# A revision of the genus *Gonatium* (Araneae: Linyphiidae)

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#### Summary

All the accessible species ascribed to the genus Gonatium have been examined, and probable synapomorphic genitalic characters for the genus have been identified. Two new taxa have been erected, viz. G. nipponicum n.sp. and G. cappadocium n.sp. G. cinctum Schenkel and G. opimum Oi are synonyms of G. japonicum Simon, and G. büttneri Schenkel is a synonym of G. rubens (Bl.). G. nemorivagum (O. P.-Cambridge), confused in the past with G. hilare (Thor.), is a separate species. G. rubens is replaced in N. America and Japan by the closely related species G. crassipalpum Bryant and G. nipponicum n.sp. respectively. A number of the reported Gonatium species have been removed from the genus; these are: G. amdoensis Schenkel (nomen dubium), G. convexum Kulcz., G. crassiventris Strand (nomen dubium), G. femineum Roewer, G. fuegianum Tullgren, G. griseolineatum Schenkel, G. lividulum Simon (nomen dubium), G. petrunkevitchi Caporiacco, G. rufum Caporiacco (nomen dubium) and G. strugaensis Drensky. The palps and epigynes of all the true Gonatium species are figured, and brief descriptions of the less common species are given.

### Introduction

The genus Gonatium was erected by Menge (1868) for the two European species Theridion cheliferum Wider (=Neriene rubens Blackwall) and Micryphantes isabellinus C. L. Koch (=Neriene rubellum Blackwall). Since that time, additional Gonatium species have been reported from Europe, China, Japan, north and central Africa, and north and south America. The revision of the genus which is reported in this paper was undertaken principally to identify apomorphic characters which are common to all species in the genus, and to establish whether all the reported species are correctly assigned to Gonatium. Examples

of all the recorded species (Roewer, 1942b; Bonnet, 1957; and references in Zoological Record from 1940 onwards) which could be obtained were examined during the course of the work. On the basis of the identified synapomorphies, it was established that a number of the reported species are not assignable to Gonatium. The commoner species of the genus have been well described in the literature, and redescriptions would be superfluous, but in order to illustrate the generic characters figures are given of the palps (or parts of the palps) and of the epigynes/vulvae of all the species. Brief descriptions of two new species and of the less well-known species are provided.

## Genus Gonatium Menge

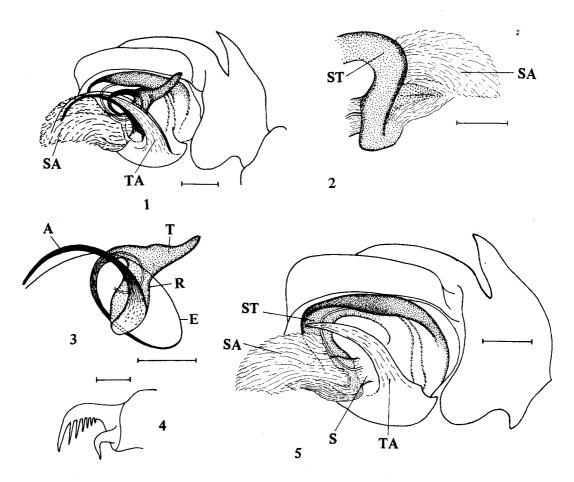
Gonatium Menge, 1868: 180 (type species Neriene rubens Bl.); Simon, 1884: 546, and 1926: 428, 429, 514; Roewer, 1942b: 628; Locket & Millidge, 1953: 229; Bonnet, 1957: 2031; Wiehle, 1960: 335.

The members of this genus have a total length of 2.0-3.7 mm, cephalothorax length 1.0-1.4 mm. The cephalothorax and legs are bright orange to orange-red, and the abdomen is also sometimes reddish, but these colours may fade in alcohol. In the male, the carapace is raised anteriorly, but there is no lobe; the males of some species have short sulci running back from the lateral eyes (Figs. 49-51). In both sexes the files on the lateral margins of the chelicerae are very weak. The abdomen is rather globular, with no scutum but with 4 impressed dots dorsally. The sternum is at least as broad as long, with coxae IV widely separated. The legs are relatively long and slender, with tibia I 1/d 6-9 (2). The tibial spines are 1111 in both sexes, though short and weak in the male; a trichobothrium is present on each metatarsus, with TmI 0.75-0.95 (Pd). In the male, tibiae I (and to a lesser extent tibiae II) are somewhat curved and swollen distally, furnished ventrally with numerous long hairs or bristles; there are paired rows of short spines ventrally on metatarsi I, reduced to stout bristles on metatarsi II, and femora I and II have numerous short spines or bristles ventrally. The tarsal claws are pectinate (Fig. 4), with narrow. needle-like teeth, similar in all the species. In the type species and three related species the femur of the male palp is swollen distally and armed with a stout

dorsal apophysis and numerous black pointed warts (Figs. 6-9); the palpal patella is almost globular in a few species (Figs. 29-31). The male palpal tibia is extended distally into an apophysis which is thin and semi-transparent on its outer side (Figs. 13, 75), and there are several additional apophyses towards the base of the tibia.

The paracymbium of the male palp is U-shaped, with the distal arm fairly short and pointed (e.g. Fig. 45). The palpal organ appears at first sight to be rather complex, but it has essentially the same pattern as in other genera which have a coiled embolus (Millidge, 1977). The tegulum is extended from the base on the mesal side into a lightly sclero-

tised apophysis; in the type and several other species this apophysis is long and narrow, pointed distally (e.g. Figs. 1, 5), but in others it is short and weakly developed (e.g. Fig. 42). The suprategulum (ST, Fig. 5) is stout and strongly sclerotised, curving downwards distally; the suprategular apophysis (SA), which has a membranous, plumose structure (SA, Figs. 1, 5), projects forwards from the distal end of the suprategulum and could be regarded as an extension of the stout translucent stalk (S) which carries the seminal duct to the embolic division. The embolic division (ED) (Figs. 3, 44, 73) comprises: i. a short tailpiece (T); ii. a radical (median) section (R); iii. a long thin embolus (E), forming a coil of about one



Figs. 1-5: Gonatium rubens. 1 male palp, mesal; 2 suprategulum and suprategular apophysis, ectal (embolic division removed); 3 embolic division; 4 tarsal claw, leg I; 5 male palp, mesal, embolic division removed. (A = apophysis of embolic division, E = embolus, R = radical section of embolic division, S = stalk, SA = suprategular apophysis, ST = suprategulum, T = tailpiece, TA = tegular apophysis). Seale lines 0.1 mm, except 4, 0.02 mm.

turn; and iv. a forward-directed pointed apophysis (A) which arises from the base of the radical section, and which is sclerotised to a variable degree. The ED is firmly attached to the ST, and attempts to break off the ED usually result in fracture of the SA rather than of the stalk. The basal part of the embolus runs beneath the ST posterior to the SA, and then downwards between the tegulum, which is hollowed out in this region, and the radical part of the ED, and emerges at the base of the tegular apophysis (Figs. 1, 47, 74). The distal part of the embolus then curves upwards and forwards, lying along the tegular apophysis (when this is long), the ED apophysis and the SA, which appear to act jointly as "conductor" for the embolus. All the Gonatium species have the palpal organs of the same basic pattern; the principal differences between the species lie in the length of the tegular apophysis, the length of the embolus, and the form of the ED apophysis which can be either sclerotised and narrow (e.g. Fig. 1) or more membranous and wider (e.g. Fig. 44).

