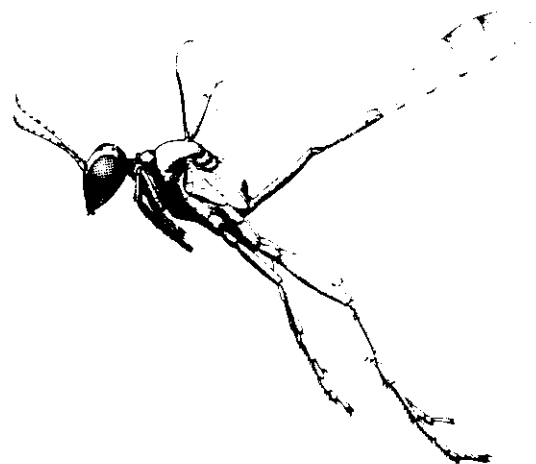


# SPHECOS



Number 11 - June 1986

A Forum for Aculeate Wasp Researchers

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## Editor's Notes

Considerable time has elapsed since Sphecus 10 appeared in October of 1985, and I'm sorry for the delay. To make up for it, two concurrent issues have been produced. The reason for two issues is that so much material has accumulated since number 10 that the 50 page maximum dictated by the USDA duplicating office was exceeded. Hence, I had to make two issues.

The FORUM was introduced last time, and my piece on subgenera generated considerable comment from some readers. In particular Michael Archer and James Carpenter have engaged in a sparring match over vespine genera and subgenera, and others have joined the fray, as you will see a few pages farther on in this issue. Such discussions are very useful and I hope that more of you will join the action. Lets have some other subjects brought out. No one responded to Chris Starr's treatise on social dominance. Looks like behaviorists are less inclined to discuss controversial things than taxonomists.

The Directory issued in 1984 is now outdated and a new one will be forthcoming. In order to improve on the old one, I have drafted up a new questionnaire for each of you to fill out and return to me. I hope that ALL OF YOU will take the time to do this. The accuracy and completeness of the new directory will depend entirely on YOUR cooperation.

Terry Nuhn typed practically all of this issue for me, and I thank him profusely.

## Research News/Help Needed

Enrique Ruiz C. (Tordillo 2308, Fracc. Valle del Huajuco, Monterrey, N.L., Mexico) writes: "As a thesis work, I'll collect and classify Vespidae of Tamaulipas, Nuevo Leon and Coahuila states, also the vespids present in the collections of 4 universities. Until now, I've seen more than 15 species or subspecies of Polistes, 3 spp. of Mischocyttarus, one Polybia and one Brachygaster. We found Stelopolybia in Tamaulipas and Nuevo Leon not reported by Richards (1978) of NE Mexico. Moreover, we have 3 spp. of Vespula: V. squamosa obtained mainly over 1000 msnm in forests of Quercus, this species being the more common, and other two species not identified which are different to those reported by Akre et al. in "Yellowjackets of N.A."

Jeff Cumming (Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario K1A 0C6, Canada) writes: "I have recently accepted a permanent curatorial position at the Biosystematics Research Centre in Ottawa, after

having completed my graduate studies in Edmonton. I am now preparing my dissertation 'Classification and evolution of the eumenine wasp genus Synmorphus Wesmael (Hymenoptera: Vespidae)' for publication, hopefully to appear as a Memoir of the Canadian Entomological Society in 1988. After considerable new synonymy, I recognize 35 species worldwide, including a few new speices and subspecies. Phylogenetic and zoogeographic aspects of the genus are also considered. My new job is research oriented and although I should have a little time to work on aculeates, I am now a Dipterist (Jim Carpenter now referring to me as 'traitorous running dog'), being primarily responsible for Empidoidea as well as some other predaceous groups. Recently, along with my new duties, I have begun to examine the acarinarina of eumenines and would appreciate receiving any mite-bearing specimens colleagues can spare."

Robin Edwards (Rentokil Ltd., East Grinstead, W. Sussex RH19 2JY) writes: "I have a list of predators, parasites and commensals of the Vespinae of the world. If anyone finds Shun'ichi Makino's list for the Polistines of value, then they may wish to compare it with mine. It is a very long list, handwritten and a bit of a mess in places - but I could tidy up the worst and send a photocopy to anyone really interested. There are about 30 pages, plus over 70 references.

"I wish to apologise to Philip Spradbery for forgetting the drawing in his book "Wasps" that showed Vespula vulgaris using mud to cover a damaged nest (Fig. 40). The situation was identical to mine (Sphecos 9:10), only the species, V. germanica, was different."

Raimond V. Hensen (Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, postbus 9517, 2300 RA Leiden, Nederland) writes: "I have nearly finished my present work on the Sceliphronini. Van der Vecht has requested me to try and finish also his remaining work on the sphecline genera Spheex and Isodontia."

John F. MacDonald (Department of Entomology, Purdue University, West Lafayette, Indiana 47907) writes: "Roger Akre and I contributed a manuscript, 'Biology, Economic Importance and Control of Yellowjackets', in part of which we attempt to quantify the economic and medical impact of social wasps, and we present a condensed review of the literature on pure venom immunotherapy. For those interested, look for it in S. B. Vinson (Ed.), Economic Impact and Control of Social Insects, Praeger Press (1986). Completed in early 1983 ('in press' since then), our review of this rather rapidly developing field is already out of date, but is an available starting point for reading about this interesting topic."

Stephen G. Reyes (Dept. of Zoology, University College, P.O. Box 78, Cardiff CF1 1XL S. Wales, United Kingdom) writes: "My work on Cerceris is rather very slow and so far I have only submitted a paper on the new species of Philippines Cerceris. I hope to submit the revisionary work before the end of the year. The species-groupings and other notes on the Oriental species have to follow next year. While here in U.K., I also plan to review our Eumenid fauna and I am planning to arrange to see Dr. van der Vecht and consult him especially with the problems in the stenogastrines. I hope my stay here could be as productive as I envisioned."

Alicia Rodriguez P. (Estacion de Biologia Chamela, Apartado Postal 21, San Patricio, Jalisco 48980, Mexico) writes: "Currently, I am working at the Chamela Biological Station of U.N.A.M. on the coast of Jalisco, where I am studying the Vespidae of the region and developing a thesis project for my B.Sc. on the biology of Mischocyttarus pallidipectus."

