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Revision of the subspecies of Onychogomphus forcipatus (Linnaeus, 1758) in Europe and Asia Minor, and the true distribution of Onychogomphus forcipatus unguiculatus (Vander Linden, 1823) (Odonata, Gomphidae)

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Abstract

Many specimens from several parts of Europe, North Africa, and Asia Minor have been examined to revise Onychogomphus forcipatus (LINNAEUS, 1758). *Colour pattern is unreliable for subspecific demarcation, whereas the morphology of the apical part of the male inferior appendage allows to distinguish three subspecies. These subspecies, which are connected by intermediate specimens but not by intermediate populations, are* Onychogomphus forcipatus forcipatus (LINNAEUS, 1758), O. f. unguiculatus (VANDER LINDEN, 1823), *and* O. f. albotibialis SCHMIDT, 1954. O. f. meridionalis *auct. and* O. f. siculus (VANDER LINDEN, 1825) *are synonymized with the nominal subspecies.* O. f. cypricus SCHMIDT, 1954 *is synonymized with* O. f. albotibialis SCHMIDT. *The synonymy of* O. f. lucidostriatus SCHMIDT, 1954 *with* O. f. albotibialis *is likely but not demonstrated. Females are poorly differentiated at subspecific level. A key is provided for the males, and the range of each subspecies is defined.* O. f. unguiculatus *is restricted to the West Mediterranean countries, and is replaced by the nominal subspecies in the Balkan area and Sicily.* O. f. albotibialis *inhabits Asia Minor, but its range boundaries remain unclear.*

Résumé

*De nombreux exemplaires d'*Onychogomphus forcipatus (LINNAEUS, 1758) *ont été examinés dans plusieurs régions d'Europe, d'Afrique du Nord et d'Asie Mineure, en*

*vue d'en redéfinir les sous-espèces. Les critères de coloration ne permettent pas de distinction subspécifique claire. Seule l'observation de certains caractères structuraux, et en particulier de la morphologie de la lame supra-anale des mâles, permettent d'identifier trois sous-espèces, reliées entre elles par des individus intermédiaires mais non par des populations intermédiaires. Il s'agit d'*Onychogomphus forcipatus forcipatus (LINNAEUS, 1758), O. f. unguiculatus (VANDER LINDEN, 1823) *et* O. f. albotibialis SCHMIDT, 1954. O. f. meridionalis *auct. et* O. f. siculus (VANDER LINDEN, 1825) *sont rapportés à la sous-espèce nominale.* O. f. cypricus SCHMIDT, 1954 *est synonyme d'*O. f. albotibialis SCHMIDT. *La synonymie d'*O. f. lucidostriatus SCHMIDT, 1954 *et* O. f. albotibialis *est possible mais non démontrée. Les femelles ne sont que très peu différenciées à un niveau subspécifique. Une clé de détermination est proposée pour les mâles et la répartition des différentes sous-espèces est établie.* O. f. unguiculatus *n'occupe que le bassin méditerranéen occidental et est remplacé par la sous-espèce nominale dans les Balkans et en Sicile.* O. f. albotibialis *occupe au moins la Turquie d'Asie, mais sa répartition précise reste à établir.*

1. Introduction

Onychogomphus forcipatus (LINNAEUS, 1758) is a polymorphic species, exhibiting considerable colour and structural variation throughout its range, but also within populations. Broadly speaking, thoracic and abdominal black markings become progressively reduced from northern to southern Europe, whilst the subterminal projection arising from the dorsal surface of the male inferior appendage more or less follows its main curvature, and is directed caudad, in northern populations, but is abruptly recurved and directed cephalad in some southern ones. Many taxa were named on the basis of these findings, usually without detailed descriptions.

O. f. forcipatus (LINNAEUS, 1758) applied at first to populations having the dorsum of the 8th abdominal segment entirely black or with only a rounded yellow spot (SELYS & HAGEN, 1850). Such populations usually exhibit continuous meso/metapleural black stripes on the thorax and this feature became the main valid criterium in more recent works (AGUESSE, 1968). This taxon was assumed to inhabit from western France to northern and central Europe, and to extend up to the Balkans and Anatolia through mountainous areas (SELYS & HAGEN, 1858; MORTON, 1915; FUDAKOWSKI, 1930; BUCHHOLZ, 1954, 1963; AGUESSE, 1957; DUMONT, 1977a, 1977b). The name *O. f. siculus* (VANDER LINDEN, 1825) was given to the very yellow Sicilian populations, in which the yellow spots on the 3 last abdominal segments of the males are more extensive than the black markings (SELYS & HAGEN, 1858). Later SELYS (1860) named *O. f. unguiculatus* (VANDER LINDEN, 1823) all the mediterranean populations (including *O. f. siculus*) in which the dorsum of the 8th abdominal segment was profusely marked with yellow. They generally exhibit interrupted meso/metapleural black stripes, which was later considered as the main differential character (AGUESSE, 1968). Such populations were recorded from central France and Auvergne (DOMMANGET, 1982; FRANCEZ, 1985), from the western Mediterranean area including the whole of Italy (AGUESSE, 1968), and from the Balkans up to Rumania, Armenia, Cyprus and Asia Minor at low altitude (AKRAMOWSKI, 1948, ADAMOVIC, 1967, DUMONT, 1977a, 1977b). STEIN (1863) named "*Gomphus forcipatus* LINN. var *meridional.*" (nec "*meridionalis*"!) the very yellow and slender specimens from Greece and Dalmatia, an obvious reference to SELYS "variété méridionale" (SELYS & HAGEN, 1850),

