

## The world distributions of species within the *Enoplognatha ovata* group (Araneae: Theridiidae): implications for their evolution and for previous research

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### Summary

The world distributions of species within the *Enoplognatha ovata* group (*sensu* Hippa & Oksala, 1983b) — *E. ovata s.s.*, *E. latimana*, *E. afrodite*, *E. penelope* and *E. margarita* — are described for the first time. *E. ovata s.s.* and *E. latimana* are widespread in Europe and in North America, while the other three species are more limited in their ranges. The concentration of species in the Mediterranean region may suggest this as a possible centre of origin for the group, although alternative explanations cannot be eliminated. The status of previous work on *E. ovata s.l.* is discussed in the light of the distributions of the five sibling species.

### Introduction

The spider *Enoplognatha ovata* (Clerck) has been the specific subject of a number of studies during the past 60 years. Most have concerned the striking colour and pattern polymorphism found in virtually all populations (e.g. Bristowe, 1931; Geyer, 1967; Hippa & Oksala, 1979, 1981; Oxford, 1976, 1983, 1985a; Oxford & Reillo, in press; Oxford & Shaw, 1986; Reillo, 1989a; Reillo & Wise, 1988a,b,c; Tweedie, 1970; Wise & Reillo, 1985), but the genetics of other phenotypic variation (Oxford, 1983, 1985b, 1989; Reillo & Wise, 1987), post-embryonic development (Seligy, 1971), allometric growth (Lockett, 1932), biochemistry of pigments (Seligy, 1969, 1972), parasitism by mites (Reillo, 1989b), reproductive strategies (Hippa & Oksala, 1981), fecundity (Tarwid, 1984), ecology (Juberthie, 1954; Stevenson & Dindal, 1982) and the physiological effects of industrial pollution (Zimakowska-Gnoińska & Tarwid, 1984) have also received attention. In all these studies it was assumed that *E. ovata* is a single, widely distributed species.

In the early 1980s, Hippa & Oksala (1982) re-examined material from western Europe and discovered within *E. ovata* three sibling species, *E. ovata sensu stricto*, *E. latimana* Hippa & Oksala and *E. penelope* Hippa & Oksala. Further examination of material from the Mediterranean region together with published information from Japan added another two species, *E. afrodite* Hippa & Oksala and *E. margarita* Yaginuma (Yaginuma, 1964), to what Hippa & Oksala described as the *Enoplognatha ovata* group (Hippa & Oksala, 1983b).

Hippa & Oksala (1983b) deduced the cladogenesis of species within this group on the basis of morphological characteristics (Fig. 1).

Obviously the presence of previously unrecognised sibling species may complicate interpretation of the results of the studies cited above, but this will depend on the geographical ranges of the species concerned. In this paper, we present information on the world distributions of the five sibling species presently placed in the *Enoplognatha ovata* group, and consider the implications for their evolution and for previous work.

### Materials

Hippa & Oksala (1982, 1983a,b) gave the locations of collected material in their original descriptions of species. We collected many specimens from France, The Netherlands, Germany, Switzerland and Italy during August 1991 (Oxford & Reillo, in press). Information for the British Isles is based on a number of surveys (Oxford, 1985a, 1991, 1992; Snazell, 1983), augmented with unpublished records from members of the British Arachnological Society. Distributional data from Belgium, Switzerland and the French Pyrenees came predominantly from recent surveys (Van Keer & Vanuytven, in prep.; Maurer & Hänggi, 1990; Bosmans & De Keer, 1985, respectively). All other data are from examination of museum material of *E. ovata sensu lato* or determinations made by correspondents. Information based on personal or museum collections made before the revision of the group (Hippa & Oksala, 1982, 1983b) was rejected if it had not subsequently been re-examined by us or by the correspondent. Likewise, data from more recent collections were rejected if the correspondent was not aware of the revision and the material was not available for us to examine. All specimens available to the authors were determined by G. S. Oxford using the palp and epigyne characteristics described by Hippa & Oksala (1982, 1983a,b). Symbols on the accompanying maps may indicate individual spiders or one or more collections, each of a few to many spiders, from adjacent localities.