The epigynes of all the Gonatium species have the same general pattern. Posteriorly the spermathecae are visible on either side of a roughly rectangular or semi-circular area enclosed by thick dark lines (e.g. Figs. 17, 58) which are the apodemal structures carrying the spermathecae and associated ducts. The shape of the enclosed area always shows some intraspecific variation. Anteriorly lie the entrances to the spermathecal ducts, these entrances being clearly visible in most of the species. The openings may be funnel- or tube-like, and can be large (e.g. Figs. 36, 60) or small (e.g. Figs. 17, 61), or partially concealed behind an overhang (Fig. 62). Some species have two cusp-shaped markings, which appear to be small pockets, on the epigynal surface adjacent to the spermathecae (Figs. 58-64). Internally, the spermathecal ducts arise on the dorsal side of the spermathecae, and in most species pass by an S-shaped pathway to the external openings; in two species, G. japonicum Simon and G. arimaense Oi, however, the ducts are lengthened considerably by the insertion of a coiled section into the normal pathway (Fig. 27). This lengthening of the internal ducts is associated, in Gonatium as in some other genera, with the presence in the males of these species of a particularly long embolus; a similar situation exists, e.g. in Spirembolus Chamberlin (Millidge, 1980), in Walckenaeria Bl.

(Millidge, in preparation), and in *Bathyphantes* Menge (Merrett, 1963).

The form of leg I of the males (the swollen tibia, and the ventral armature of bristles) seems to be characteristic of the genus, though somewhat similar characters can occur in some members of other genera, e.g. Satilatlas Keyserling and Grammonota Emerton (Millidge, in press).

The palpal organs of Gonatium differ from those of other genera which have a coiled embolus, by the form of the ED and of the SA, and by the presence of the particular form of the tegular apophysis. On current knowledge, the structure of the epigyne/vulva of the Gonatium species differs from those of other erigonine genera, particularly by the form and position of the genital openings. The conformation of the palpal organs and of the epigynes, as described above, are probably amongst the most recent derived characters of the group, and these synapomorphies support the hypothesis that the genus forms a monophyletic group.

The members of the genus can be recognised, in both sexes, by a combination of somatic characters, viz. the presence of a trichobothrium on metatarsus IV, the value of TmI, the presence of a single spine on each tibia, and the form of pectination of the tarsal claws (Fig. 4). The generalised character "tarsal claws pectinate" occurs in many families and must be regarded as plesiomorphic; the specific pattern of pectination in *Gonatium* is however different from that in *Walckenaeria*, *Tapinocyba* Simon and *Tiso* Simon, but a very similar pattern seems to be present in the genus *Oia* (Wunderlich, 1973).

#### Species included in the genus

On the basis of the present investigation, the genus *Gonatium* now comprises the following 16 species:

rubens group — G. rubens (Bl.)
G. crassipalpum Bryant
G. nipponicum new species
G. ensipotens (Simon)
rubellum group — G. rubellum (Bl.)

G. geniculosum Simon G. orientale Fage



Figs. 6-9: Male palps, ectal. 6 Gonatium rubens; 7 G. crassipalpum; 8 G. nipponicum; 9 G. ensipotens. Scale lines 0.1 mm.

hilare group — G. hilare (Thorell)

G. nemorivagum
(O. P.-Cambridge)

G. occidentale Simon

G. biimpressum Simon

G. cappadocium new species

G. paradoxum (L. Koch)

G. davense Simon

japonicum group - G. japonicum Simon

G. arimaense Oi

The species fall as shown into four groups, which are characterised as follows:

rubens group:

- (a) the palpal femur is widened distally and bears a pointed apophysis and numerous black pointed warts (Figs. 6-9);
- (b) the distal tibial apophysis is long and curved, and there is a stout basal apophysis (Figs. 13-16);
- (c) the tegular apophysis is long (Fig. 1);
- (d) the epigyne is of the form shown in Figs. 17-21, with the genital openings small and more or less circular.

rubellum group:

- (a) the palpal patella is swollen, almost globular in shape (Figs. 29-31);
- (b) the distal tibial apophysis is long and curved as in the *nubens* group (Figs. 29-31), but there is no stout basal apophysis;
- (c) the tegular apophysis is long (Fig. 33);
- (d) the epigyne is of the form shown in Figs. 34-36, with the genital openings large.

hilare group:

- (a) the male has sulci behind the lateral eyes (weak in G. dayense);
- (b) the distal tibial apophysis is much shorter than in the other groups, and is not curved; there are 3 additional apophyses (Figs. 52-57) (reduced in *G. paradoxum* and *G. dayense*), including a basal one which carries small warts;
- (c) the ED apophysis is broader and less sclerotised (e.g. Fig. 44);
- (d) the tegular apophysis is weakly developed (e.g. Fig. 42);
- (e) the epigyne has a cusp-shaped "pocket" on either side over the spermathecae (Figs. 58-64).

iaponicum group:

- (a) the distal apophysis of the palpal tibia is very long and curved (Figs. 75, 77);
- (b) the palpal organs have the embolus and the SA much longer (Fig. 74) than in the other groups;
- (c) the tegular apophysis is long;
- (d) the epigyne has clear openings anteriorly, and the internal ducts follow, in part, a spiral path (Figs. 27, 28).

## Synonyms

Gonatium büttneri Schenkel, 1947 = G. rubens (Bl.) – new synonym. This synonymy was established by Prof. R. Braun (Mainz) and by Dr K. Thaler (Innsbruck) some years ago, but not published (K. Thaler, pers. comm.); it has been confirmed by the author by examination of the type female (Naturh. Museum, Basel).

Gonatium cinctum Schenkel, 1936 = G. japonicum Simon, 1894 — new synonym. This was established by comparison of the types of G. cinctum (Naturh. Riksmuseet, Stockholm) with the type of G. japonicum (MNHN, Paris).

Erigone (Gonatium) corallipes O. P.-Cambridge, 1875 = Erigone (Gonatium) paradoxa L. Koch, 1869 (Thaler, 1972: 40). Koch's name unfortunately has to take priority.

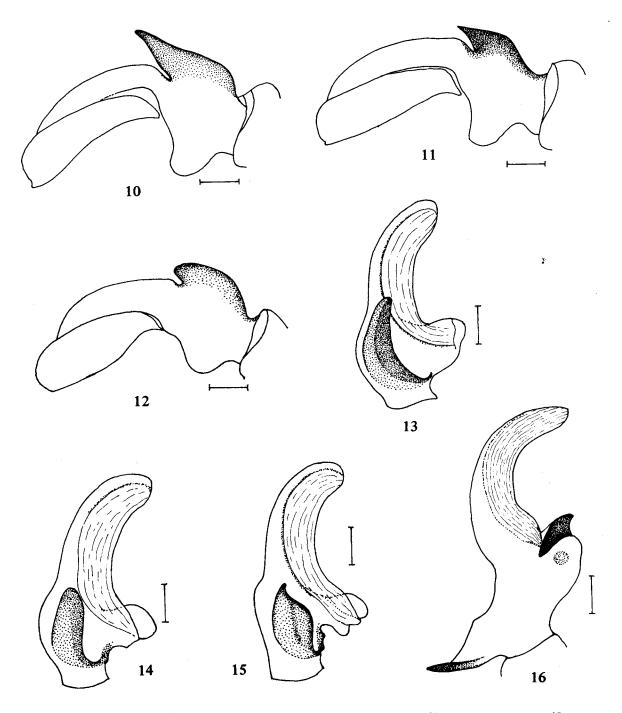
Gonatium opimum Oi, 1960 = G. japonicum Simon, 1894 — new synonym. Established by comparison of males provided by Dr Oi (Osaka) with the Simon type.

#### Synonym rejected

Gonatium nemorivagum (O. P.-Cambridge, 1875) is not, as universally assumed (Simon, 1926; Roewer, 1942b; Bonnet, 1957; Wiehle, 1960), a synonym of G. hilare (Thorell, 1875). The distinguishing characters of the two species are given under the species descriptions.

## Species excluded from the genus

Gonatium (?) acripes Denis, 1962 from Madeira was later transferred to Grammonota (Denis, 1964). It is certainly not a Gonatium.



Figs. 10-16: Male palpal tibiae. 10 Gonatium rubens, mesal; 11 G. crassipalpum, mesal; 12 G. nipponicum, mesal; 13 G. rubens, dorsal; 14 G. crassipalpum, dorsal; 15 G. nipponicum, dorsal; 16 G. ensipotens, dorsal. Scale lines 0.1 mm.