later (1860) classified under *O. f. unguiculatus*. This designation was recently improperly turned into "*O. f. unguiculatus* SELYS, 1850" (BILEK, 1967) or "*O. f. meridionalis* (STEIN, 1863)" (GALLETTI & PAVESI, 1983). SCHMIDT (1954a, 1954b) attempted to classify the *O. forcipatus* from Turkey, Cyprus, and Iran on the basis of colour-pattern and some unexplained structural characters, which were later partly illustrated by DEMIRSOY (1982). *O. f. lucidostriatus* SCHMIDT, 1954 was described from northern Iran (southern fringe of the Caspian Sea and adjacent highlands), based on only 2 males. It was assumed to differ from the nominal subspecies only by the presence of yellowish streaks on the legs. *O. f. albotibialis* SCHMIDT, 1954 from Anatolia was supposed to differ from the nominal subspecies by yellowish streaks on the tibiae and by some, advocated but not described, structural particularities. The name *O. f. cypricus* SCHMIDT, 1954 applied to Cyprus populations, which show the same elusive "structural particularities" as the foregoing taxon, but lack yellowish streaks on the tibiae.

Indeed, basing on such colour-pattern criteria, intermediate populations were extensively found so that a number cannot be satisfactorily assigned to any subspecies (AGUESSE, 1968, DUMONT, 1977b). Thus the respective range of the components of the species can not be assessed with accuracy.

To solve these difficulties some works used the structural features previously emphasized by HAGEN (SELYS & HAGEN, 1858). LIEFTINCK (1966) claimed that the only reliable criteria are structural. Males with the subterminal dorsal projection in line with the main curvature of this appendage, and with a poorly defined ventral subterminal protuberance, were considered to be typical *O. f. forcipatus*. Those having a strongly recurved subterminal dorsal projection and a well-defined, swollen, subterminal ventral protuberance were assigned to *O. f. unguiculatus*. In LIEFTINCK's mind populations from Sicily and Cyprus were sufficiently recognizable on the basis of their colour-pattern to merit racial distinction. No structural differentiation occurs, however, in *O. f. siculus*, as compared to the nominal subspecies (SELYS & HAGEN, 1858; GALLETTI & PAVESI, 1983).

On such a structural basis the ranges assigned to the previous taxa were markedly changed. In France *O. f. unguiculatus* sensu LIEFTINCK was recorded from the Mediterranean fringe only (SELYS & HAGEN, 1858; LIEFTINCK, 1966; BILEK; 1967; DE MARMELS & SCHIESS, 1978), but its northern limit remained unknown. All the populations from NE Italy, Yugoslavia, Greece and Bulgaria proved to belong to the nominal subspecies (BUCHHOLZ, 1954, 1963; LIEFTINCK, 1966; BILEK, 1967; KIAUTA, 1969; GALLETTI & PAVESI, 1983). The identity of the populations from Asia Minor remains uncertain, because of the poor descriptions by SCHNEIDER (1845) and SCHMIDT (1954). From this mixed-up situation, it follows that common criteria for subspecies identification are necessary. All previously used characteristics are in need of revision.

For this purpose, we first examined numerous specimens from NE, SW and S France, then from other countries such as Morocco, Spain, Italy, Finland, the Balkans and Asia Minor. This made it possible to sort out reliable characters and to provide a fair assessment of the differentiation and distribution of the *O. forcipatus* subspecies in most of the West Palaearctic.

2. Definition of the subspecies in Onychogomphus forcipatus

2.1. Variation of the colour-pattern in the imago

The main colour-pattern features noted in a number of males from various parts of Europe and Asia Minor are summarized in Table 1. They often show a strong heterogeneity within a given locality, and never vary simultaneously from an area to another. Thus, in a number of populations most specimens exhibit both dark 8th and 9th abdominal segments and discontinuous thoracic meso/metapleural black stripes. Such specimens cannot be satisfactorily ascribed to a known subspecies. Many specimens from the french southern Alps and Provence exhibit a noteworthy pale condition with sometimes the meso/metapleural black stripes reduced to their basal part; they resemble those at hand from Sicily and Greece. Such specimens should not be considered as typical of the Balkans and Sicily. The heterogeneousness of specimens from Asia Minor was previously emphasized by DUMONT (1977b), who failed to identify a natural grouping among them on evidence of colour criteria.

Thus, although a progressive reduction in black surfaces is, on average, evident from northern and western Europe to the Mediterranean and Asia Minor, and from the highest to lowest altitudes, colour-pattern does not provide a reliable criterion to establish well-defined entities with clear geographic limits.

2.2. Variation in the shape of male inferior appendage

2.2.1. European populations

Considering the set of populations from the whole of Europe, the values of the angle between the subterminal dorsal projection and the rest of the male inferior appendage ("δ" in figures 1 and 3) cluster around 2 distinct values (90° and 150°) (Fig. 1). This emphasizes the existence of 2 different subsets, linked together by a small number of intermediate specimens with a δ value around 120°. This bimodal distribution disappears in every single locality. Thus, males belong to one or the other of these 2 entities.