### Results

Of the five *Enoplognatha* species considered here, *E. ovata s.s.* and *E. latimana* are by far the most widely

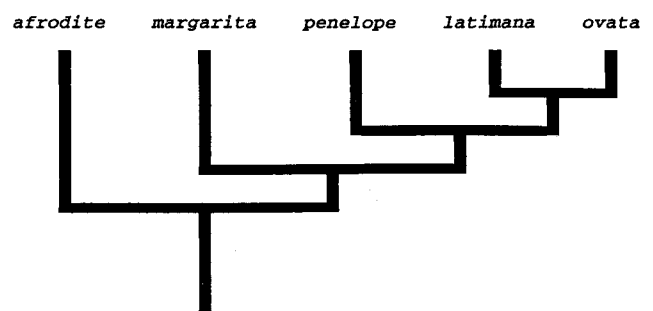


Fig. 1: Cladogram of species in the *E. ovata* group (after Hippa & Oksala, 1983b).

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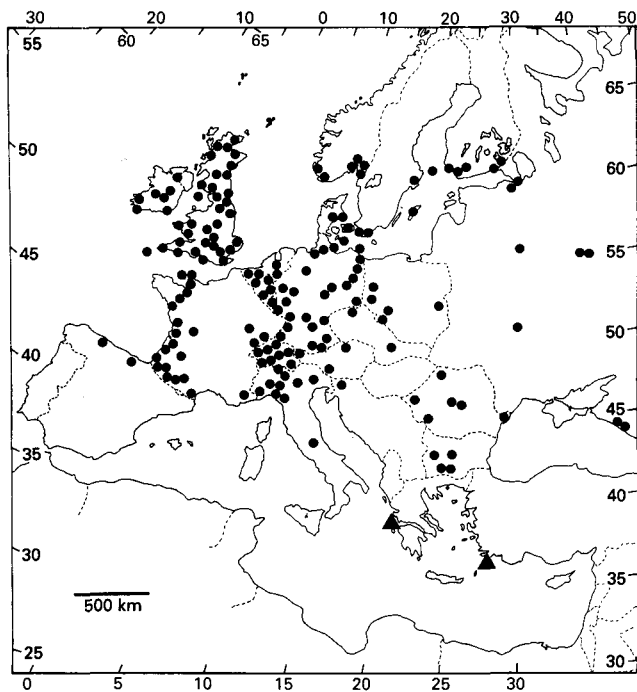


Fig. 2: Map of Europe showing the known distributions of *E. ovata s.s.* (closed circles) and *E. penelope* (closed triangles).

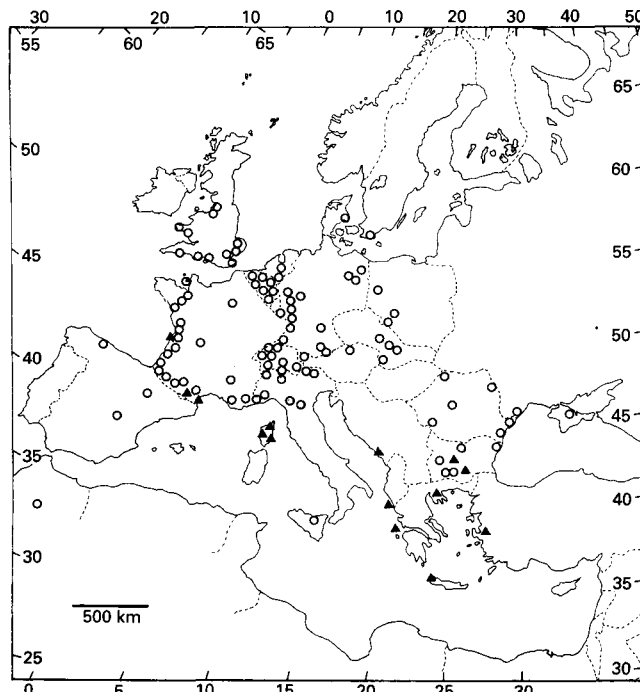


Fig. 3: Map of Europe showing the known distributions of *E. latimana* (open circles) and *E. afroditae* (closed triangles).

distributed (Figs. 2–6), being found in both North America and Eurasia and, for *E. latimana*, in North Africa. The other three species are more restricted, *E. afroditae* to the northern Mediterranean (Fig. 3), *E. penelope* to Greece (Fig. 2) and *E. margarita* to the Far East (Yaginuma, 1986, and pers. comm.). A report of *E. ovata s.l.* (as *Theridion venustum* Walck.) from Jerusalem, Israel by Cambridge (1872) is based on a misidentification of an immature *Steatoda triangulosa* (Walck.) (Levy & Amitai, 1981). Very few specimens were available from the Iberian peninsula, from central and southern Italy or from the former USSR, and this should be borne in mind when the distributions of the species are discussed. The following is a more detailed discussion of the distributions of individual species.

