

RETURN TO THE SUBSPECIES CONCEPT IN THE GENUS *ZETA* (HYMENOPTERA: VESPIDAE; EUMENINAE)

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Abstract.- The subspecies recognized in the eumenine wasp genus *Zeta* are confirmed as synonyms.

Resumen.- Las subespecies reconocidas en el género de avispa eumenina *Zeta* son inveteradas como sinónimos.

In 1987, I published a study of the subspecies of two species of the neotropical potter wasp genus *Zeta*. At that time, the four recognized species in *Zeta*, were divided into 15 subspecies, with most of the subspecies proposed by Giordani Soika (1975). I documented that the color characteristics by which most of the subspecies were distinguished: (1) showed discrepancies between actual specimens and Giordani Soika's (1975) key, (2) were transitional. Distributional overlap was also noted. I concluded that these subspecies were not really distinct, and sank most of them. I also opined that "Recognition of subspecies is in my view a poor way of dealing with color variation in vespids anyway" (Carpenter, 1987: 257).

Giordani Soika (1990: 166-170) took issue with this conclusion, in an appendix to a publication dealing with some other neotropical eumenine genera. Below I quote the full appendix:

"In una recente pubblicazione (1987, PSICHE [sic], 94:253-259) il Carpenter enuncia 'A review of the subspecies concept in the eumenine genus *Zeta*', basata sullo studio tassonomico di alcune specie di questo piccolo genere neotropicale. Il Carpenter si mostra altamente meravigliato dal fatto che alla specie *argillaceum* (L.) vengono attribuite 10 sottospecie: 'Giordani Soika recognizes only four species in *Zeta*, but these are divided into no fewer than 15 subspecies, 10 of which are in *argillaceus*'.

Ma che dire allora delle 16 sottospecie dell' '*Eumenes flavopictus* (Blanch.)' riconosciute e descritte del Van der Vecht (1959, Zool. Verh. Leiden, 41:1-71); o delle 15 sottospecie del *Polistes rothney* Cam., pure studiate dal Van der Vecht (1978, Bijdr. Dierk., 38/97-109); o delle 17 sottospecie di *Polistes stigma* (F.) del Petersen (1987, Ent. Scand., 10:227-259); o delle 9 'color forms' dell' '*Eumenes lepeleteri* Sauss.' del Bequaert; od anche le 10 «color varieties» dell' '*Eumenes maxillosus* (DG), pure del Bequaert (1918, Bull. Am. Mus. nat. Hist., 39: 276-278, e 60: 279-281). È però opportuno ricordare che molte delle «color varieties» del Bequaert sono oggi considerate buone specie. E non è impossibile che qualche sottospecie dell' '*argillaceum* si riveli, ad un più attento studio, anch'essa valida specie. Posso già dire che lo studio dell'apparato copulatore di alcune ha già messo in evidenza significative differenze, specialmente nei lobi basali dell'edeago e negli apodemi, come risulta dall'esempio delle figg. 8991: le differenze tra le sottospecie *incarnum* ed *apurimacense* dell' '*argillaceum* non sono minori di quelle dalla specie *mendozanum* (Schr.).

Il Carpenter ritiene fonte di difficoltà un 'couplet' della mia Tabella per le sottospecie dell' '*argillaceum*, che definisce 'vague', e così traduce;

'Ferrugineous, or brown-ferrugineous and black, without yellow markings. In some examples (transitional to *hubrichi*) part of the posterior margin of the pronotum

and apex of tergum 1 may be yellow'.

'Yellow markings fairly extensive both on thorax and abdomen'.

A dire il vero, questo 'couplet' mi sembra assai più chiaro di molti di cui abbonda la letteratura: mi limito a citare - come esempio - parte della Tabella per la determinazione delle *specie* di *Stenodynerus* (= *Nannodynerus* Bl.) nella fondamentale Monografia del Bliithgen, pubblicata dall'Accademia delle Scienze di Berlino (Die Faltenwespen Mitteleuropas, 1961, Abh. Deutsch. Ak. Wiss. Berlin, Kl. Chem. Geol. Biol., Jh. 1961, 2: 109-110).

'Flügelsschuppen zitronen-, hell- oder weisslinchgelb, mit nicht pigmentiertem, durchsichtig gelblichem Mittelfleck, und linearem solchen Saum, am Innerrand geschwärzt; ausnahmsweise sind sie braunschwarz, mit oder ohne schmale gelbe Randbinde, aber nie gerötet'.