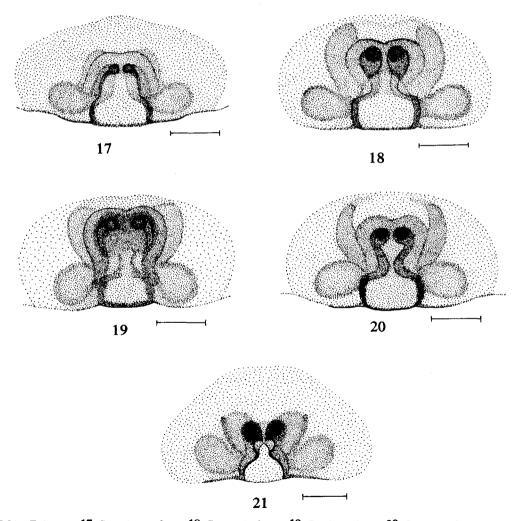
G. amdoensis Schenkel, 1963. This species was based on a single female from Kansu, China. The description and figure given are quite inadequate for identification, and the type specimen cannot be found in MNHN, Paris or in Basel; under these circumstances the name must be regarded as a nomen dubium.

G. convexum Kulczynski, 1885. This species was based on a female from Kamtkatscha; the type does not seem to be present in the Kulczynski Coll. in Warsaw (J. Proszynski, pers. comm.). The description given by Kulczynski would not identify the species; the epigyne figured is probably too simple to

be that of a Gonatium.

G. crassiventris Strand, 1913. This species was described on a female from central Africa; the location of the specimen, if it still exists, is unknown. The species could never be recognised from the description, and no figures were provided. The name must inevitably be considered as a nomen dubium.

G. femineum Roewer, 1942a. The type females (Senckenberg, Frankfurt) from Fernando Poo, West Africa, have been examined; on the basis of the epigyne and of the value of TmI, this species is possibly a Diplocephalus, but certainly not a Gonatium.



Figs. 17-21: Epigynes. 17 Gonatium rubens; 18 G. crassipalpum; 19 G. nipponicum; 20 G. crassipalpum, another specimen; 21 G. ensipotens. Scale lines 0.1 mm.

G. fuegianum Tullgren, 1901. This species was based on a male from Patagonia. The type (Naturh. Riksmuseet, Stockholm) has been examined; the palpal organs and other characters show that the species is not assignable to Gonatium.

G. griseolineatum Schenkel, 1936. This species was described on a female from Kansu, China; the type (Naturhist. Riksmuseet, Stockholm) has been examined. The chaetotaxy is similar to that of Gonatium, but the tarsal claws are not pectinate and the epigyne is not of the Gonatium pattern. It can be concluded that this species should not be retained in Gonatium.

- G. inflatum Soerensen, 1898 = Scotinotylus (Cochlembolus) alpinus (Banks) (Holm, 1967).
- G. insigne Bösenberg, 1902 = Oedothorax retusus (Westring) or O. apicatus (Blackwall) (Wunderlich, 1974).

G. lividulum Simon, 1908. This species was based on a female taken in south-west Australia by the 1905 Hamburg University Expedition, and was placed doubtfully in Gonatium by Simon. The description given, with no figures, is inadequate to identify either the species or the genus, and since the specimen cannot be found either in MNHN, Paris, or in Zoologisches Institut, Hamburg, the name must be regarded as a nomen dubium.

G. petrunkevitchi Caporiacco, 1949. The male holotype, from east Africa, has been examined by Dr Å. Holm, who kindly sent me figures of the male palp. I agree with him that, on the basis of the palpal organs, the species is not a Gonatium.

G. rufum Caporiacco, 1934. This species was based on a female from Cyrenaica, N. Africa. The description given, with no figures, is inadequate for identification, and all attempts to locate the type have been fruitless. The name must therefore be regarded as a nomen dubium.

G. strugaensis Drensky, 1929. No specimens of this Macedonian species can be found in the Drensky material in Sofia (C. Deltshev, pers. comm.). The figures given by Drensky for the male palp suggest that this species is not a Gonatium.

The identities of G. fuscum Bösenberg, 1902, G. gibbum Bösenberg, 1902 and G. pallidum Bösenberg, 1902 are uncertain (Wiehle, 1960), but it appears unlikely that any of these species are assignable to Gonatium.

#### **Conclusions**

The genus Gonatium which emerges from this study is a homogeneous one, with clearly recognisable genitalic characters. It appears to be limited to the non-tropical areas of the northern hemisphere, where its range extends from ca 35°N to ca 80°N. The largest concentration of species is located in and around the Mediterranean area: N. America seems to have only a single species. The genus contains several small groups of closely related species; the species triplet G. rubens (endemic to Europe/W. Asia). G. crassipalpum (endemic to N. America) and G. ninnonicum (endemic to Japan) forms an interesting example. G. rubens is clearly a very adaptable species. being found commonly over a wide geographical range, and this seems also to be true of G. crassipalpum and G. rubellum; the majority of the species. however, seem to be much more restricted in range. In most of the species the chief period of male maturity is in late summer and autumn, particularly in August-October.

## Species descriptions

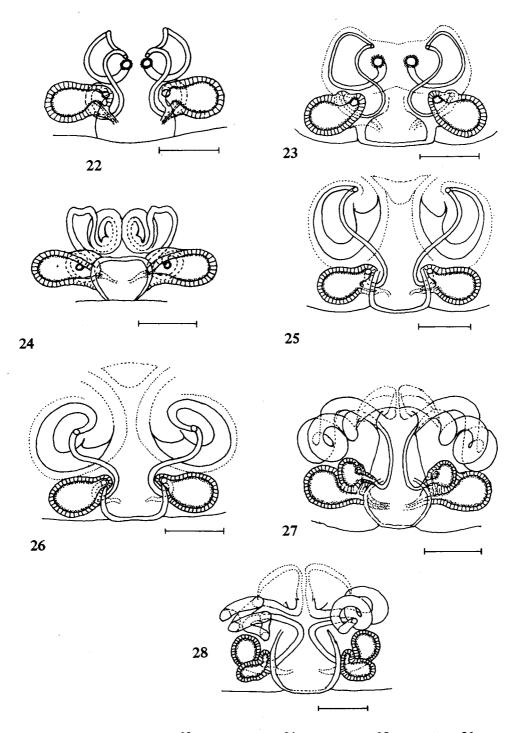
Gonatium rubens (Blackwall) (Figs. 1-6, 10, 13, 17, 22)

Neriene rubens Blackwall, 1833: 189, and 1861-4: 270. Gonatium rubens: Simon, 1884: 554 and 1926: 430, 434, 514; Roewer, 1942b: 629 (in part); Locket & Millidge, 1953: 229; Bonnet, 1957: 2036 (in part); Wiehle, 1960: 336. Complete lists of synonyms are given by Roewer (1942b) and Bonnet (1957).

Not Gonatium rubens: Bishop & Crosby, 1935: 255; Kaston, 1948: 172; and most N. American authors.

Type: Trafford Park, near Manchester, England; lost.

Description and diagnosis: This common European species has been adequately described in the literature. It is readily distinguished in both sexes from the two closely related species G. crassipalpum and G. nipponicum (see descriptions of these). G. nubens is quite similar to G. ensipotens, but the female epigynes (Figs. 17, 21) and vulvae (Figs. 22, 24) are sufficiently distinct to make confusion unlikely; the males of both species have similar palpal femora (Figs. 6, 9), but the tibial apophyses are distinct (Figs. 6, 13 cf. Figs. 9, 16).



Figs. 22-28: Vulvae. 22 Gonatium rubens; 23 G. crassipalpum; 24 G. ensipotens; 25 G. rubellum; 26 G. orientale; 27 G. japonicum; 28 G. arimaense. Scale lines 0.1 mm.