*E. ovata s.s.* (Figs. 2, 4, 5, 6)

In Eurasia, *E. ovata s.s.* occurs from the Atlantic coasts of Ireland and France eastwards to a line drawn from the Russian-Finnish border to the Caspian Sea (Figs. 2, 4). Locket, Millidge & Merrett (1974) record *E. ovata s.l.* as present on the Shetland Isles, UK, but no material was available for examination. The northerly limit of the species in the west of its range therefore roughly coincides with latitude 61°N. This limit may be lower further east but information from the former USSR is scanty. In the south, the species ranges to approximately latitude 42°N.

*E. ovata s.s.* occurs on the eastern and western sea-boards of the northern United States and southern Canada (Figs. 5, 6), ranging from latitude 40°N to 50°N on both coasts. In the west, most records are from a 200 km wide coastal strip but a small number of localities are much further inland. On the east coast, the

species is widespread up to 1000 km inland. Additional distributional data from the east coast is provided by samples of *E. ovata s.l.* containing the plain red (*ovata*) colour morph (Wise & Reillo, 1985; Reillo & Wise, 1988a,c; Reillo, 1989a). As far as is known, this particular morph is restricted to *E. ovata s.s.*, although the other principal colour morphs (*lineata* and *redimita*) are common to both *E. ovata s.s.* and *E. latimana* (Snazell, 1983; Oxford, 1991, 1992; Oxford & Reillo, in press).

*E. latimana* (Figs. 3, 4, 5, 6)

*E. latimana* in continental Eurasia is found from the west coast of Wales and the Atlantic coast of France through central southern Russia (Tadzhikistan and Kirgizia) (Figs. 3, 4). In the west, its northern latitudinal

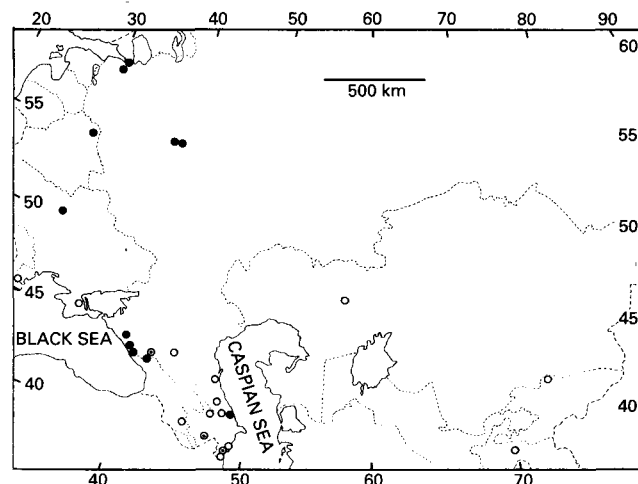


Fig. 4: Map of the former USSR indicating the known eastern ranges of *E. ovata s.s.* (closed circles) and *E. latimana* (open circles). Open circles enclosing a dot represent mixed species samples.

boundary is at about 56°N (53° 30'N in Britain). Further east, this northern limit seems to move progressively southwards and in the former USSR occurs at about latitude 45°N. The southern boundary is approximately at latitude 42°N but seems to be further south on the Iberian and Italian peninsulas. Two collections of *E. ovata s.l.* from montane habitats (1600 m) in Morocco (Jocqué, 1977) have been re-examined by both R. Jocqué and G. S. Oxford and are definitely *E. latimana* (Fig. 3). They represent the first record of this species from the African continent.

Apart from a single male from Port-au-Saumon, Quebec (Fig. 5), in North America *E. latimana* appears to be confined to the west coast (Fig. 6). Here it ranges from northern California (latitude 41°N) to central British Columbia (latitude 54°N). As for *E. ovata s.s.*, most locations are in a 200 km wide coastal strip, but a few are considerably further inland. Although sample sizes at the extremes of the ranges of these species are often very small, there is a suggestion that a higher proportion of the spiders from southern Oregon and California are *E. latimana*.