Male from the southernmost lowland french localities, from central Italy, from Morocco and Tunisia, and from central and southern Spain, have a strongly backturned subterminal projection at their inferior appendage [δ = (28°) 80° - 100° (118°)], that looks either straight or slightly curved upwards (Fig. 2, e to h). They represent *O. f. unguiculatus* (CAPRA & GALLETTI, 1978).

In males from northern or altitudinal areas in France, and from Finland, Yugoslavia, Greece and adjacent islands (up to the Cyclades), Bulgaria, and Sicily, the δ angles are much more obtuse and their values range from 120° to 170°, (Fig. 2, a to d; see also drawings by SELYS & HAGEN (1858), and GALLETTI & PAVESI (1983)). They belong to the nominal subspecies, sensu LIEFTINCK.

No intermediate population was found, such that it would exhibit a modal frequency for δ values around 120°. Nevertheless, the existence of intermediate specimens in almost all localities, make it mandatory to examine a great number of specimens in order to produce an accurate diagnosis.

Table 1. Main colour-pattern features in several populations of *Onychogomphus forcipatus* from various parts of Europe and Asia Minor.

Country	Number of specimens observed	Dorsum of abdominal segment n° 8th A	8th B	8th C	9th A	9th D	9th E	Meso/metapleural stripes: Continuous	Interrupted	Reduced to basal part
Finland	2	+++			+++			+++		
France										
Lorraine + Jura	31	+++			+++			++	+	
Central Massif	29	++	+		++	+		+	++	
Indre to Aquitaine	43	++	++		+++			+	+++	
Vaucluse lowland	27	+	++	++	++	++		+	+++	+
Southern Alps Côte d'Azur to Provence and Roussillon	154	+	+	+	++	++	+	+	+++	
	222	+	+++	++	+	+	+	+	+++	+
Spain	5		++	++		+++			+++	
Central Italy	2			+++		++	++		+++	
Morocco and Tunisia	9		+	++	+	++	++		++	+
Balkans	11	++	+		++	++		++	+	
Sicily	3			+++			+++		++	++
Turkey	34	+	++	++	+	++	+++	+	+++	+++
Cyprus and southern Sporades Islands	4		++	++					++	++

A: black surface > 95%
B: with a rounded yellow spot
C: with an elongated yellow spot, or with yellow surface > 50%
D: black surface ranging from 50 to 100%
E: yellow surface > 50%
The number of "+" indicates the proportion of the given form upon the others in each area.

The subterminal ventral protuberance is either present or absent in each subspecies, in every locality studied (Fig. 2, a to f), and does not supply further help for subspecific identification.

In France, the geographic separation of these 2 entities coincides with a topographic differentiation, with the exception of the lower Rhône Valley. In Italy, where the same 2 forms occur, their respective distribution is also well understood (LIEFTINCK, 1966; CAPRA & GALLETTI, 1978; TERZANI, 1980; GALLETTI, 1981). Indeed, such a structural character, which allows differentiation between 2 pools with a clear geographic distribution, is of more taxonomic interest than colour-pattern criteria, which cause only confusion.