A. Giordani Soika (Museo Civico di Storia Naturale di Venezia, S. Croce 1730, 30125 Venezia, Italy) writes "In the last months I continued my research on the taxonomy and biology of the solitary wasps. I have recently [February] been in London, where I have studied several types of Oriental Eumenidae. In March I went to Berlin for the study of Blüthgen's and Bingham's collections. A revision of the Afrotropical species of the genus Antepipona and allied genera has been recently published, with the drawings of the well known venetian artist Gea D'Este. This paper contains the descriptions of two new genera, 20 new species or subspecies, and 13 new synonyms. I have now in print a second contribution to the knowledge of the Afrotropical Eumenidae, where 45 new species or subspecies are described, together with descriptions of 5 new genera and 3 new subgenera. I have also in print a paper on Eumenidae of the Palearctic region, especially from north Africa and the far East (China, Korea, Japan, the Philippines, etc.)"

"This spring I have been in north and central Sahara: in El-Oued Oasis I collected a Polistes probably new. So I began to study the Mediterranean species of this genus, still very little known and I went to Sardinia, Macomer, and collected topotypes - and the neotype because the type is destroyed - of the enigmatic Polistes bischoffi Weyr."

"I am grateful to anyone who will send me for study Eumenidae of the world, especially from the Palearctic, Afrotropical and Oriental regions."

Barbara J. Hager (Dept. of Biology, 173 Castetter Hall, Univ. of New Mexico, Albuquerque, N.M. 87131) writes: "I completed my M.S. in 1984 from the college of environmental science and forestry (Syracuse, N.Y.) where I worked on the general behavior of Ammophila harti. Currently I am a doctoral student working on sex ratio biases in solitary wasps. Right now I am in the process of trying to determine suitable species to study and am basing my criteria on size differences between males and females and on mating systems (I'm looking for species in which males are larger than, equal in size to, and smaller than females). I am interested in using a couple of Ammophila species, particularly since I have had some experience with this genus."

Henry Townes (American Entomological Institute, 3005 SW 56th Avenue, Gainesville, Florida 32608, USA) wants to alert everyone to the fact that he has discontinued work on the Plumariidae.

## Help Needed On Chrysididae

As part of our world revision of the Chrysididae, we are preparing detailed species lists for each genus. These lists will include type repositories. There are a variety of private collections housing types as well as the types of some of the older authors that we have been unable to locate. If any of you know the whereabouts of any of the material listed below, we would really appreciate hearing from you. - Lynn S. Kimsey and Richard M. Bohart (Dept. of Entomology, Univ. of California, Davis, Calif. 95616).

Chrysidid collections containing types - locations unknown,  
with name and date of author in parentheses

[In brackets after each entry I have added information on the whereabouts of the material according to Horn and Kahle (1935-1937, Ent. Beihefte Berlin-Dahlem, vol. 2, 3, 4) "Über ent. Sammlungen" with an update by Sachtleben (1961, Beiträge Ent. 11:481-540). Perhaps the readership can confirm or clarify these facts. - A. S. Menke.]

F. Ancey coll. (Mocsary 1914) [Hymenoptera to J. Lichtenstein (some of the latter's material to Budapest)].  
Beaumont coll. (Linsenmaier 1959) [His collection is in the museum in Lausanne, Switzerland].  
Drewsen Museum (Dahlbom 1854) [In Copenhagen].  
Dufour coll. (we were unable to locate this at Paris) [In Paris].  
Loew coll. (Dahlbom 1854) [Flies to Berlin, other stuff to Halle, Stockholm, and Vienna (again all flies)].  
Mus. Lugdunense (Mocsary 1889) [somewhere in France, Lyon perhaps??]  
Mochi coll. (Zimmermann 1940) - Cairo?  
Naef coll. (Linsenmaier 1959) [Some beetles to Muritz Museum, Waren (Mecklenbg.)].  
Nylander coll. (Dahlbom 1854) [Mus. in Helsingfors].  
Rudow coll. (Buysson 1887) [Mus. Jena ("Sammlung hatte stark gelitten und war vielfach falsch bestimmt")].  
Schrottky coll. (Br  thes 1903) [His material was destroyed according to everything I've ever found out. Some material identified by him may be found in Buenos Aires and La Plata.].  
Schulthess-Rechberg coll. (Mocsary 1889) - [Zurich?]  
Wustneii coll. (Mocsary 1890) [Some stuff to Mus. Altona. Some to Copenhagen and Mus. in Lubeck.].  
Zeller coll. (Dahlbom 1854) [Some stuff to London, some to Leningrad].

Type repositories of the following authors are unknown to us.

Christ, J.L. 1791 [Heh, heh, heh. You must be dreaming.]  
De Stefani, T. 1888 [According to Italo Currado, his stuff is in Sicily in the "Castelbuona". Curator is Dr. Romano, Farmacia, Capaci (Palermo)].  
Fourcroy, A. F. de 1785 [Heh, heh, heh. Incidentally, all species are Geoffroy in Fourcroy.]  
Montrouzier, R. P. 1864 [Australasian material: some lost, some auctioned, some to Mus. Paris, some in Tervuren.]  
Pallas, P. S. 1771 [Mus. Berlin, Leningrad and Vienna.]  
Panzer, G. F. W. 1801 [Mus. Berlin]  
Rossi, P. 1790 [His collection to F. de Sanvitale (Parma), then all or part to Mus. Berlin.]

## Translations Requested

I am wondering if any of Spheco's readers has in his possession an English translation of any of the following papers which were originally written in German:

Adriaanse, A. 1948. Ammophila campestris Latr. und Ammophila adriaansei Wilcke, eind Beitrag zur vergleichenden Verhaltensforschung. Behaviour 1:1-35.  
Baerends, G. P. 1941. Forpflanzungsverhalten und orientierung der Grabwespe Ammophila campestris. Jur. Tijdschr. Entomol. 84:68-275.  
Olberg, G. 1952. Die Sandwespen. Die neue Brem-Bucherei, Heft 68, 55pp.  
Teschner, W. 1959. Starrheit und variabilit  t in Verhalten von Sandwespen. Zool. Beitr. (n.s.) 4:411-472.

I would greatly appreciate the chance to read these papers that I see cited so often, and will gladly pay reproduction and postage costs. thanks. - Jay Rosenheim (Dept. of Entomological Sciences, Univ. Calif. Berkeley, Berkeley, Calif. 94703)

## Forum

My article (some would say diatribe) titled "Subgenera vs. Species Groups" that helped to launch the FORUM in Sphecos 10 generated a fair amount of reader response. These are presented below for your amusement, amazement, consternation, or whatever response they illicit from you. Hopefully more of you will send in your own views on these and other subjects - your old editor.