'Flügelsschuppen rot oder orange oder hellgelb, mit durchsichtiger roter iiberlagerung'.

Il nuovo concetto di sottospecie del Carpenter è imperniato sul non riconoscimento della validità delle sottospecie, che sarebbero 'artificial taxa'. Questo concetto è ripreso dal Carpenter in SPHECOS (1988, n° 17:12), ove approva l'eliminazione delle sottospecie proposta dall'Archer 'especially to the extent that subspecific taxa are eliminated'. E rafforza questo principio ricordando le ricerche di McLean (in realtà precedute da molte altre di vari AA., specialmente su Lepidotteri) che hanno 'even shown experimentally that such 'subspecies' in *Polistes* can be produced by manipulation of humidity!«.

In realtà, il fatto che variando alcuni fattori ambientali si inducono variazioni di colore in molti insetti, è del tutto ininfluenza nei casi in esame, in quanto tali variazioni sono limitate alla generazione che li ha subiti, e scompaiono completamente già alla prima generazione successiva. Ciò mi ricorda le ricerche, riportate dai vecchi testi universitari di Zoologia, di alcuni 'scienziati' che, avendo tagliata la coda ad alcuni topi, si attendevano che la loro prole nascesse priva di coda. Questo non

avvenne, e gli sperimentatori, del tutto stupiti, conclusero per la non trasmissibilità ereditaria dei caratteri acquisiti, e ne fecero una pubblicazione.

Oggi noi potremmo ritornare al concetto linneano: 'Species tot sunt quot diversas formas ab initio produxit Infinitum Ens; quae deinde formae secundum generationis inditas leges produxere plures, at sibi semper simi les, ut species nunc nobis non sint plures, quam quae fuere ab initio'. (C. Linnaei, Genera Plantarum, Ed. V, 1754, p. III).

Ma è oggi difficile accettarlo, e dobbiamo ammettere la speciazione, e la razzazione che ne è l'inevitabile fase intermedia. E se diamo un nome alle specie dobbiamo, per chiarezza, precisione, ed anche per semplicità, dare un nome anche alle sottospecie. Ovviamente quando le caratteristiche delle sottospecie sono nettamente al di fuori dei limiti di variabilità della forma nominale o delle altre sottospecie, e sono geneticamente stabilizzate, si da ripresentarsi eguali nelle successive generazioni.

A conferma del punto di vista del Carpenter interviene Mud D'aub (1988, SPHECOS, n° 17:12): 'The use of subspecies is akin to putting stamps into albums that have rectangles for each issue'. Non è forse tanto pertinente il confronto con insetti che, certamente, non hanno caselle predisposte; comunque siamo nel più pieno concetto linneano «Species tot sunt...», ove l'«Infinitum Ens» è l'uomo, che stampa gli immutabili francobolli.

Riservandomi di discutere più ampiamente la questione in un lavoro di prossima pubblicazione, confermo la validità delle sottospecie da me segnalate nella mia nota del 1975 sul genere *Zeta* Sauss."

which I translate (after correcting a few typographical errors) as:

"In a recent publication (1987, Psyche, 94:253-259) Carpenter enunciates 'A review of the subspecies concept in the eumenine genus *Zeta*', based on taxonomic

study of some species of this small neotropical genus. Carpenter marvels highly at the fact that to the species *argillaceum* (L.) 10 subspecies are attributed: 'Giordani Soika recognizes only four species in *Zeta*, but these are divided into no fewer than 15 subspecies, 10 of which are in *argillaceus*!'.

But is what one to say then of the 16 subspecies of '*Eumenes flavopictus* (Blanch.)' recognized and described by van der Vecht (1959, Zool. Verh. Leiden, 41:1-71); or of the 15 subspecies of *Polistes rothney* Cam., also studied by van der Vecht (1978, Bijdr. Dierk., 38/97-109); or of the 17 subspecies of *Polistes stigma* (F.) of Petersen (1987, Ent. Scand., 10:227-259); or of the 9 'color forms' of '*Eumenes lepeleteri* Sauss.' of Bequaert; or also 10 'color varieties' of *Eumenes maxillosus* (DG), also of the Bequaert (1918, Bull. Am. Mus. nat. Hist., 39: 276-278 and 60: 279-281). It is opportune to remember however how a lot of the 'color varieties' of Bequaert are considered good species today. And it is not impossible that some subspecies of *argillaceum* will be revealed, to a more careful study, also valid species. I can already say that the study of some copulatory apparatus of some has already put in evidence meaningful differences, especially in the basal lobes of the aedeagus and in the apodemes, as results from the example of the figs. 89-91: the differences between the subspecies *incarum* and *apurimacense* of *argillaceum* are not smaller than those from the species *mendozanum* (Schr.).