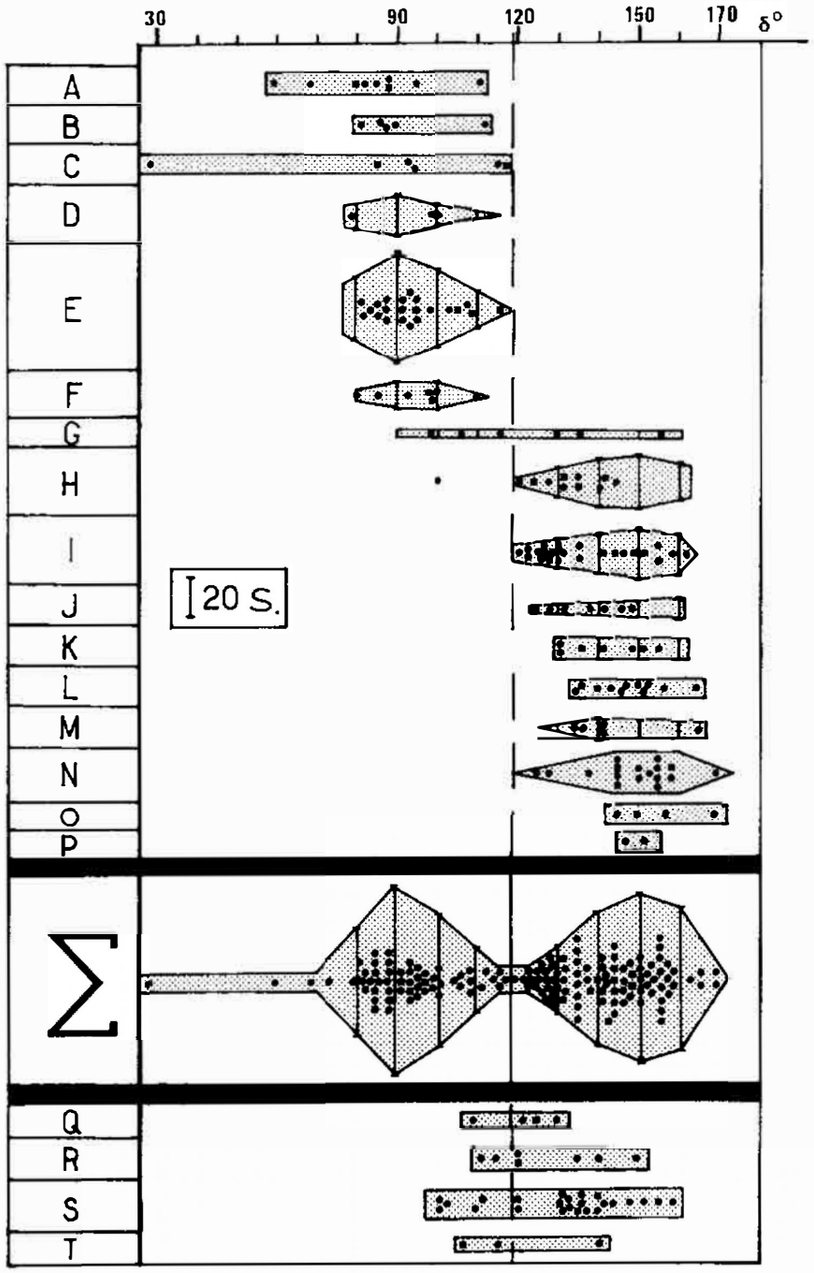

Figure 1. δ values of the angle joining the subterminal dorsal projection with the rest of the inferior appendage, in males of *Onychogomphus forcipatus* from Europe, Northern Africa, and Asia Minor.

•: precise determination on collected specimens (accuracy = 3°).
I: estimation in natura on living specimens (accuracy = 10°). (I = 20 s.: 20 specimens).
A: Morocco (Rif and atlantic coast) and Tunisia (Oued Ghezala).
B: Spain (Andalusia: Cordoba; Pyrenees: Santa-Cruz near Jaca) (authors' collection and coll. VERSCHUREN).
C: Northern to Central Italy (coll. DOMMANGET: Erro river at Pian Botello, Mioglia (SV); GALLETTI & PAVESI (1983); CAPRA & GALLETTI (1978); DE MARMELS & SCHIESS (1978)).
D-M: France
D: Roussillon and South-Western Languedoc.
E: Languedoc north-east of Canal du Midi, up to the eastern slopes of Cevennes and the southern ones of the Plateau of Coiron.
F: Provence - Côtes d'Azur east of the Rhône river.
G: Contact localities between *O. f. forcipatus* and *O. f. unguiculatus* (Coulon river between Apt and Avignon, and Asse river between Digne and Gréoux-les-Bains).
H: Southern Alps, except Vaucluse and Drôme.
I: Vaucluse and Drôme north of Avignon and Apt.
J: Massif Central (Tarn river and tributaries).
K: Aquitaine westward of Mazamet, Carcassonne and Ax-les-Thermes, and southward from Dordogne.
L: Western France (Indre, Indre-et-Loire, Vienne, and Haute-Vienne) (coll. DOMMANGET).
M: Lorraine.
N: Balkans (Yugoslavia: Dinaric Alps near Gospic; Montenegro near Niczic and Danilovgrad; Greece: Olympia, Lefkas, Thasos Island; Cyclades Islands: Tinos; Bulgaria: Malko Tarnovo) (authors' collection and coll. DOMMANGET; GALLETTI & PAVESI (1983); BILEK (1967)).
O: Sicily (authors collection; GALLETTI & PAVESI (1983))
P: Finland (Hakulinjaki) (coll. DOMMANGET).
Σ: all European countries combined.
Q-T: Asia Minor.
Q: Cyprus and Southern Sporades Islands (Samos).
R: Northern part of Turkey: Pontic Alps and Black Sea coast (Bolu, Taflan, Persembe, Esbiye, Trabzon).
S: Taurus Mountains in Turkey: Barla, Egridir, Galvaç, Hazar Gölü, Elmali, Beysehir Gölü.
T: Southern coast of Turkey: Demirtas, Silifke, Adana.

(The material studied resides either in the authors' collections, or in other indicated ones).