### A WORKING CLADOGRAM FOR THE VESPINAE

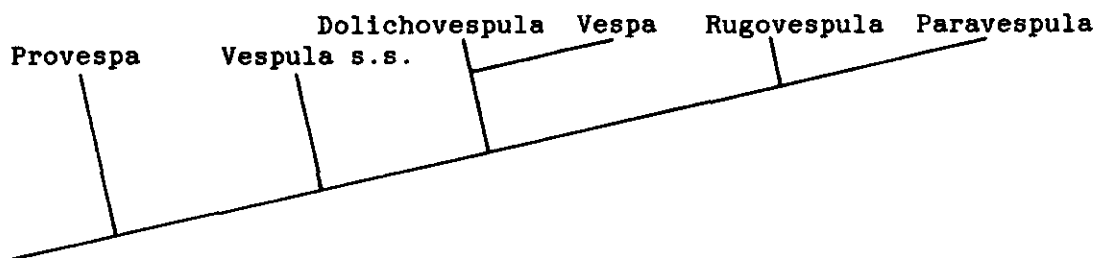
by

Michael E. Archer

(the College of Ripon & York St. John,  
Lord Mayor's Walk, York YO3 7EX, England, U.K.)

In response to Arnold Menke's comments on the Vespinae (Sphecos 10:11-13) I can perhaps contribute to the discussion by giving some preliminary details of my phenetic and cladistic studies of the Vespinae. Vespa, in which I recognise currently 23 species, seems to consist of a group of closely related species with at most V. basalis and V. binghami as isolates. Vespula s.s. is as similar to (or different from) Paravespula as from Dolichovespula so there is no justification to associate Vespula s.s. more closely with Paravespula than with Dolichovespula as is the usual procedure. Vespula s.s. also turns out to have many primitive characters with their derived states in Paravespula and Dolichovespula. Incidentally Vespula squamosa and V. sulphurea are clearly closely associated with Vespula s.s. and should not be left 'in limbo' as is generally the case. Provespa and Vespula s.s. both have unique derived characters so that they are isolated, particularly Provespa, from the rest of the Vespinae.

However the most interesting finding is that Vespa is the sister-group of Dolichovespula so that the traditional taxon Vespula (or rather Dolichovespula + Vespula) is paraphyletic - i.e. the observation of most taxonomists, as quoted by Arnold Menke, that this taxon is monophyletic does not seem to be the case (this finding also came as a surprise to me). In fact the yellowjackets of vespine wasps turn out to be a rather loose group of four or five closely related taxa. My working cladogram is thus:



I shall, therefore, be proposing that the Vespinae consist of 5 genera and 2 subgenera only and all other groupings be called species-groups. The listing with the number of species in brackets is:

Genus Provespa (3)

Genus Vespula s.s. (10) viz.: squamosa, sulphurea, consobrina, acadica,  
atropilosa, vidua, rufa, kingdonwardi, nursei,  
austriaca.

Genus Vespa (23)

Genus Dolichovespula (18) viz.: maculata, media, floral<sup>1</sup>, sylvestris,  
asiatica, adulterina, omissa, lama, panda,  
norwegica, saxonica, sinensis<sup>1</sup>, arenaria,  
"alpicola", norvegicoides, pacifica (this  
includes lockenae), xanthicincta, baileyi<sup>1</sup>.

Genus Paravespula (10)

Subgenus Rugovespula (2) viz.: koreensis, orbata.

Subgenus Paravespula s.s. (8) viz.: germanica, pennsylvanica, vulgaris,  
maculifrons, flavopilosa, structor,  
flaviceps, shidai.

I have listed the species of vespine wasps to avoid some confusion. Names with superscript 1 are new species in the process of being described, i.e. in press. As to "alpicola", I am confused as to whether or not Robert Wagner has described this new species, perhaps someone can help me [see remarks in Carpenter's response and Archer's rebuttal below - edit.].

Of course Vespa, at present, is very rich in subspecies but some of these are being raised to species level as knowledge of their distributions increases. The vespine wasps are less rich in subspecies but some of these may yet be raised to species level.

Thus the Vespinae would seem to have more genera than might be at first supposed but I have succeeded in eliminating most of the subgenera and turning them into species-groups, which as Arnold Menke remarks, that is what they are really. The number of species in each genus except for Provespa, which is the isolated group of the Vespinae, is probably larger than the current size of most zoological genera. Further in order to make the species-groups as nearly equivalent as possible, they will be primarily founded on the bases of differences in the male genitalia.

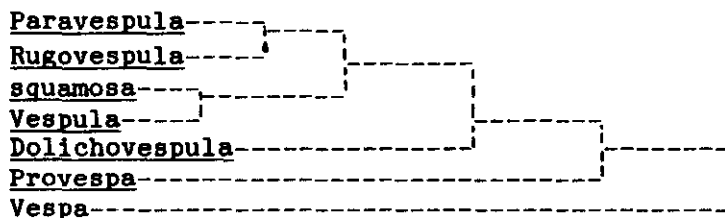
REPLY TO ARCHER

by

James M. Carpenter

(Museum of Comparative Zoology, Cambridge Mass. 02138)

The most serious deficiency of Archer's contribution is obviously that no supporting evidence whatsoever is cited. I have completed my own cladistic analyses of the vespine genera and subgenera (Carpenter 1986a & b) which has been presented at the Eastern Branch of the ESA meeting in Oct. 1985. My results completely contradict Archer's. The scheme is: Vespa + (Provespa + (Dolichovespula + (Paravespula = Vespula))).



The squamosa group is the sister-group of the remainder of Vespula, and Rugovespula the sister-group of Paravespula; that is the extent of the agreement between our systems. When I first saw Archer's comment, I sent him the initial draft of Carpenter (1986a), as well as the results of my analysis of the data matrix of Matsuura & Yamane (1984), and queried him about the characters he used. Archer (in litt.) only indicated that he used some characters that I did not in the 1986a paper, but that I used some that he did not. It is impossible to identify the basis of this disagreement as no characters were provided by Archer, but I can at least compare both systems in terms of my data and that of Matsuura & Yamane. In what follows I shall restrict discussion to those five taxa whose position is in dispute.