#### *E. afrodite* (Fig. 3)

This species has a northern Mediterranean distribution which, with the exception of one record from the west coast of France, is restricted to south of latitude 43°N. Many collections have been made from Corsica and all are *E. afrodite*. Canard (1989) records *E. ovata* from the island but gives the sampling dates of mature spiders as March and July/August. These dates agree with information for *E. afrodite* (Oxford, unpublished)

which suggests that the species may have two generations per year. It is probable, therefore, that Canard's specimens were *E. afrodite*, and indeed, this may be the only species in the *E. ovata* group on Corsica. It seems likely that *E. afrodite* will be found in other northern Mediterranean countries, on other islands and possibly elsewhere.

#### *E. penelope* (Fig. 2)

To date only two records of *E. penelope* are available, both from Greek islands. Whether this is a true reflection of a very limited distribution or a result of poor recording remains to be seen.

#### *E. margarita*

This species was first described from montane habitats (900 m and 1300 m) in Nagano Prefecture, Honshu, Japan, by Yaginuma (1964). Later, Matsuda (1985, 1987) recorded it from the Taisetsuzan National Park and the Tokachi plain on Hokkaido, where it is common on low plants and bushes (M. Matsuda, pers. comm.). *E. margarita* has also been found in Korea and China (T. Yaginuma, pers. comm.; Y. M. Marusik, pers. comm.), Inner Mongolia (eastern slopes of the Great Khingan Range), and Maritime Province and Sakhalin (both in the former USSR) (Y. M. Marusik, pers. comm.). The belief that *E. ovata* (as *Theridion redimitum*) occurs in Japan (Bristowe, 1939: 61) may be based on a misidentification of *E. margarita*.

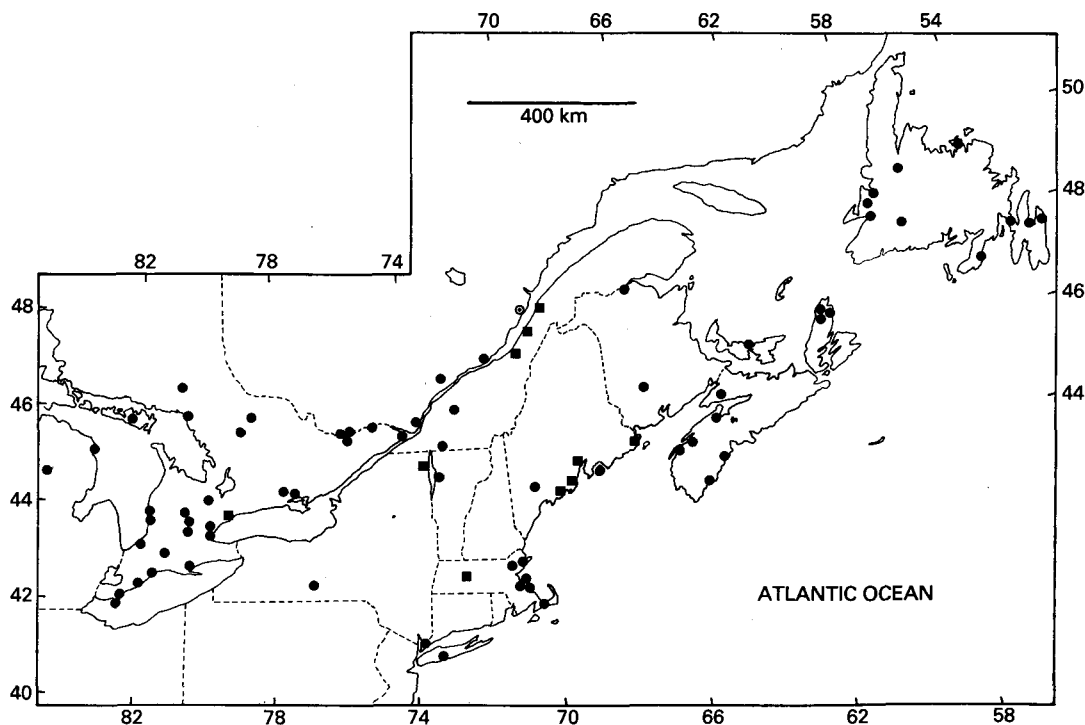


Fig. 5: Map of eastern central North America showing the known distributions of *E. ovata s.s.* (closed circles) and a mixed species population with *E. latimana* (open circle with dot). Closed squares denote sites from which the *ovata* morph of *E. ovata s.l.* has been reported (Reillo, 1989a; Reillo & Wise, 1988a,c; Seligy, 1971; Wise & Reillo, 1985); since this morph has yet to be found in *E. latimana*, these almost certainly represent individuals of *E. ovata s.s.*