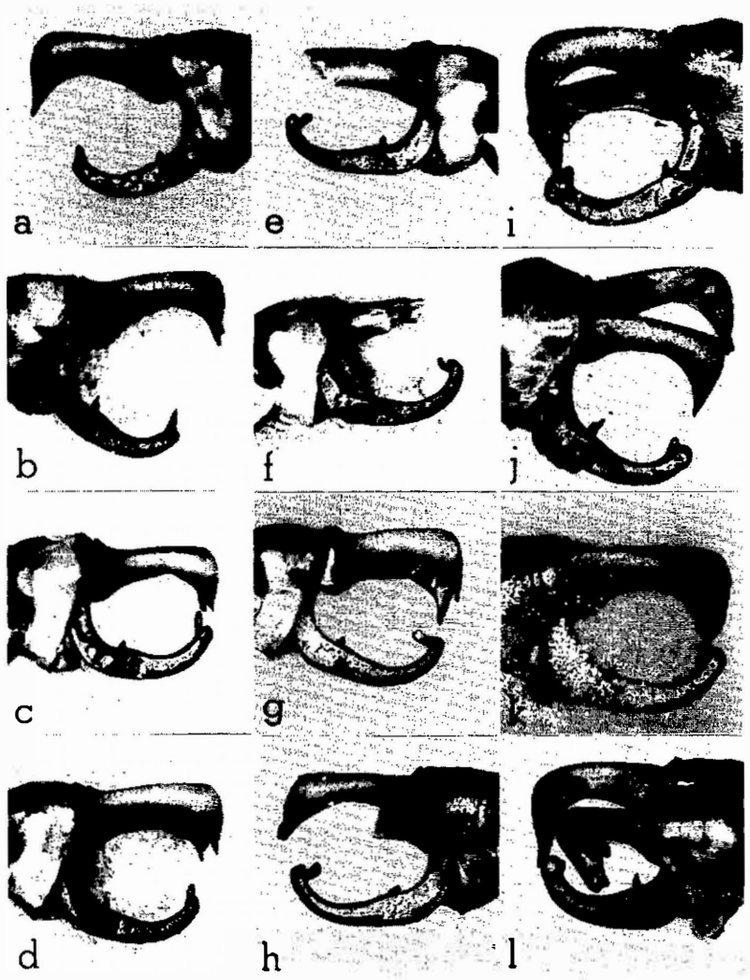

Figure 2. Morphology of the inferior appendage of males in several subspecies of *Onychogomphus forcipatus*. a - d: *O. f. forcipatus* (France; a-b: Lorraine; c: Vaucluse; d: Ariège). e - h: *O. f. unguiculatus* (e: France, Ardèche; f: France, Gard; g-h: Morocco, Rif). i - l: *O. f. albotibialis* (Turkey; i: Beysehir Gölü; j-l: Hazar Gölü). (Length of each inferior appendage: 3 mm).

2.2.2. Populations from Asia Minor

Males from Turkey and adjacent islands (Cyprus and southern Sporades) were found to be distinct from European ones on a structural basis, but here too observations must be carried out at a population, not at an individual, level.

All δ values cluster around 135°, and, in 38 specimens studied, range from 100° to 160° (Fig. 1). However, another useful aid for distinction resides in the shape of the subterminal dorsal projection itself. It is mostly short and thick, as wide as long, or wider than long, rounded and of the same size and shape or smaller than the subterminal ventral protuberance, so that the posterior part of the inferior appendage is shaped like the head of a human femur (Fig. 2, i to l). Thus, the length to width ratio (determined as in figure 3, and noted a:b) is generally less than 1 (Fig. 4). The subterminal ventral protuberance itself mostly looks like a rounded, swollen, and well-defined, apex.

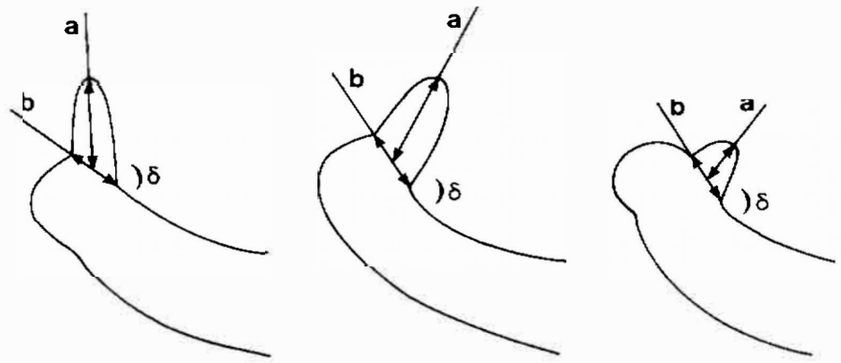

Figure 3. Main values allowing to separate males of *Onychogomphus forcipatus* in several subspecies (see text for explanations).

In European and African males, the subterminal dorsal projection is longer than wide, both in the nominal subspecies and in *O. f. unguiculatus*. Its length to width ratio ranges from 1 - 2.5, with only few individual exceptions (Fig. 4). The subterminal ventral protuberance is variable and may be absent.

Within the limits of the series from Asia Minor studied, males from various parts of Turkey (including the whole of Anatolia and the Bosphorus asiatic shore), Cyprus and the southern Sporades seem structurally homogeneous (Fig. 1 and 4), despite their wide colour variation, which is of the same magnitude as in the nominal subspecies. They should be called *O. f. albotibialis* (with *O. f. cypricus* as a junior synonym). Perhaps *O. f. lucidostriatus* is another synonym, but the question remains open, for we did not have the opportunity to study the only 2 known specimens from Iran. Moreover they do by no means constitute a valid sampling, since a subspecies must be determined at the population level. Observation should be carried out on a more important Iranian material before coming to a conclusion.

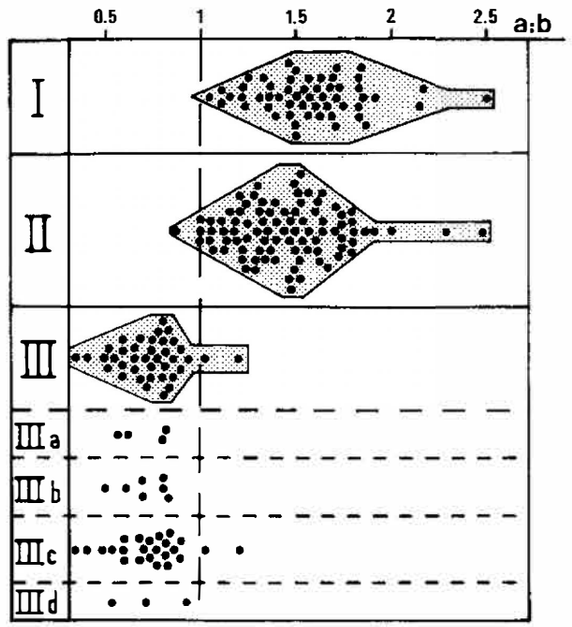

Figure 4. Length to width ratio (a:b) of the subterminal dorsal projection of the male inferior appendage, in several subspecies of *Onychogomphus forcipatus*. I: *O. f. unguiculatus*. II: *O. f. forcipatus*. III: *O. f. albotibialis* (detailed regional distribution: IIIa: Cyprus and Samos Islands; IIIb: Turkey: northern coast; IIIc: Turkey: Taurus Mountains, Central and Eastern Anatolia; IIId: Turkey: southern coast)