Carpenter (1986a) used 17 characters, polarized with reference to the Polistinae, sister-group of the Vespinae (Carpenter, 1981). Eight of these (nine states) are autapomorphies of Vespa, Provespa and Dolichovespula and so

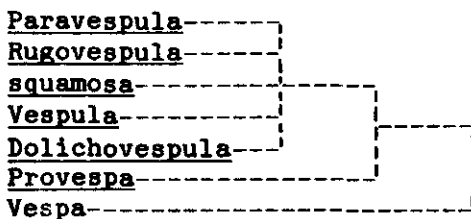
are not at issue here. Vespula and Paravespula shared two synapomorphies: loss of tylodes in the male antenna and complete loss of pronotal carina. The former feature also occurs in a few species of the other vespine genera, but are present in the polistine ground-plan and so is primitive for Vespinae (*contra* Yamane, 1976). The second is perfectly consistent; a carina is present at least laterally in other Vespinae.

There are four synapomorphies for Provespa + (Vespula + Dolichovespula): apex of discal cell truncate, clustering of hamuli basad of SC, loss of pronotal carina dorsally and loss of pretegular carina. The pronotal carina shows homoplasy: it is lost dorsally in a few Vespa, and is present dorsolaterally in a few Dolichovespula (Yamane & Matsuura, 1984, consider Dolichovespula to have the primitive state. I do not believe this to be correct but will defer argument here.). Vespula and Dolichovespula share three synapomorphies: loss of the strong seta on the third labial palp segment, reduction of the scutal lamella and presence of a twisted pedicel in embryo nests.

About the only ground-plan apomorphy shared by Vespa and the Dolichovespula that I can come up with is branched processes of the larval spiracle. Diagnosing my cladogram (Farris, 1979, 1980) with only the nine informative characters mentioned above and this larval character, the number of entries is 11, compared with a minimum possible of 10 (I am ignoring the homoplasy mentioned above - Archer's cladogram requires the same amount). The number of diagnostic entries for Archer's cladogram is 22. Whereas it accounts for the single larval character better (as a single origin), Archer's arrangement is otherwise inferior by a wide margin for these data because it requires twice the number of diagnostic entries. Viewing these diagnostic statements as character origins on the tree, this means Archer's tree requires all but one of the characters to have evolved more than once. Without strong justification for believing this massive convergence, Archer's system must be rejected.

Matsuura & Yamane (1984) published a matrix of 42 characters for the Vespinae (including Rugovespula and the squamosa group). Six characters are invariant in the subfamily, one applies only to parasitic species, and one (#13, ovarioles per ovary) in my view questionably homologizes all numbers above 6. I have analyzed the remaining 34 characters (including 16 autapomorphies). There is a considerable number of missing entries, so I have used a computer system (PHYSYS) that can process missing data. I included an outgroup node. (It should be noted that two of Matsuura & Yamane's polarities are erroneous, #1 and 6 - ocelloccipital distance and hind coxal carina. The addition of the outgroup corrected for these. Additionally, they failed to code #22, pedicel of embryo nest, for Provespa, although the text indicates that it should be zero. #25, occipital carina, has an error. I have changed these. Finally, for characters that vary within taxa the ancestral state is used. I disagree with certain other of their interpretations, but follow them here.)

The matrix is ambiguous; there are six equally parsimonious cladograms (I used the branch-and-bound routine to get exact solutions). However, they only disagree on the interrelationships of the Vespula subgenera/squamosa group/Dolichovespula. The strict consensus tree (Nelson, 1979) - the tree that has only the groups found on all six of the cladograms - is:



The Adams consensus tree (Adams, 1972), which takes the intersection of groups, differs in having Vespula and the squamosa group as sister groups. That is, Vespula s.l. is monophyletic on every tree. Provespa is always its sister-group, and Vespa is always the sister-group to this. Thus, these results are broadly compatible with my treatment outlined above, and contradict Archer's. The length of the five trees is 45 (consistency .80). Diagnosing Archer's tree with this matrix, the length of his tree is 52 (consistency .69). For that matter, the strict consensus tree is diagnosed with a length of 50 (consistency .72), and the Adams consensus tree with 48 (.75), so even a less resolved tree is better than his for these data.

I have even performed some phenetic analyses in order to ascertain if Archer's tree might be obtained this way, as he stated he was also doing some phenetic studies of Vespinae (one might reasonably ask why). The dot matrix obtained from Matsuura & Yamane was converted first into a Manhattan distance matrix and then into a Euclidean distance matrix. Both were clustered on with UPGMA, WPGMA, complete linkage and single linkage. All combinations except single linkage produced the same topology, differing only in clustering levels. The topology for most of the combinations is: Dolichovespula + (Vespa + (Provespa + ((Paravespula + Rugovespula) + (Vespula + squamosa))))). That for a single linkage is Dolichovespula + (Vespa + Provespa + (Vespula + squamosa = (Paravespula + Rugovespula)). Neither result is similar to Archer's tree, and his does not fit the distances very well, for example having a cophenetic correlation of .76 for the Manhattan matrix. (Dolichovespula clusters basally because of its numerous autapomorphies, which cause it to have a large distance from the other groups. This treatment of unique characters is a major reason for the inferiority of phenetic techniques in constructing informative classifications (Farris, 1979).)

To summarize, there is considerable reason for thinking Archer's result is erroneous. Vespula s.l. is well supported by both data sets used here, and mine supports the closer association of Vespula s.s. with Paravespula than with Dolichovespula. The traditional view of relationships thus remains the best. I would also add that the subgenus Nyctovespula should be sunk, as it renders Vespa paraphyletic, and the same applies for Boreovespula in relation at least to Metavespula. In fact, to turn to a more subjective matter, I would say the most practical classification is one that recognizes only the usual four genera (Vespa, Provespa, Vespula and Dolichovespula), with at most two subgenera (Vespula and Paravespula). And although the two subgenera each have several unique derived characters, I am in general agreement with Menke on this matter. They are small groups that would be better recognized as species groups. Menke's comments about the forest and the trees are quite incisive in relation to Archer, regardless of whether Archer's results are in error or not. Archer characterizes the vespines as "a rather loose group of four or five close-related taxa. Of course, any group of four or five taxa is more or less closely related, but the terming of the vespine genera as a "rather loose group" is certainly incorrect when the other vespine subfamilies are considered. The differences are very slight in comparison to, say, Masarinae, Eumeninae or Polistinae.

Finally, in regard to the name "alpicola", Wagner has not yet published it, but Eck (1984) has - by mistake, in her key to Dolichovespula.