## Discussion

For many years, *E. ovata* was regarded as a cosmopolitan species (Bristowe, 1939; Levi, 1967), showing marked intraspecific variation in epigyne and palp characteristics (Levi, 1957, 1967). The recognition that *E. ovata s.l.* actually comprises five species helps to explain some, but by no means all, of this variation in reproductive structures (Hipps & Oksala, 1982, 1983a; Oxford, unpublished).

The broad distributions in Europe suggest that the species may differ in their latitudinal tolerance, possibly as a result of climatic factors. Thus, *E. ovata s.s.* is found the furthest north, occurring throughout the British Isles and over the southern parts of Scandinavia. (*E. ovata s.l.* is reported throughout southern Sweden (S. Almquist, L. J. Jonsson, pers. comm.) although only a few specimens have been positively identified as *E. ovata s.s.*). *E. latimana* occurs in the southern half of Britain and in the Scandinavian countries has been found only on the southernmost tip of Sweden (L. J. Jonsson, pers. comm.). The southern limits of both species seem to be about the same in eastern Europe. There is, however, some suggestion that the southern limit of *E. latimana* in western Europe may be at lower latitudes than *E. ovata s.s.*, and lower than it is further east. This may reflect either the moderating influence of the Atlantic Ocean and/or the absence of congeners, e.g. *E. afrodite*. If *E. latimana* does have a more southerly distribution than *E. ovata s.s.*, then the relative proportion of the former in mixed species populations might be expected to increase

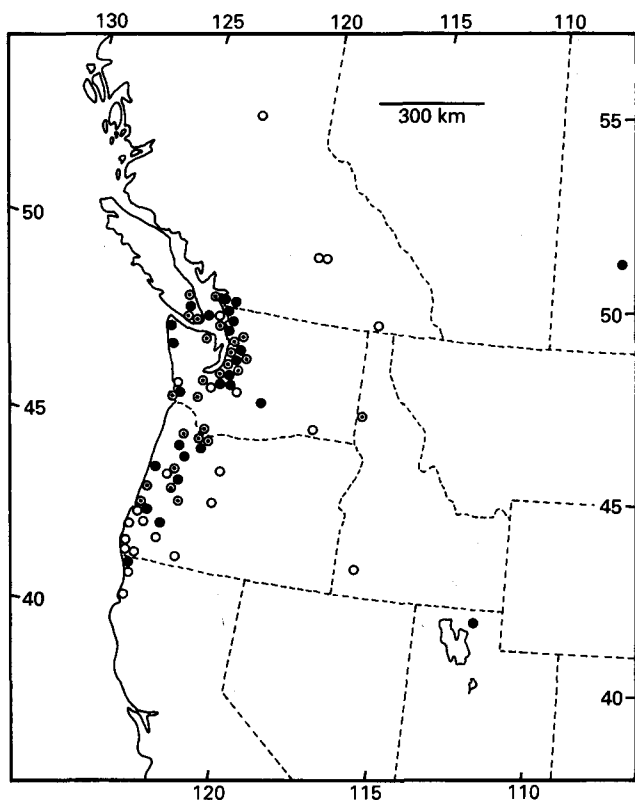


Fig. 6: Map of western central North America showing the known distributions of *E. ovata s.s.* (closed circles) and *E. latimana* (open circles). Open circles enclosing a dot represent mixed species samples.