Distribution: This species appears to be endemic to Europe and parts of western Asia. It is known from practically the whole of Europe, though it is commoner in the north than in the south. It has been recorded from as far north as Swedish Lapland (Holm, 1950) and the extreme north of Finland (Palmgren, 1976), but the southern limits of its distribution are not precisely known. The only Asian records seem to be from Siberia (e.g. Holm, 1973). It has been taken in Iceland (Braendegaard, 1958), but not in Greenland (Bonnet's record (1957) is an error). G. rubens is not, so far as is known, sympatric with either G. crassipalpum or G. nipponicum; its range may just overlap with that of G. ensipotens.

Gonatium crassipalpum Bryant (Figs. 7, 11, 14, 18, 20, 23)

Gonatium crassipalpus E. Bryant, 1933: 173; Roewer, 1942b: 630.

G. crassipalpe: Bonnet, 1957: 2032.

G. rubens (not G. rubens (Bl.)): Bishop & Crosby, 1935: 255, figs. 44-46; Roewer, 1942b: 629 (in part); Kaston, 1948: 172, figs. 471, 472, 484, 485; Bonnet, 1957: 2036 (in part); Holm, 1960: 118; and probably all N. American authors except Bryant (1933).

Type: Holotype male from Long Lake, Colorado, U.S.A., 28 August (T. D. Cockerell); in Museum of Comparative Zoology, Harvard University, examined.

Description and diagnosis: This species, which is closely similar in size and general appearance to G. rubens, has been well described by Bryant, and it is only necessary to add the value of TmI: 9d 0.80-0.88. The palpal organs of G. crassipalpum, G. rubens and G. nipponicum are indistinguishable, and diagnosis of the male is based on the form of the apophyses of the palpal tibia (Figs. 7, 11, 14); the clear differences between G. crassipalpum and G. rubens were obvious in the figures given both by Bryant (1933) and by Bishop & Crosby (1935). The differences in the number and form of the pointed warts on the femur are not significant, there being some intraspecific variation in all three species. The female of G. crassipalpum is diagnosed by the epigyne, which is of similar form to that of both G. rubens and G. nipponicum. The genital openings are further forward from the spermathecae than in G. rubens (Figs. 18, 20 cf. Fig. 17), but slightly less forward than in G. nipponicum (Fig. 18 cf. Fig. 19). The vulvae of

G. crassipalpum and G. rubens differ only in their proportions (Figs. 22, 23).

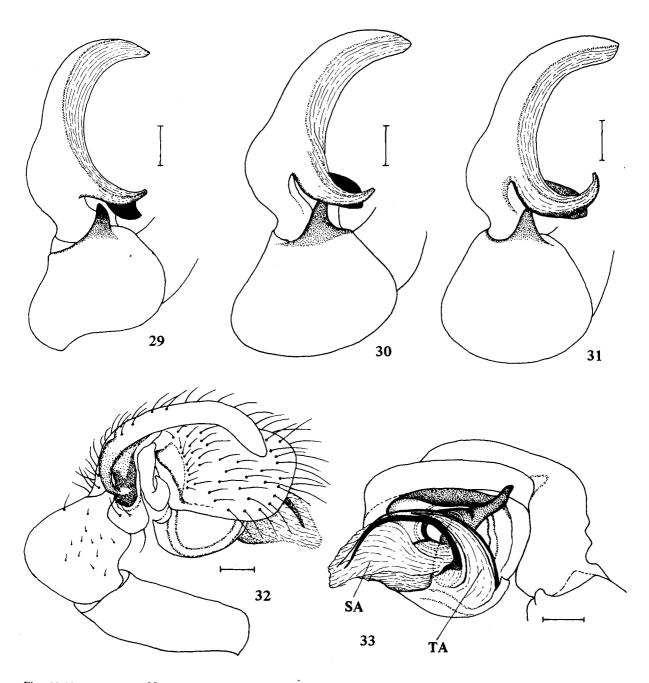
Distribution and natural history: This species appears to be endemic to N. America, There are numerous vials labelled "Gonatium rubens" in the American Museum of Natural History, but without exception these proved to be G. crassipalpum; it is very probable that G. rubens is not present in N. America. G. crassipalpum is found throughout the North American continent, apart from the extreme south; the author has seen specimens from Alaska, British Columbia, Colorado, Connecticut, Labrador, Maine, Massachusetts, Montana, New Hampshire, New York, North Carolina, Nova Scotia, Ontario, Pennsylvania, Tennessee, Wisconsin and Wyoming, and Bishop & Crosby (1935) recorded it also from Iowa, Maryland, Rhode Island, Vermont, Virginia and Washington D.C. It has not been recorded from Greenland. Males have been taken in August-November, females in February-October. Kaston (1948) mentions that it has been collected from bushes and under fallen leaves, and it has also been found ballooning from fences.

Gonatium nipponicum new species (Figs. 8, 12, 15, 19)

Gonatium rubens (not G. rubens (Bl.)): Ono, 1975: 7; Yaginuma, 1977: 383.

Type: Male holotype and female paratype from Nikko Region, Tochigi Pref., Japan, 16 September 1974 (H. Saito); deposited in the Collection of the Arachnological Society of East Asia, Ohtemon-Gakuin University, Osaka (Prof. T. Yaginuma).

Description and diagnosis: This species is closely similar in size and colour to G. rubens and G. crassipalpum. Tml: 9 0.88-0.90; & 0.80-0.86. The male palpal organs are indistinguishable from those of G. rubens and G. crassipalpum, and diagnosis of the male is based on the form of the tibial apophyses, which show clear differences from both of these species (Figs. 8, 12, 15 cf. Figs, 6, 7, 10, 11, 13, 14). The female of G. nipponicum is diagnosed by the epigyne (Fig. 19), which is very similar to that of G. crassipalpum (Figs. 18, 20), with the genital openings even further forwards from the spermathecae. G. nipponicum is structurally closer to G. crassipalpum than to G. nubens.



Figs. 29-33: Male palps. 29 Gonatium rubellum, patella/tibia, dorsal; 30 G. geniculosum, patella/tibia, dorsal; 31 G. orientale, patella/tibia, dorsal; 32 G. geniculosum, ectal; 33 G. geniculosum, mesal (SA = suprategular apophysis, TA = tegular apophysis). Scale lines 0.1 mm.

Distribution and natural history: G. nipponicum appears to be endemic to Japan. In addition to the type locality the species has also been taken in Hokkaido Prefecture. The species was taken amongst grass by sweeping; males have occurred in August and September, females in July and September.

## Gonatium ensipotens (Simon) (Figs. 9, 16, 21, 24)

Erigone ensipotens Simon, 1881: 234. Gonatium ensipotens Simon, 1884: 558, and 1926: 430, 434, 514; Roewer, 1942b: 628; Bonnet, 1957: 2032.

Type: Male and female syntypes from Collioure,

Pyr. Orient., France; in MNHN, Paris, examined. Description and diagnosis: Length: 9 2.7-3.0 mm, d 2.35 mm. Cephalothorax: length: ♀ 1.2 mm, d 1.1 mm. Orange; raised anteriorly in male, as in G. rubens, Abdomen: grey-pink. Sternum: red-brown to orange. Legs: yellow to orange. TmI: 98 0.75-0.80.

Male palp: Figs. 9, 16; the basal tibial apophysis is pointed and strongly projecting. The palpal organs are not distinguishable from those of G. rubens.

Epigyne/vulva: Figs. 21, 24.

This species can be diagnosed in the male by the form of the palpal tibia (Figs. 9, 16), which is clearly different from that of any of the other species. The female is diagnosed by the epigyne, which is sufficiently different from that of G. rubens (Fig. 21 cf. Fig. 17) and other species to make confusion unlikely.

Distribution and natural history: This species has been reported from southern France (Drôme, Vaucluse, Pyr. Or.), northern Spain (Basque provinces and Catalonia), Portugal and Minorca. Brignoli's record for Italy (1971, fig. 109) probably refers to G. biimpressum. The maturity period and habitat preferences of G. ensipotens are not known. Hull (1951) recorded G. ensipotens from England, but this was based on a misidentification.