2.3. Structural differentiation of the females

According to the mating scheme of the species and considering the structural differences in male appendages, we have searched for morphological particularities on the frons of the females. Differences really exist between the three subspecies, but the variation range in every one is so wide that this cannot be used as a reliable character for a precise subspecific determination.

Some general tendencies have been, however, recognized, which are illustrated on figure 5.

In *O. f. albotibialis* (7 females studied), the central region of the upper part of the frons is moderately depressed and generally shows a deep triangular or rounded pit just before the central ocellus (in 4 specimens) (Fig. 5a). In the other 3 specimens, this excavation was only slightly marked, or was almost lacking. The shoulderings on both sides of the pit are posteriorly rounded.

In *O. f. forcipatus* (6 females studied), the median area of the upper part of the frons is very slightly depressed, but has a triangular pit (rarely rather rounded) which is always present and generally deep (in four specimens at least). This pit is bordered posteriorly by a well visible pad and anteriorly by a median bulge, more or less prominent. In three specimens this bulge was very important and separated 2 grooves diverging backwards (Fig. 5b). This structure, when present, seems to be a good criterium to identify the nominal subspecies. The lateral shoulderings are rounded.

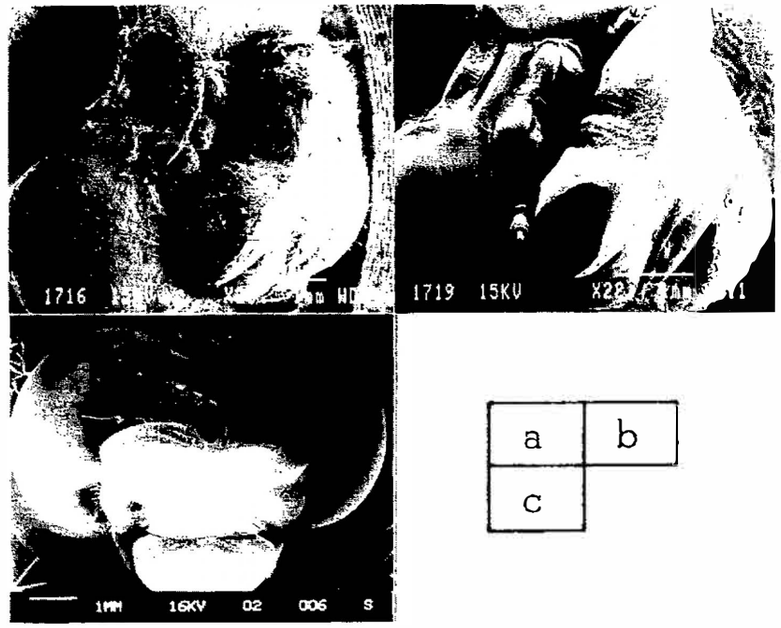

Figure 5. Structural characters of the frons of the females, in several subspecies of *Onychogomphus forcipatus*. a: *O. f. albotibialis* (Turkey); b: *O. f. forcipatus* (France); c: *O. f. unguiculatus* (Morocco).

In *O. f. unguiculatus* (8 females studied), the structure of the frons area is variable. Nevertheless the central part is generally depressed, often forming a deep groove with a rounded bottom (Fig. 5c), ending, in front of the central ocellus, in a hollow which is generally deep, rounded and widely opened forwards. The lateral shoulderings are posteriorly very marked in most specimens, steeply dominating the bottom of the pit.

Thus it remains impossible to identify with certainty an isolated female at a subspecific level. The study of the frons area provides only a probability, which may be improved by increasing the number of specimens studied.

3. Key to subspecies of males Onychogomphus forcipatus

1 - Subterminal dorsal projection of the male inferior appendage longer than wide, with a length to width ratio value ranging from 1 to 2.5 at a population level (only few individual exceptions). Subterminal ventral protuberance of variable size and shape, either large and swollen, poorly defined, or absent.

2 - Subterminal dorsal projection of the male inferior appendage following more or less its main curvature, directed caudad or weakly backturned. Angle between this projection and the rest of the appendage always obtuse, with values ranging from 120° to 170° at a population level (median frequency around 140°-160° in every population) . . . . . *Onychogomphus forcipatus forcipatus* (LINNAEUS, 1758)

2 - Subterminal dorsal projection of the male inferior appendage strongly backturned by an angle ranging from 25° to 120° at a population level (median frequency around 90° in every population) . . . . . *Onychogomphus forcipatus unguiculatus* (VANDER LINDEN, 1823)

1 - Subterminal dorsal projection of the male inferior appendage short and thick, about as wide as long or wider than long, with a length to width ratio ranging from 0.5 to 1 at a population level (only few individual exceptions). Size and shape generally similar or smaller than that of the subterminal ventral protuberance. This latter often well-defined, rounded, and swollen . . . . . *Onychogomphus forcipatus albotibialis* SCHMIDT, 1954

4. Distribution of the subspecies of Onychogomphus forcipatus

4.1. *Onychogomphus forcipatus unguiculatus* (VANDER LINDEN)

Figure 6 shows the exact distribution of *O. f. unguiculatus* in France, and Figure 7 illustrates its entire range.