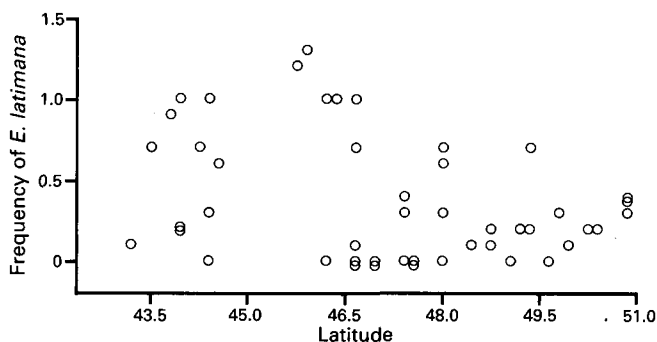


Fig. 7: Plot of frequency of *E. latimana* against latitude in mixed-species samples ( $n = 47$ ) of *E. latimana* and *E. ovata s.s.* from western Europe containing 20 or more individuals. Frequencies are arcsine transformed (radians). The weighted regression equation describing the relationship is:  $\text{freq. latimana} = 3.385 - 0.065 * \text{latitude}$  ( $p = 0.009$ ). Weights used are individual sample sizes.

with decreasing latitude. An analysis of the proportion of *E. latimana* in samples taken along two, approximately north-south, transects in this region (Oxford & Reillo, in press) suggests that this is the case. In collections consisting of 20 or more individuals, the frequency of *E. latimana*, as a proportion of *E. latimana* plus *E. ovata s.s.*, is significantly negatively associated with latitude (weighted regression coefficient =  $-0.065$ , d.f. = 45,  $p = 0.009$ ; weights = sample size, frequencies arcsine transformed) (Fig. 7). Although there is, not surprisingly, a large amount of variation between samples, the general trend is for *E. latimana* to become relatively more common further south. A similar pattern may be present on the west coast of North America (Fig. 6). Large samples taken at altitude in the Swiss Alps (Oxford & Reillo, in press) yielded just one individual of *E. latimana*, which again is consistent with this general thesis.

The northern limit of *E. afrodite* appears to be the south coast of France, while *E. penelope* seems to be confined, as far as is known, to the Greek islands. A climatic influence on distribution is also suggested by the apparently progressive reduction in the northerly limit of *E. latimana*, compared with *E. ovata s.s.*, with distance into the Eurasian landmass (Figs. 3, 4). However, data in these areas are scarce and these patterns may be misleading.

It is also the case that species may become more specialised in their habitats at the extremes of their distributions. For example, *E. latimana*, at the northern edge of its range in Britain, tends to be found in dry, very sunny sites (e.g. open heathland, cliff tops, sand dunes and chalk grassland) often associated with the coast (Fig. 3) (Snazell, 1983; Oxford, 1991, 1992). In south-eastern England populations also occur further inland, but in similar sorts of open, often pioneer, habitats (Oxford, 1992; P. R. Harvey, pers. comm.). In Sweden, the one known population lives on a 40 m high, south-facing gravel/sand ridge (esker) just a few metres from the shoreline, and therefore conforms to the same pattern (L. J. Jonsson, pers. comm.). Elsewhere in Europe, however, *E. latimana* is widespread and occurs in much the same habitats as *E. ovata s.s.* (Oxford &

Reillo, in press). The most southerly and easterly records of *E. latimana* are all from montane regions where the species is presumably tracking a favoured habitat by adjusting its altitude.

Hippa & Oksala (1982) suggested that both *E. ovata s.s.* and *E. latimana* occur in North America, citing as evidence drawings of male palps and female epigynes in Levi (1957). This is now confirmed. Levi (1957) argued that because different species in the genus *Enoplognatha* are found in Europe and in North America, the two that are common to both continents (*E. ovata s.l.* and *E. thoracica*) have probably been introduced into North America from Europe. If this is the case, introductions would be expected to occur infrequently and the chances of transportation of not one but two species of the *Enoplognatha ovata* group from Europe might seem extremely remote. However, in western continental Europe at least, a very large proportion of populations contain both species (Oxford & Reillo, in press). If the North American representatives of these species really were imported, and the source was western Europe, then the chance of *both* species being introduced is high. Of course the reverse hypothesis, that *E. ovata s.s.* and *E. latimana* were introduced into Europe from North America, cannot entirely be eliminated, but seems less likely.