## Gonatium rubellum (Blackwall) (Figs. 25, 29, 34)

Neriene rubella Blackwall, 1841: 648, and 1861-4: 281. Micryphantes isabellinus C. L. Koch, 1841: 109. Gonatium rubellum: Simon, 1884: 556, and 1926: 431, 433, 514; Roewer, 1942b: 629; Locket & Millidge, 1953: 231; Bonnet, 1957: 2034; Wiehle, 1960: 340.

Type: The type specimens were taken near

Llanrwst, N. Wales; they are probably no longer in

Description and diagnosis: This common European species has been adequately described in the literature. The diagnosis of G. rubellum offers no problems except in those areas of Europe where one or other of the two closely related species, G. geniculosum and G. orientale, may also occur. The male is diagnosed by the form of the palpal patella and tibial apophyses. The rounded patella of G. rubellum is drawn out into a shallow cone (Fig. 29), which is absent in G. geniculosum (Fig. 30) and in G. orientale (Fig. 31). The basal lateral apophysis on the tibia is shorter and less curved in G. rubellum (Fig. 29) than in G. geniculosum (Fig. 30), but the difference is small; in G. orientale the basal lateral apophysis is even longer and more curved distally than in G. geniculosum (Fig. 31). Diagnosis of G. rubellum female is based on the epigyne, but the differences from G. geniculosum and G. orientale are rather small. The central area in G. rubellum tends to be wider than in G. geniculosum (Fig. 34 cf. Fig. 35), but there is variation in both species, and separation of the females by the epigynes must be regarded as unreliable. In G. orientale the genital openings are nearer to the spermathecae than in G. rubellum or G. geniculosum, and the anterior septum is narrower (Figs. 26, 36); although the epigyne of G, orientale is somewhat variable in appearance, the position of the genital openings seems to be a constant character.

Distribution and natural history: G. rubellum has been reported from practically the whole of Europe, from the north of Finland (69°N) (Palmgren, 1976) to the Balkans. Possibly it is replaced by G. orientale in south-eastern Europe, but it is not known whether the two species overlap in distribution. The typical habitat of G. rubellum is on low vegetation and in the ground layer beneath low shrubs, etc. The chief period of male maturity is in August and early autumn.

Gonatium geniculosum Simon (Figs. 30, 32, 33, 35)

Gonatium geniculosum Simon, 1918: 158, and 1926: 430, 433, 514; Roewer 1942b: 628; Bonnet, 1957: 2033.

Type: Male and female syntypes from La Madonedes-Fenêtres, Forêt de Turini, Peira Cava, Alpes Maritimes, France, September 1915 (de Dalmas); in MNHN, Paris, examined.

Description and diagnosis: Length: \$ 3.0-3.3 mm, \$ 2.8 mm. Cephalothorax: length: \$ 1.3-1.4 mm, \$ 1.3 mm. Orange with faint darker margins. Abdomen: grey-pink. Sternum: orange. Legs: yellowbrown to orange. TmI: \$ 0.88, \$ 0.82. Male palp: Figs. 30, 32, 33. Epigyne: Fig. 35.

The diagnosis of this species is based on the male palpal tibia and patella, and on the female epigyne: see G. rubellum diagnosis.

Distribution and natural history: G. geniculosum is known only from the Alpes Maritimes in south-

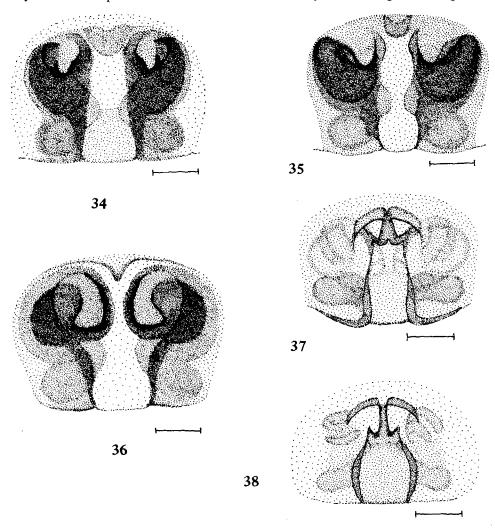
eastern France. Adults of both sexes were taken in subalpine forest in September.

## Gonatium orientale Fage (Figs. 26, 31, 36)

Gonatium orientale Fage, 1931: 144; Roewer, 1942b: 629; Denis, 1952: 7; Bonnet, 1957: 2034.

Type: The male holotype was taken in a cave at Corobana mica la N. de Poarta lui Ionel, Romania; this specimen is not in MNHN, Paris, and appears to have been lost.

Description and diagnosis: Length: 9 3.0-3.7 mm,



Figs. 34-38: Epigynes. 34 Gonatium rubellum; 35 G. geniculosum; 36 G. orientale; 37 G. japonicum; 38 G. arimaense. Scale lines 0.1 mm.

ở 2.9 mm. Cephalothorax: length: ♀ 1.25-1.55 mm, ở 1.35 mm. Orange-brown, with darker markings and margins. Abdomen: grey-pink. Sternum: redbrown, with darker margins, Legs: orange. TmI: ♀ 0.83-0.86, ♂ 0.86. Male palp: Fig. 31. Epigyne/vulva: Figs. 26, 36.

This species is diagnosed by the male palpal tibia/patella and by the female epigyne: see G. rubellum diagnosis.

Distribution and natural history: Known only from Romania, where it has been taken inside and at the entrance to caves (Fage, 1931; Denis, 1952), and in woodland at ca 900-1100 m in the eastern Carpathians (Weiss et al., 1979). Adults were taken in July and August-October (caves) and in May and July-September (woodland).

## Gonatium hilare (Thorell) (Figs. 39, 44, 49, 50, 52, 58, 65)

Erigone hilaris Thorell, 1875: 88.

Gonatium nemorivaga: Simon, 1884: 549 (probably in part). G. hilare: Simon, 1926: 432, 434, 515 (in part); Roewer, 1942b: 628 (in part); Bonnet, 1957: 2033 (in part); Wiehle, 1960: 346; Miller, 1971: 264, 289.

Not Erigone nemorivaga O. P.-Cambridge, 1875: 326. There has been confusion in the past between G. hilare and G. nemorivagum.

Type: Male type (consisting of a single palp) from N. Italy; in Thorell Collection, Naturh. Riksmuseet, Stockholm, examined.

Description and diagnosis: This species has been well described by Wiehle (1960), who probably examined a pure sample of G. hilare. The male has short sulci running back behind the lateral eyes (Figs. 49, 50).

The diagnosis of this species requires careful distinction from the closely related G. nemorivagum. The male is diagnosed by the palpal tibial apophyses; viewed dorsally, the lateral apophyses are rather larger and differently shaped than in G. nemorivagum (Fig. 52 cf. Fig. 53), and viewed laterally the gap between these two apophyses is rather wider (Fig. 39 cf. Fig. 41). The rounded, wart-bearing basal apophysis is similar to that of G. nemorivagum, but slightly larger. The female is diagnosed by the epigyne/vulva, which have the genital openings significantly larger than in G. nemorivagum (Figs. 58, 65 cf. Figs. 59, 66). As noted in the genus descrip-

tion, the variable shape of the posterior area of the epigyne is of no significance.

Distribution and natural history: The species has been reported from metropolitan France (central and southern), Corsica, Spain, Germany, Switzerland, Austria, Italy, Yugoslavia, Czechoslovakia, Hungary, the Balkans and European Russia, Most of the published localities are south of the Alps (Thaler, 1969), but some of these records probably refer to G. nemorivagum and others possibly to G. biimpressum. Thorell's record for Algeria is erroneous; his specimen (Naturh. Riksmuseet, Stockholm) is G. occidentale. The author has seen specimens of G, hilare only from France (mixed with G. nemorivagum), Germany, Austria, Czechoslovakia and Italy (the type). The species is found on the lower branches of trees, e.g. pine, chestnut, or on bushes, but also in the ground layer (Wiehle, 1960; Thaler, 1969), at moderate altitudes, e.g. 500-1000 m. Males are adult in August-October.