In France, this subspecies inhabitats only the Mediterranean fringe and an asymmetric part of the lower Rhône Valley. To the West, its range boundary closely follows the divide between the Mediterranean and Atlantic ocean watersheds. Northwards, it is limited by the southern foothills of the southern Alps and the Central Massif, and it does not occur above 450 m (calcareous rocks) or 280 m (acid rocks). In the lower Rhône Valley, *O. f. unguiculatus* inhabits the right bank south of Montélimar and the Coiron Plateau, whereas the nominal subspecies inhabits the left bank up to Avignon, i.e. the Drôme and almost the whole Vaucluse area. The reasons for this strange asymmetric distribution are unclear.

Thus, *O. f. unguiculatus* as defined here is much more of a southern subspecies in France than was hitherto believed, and the limits of its range are better defined than on the basis of colour-pattern criteria. The 2 french subspecies exhibit distinct ranges and rarely contact each other in mixed populations (only in 2 localities did we find great numbers of both *forcipatus* and *unguiculatus*- phenotypes). The isolation of the 2 taxa in regions with different climatic features, together with structural differentiations, provides restrictions to hybridization and

favours the preservation and fixation of their characteristics.

In a broader context, *O. f. unguiculatus* inhabits the greater part of mainland Italy, except for the NE and possibly Calabria (and Basilicata ?) (BUCCIARELLI, 1977). In Spain, the structural details needed for correct identification of the inhabiting subspecies are rarely explicited in the published accounts available. LIEFTINCK (1966) records *O. f. unguiculatus* from southern Spain on evidence of the morphology of the male inferior appendages. Our specimens from Andalusia and one from the surroundings of Jaca in northern Spain (Coll. D. VERSCHUREN, Gent), also belong to this subspecies. Moreover, Ocharan (in litt.) claims that specimens from the southern slopes of the Cantabric and Iberian Mountains up to 1100 m above sea level (northern Duero basin), and from the Tajo basin in Central Spain, are true *O. f. unguiculatus*. Neither *O. f. forcipatus* nor *O. f. unguiculatus* have been recorded north of the Cantabric Alps, along the Atlantic coast. The possibility remains that the nominal subspecies inhabits the NW corner of Spain (Galicia), in close relation with its specific oceanic climate, but this assertion remains to be proved.

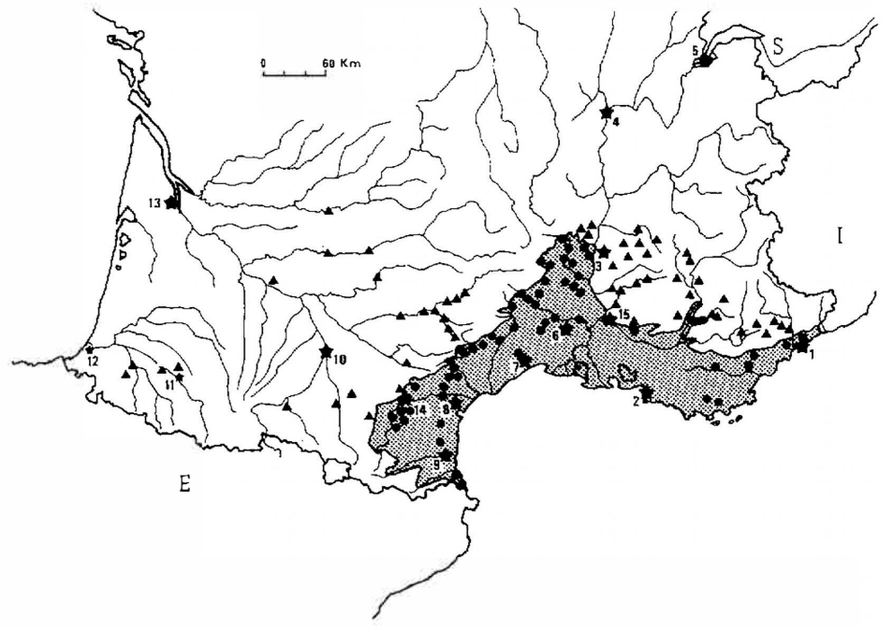

Figure 6. Distribution of *Onychogomphus forcipatus unguiculatus* in France. ●: *Onychogomphus forcipatus unguiculatus*; ▲: *Onychogomphus forcipatus forcipatus*; ★: Main towns (1= Nice; 2: Marseille; 3: Montélimar; 4: Lyon; 5: Genève; 6: Nîmes; 7: Montpellier; 8: Narbonne; 9: Perpignan; 10: Toulouse; 11: Pau; 12: Bayonne; 13: Bordeaux; 14: Carcassonne; 15: Avignon); E: Spain; I: Italy; S: Switzerland.