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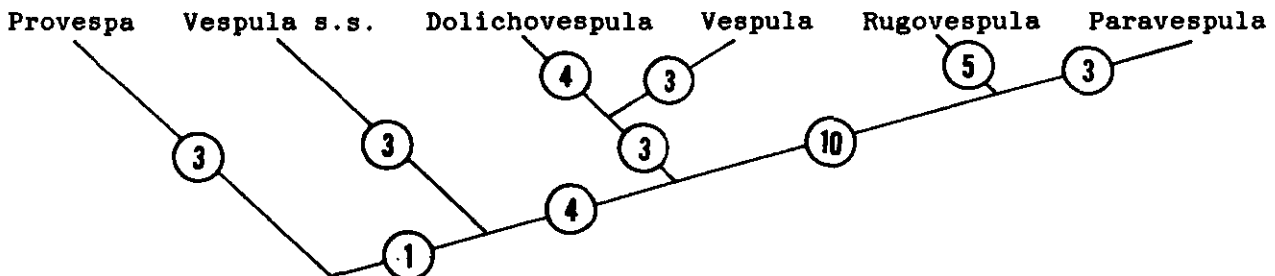
# A JUSTIFICATION FOR MY WORKING CLADOGRAM FOR THE VESPINAE

by

Michael E. Archer

I welcome Carpenter's comments on my preliminary investigations into the taxonomy of the Vespinae. Such comments help me focus more clearly on the problems that interest me and highlight the data I am considering. I am really interested in producing a classification with supporting keys to the adults and as such the characters I study are from the external morphology of the adults. However with an interest in the strategy ecology of nest structure and life-history characteristics it is hoped that the strategy ecology and morphological variations will bear some relationships to each other. To produce a classification I am quite prepared to use both phenetics and cladistics but I will concentrate on the cladistic part of my argument since it is about this part that Carpenter is critical.

I must emphasize that my comments are interim and could change with further experience and investigation. The previous statement was produced for the IUSI Congress in Munich in the summer of 1986 and a copy was sent to Sphecos because of the current discussion about sub-genera and species groups. My investigation is based upon 25 characters which can take about 72 character states and is thus much more extensive than Carpenter's study. I have considered various cladograms but the current one favoured is given below with the number of synapomorphies and automorphies in circles. The selection



of the cladogram used, although ideally derived by parsimonious methods with characters given equal weighting, in practice must involve subjective judgement if only because not all possible characters are used.

In this cladogram, and others considered, the usual arrangement is for Rugovespula and Paravespula to be on the right and Provespula on the left with Vespula s.s., Dolichovespula and Vespa largely interchangeable. The above cladogram with my phenogram causes me to suggest a classification of five

genera (Provespa, Vespula s.s., Dolichovespula, Vespa and Paravespula) with two subgenera for Paravespula. I do not see the need to convert the cladogram directly into a classification.

Taxonomic investigations should also help to formulate answers to other problems. I will consider a biogeographical and a strategy ecology problem. Why is North America so rich in Vespula s.s. species including two species, V. sulphurea and V. squamosa, which show developments approaching those of Paravespula? Assuming that the Vespinae arose somewhere in Asia my cladogram agrees with the proposition that Vespula s.s. invaded North America before Paravespula and diversified in the time-lag before Paravespula arrived. In the Old World the time lag between the Vespula s.s. and Paravespula expansions would be much smaller.

Paravespula would seem to be rather remote from the other Vespinae and this surely can be related to its distinctive characteristics of having deep underground nests, long-cycle development and small investment per worker resulting in large colony size with large queen production in the autumn. It will be interesting to see if Rugovespula shows the same characteristics as Paravespula s.s.

Provespa seems to have been an early attempt to adapt to the nocturnal habit which judging from the small number of species was not a very successful venture. Vespa with its increased size has resulted in a successful proliferation of many species and subspecies. Dolichovespula has pioneered the aerial nest and with large investment per worker and small colonial size has probably retained short-cycle development and produces its queens during the summer. Vespula s.s. would then be considered primitive retaining short-cycle development and nest sites just below the surface of the ground.

Taxonomic investigations of the Vespine via phenetic and cladistic disciplines are very recent and it should not be surprising that two workers should come up with solutions which appear so different from each other. If this controversy causes other workers to take up the study of the Vespinae or causes the current workers to enlarge the number of characters they investigate it will have served a good purpose.

Concerning the 'alpicola' name on the advice from Mick Day the situation would seem to be:

(Dolichovespula saxonica (Fabricius) sensu Wagner, 1978, female, worker, male, misidentification)

Dolichovespula alpicola Eck 1984:40,44, figs. 2C, 3L,4M,N

Jim Carpenter and Regina Eck accept this solution which means that a lectotype will need to be declared from the syntype series of Eck.

#### COMMENT

Robert E. Wagner (Dept. of Entomology, Univ. California, Riverside, Calif. 92521) writes: "I was pleased to read your FORUM article, SUBGENERA vs. SPECIES GROUPS (Sphecos 10:11-13) and must say that I agree with your views almost entirely. In articles regarding vespine taxonomy during the past few years it seems that most authors have favored species groups rather than coining superfluous subgeneric names. I must admit that in my 1978 article on a new Dolichovespula species from North America, that I used Bluthgen's subgeneric names for convenience but would have been wiser to use species groups."

"Incidentally, the wasp which I assigned to D. saxonica and later have named D. alpicola is alive and well and a formal description will be ready for publication soon" [According to Carpenter's response to Archer above, and also Archer's subsequent rebuttal, Eck has already inadvertently described the wasp - edit.] "I have been trying to 'fine tune' the key so that some on our peers will have less trouble determining this species. It still eludes me how Akre

et al. (1981) could have found 'head-width to oculo-malar space ratios intermediate in value' to the ones I published when I gave but a single value on either side of which were different taxa."

"I appreciated the chance to preview Dr. Archer's proposed cladogram for the Vespinae. I could not agree with his analysis unless an enormous amount of conclusive evidence were presented to support such a radical proposal. His concept of Vespula s.s. was not clarified but I hope he is including the entire V. rufa group rather than the ridiculous thought that a single parasitic form constitutes a genus. Realistically, considering the paucity of knowledge available about the Vespinae except in North America, Europe and Japan, any cladistic revision would be speculative at best. When only museum specimens are available, especially if they are few in number and from widely separated locations, not associating all castes of a species with nest series can result in total misunderstanding even at the species level."

"Within the Vespinae, it seems that the more data which is obtained about poorly known taxa the more affinities show up to bring closer the entire assemblage."