## Gonatium nemorivagum (O. P.-Cambridge) (Figs. 41, 42, 51, 53, 59, 66)

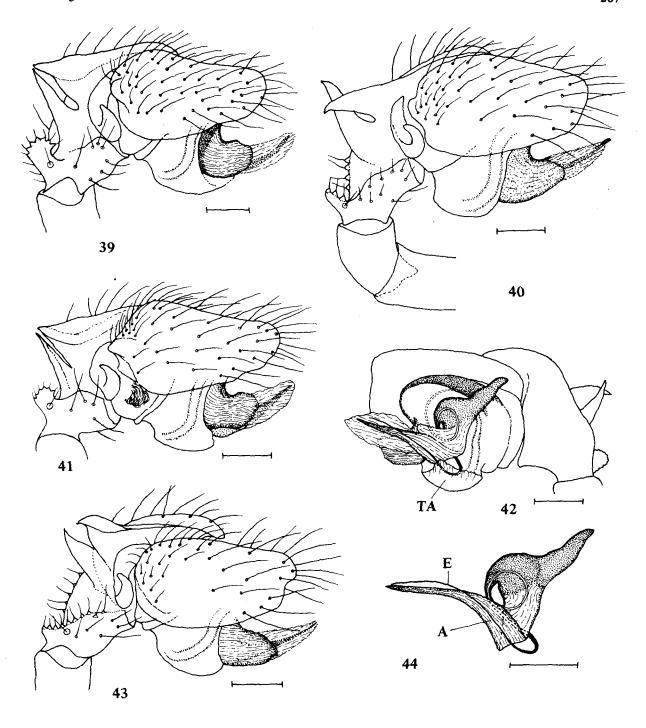
Erigone nemorivaga O. P.-Cambridge, 1875: 326. Gonatium nemorivaga: Simon, 1884: 549 (in part). G. hilare: Simon, 1926: 432, 434, 515 (in part): Roewer, 1942b: 628 (in part); Bonnet, 1957: 2033 (in part). Up to now, E. nemorivaga Cambridge has been regarded as a junior synonym of E. hilaris Thoreli.

Type: Male and female syntypes from Troyes, France, 1871 (from E. Simon); in Hope Entomological Collections, Oxford, examined.

Description and diagnosis: Length: \$ 2.5-2.7 mm, \$ 2.2-2.5 mm. Cephalothorax: length: \$ 1.1 mm, \$ 1.0-1.05 mm. Orange-brown, with faint grey markings and margins. Raised anteriorly in male, as in G. hilare, with short sulci running back from the lateral eyes (Fig. 51). Abdomen: grey to black. Sternum: orange, with blackish margins. Legs: yellow to orange-brown; TmI: \$ 0.78-0.84, \$ 0.76-0.83. Male palp: Figs. 41, 42, 53; the palpal organs are indistinguishable from those of G. hilare and the other members of the hilare group. Epigyne/vulva: Figs. 59, 66.

This species is very close to G. hilare, and its diagnosis is dealt with under that species.

Distribution and natural history: Some of the



Figs. 39-44: Male palps. 39 Gonatium hilare, ectal; 40 G. occidentale, ectal; 41 G. nemorivagum, ectal; 42 G. nemorivagum, mesal; 43 G. biimpressum, ectal; 44 G. hilare, embolic division. (A = apophysis of embolic division, E = embolus, TA = tegular apophysis). Scale lines 0.1 mm.

published records for G. hilare probably refer to G. nemorivagum, which is almost certain to be present in some of the same geographical areas, though the ecology of the two species will be different. The author has seen specimens of G. nemorivagum only from metropolitan France (the types, and numerous specimens mixed with G. hilare in a tube from MNHN, Paris), Corsica, Sardinia and Yugoslavia; it might be expected to occur in mainland Italy and probably in other parts of central and south-eastern Europe. In Corsica, both sexes were frequent in one locality near the coast, north of Ajaccio, on low plants in May 1974; in Yugoslavia a male was taken (C. Deeleman) in a cave entrance. The species seems

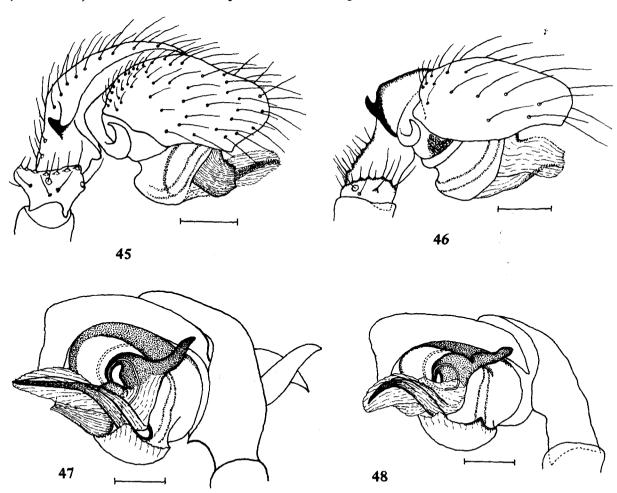
to inhabit lower altitudes than G. hilare, and to be adult at an earlier season (May-June).

Gonatium occidentale Simon (Figs. 40, 47, 54, 60, 67)

Gonatium occidentale Simon, 1918: 115, and 1926: 432, 433, 515; Roewer, 1942b: 629; Bonnet, 1957: 2034.

Type: Male and female syntypes from Basses-Pyrénées, France; in MNHN, Paris, examined.

Description and diagnosis: Length: 9 2.35 mm, & 2.2 mm. Cephalothorax: length: 9 1.2 mm, & 1.0 mm. Orange-brown, with darker markings and margins. Raised anteriorly in the male, with short



Figs. 45-48: Male palps. 45 Gonatium paradoxum, ectal; 46 G. dayense, ectal; 47 G. occidentale, mesal; 48 G. dayense, mesal. Scale lines 0.1 mm.

sulci behind the lateral eyes. Abdomen: black. Sternum: orange-brown, with margins suffused with grey. Legs: orange-brown, with tarsi rather paler. TmI: \$\inp 0.88\$, \$\inp 0.80\$. Male palp: Figs. 40, 47, 54; the palpal organs are not distinguishable from those of the other members of the hilare group. Epigyne: Fig. 60; the genital openings, which are large and more or less circular, are sometimes obscured by a thin skin of exudation which can be removed with a fine needle after soaking the specimen for 1-2 minutes in 5% KOH. The spermathecal ducts follow a smooth S-shaped path (Fig. 67).

The male is diagnosed by the form of the tibial apophyses; the lateral apophyses cross one another (Figs. 40, 54), while the basal wart-bearing apophysis is not rounded as in G. hilare and G. nemorivagum, and differs also from that of G. biimpressum (Fig. 43). The female is diagnosed by the epigyne (Fig. 60), which is quite distinct from that of the other species of the group, with the genital openings wide and approximately circular in shape.

Distribution: This species is known only from the western Pyrenees area of France, from Spain and from N. Africa (Algeria). G. occidentale is probably not sympatric with G. biimpressum, but there is no information to show whether it overlaps in distribution with either G. hilare or G. nemorivagum.

## Gonatium biimpressum Simon (Figs. 43, 55, 61, 68)

Gonatium biimpressum Simon, 1884: 551, and 1926: 432, 515; Roewer, 1942b: 628; Bonnet, 1957: 2032; Denis, 1966: 122.

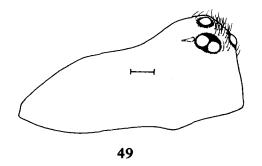
Type: Male type from Bonifacio, Corsica; lost

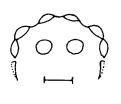
(Simon, 1926: 515, footnote; but see also Denis, 1966: 122, footnote).

