, taken near Kew Gardens, Surrey, in August 1975 was found to be brachypterous, as was a female collected at Nevendon, Essex, during the same month. On the other hand, a small series (twelve specimens) collected near Kew Gardens during March and April of 1975 and 1976 included four (33%) fully-winged individuals. In addition, a single gravid female with fully-developed wings, captured at Turnham Green, London in 1974, laid eggs from which eighteen adults were successfully reared (Richards *et al.*, 1976) and one of the progeny had fully-developed wings.

An attempt to correlate the recent history of *S.24-punctata* in the British Isles with the discoveries set out above produced a number of interesting points. J. F. Stephens (1832, p. 391) commented that to him the species was 'very abundant in hedges and grassy places throughout the metropolitan district' and that it was 'mostly winged'. J. A. Power's material (collected between 1857 and 1866) totalled twenty-six specimens, of which fifteen were taken between 1857 and 1861, ten of these being from two localities during the latter year. W. W. Fowler (1888, p. 157) regarded the species as 'locally common' in the south, 'apparently very rare in the Midland counties' and 'rare in Scotland'. More recent writers, such as N. H. Joy (1932, p. 521) and E. F. Linssen (1959, p. 47) simply record the species as widespread, but local. Collecting records for the Kew Gardens area between 1963 and 1976 (Eastop & Pope, 1966, p. 288; 1969, p. 163; and unpublished data) show a marked rise in the number of individuals taken between 1967 and 1970 (90, 102, 174 and 125) compared with those captured between 1964 and 1966 (1, 33 and 6).

Using the material from the Stephens collection and twenty-two examples from Czechoslovakia (one of the series of twenty-three lacked an abdomen) the relationship between wing development and sex was investigated. Stephens' sixty-seven specimens consisted of seventeen *males* and fifty *females*. Of the sixteen fully-winged examples among his material, four were *males*, twelve *females*. Thus, the *male/female* ratio of the whole series was almost perfectly maintained among the fully-winged forms. The twenty-two specimens from Czechoslovakia included nine *males* and thirteen *females*. The fourteen fully-winged examples in the series comprised six *males* and eight *females*. This gives a *male/female* ratio for the entire series of 41/100 and for the fully-winged forms alone of 43/100.

A series of carefully controlled breeding experiments, backed up by systematic, environmental-correlated collecting over a period of years might disclose the mechanisms determining wing development in *S.24-punctata* and show how external factors may influence the process. In the meantime, certain inferences seem possible from the results so far obtained and the available information concerning the distribution and ecology of the species.

Firstly, the specimens from the Stephens collection and those from Czechoslovakia show quite clearly that the distribution of fully-winged forms in a population occurs irrespective of sex.

Secondly, it is clear that, although not simply expressed over a considerable part of the distribution of the species, brachyptery is dominant in *Subcoccinella*. The appear-

ance of one fully-winged individual among eighteen progeny from a fully-winged female and the discovery of a few cases of intermediate wing development support the suggestion that modifiers operate on the normal inheritance.

Thirdly, the distribution of fully-winged forms (Tables 4 and 5, Fig. 1) is supported by evidence from the literature (Mulsant, 1846, p. 208; Grandi, 1913, p. 298) Yakobson, 1905–15, p. 970; Porta, 1929, p. 244; Tanasijevic, 1958) and seems to be, at least in part, explicable in terms of the relative stability of either the species, the environment, or both. Over most of Europe, a balanced polymorphism exists, fully-developed wings occurring at an average rate of 26.5%. The recent appearance in America provides a special circumstance. The extreme instability of an expanding population, establishing itself in a new territory could well result in a predominance of fully-winged forms (Darlington, 1943, pp. 43–44). On the other hand, the offspring of a single fully-winged female, mated with a flying male, would be a generation entirely lacking in the genes for brachyptery. A parallel case exists in the palaearctic weevil *Sitona hispidula* (F.), first recorded from the United States in 1876 (Jackson, 1928, pp. 689–691).

In Britain, *S.24-punctata* has been in a contracting phase for most of the last 140 years and shows a corresponding diminution of fully-winged forms. Above-average incidence of fully-developed wings is clearly linked with the periods of instability associated with an unusual increase in population density.

The high incidence of fully-winged individuals in southeast Europe and the Near East (95%) may, perhaps, be explained in terms of climate, flora and land use. *S.24-punctata* can complete its lifecycle on plants from several families (Tanasijevic, 1958, p. 44). However, the most favoured foodplant is Lucerne (*Medicago sativa* (L.)), thought to have had its origins in western Iran (Belov, 1929; Klinkowski, 1933) and abundant naturally in several forms throughout southeast Europe, which is where Lucerne is cultivated on a very large scale and also where *Subcoccinella* is regarded as a pest. Cultivated Lucerne is mown to within a few inches of the ground several times each year, including during the hottest parts of the summer (Tanasijevic, 1958, p. 49). This not only removes most of the food available to the beetles in the fields, but drastically reduces the amount of shade at a time when the temperature may reach 37°C. Thus, for a significant proportion of the population, the environment will be highly unstable and there will be strong selective pressures against brachyptery.

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