Akre, R. D. et al., 1981. The Yellowjackets of America North of Mexico. USDA Agricultural Handbook Number 552. (p. 12)

#### SUBGENERA vs. SPECIES GROUPS

by

Robin Edwards

(Rentokil Ltd., East Grinstead, W. Sussex RH19 2JY, England)

I was pleased to see that Menke found the section in my book on the history of the naming of the Vespinae of some value for his contribution to "Forum". I never expected anyone to read that bit!

By referring to the Vespinae, Menke has clearly stirred up a hornets' nest (!) but I fail to see what all the fuss is about. If groups of insects can be separated morphologically and/or behaviourally, then surely it must be useful for them to have different names. The Menke's of this world call them "species-groups", others give them "subgeneric names". What is the difference? I find the use of species-group names rather cumbersome - if a group of insects is so distinctive as to be placed together, why not give them a one-word name and be done with it? The "species-group" folk seem to forget that they are actually giving the insects a new name and all that happens is that we end up with two names for a group instead of one - where's the sense in that?

What next will they try to do to taxonomic names? I foresee the species-group people trying to eliminate generic names - after all, a genus is only a group of species. Why not divide the Vespinae into the "Vespa species-group" and the "Vespula species-group"? That way we could get rid of subfamily names as well!

If one erects, sorry Arnold, if one describes a new genus which was previously known as a subgenus, then there should be very good reasons for it. But who is to say whether the reasons are good enough or not? Obviously everyone has their own ideas of this: for instance I like the scheme of dividing what the Americans call yellowjackets into two genera, Dolichovespula and Vespula, but I do not at present see large enough differences to separate out Paravespula and put these species on a level with Dolichovespula.

The only way round this problem is to have a committee to decide before publication whether an author can be allowed to change a subgenus to a genus. My goodness wouldn't they be kept busy!!

RESPONSE TO EDWARDS

by

Arnold S. Menke

Robin evidently did not read the first paragraph of my diatribe on subgenera and species groups carefully enough. Robin says "what is the difference [between them]?". The difference is simple: subgenera are formal names that must be accounted for in zoological nomenclature, and we all know how overburdened insect nomenclature is already (not to mention all of zoology). Furthermore, authors who use subgenera often end up with species that don't fit anywhere but which (apparently) don't have sufficient distinctions to be put into subgenera of their own (see Lomholdt's comments further on). I have even seen authors use double subgeneric names for certain problematic species! On the other hand, species groups, being informal names, do not clutter our nomenclature, and do not necessarily have to be of equivalent rank. Thus problematic species can be placed in their own species group without qualms. Finally species group names are not necessarily "cumbersome". For example the "vulgaris group" is nearly as brief as Paravespula.

COMMENT

Dave Legrys (Rt. 4 Box 131F, Pittsboro, NC 27312) comments on Menke's contribution: "I share your view that hypersubgenerization must be stamped out! Your example of the Vespula is well taken - I am very interested in this group. The problem of Vespula/Dolichovespula/Paravespula only tends to dilute the information on these wasps. I would think that 2 genera would be quite adequate. I'm working with D. maculata right now and feel that there are several good morphological and behavioral grounds to distinguish between Dolichovespula and Vespula."

COMMENT

Roy R. Snelling (Natural History Museum of Los Angeles County, 900 Exposition Blvd., L.A., Calif. 90007) writes: "I think that the argument "subgeneric names compete with generic names in terms of zoological nomenclature" is a trivial one that should be dropped as irrelevant. Sure, they do compete, but so do generic names. And, horror of horrors, subgenera have been elevated to generic status. All in all, the argument is thin." [Come now, Roy, species groups are not as easily elevated! - edit.]

"The real point is: Do subgenera exist? Systematics is an attempt to understand the interrelationships and evolutionary history of a group of organisms. We expend a great deal of energy in our effort and wind up with a theoretical concept. And that's all it is--a hypothetical construct that we believe may reflect the relationships and origins of the taxa involved. The consensus seems to be that while species are "real," all else is "artificial," a creation built to satisfy our human need to fit everything into a tidy little system."

"Personally, I do believe that subgenera have a place in systematics, that they can be a useful tool in helping to understand relationships, especially in very large and complex genera. Like you, I think that they should represent major divisions within genera that could almost be recognized as genera (and often are). If I understand you correctly, it is the naming of "species groups" as subgenera that you object to. I concur. Bombus, with its horrendous proliferation of subgenera is one of the more outstanding examples

of such silliness (how come nobody has named "Sillibombus" and "Boobobombus"? How about "Proliferibombus")."

"The idea that a genus with 2 or 3 species should be divided into 2 or 3 subgenera, however, is absurd. There has been a lot of that in the past, and it still happens. But, for moderate-sized or large genera, then subgenera can be useful, if they are established on a unique set of morphological characteristics. I would be very hesitant about subgenera based on only one sex."

"The Vespula problem is, as you already know, one that makes me unhappy, too. My preference is the single genus Vespula, with Dolichovespula as a subgenus. But, I can learn to live with 2 genera (but in the LACM collection, only one genus). The additional formal groups such as Paravespula are nothing more than species groups that are not worthy of formalized names. A similar, and even more extreme case, is that of Trigona in the bees. Too commonly, the decision to 'elevate' a name is made by an ignoramus who cannot see the forest. Worse yet, such ignorami are often not even systematists. Often they are ecologists or behaviorists so impressed by ecological or behavioral features that they reason the animals must be fundamentally different. Such assumptions are commonly made with little or no understanding of the full range of ecological or behavioral repertoire of the larger taxonomic unit."

"But in answer to your question, yes, there are too many subgenera. Is there a solution? I doubt it, short of doing away with subgenera altogether. This, of course, is the solution a la W. L. Brown, Jr. in ant systematics. But as long as we have systematists with differing philosophies, we cannot expect the situation to improve in the near term. I cannot envision any acceptable formal or 'legalized' method by which the proliferation of such names can be discouraged."

"So much for subgenera: I believe they are a useful category, but much over-used."

#### THE SUBFAMILY, -GENUS, -SPECIES GROUP PROBLEM

by

Ole Lomholdt

(Zoologisk Museum, Universitetsparken 15, DK 2100 Copenhagen, Denmark)

An analysis of the phylogeny within a given group can be described and illustrated in several ways, but whenever categorical names are used they should - theoretically - represent monophyletic units. This is often impossible since in very many cases it is not possible to define the exact/true phylogenetic relationships between the taxa in question. If we shall retain terms describing groups of higher categorical rank than the species, but below the order level, the most that I find acceptable is the use of Suborder, Family and Genus. A genus containing many species usually can be subdivided, but I certainly prefer species-group names such as the vulgaris-group instead of a subgenus name. The reasoning is that every time you revise a genus you will end up with a "residual" group which is not at all monophyletic. - I fully agree in your viewpoints concerning the uselessness of subgenera. The yellowjackets represent an excellent example because we all know it, but there are many more, especially in the apids. This is a problem for museum curators. In case that no catalogue exists, I sometimes rearrange a part of the collection according to the most recent revision and place a reprint of the actual paper close to the species in question. Two years later a new revision may turn up including numerous alterations in nomenclature and systematics. - Horrible.