Description and diagnosis: The female (taken with the male) has not previously been described. Length: \$\times 2.7-3.3\$ mm, \$\delta 2.2\$ mm. Cephalothorax: length: \$\times 1.05-1.3\$ mm, \$\delta 1.2\$ mm. Orange, with faint darker markings and margins; raised anteriorly in the male, with short sulci behind the lateral eyes. Abdomen: grey to black. Sternum: orange, with darker margins. Legs: yellow-brown. TmI: \$\times 0.86-0.90\$, \$\delta 0.81-0.83\$. Male palp: Figs. 43, 55; the palpal organs are closely similar to those of the other species in the group. Epigyne: Fig. 61; the genital openings are ovoid, with the long axis more or less horizontal, and the internal ducts follow a smooth curve (Fig. 68).

The male is diagnosed by the form of the tibial apophyses (Figs. 43, 55), which show clear differences from those of the other members of this group, with the exception of G. cappadocium; G. biimpressum male is probably not distinguishable from G. cappadocium. The female of G. biimpressum is diagnosed by the form of the epigyne/vulva (Figs. 61, 68). The species with which it might most easily be confused are G. nemorivagum and G. cappadocium; it is separated from the former by the shape and position of the genital openings, and by the more posterior setting of the cusps (Fig. 61 cf. Fig. 59), and from the latter by the angle of the ovoid genital openings and by the convoluted pathway of the internal duct in G. cappadocium (Figs. 61, 68 cf. Figs. 63, 70).

Distribution: The species has been taken in Corsica, Sardinia, the Pontine Islands and mainland Italy (Lazio, Abruzzi National Park and probably Campania ("G. ensipotens", Brignoli, 1971)). G.







50

51

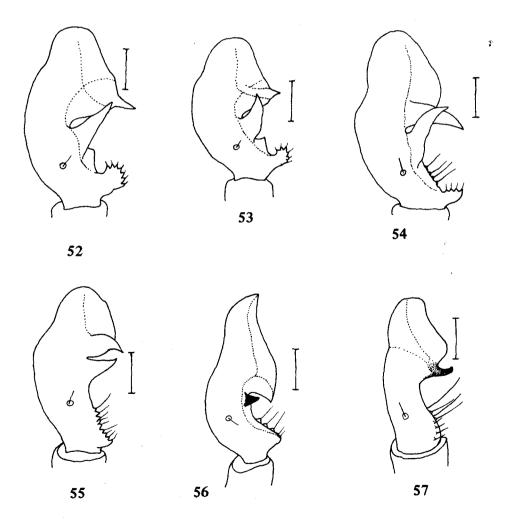
Figs. 49-51: 49 Gonatium hilare &, carapace, lateral; 50 G. hilare &, eyes and sulci, dorsal; 51 G. nemorivagum &, eyes and sulci, dorsal. Scale lines 0.1 mm.

nemorivagum has also been taken in Corsica and Sardinia, but whether G. biimpressum overlaps in distribution with G. hilare or G. cappadocium is not known. Males have been taken in June and August, females in August, October and December.

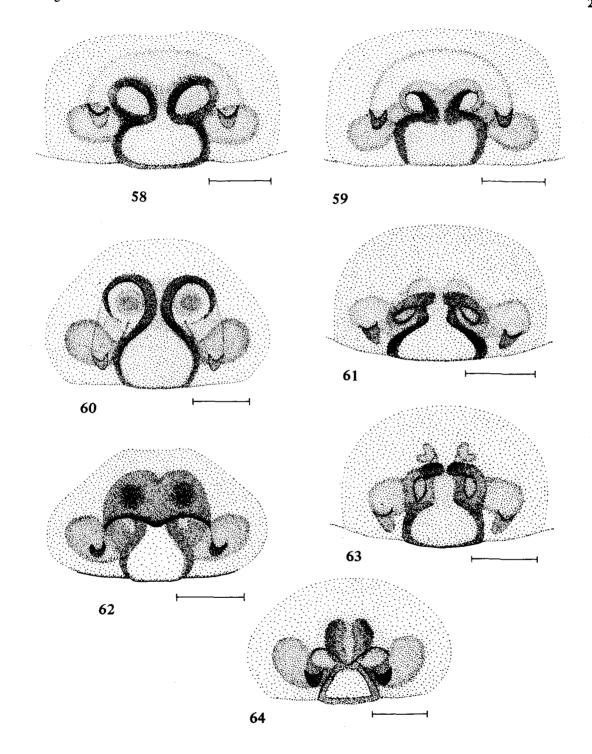
## Gonatium cappadocium new species (Figs. 63, 70)

Type: Holotype female from Antitaurus, eastern Turkey (Kumerloewe leg.); in Roewer Collection, Senckenberg Museum, Frankfurt (SMF 24712). This specimen, accompanied by a paratype male, was labelled "Gonatium hilare".

Description and diagnosis: Length: 92.55 mm, 32.25 mm. Cephalothorax: length: 91.2 mm, 31.05 mm. Raised anteriorly in male, with sulci behind the lateral eyes, as in G. biimpressum. Abdomen: grey to black. Sternum: orange, suffused with brown. Legs: orange-brown. TmI: 90.88, 30.81-0.83. Male palp: identical with that of G. biimpressum, except that the warts on the basal apophysis are slightly larger and more numerous; this difference may not however be constant. Epigyne: Fig. 63; the genital openings are ovoid, with the long axis more or less longitudinal, and the internal ducts are distinctly convoluted anterior to the openings (Fig. 70).



Figs. 52-57: Male palpal tibiae, dorsal. 52 Gonatium hilare; 53 G. nemorivagum; 54 G. occidentale; 55 G. biimpressum; 56 G. paradoxum; 57 G. dayense. Scale lines 0.1 mm.



Figs. 58-64: Epigynes. 58 Gonatium hilare; 59 G. nemorivagum; 60 G. occidentale; 61 G. biimpressum; 62 G. paradoxum; 63 G. cappadocium; 64 G. dayense. Scale lines 0.1 mm.

The female is diagnosed by the form of the epigyne/vulva, which is distinguished from G. biimpressum by the position of the genital openings and by the convulution of the internal duct, which is visible through the integument (Figs. 63, 70 cf. Figs. 61, 68). Diagnosis of the male of G. cappadocium may be impossible if it is taken without the female, because of its close structural similarity to G. biimpressum male. With greater knowledge of the geographical distributions of G. cappadocium and G. biimpressum it may be possible to separate the males on the basis of their distributions. It may be that G. cappadocium should be regarded as a subspecies of G. biimpressum, but the capture of more specimens of both species (in order to explore the extent of intraspecific variability) will be necessary to decide this point.

Distribution: Known only from the type locality; there is no information on the date of capture or the type of habitat.

## Gonatium paradoxum (L. Koch) (Figs. 45, 56, 62, 69)

Erigone paradoxa L. Koch, 1869; 184; Bonnet, 1956: 1771; Thaler, 1972: 40.

Erigone corallipes O. P.-Cambridge, 1875: 328.

Gonatium corallipes: Simon, 1884: 552, and 1926: 432, 434, 514; Roewer, 1942b: 628; Bonnet, 1957: 2032; Wiehle, 1960: 343; Locket, Millidge & Merrett, 1974: 81; and other European authors.

Type: Male type from Höttinger Alps, near Innsbruck, Austria, 22 September (Ausserer); in Koch Collection, BMNH, London.

Description and diagnosis: This species has been adequately described in the literature under the name G. corallipes. The male palpal organs are very similar to those of the other members of the group, and the male is diagnosed by the form of the tibial apophyses (Figs. 45, 56), which are simpler than those of the other members of the group except G. dayense. The female is diagnosed by the epigyne/vulva (Figs. 62, 69), which are readily distinguishable from those of the other members of the group.