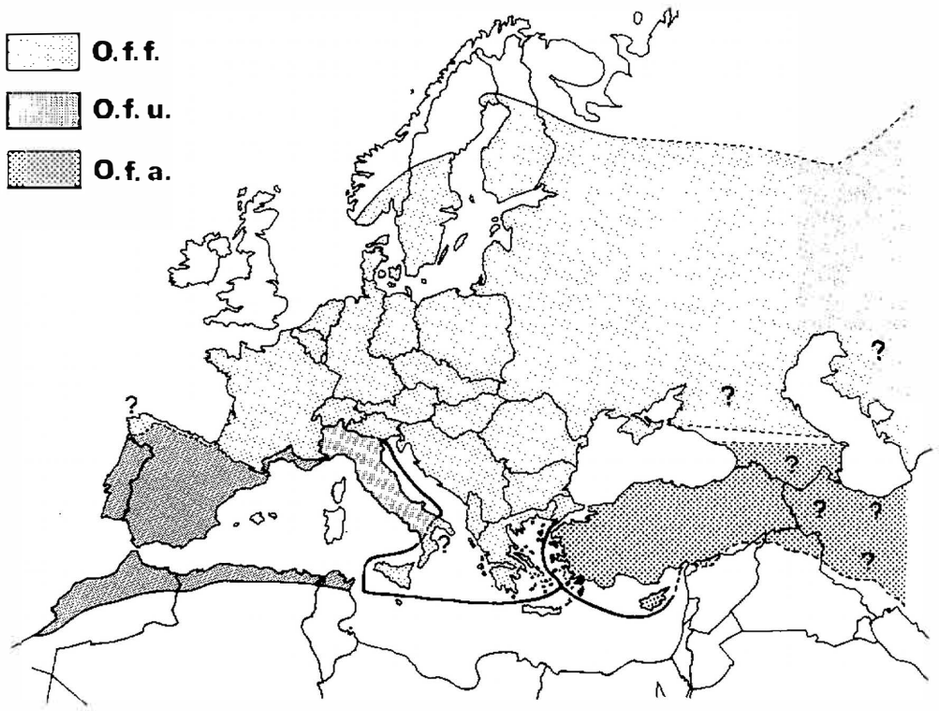

Figure 7. Assessment of the distribution of the subspecies of *Onychogomphus forcipatus* in Europe and Asia Minor. O.f.f.: *O. f. forcipatus*; O.f.u.: *O. f. unguiculatus*; O.f.a.: *O. f. albotibialis*; ?: possible, but uncertain, presence of the given subspecies; ------: imprecise limits.

In Africa, *O. f. unguiculatus* inhabits only the Mediterranean and Atlantic fringes of Morocco (LIEFTINCK, 1966; DUMONT, 1972), Algeria [SELYS & HAGEN, 1858; SELYS, 1871; MCLACHLAN, 1897; MORTON, 1905 and MARTIN, 1910 (sub. *O. forcipatus* (L.))], and Tunisia (DUMONT, 1977c). It does not live south of the Atlas and Tellian Atlas, and is absent from Lybia (D'AGUILAR *et al.*, 1985) and Egypt (DUMONT, 1980).

O. f. unguiculatus thus appears to be a true West-Mediterranean subspecies, which does not extend east of Tunisia and Italy, and is restricted to the margins of the Mediterranean, without penetration of the continental areas, with the exception of Spain.

4.2. *Onychogomphus forcipatus albotibialis* SCHMIDT

The range of this subspecies, which inhabits both running waters and lakes, remains undefined, and its assessment depends upon the true identity of the Iranian *O. f. lucidostriatus*. *O. f. albotibialis* seems to be the single subspecies present in Turkey (where it reaches eastern Anatolia), Cyprus, and the southern Sporades. It is not known from Syria and Iraq, but its presence remains possible in the northern provinces of these countries. *O. f. lucidostriatus* is in need of reexamination on a great number of specimens. If it is a synonym of *albotibialis*, this subspecies extends at least to northern Iran, and possibly south of the Caucasus (Georgia, Armenia, and Azerbaïdjan). It does not reach Afghanistan.

4.3. *Onychogomphus forcipatus forcipatus* (L.)

The nominal subspecies inhabits what is left of Europe, including the french southern Alps up to 1100 m or more and the Atlantic rivers in the Central Massif, but excluding the British Islands and northern Scandinavia. It extends up to the Ural Mountains, western Siberia, and, possibly, the northern slopes of the Caucasus. Its range includes Sicily, the Balkan countries (Yugoslavia, Albania, Greece, Bulgaria), the Cyclade Islands and, probably, Rumania. Additional data are needed, however, from Bulgaria, Rumania, southern USSR, southern Italia, and from some Egean islands. From a structural point of view, the so-called *O. f. meridionalis* auct. and *O. f. siculus* are only pale conditions of typical *O. f. forcipatus*, without any systematic value.

5. Conclusion

The splitting of *O. forcipatus* into several subspecies is impossible on colour-pattern criteria. From western and northern Europe to the Mediterranean countries, and from the highest to the lowest altitudes, populations are subjected to an irregular reduction in black markings. No demarcations can be traced between pale and black populations. Quite to the contrary, the angle of the subterminal dorsal projection and the rest of the inferior appendage in males, together with the length to width ratio of this projection, provide reliable criteria for establishing subspecies. Observations need to involve, however, a great number of specimens, and populations rather than individuals. From these structural characteristics, it is possible to derive three entities exhibiting a distinct geographic distribution: *O. f. forcipatus*, *O. f. unguiculatus*, and *O. f. albotibialis*. The females are, however, poorly differentiated at the subspecies level.

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