Carpenter thinks a source of difficulty a couplet of my key for the subspecies of *argillaceum*, that he terms 'vague', and so translates;

'Ferrugineous, or brown-ferrugineous and black, without yellow markings. In some examples (transitional to *hubrichi*) part of the posterior margin of the pronotum and apex of tergum 1 may be yellow.'

'Yellow markings fairly extensive both on thorax and abdomen.'

To say the truth, this 'couplet' seems me a great deal clearer than many of which

literature abounds: I confine to quote - as example - part of the key for the determination of the species of *Stenodynerus* (= *Nannodynerus* Bl.) in the fundamental monograph of Blüthgen, published by the Academy of Sciences in Berlin (Die Faltenwespen Mitteleuropas, 1961, Abh. Deutsch. Ak. Wiss. Berlin, Kl. Chem. Geol. Biol., Jh. 1961, 2: 109-110).

'Tegulae lemon -, brightly - or whitish-yellow, with not pigmented, lucidly sallow middle-stain, and linear such margin, at the inner-edge blackened; as an exception, they are brown-black, with or without narrow yellow edge-bands, but never reddened'.

'Tegulae red or orange or light-yellow, with transparent red superimposition'

The new concept of subspecies of Carpenter has hinged on not recognizing the validity of the subspecies, that are 'artificial taxa'. This concept is taken from Carpenter in SPHECOS (1988, no. 17:12), who approves the elimination of the subspecies proposed by the Archer 'especially to the extent that subspecific taxa are eliminated'. And reinforces this principle citing the research of McLean (really preceded by a lot of other varied authors, especially on Lepidoptera) who have 'even shown experimentally that such 'subspecies' in *Polistes* can be produced by manipulation of humidity!'.

Really, the fact that varying some environmental factors induces variations of color in many insects, it is entirely influential in the cases in examination, in how much such variations are limited to the generation that has suffered them, and they already completely disappear in the first following generation. This recalls to me the research, reported by the old university texts of zoology, of some 'scientists' that, having cut the tail of some mice, were expecting that their issue would be born deprived of tail. This didn't happen, and the experimenters, entirely surprised, concluded for no hereditary transmissibility of the acquired characters, and they made a publication of it.

Today we could return to the Linnaean concept: 'There are as many species as those diverse forms which the Infinite Be-

ing has produced from the beginning; subsequently these forms produced more in accordance with the inherent laws of generation, but always similar to themselves, with the result that we do not now have more species than have existed from the beginning'. (C. Linnaeus, *Genera Plantarum*, Ed. V, 1754, p. III).

But it is difficult to accept it today, and we have to admit speciation, and the racination that is the inevitable intermediary phase of it. And if we give a name to the species we ought, for clarity, precision, and also for simplicity, to also give a name to the subspecies. Obviously when the characteristics of the subspecies are clearly out of the limits of variability of the nominal form or the other subspecies, and they have stabilized genetically, is affirmed by equal reappearance in the following generations.

To confirmation of the point of view of the Carpenter Mud D'aub intervenes (1988, SPHECOS, no. 17:12): 'The use of subspecies is akin to putting stamps into albums that have rectangles for each issue'. It is not so much perhaps pertinent the comparison with insects that, certainly they don't have predisposed boxes; however we are in the fuller Linnaean concept 'Species tot sunt...', where 'Infinitum Ens' is man, who stamps the unchangeable postage stamps.

Reserving to discuss more broadly the matter in a work of next publication, I confirm the validity of the subspecies recognized by myself in my note of 1975 on the genus *Zeta* Sauss."

Borsato and Ratti (1999), in their list of taxa, followed Giordani Soika (1990) in treating the subspecies of *Zeta* as valid. Therefore, I now retort.