Distribution and natural history: This species is known throughout Europe, with records from Finland, Sweden, southern England, France, Netherlands, Germany, Switzerland, Austria, Italy, Poland, Hungary, Czechoslovakia, Romania, the Balkans,

Estonia and European Russia. Males are mature in August-September; the species is found in moss and grass, on heather, and on the lower branches of pine, oak and alder.

Gonatium dayense Simon (Figs. 46, 48, 57, 64, 71)

Gonatium dayense Simon, 1884: 553; Roewer, 1942b: 628; Bonnet, 1957: 2032.

Type: Male and female syntypes from Daya, Oran, Algeria (L. Bedel) are in MNHN, Paris. The tube of type material contains not only numerous individuals of *G. dayense*, but also several other erigonine species; I have therefore designated a lectotype male, which is deposited in MNHN, Paris.

Description and diagnosis: Length: \$\, 2.55-2.80 mm, \$\, 2.0-2.2 mm. Cephalothorax: length: \$\, 1.05-1.15 mm, \$\, 0.95-1.0 mm. Orange; somewhat raised anteriorly in male, with weak sulci behind lateral eyes. Abdomen: grey to shiny black. Sternum: orange, sometimes reticulated with black. Legs: orange to orange-yellow. TmI: \$\, 0.77-0.80, \$\, 0.75-0.80. Male palp: Figs. 46, 48, 57; the palpal organs are practically identical with those of the other species in the group, and the tibial apophyses are rather simple. Epigyne/vulva: Figs. 64, 71; the cusps are sometimes poorly developed and rather difficult to see. The genital openings are frequently obscured by an exudation which can be removed in the same way as with \$G\$, occidentale.

The male is diagnosed by the form of the palpal tibial apophyses (Figs. 46, 57), which are rather simple and quite distinct from those of the other members of the group. The female is diagnosed by the epigyne (Fig. 64), which is easily distinguished from those of the other species.

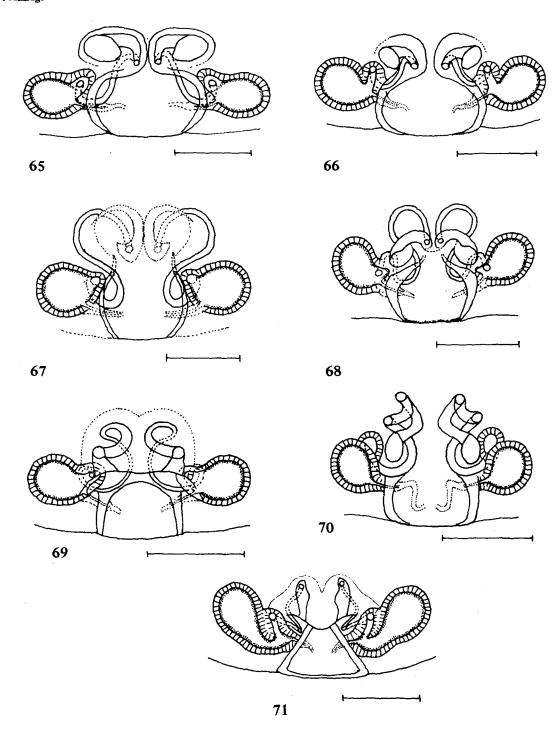
Distribution: Known only from the type locality, Algeria, where it was taken in company with a few specimens of G. occidentale. It is possible that, like G. occidentale, G. dayense may eventually be found to occur in Spain.

Gonatium japonicum Simon (Figs. 27, 37, 72-76)

Gonatium japonicum Simon, 1894: 630; Bonnet, 1957: 2034.

G. cinctum Schenkel, 1936: 55; Roewer, 1942b: 628; Bonnet, 1957: 2032.

G. opimum Oi, 1960: 155.



Figs. 65-71: Vulvae. 65 Gonatium hilare; 66 G. nemorivagum; 67 G. occidentale; 68 G. biimpressum; 69 G. paradoxum; 70 G. cappadocium; 71 G. dayense. Scale lines 0.1 mm.

Type: Male type from Yokohama, Japan; in MNHN, Paris, examined.

Description and diagnosis: Simon's description (1894) is rudimentary, but the name japonicum is considered to be just this side of a nomen nudum. The species has been well described, under the name G. opimum, by Oi (1960). The values of TmI are: ♀ 0.88-0.92, ♂ 0.85-0.90. Male palp: Figs. 72-75; the distal apophysis of the tibia is long and sickleshaped, and the palpal organs have the embolus, the ED apophysis and the SA significantly longer than in all species other than G, arimaense. Epigyne: Fig. 37; the genital openings are clearly visible anteriorly. The pathway of the internal duct includes a spiral section (Fig. 27), which appears to be a coiled lamella, C-shaped in section, with a duct on each margin (Fig. 76). The duct from the genital opening seems to pass down one margin of the spiral, returning up the other margin, i.e. the path is a double helix; thereafter the duct follows the usual S-pathway to the spermatheca.

G. japonicum cannot be confused with any other species apart from G. arimaense. The male palps of these two species are very similar, but the retrograde basal apophysis of the tibia is significantly shorter in G. japonicum than in G. arimaense (Fig. 75 cf. Fig. 77). The female epigynes and vulvae are of similar form (Figs. 37, 38 cf. 27, 28), but should be readily distinguishable; the internal duct coils seem to be somewhat smaller in G. arimaense than in G. japonicum,

Distribution: Known from Japan (Yokohama, and Osaka Prefecture) and from central China (S. Kansu: G. cinctum). Both sexes have been taken in October and December.

## Gonatium arimaense Oi (Figs. 28, 38, 77)

Gonatium arimaensis Oi, 1960: 154.

Type: Male holotype and female paratype from Arima, 22 September 1957 (R. Oi). Specimens provided for examination by Dr Oi.

Description and diagnosis: This species has been well described by Oi (1960). The values for TmI are: 9 0.93-0.95, & 0.95. Male palp: the palpal organs seem to be indistinguishable from those of G. japonicum; tibia (Fig. 77). Epigyne: Fig. 38; vulva (Fig. 28).

This species is very close to *G. japonicum*, and the distinguishing characters are dealt with under that species.

Distribution: Known only from the type locality; both sexes were adult in September.

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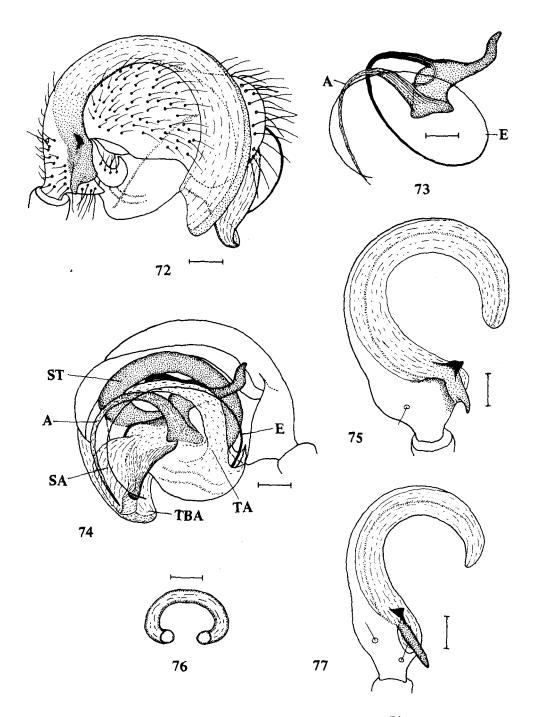
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Figs. 72-77: 72 Gonatium japonicum o palp, ectal; 73 G. japonicum, embolic division; 74 G. japonicum, o palp, mesal; 75 G. japonicum, o palpal tibia, dorsal; 76 G. japonicum, cross section of coiled lamella of spermathecal duct; 77 G. arimaense, o palpal tibia, dorsal. (A = apophysis of embolic division, E = embolus, SA = suprategular apophysis, ST = suprategulum, TA = tegular apophysis, TBA = tibial apophysis). Scale lines 0.1 mm, except 76, 0.01 mm.

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