COMMENT

Anthony Harris (Otago Museum, Great King Street, Dunedin, New Zealand) writes: "I was most interested in your article headed subgenera vs. species groups, having myself faced this problem (with New Zealand Pompilidae), and agree with the stand taken by yourself. As an aside, I wonder whether there was confusion (among students, say) over the use of the words "species-group" when they have another use, e.g., c.f. Charles Jeffrey (1977. Biological Nomenclature. Edward Arnold, in conjunction with the Systematics Association. Great Britain. 72 p.) On page 69, under glossary/index, "species-group" is defined as "the categories species and subspecies" and one is referred to p. 11. There one reads "Names of genera and subgenera and genus-group names. Names of species and subspecies are species-group names." I wonder whether students would find this a confusing synonymy? The above source accepts "group" and "an informal taxon". Perhaps species-groups could be used in the usual way, but appear in the text, say thus: CARBONARIUS GROUP (not Carbonarius species-group); i.e., simply group, and not in italics?" [In my experience most people simply say carbonarius group - edit.]

COMMENT

John F. MacDonald (Dept. of Entomology, Purdue University, West Lafayette, Indiana 47907) writes: "The FORUM section is a great idea, and I particularly enjoyed your opinion on "hypersubgenerization." I appreciated your points pertaining to a practical aspect of classifying, using formal names that convey information to the broad audience and avoiding formal names that affect zoological nomenclature when species groups suffice for specialists."

## Address Changes

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## Scientific Notes

LOMHOLDT ON LOMHOLDT, 1985  
(a summary)

A redefinition of the larrine tribes with a revision  
of the Miscophini of southern Africa and Madagascar  
(Hymenoptera: Sphecidae)(Ent. Skand. Suppl.)

by  
Ole C. Lomholdt

Without the use of computers I have tried to reconstruct some of the evolutionary events and an informative phylogenetic tree representing some of the interrelations among the larrine tribes. After a period of surveying and considering different methods of classifying relevant characters I chose (once again) the "Hennigian" way of treating this problem. A very extensive series of characters were analyzed in an effort to find the most parsimonious route leading to a plausible solution. A vast number of "trees" were elaborated, gradually minimizing the number of possibly convergently evolved characters. The result is a dichotomous arrangement of characters/character-states which reflects the use of apomorphic features only. Not all the larrine tribes as recognized by previous authors could be upheld, and especially the Miscophini "lost" many members, i.e. genera. In analyzing larrine phylogenetic relations several "outside" groups were taken into consideration, and much attention was paid to the crabronines. I have argued that the crabronine genera (incl. Mesopalarus, Plenoculus and Paranysson (!)) constitute an monophylitic group - the Crabroniformia - in the extended subfamily, the Larrinae. The remaining larrine genera have been given the informal name, the Larriformia, which is not monophyletic and does not as such constitute the sister group of the Crabroniformia. Most of you may be acquainted with my rather recent paper "On the origin of the bees" (Lomholdt, 1982) in which I suggested the apids to be a family with the Sphecoidea. [Charles Michener has told me that Apoidea is the older name and thus has priority - edit.] Consequently, the superfamily was divided into three families, viz. the Sphecidae, the Apidae and the Larridae. Because of much delay during the printing of "The Miscophini" I did not have the opportunity to compensate for the relevant nomenclatorial changes in the present paper.

In the "Redefinition of the larrine tribes..." I have concentrated on the Miscophini because of its apparent tremendous extent of diversity, and it soon became clear that the tribe at least partly was to be regarded a residual group of genera, many of which can be regarded "primitive" members of other larrine tribes. The Miscophini now consist of only nine genera (formerly 14) - a new genus is described from Namibia and two subgenera are given full generic status. The Miscophini is now defined by - I must admit - only a single apomorphic character which - unfortunately - is negative, i.e. the complete loss of the volsellar sclerite. The genera now included in the Miscophini are the following: Sphodrotes, Solierella, Miscophus, Saliostethus, Miscophoides, Saliostethoides, Namiscophus, Miscophoidellus and Auchenophorus.

Within the Miscophini of southern Africa only very few new synonyms are proposed, but 27 new species are described. Many of these originate from my collecting in Namibia (the Namib Desert), which harbours a great diversity of species. The species are difficult to catch, and the use of Malaise traps is not worth while. Some males are tiny, less than 1 mm "thick", so an ordinary insect net is quite useless. Furthermore most of the desert species will either sit quite still when trapped under the net, or they disappear by digging themselves down into the sand or by hiding under e.g. a stone. Many

Salioctethus have exactly the same colour as the sand, and therefore being well camouflaged. The most effective method for collecting these creatures proved to be the use of small glass tubes. Once detected many of the stout Salioctethus and Namiscophus could easily be followed when crawling after them with some caution. It is a rather hot and unpleasant job, especially because the sand surface temperature reaches 40 - 45°C rather early in the morning. Unfortunately we never saw any Namiscophus with prey, but I suspect the species to paralyze subterranean spiders (i.e. night active species) in their dwellings. The females walk rather slowly over the sand, constantly palpating it with their antennae, and suddenly she will dig herself down. - My patience was not sufficient, and I did not succeed in digging any specimen up in the very loose sand. Some of the further results from the work with the southern African Miscophini are briefly summarized below.

All southern African species are restricted to that area (i.e. no species occur north of the so-called South Equatorial Divide, about 10°S). Salioctethus, Miscophoides, Salioctethoides, Namiscophus, and Miscophoidellus are endemic to this area. Together with Auchenophorus (Australian) they form a monophyletic group. The minimum age of these genera is estimated to be about 90 mill. years.

It is suggested that Miscophus originated in southern Africa. Some of the most generalized and advanced Miscophus live sympatrically in the Namib Desert.

Two main types of morphological specializations are observed, viz. the slender, longlegged, fast moving species (the Miscophus ichneumonoides-group) and a compact, strongly built, shortlegged, walking type (Salioctethus (Mutillonitela) and Namiscophus).