There are many confusions exhibited in Giordani Soika's quotation, as I shall detail, but first I will deal with the one substantive claim, regarding "meaningful differences" in the male genitalia. Giordani Soika states that the differences between two subspecies of *argillaceum* are not smaller than those com-

paring both to the species *mendozanum*. The figures he provides show differences among these three taxa. How exactly are they meaningful? The differences are quite minor, but that is not the point: if they are all really different, that would be grounds for recognizing three species, not treating two as subspecies. Of course, to support such recognition, one would have to show that the differences are in fact diagnostic: that they are fixed in each species, and that one is not seeing instead intraspecific variation without taxonomic significance. That latter in fact appears to be the case. Giordani Soika has not shown that the genitalia are diagnostic in this case; but even if he had done so, it would not be grounds for retaining subspecies, for to do so would simply be inconsistent.

Giordani Soika is correct in concluding that I consider subspecies to be artificial taxa: they have no place in a phylogenetic system, in which diagnosable taxa should be treated as species. That is, phylogenetic species (Nelson and Platnick, 1981; Nixon and Wheeler, 1990), a concept which is compatible with cladistic theory, and being character-based, of greatest utility in classification, which is concerned with conveying information (Farris, 1979). However, as I have previously observed (Carpenter, 1996: 2): "But this means that taxa currently recognized as subspecies are either species or synonyms, and moreover there must be a mixture. Without careful study on a case by case basis, the proper status of subspecific taxa cannot be determined." Therefore, in catalogs and checklists (Carpenter, 1996, 2001; Carpenter and Kojima, 1997; Kojima and Carpenter, 1997), I have not proceeded with wholesale changes in status of subspecific taxa. I have only made such changes where I have documented that the subspecies represent arbitrary partitioning of continuous variation, such as the case of *Zeta*, as well as some of Giordani Soika's subspecies in other neotropical genera (Carpenter and van der Vecht, 1991).

Thus, when Giordani Soika cites other examples of species divided into subspecies in the quotation, my response is those are merely taxa whose proper status remains to be determined: either valid species or synonyms. And where he complains that the couplet I criticized as vague is better than other published couplets, that is merely a criticism of the other published couplets. That sort of citation are no more than an appeal to authoritarianism: the point of my criticism remains. And he also fails to mention that, while I termed the cited couplet "vague," I did so in the context of saying: "This vague couplet fails for numerous specimens in the MCZ" (Carpenter, 1987: 255). That is the real issue: the subspecies in *Zeta* cannot in general actually be distinguished by the characters used to describe them.

Giordani Soika likewise misses the point of my citation of experimental manipulations that produced "subspecies" in other vespids (MacLean et al., 1978): it calls the color characters into question as diagnostic indicators. If fluctuations in humidity show plasticity in coloration, and distributional overlap occurs in subspecies described solely on color differences, which moreover intergrade, it is ecological variation that is being given a formal Latin name, not genetically fixed differences. These are hardly species "in statu nascendi," which is Giordani Soika's stated rationale for formally naming subspecies, and so their naming serves no useful purpose.

Finally, regarding postage stamps, if the subspecies are arbitrary, then it is obviously Giordani Soika who has made postage stamps. And this conclusion follows even from a non-cladistic viewpoint. Criticisms of the description of subspecies are long-standing in the systematics literature. Wilson and Brown (1953) outlined a general argument against use of subspecies, discussing at length the problems presented by four features of geographical variation, which are as follows: "(1) the tendency for genetically independent characters to show independent geographical variation; (2) the

capacity for characters to recur in more than one geographical area, yielding polytopic races; (3) the common occurrence of the micro-geographical race; (4) the necessary arbitrariness of any degree of population divergence chosen as the lowest formal racial level" (Wilson and Brown, 1953: 100). They concluded: "The application of this logic to our present knowledge of geographical variation cannot fail to stir a feeling that the trinomial has outlived its usefulness in taxonomy" (Wilson and Brown, 1953: 108). Thus, even to adherents of the biological species concept and allopatric speciation (which obviously may entail divergence prior to speciation) the subspecies has no place. Far from being desirable for purposes of "clarity, precision, and also for simplicity" subspecies are superfluous. Giordani Soika's citation of Linnaeus is thus ironic: it is his taxonomic approach that is outmoded.

In conclusion, Giordani Soika has produced no argument for retention of his subspecies, which confirms that they should be considered synonyms, as detailed in Carpenter (1987).

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