The earliest museum specimens of *E. ovata s.l.* from North America that we have discovered were taken by J. H. Emerton in Beverley, Mass. in 1872 and 1880 (individuals were either immature or the epigyne had been removed, but the nature of the black spotting suggests *E. ovata s.s.*). *E. ovata s.s.* was positively identified in collections from Beverley (1904) and Victoria, B.C. (1905), indicating that the species was present on both coasts at the turn of the century. The earliest record of *E. latimana* was from Seattle, Wash. (1928). Collections made in the 1920s and 1930s show a wide geographical distribution of both species on the west coast (Washington, Oregon and, for *E. ovata s.s.*, northern California). If introduced, the present distributions of both species may, to some extent, reflect the randomness of continuing secondary colonisations. Thus the apparent extension of *E. latimana* considerably further north than *E. ovata s.s.* on the west coast, contrasting as it does with the situation in Europe, may reflect chance introductions of this species but not *E. ovata s.s.*

What are the implications of the distribution patterns outlined above for the evolution of species in the *Enoplognatha ovata* group? Conclusions must, of course, be tentative but the increase in the number of species as one progresses from north to south in continental Europe (*ovata s.s.*; *ovata s.s.* + *latimana*; *ovata s.s.* + *latimana* + *afrodite*) might indicate that the group evolved in the Mediterranean region. Alternatively, the present-day distributions of species might merely reflect different rates of recolonisation of northern Europe from more southerly refugia after the last glaciation some 10,000 years ago (Harland *et al.*, 1989). If this is the case, they throw no light on where (and when) speciation events occurred. However, ecological information for at

least *E. ovata s.s.* and *E. latimana* suggests that there are real differences between them and that current limits of distribution may be determined by environmental factors, rather than by time. Consistent with a Mediterranean origin for the group is the fact that *E. afrodite* is widespread on, and *E. penelope* apparently restricted to, Mediterranean islands; these may have played a role in isolating populations during allopatric speciation events.

*E. margarita* from the Far East poses a problem for the Mediterranean centre-of-origin hypothesis since, according to the cladogram presented by Hippa & Oksala (1983b) (see Fig. 1), it is more closely related to *E. ovata s.s.*, *E. latimana* and *E. penelope* than these three are to *E. afrodite*. Possibly the true affinities of *E. afrodite* and *E. margarita* are different from those suggested in the cladogram, and structural similarities within the group may have arisen by convergence. Certainly, decisions about which characters are considered apomorphic (derived) and which plesiomorphic (ancestral) seem to contain an arbitrary element. An alternative hypothesis is that the present geographical ranges of species in the *E. ovata* group could represent relics of previously much wider distributions. Further speculation is not worth while but a more detailed knowledge of the species composition on Mediterranean islands might be revealing, as would a molecular genetic analysis of the whole *E. ovata* group. The latter would enable confirmation or refutation of the Hippa & Oksala cladogram. In addition, application of the molecular clock principle to the genetic divergence between species would indicate whether speciation events occurred during the last ice age (10–120,000 BP) or earlier. It might also help to decide whether the group has a Mediterranean origin or not.

Finally, as mentioned in the introduction, *E. ovata s.l.* had been the subject of considerable work in the past before the sibling species within the group were recognised. Should the conclusions of these studies be re-evaluated in the light of the taxonomic revision, and the distributions of the species given here? The majority of the investigations carried out on *E. ovata s.l.* have been done either in eastern North America or in Britain. We have shown above that *E. ovata s.s.* appears to be the only member of the group which is widespread in eastern North America, so this must have been the species investigated. In Britain, both *E. ovata s.s.* and *E. latimana* are present but the latter has a relatively restricted, predominantly coastal distribution and is unlikely to have had a radical effect on any conclusions. Certainly in Nidderdale, Yorkshire, where *Enoplognatha* has been the subject of intensive study (Oxford, 1976, 1983, 1985a,b, 1989; Oxford & Shaw, 1986), *E. ovata s.s.* is the only species present. Finland, where Hippa & Oksala (1981) worked, also has only *E. ovata s.s.* A survey in which confusion between *E. ovata s.s.* and *E. latimana* certainly did occur was that of Hippa & Oksala (1979). Indeed, it was among material collected during this work that *E. latimana* was first recognised. The ecological and toxicological studies in Poland (e.g. Tarwid, 1984; Zimakowska-Gnoińska & Tarwid, 1984)

may also have unwittingly involved more than one species. Finally, Juberthie's (1954) investigation of the life cycle of *E. ovata s.l.* in southern France concluded that there the species had two generations per year. It is possible that he was confusing two species, perhaps *E. ovata s.s.* or *E. latimana* and *E. afrodite*, or was working on single species *E. afrodite* populations. Thus, by chance, the vast majority of the published work on *E. ovata* appears to have concerned *E. ovata s.s.* alone.

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