All the species are rather short-winged (nervation reduced), and they usually escape rather by running, digging or hiding than by flying. Males usually possess much better flight abilities than females, and sexual dimorphism is greater in less advanced species.

Wing and thoracic measurements clearly distinguishes the genera and some species groups in Miscophus.

The book is available from Scandinavian Entomology Ltd. O.O. Box 24, S-240 17 S. Sandby, Sweden.

#### A NOTE ON THE BIOLOGY OF AULACOPHILUS EUMENOIDES DUCKE (SPHECIDAE)

by

Martin Cooper

("Hillcrest", Ware Lane, Lyne Regis, Dorset DT7 3EL, England)

While collecting in Ecuador in February of 1982 (Morona-Santiago, Rio Upano 6k east of Sucua) a female of A. eumenoides was caught when it entered a hole in the side of the hollow stem of a dead herbaceous plant which was lying on the ground beneath an overhanging rock face. The cavity of the stem was 0.5cm in diameter and extended downwards for 5 cm from the entrance hole. The bottom 2cm of this cavity were lined with a very thin layer of mud within which were packed 53 immature spiders. These Mr. P. Hillyard of the British Museum has kindly identified them as 3 species of Thomisidae. They varied in length from 1-2.5mm. Two of the largest of these had an egg 1.6mm long attached to the ventral side of their abdomens. There was no trace of a transverse partition dividing the nest cavity. The wasp and its prey are preserved in my collection.

LECRENIERUS GASPARI LECLERQ (SPHECIDAE) [Colombia, Narino, Barbacoas 50m. 3.vii.1986]. A female of this species was caught with its prey: a legless tipulid fly 9mm in length. - Martin Cooper.



NEST OF QUEXUA VERTICALIS (F.SMITH)(SPHECIDAE - CRABRONINI)

by  
Martin Cooper

Several wasps of this species were seen hovering along the face of a vertical earth bank in Ecuador (Morona-Santiago, Lucua 3-viii-81). They would alight a moment at the entrance to burrows in the bank, and then move on. Some of these were caught and found to be males. A female was seen to enter a burrow and was caught as she emerged. The nest was a simple horizontal tunnel 0.2cm in diameter which was slightly expanded at its termination 7.5cm from the entrance. At the end of the burrow was the larva of the wasp with prey: 6 small adult leafhoppers (Cicadellidae) belonging to 5 species. Q. verticalis is therefore a progressive provisioner. The species is rather common in open habitats in the rain forest zone of S. America. Adults, larva and prey are preserved in my collection.

NESTS OF STELOPOLYBIA CAJENNENSIS (F.)(VESPIDAE - POLISTINAE)

by  
Martin Cooper

Richards in his book "The Social Wasps of the Americas" states that the only Stelopolybia known to make nests with envelopes are areara (Say) and flavipennis (Ducke). I have on two occasions found nests of the common Stelopolybia cajennensis (F.) covered with an envelope. Both were attached to the underside of leaves.

The first from Colombia (Vaupes, Mitu, identified by Richards and now in the British Museum) was under a slender leaf 15cm long which overhung a stream. The sides of the leaf curved down to form a semi-circle across the diameter of which extends the envelope. The length of the envelope is 10cm and the diameter 3.5cm with the entrance at the distal end. A single comb with several pedicels fills the interior of the envelope. The second nest from Ecuador (Morona-Santiago, Cordillena de Cutucu, 1,100m, in my collection) was found in primary forest. It is very similar to the first in structure, 10cm long by 4-5cm wide. A second leaf has been incorporated into the envelope.

The structural characters which separate cajennensis from Angiopolybia, a genus which builds nests with envelopes, are rather slight.

SCENT MARKING IN MONTEZUMIA ANALIS SAUSSURE (EUMENINAE)? I caught a male of this species in Bolivia (Santa Cruz, Puerto Grether) as it was rubbing its abdomen on the surface of a leaf. It seemed to be scent marking but I know of no other observation of such behaviour in this genus. - Martin Cooper.

## Necrology

AIMO K. MERISUO  
(1907-1984)

See Pekkarinen (1985) for obituary of this Finnish wasp scientist.

SIMONE KELNER-PILLAULT  
(? - 1985)

Word was received late last year from J. C. Weulersse of the Museum in Paris that Ms. Pillault was tragically killed in an automobile accident Sept. 29, 1985 - two days before her retirement. Hopefully we will be able to present an obituary for her in Sphecos 13.

## Obituary

JACQUES DE BEAUMONT

(26 September 1901 - 29 September 1985)

by

Wojciech J. Pulawski

(partly adapted from an obituary by Claude Besuchet with his permission)

Jacques de Beaumont came from a prestigious Swiss family. His forefathers settled in Geneva in 1700-1710. General Guillaume-Henri Dufour, who defeated a secessionist alliance of seven catholic cantons in November 1847 and saved the unity of Switzerland, was Jacques' great-grand-father. His equestrian statue graces a public square in Geneva, and his likeness was for many years printed on Swiss bank notes. Moreover, the family owns a mansion in Auviernier near Neuchâtel dating from the beginning of XVIIth century.

Jacques de Beaumont was born, raised and educated in Geneva. While at the university, he studied under Professor E. Guyénot and became his assistant. It was under Guyénot's direction that de Beaumont began research in the fields of cytology and experimental biology and published several papers, including his doctoral thesis, defended in 1928. In this same year, he married Renée Mallet. They had two sons: Gérard (born 1930) who is Curator of Vertebrate Paleontology at the Natural History Museum of Geneva, and François (1932-1982) who became a medical doctor in Neuchâtel.

While working for professor Guyénot, de Beaumont became acquainted with his lifelong friend Robert Matthey; together, they began collecting insects. However, they concealed this activity from their master, because Professor Guyénot had little tolerance for entomology and even less for studies in systematics. In 1931, R. Matthey was appointed extraordinary professor of zoology at the Lausanne University, and helped his friend de Beaumont gain a position there in 1933, first as lecturer (chef de travaux) at the Laboratory of Zoology, then as privat docent in 1934. Also in 1933, he began a brilliant entomological career at the Musée Zoologique of Lausanne, where he was a curator. In 1943 he was appointed director. At Lausanne University he was an Assistant Professor (chargé de cours) at the Ecole de Pharmacie between 1938 and 1949, Assistant Professor of entomology between 1942 and 1953, and finally an Extraordinary Professor from 1953 until retirement.

J. de Beaumont reorganized and significantly developed the exhibits, the scientific collections, and the library of the Musée Zoologique de Lausanne. He converted the Museum into an active research center. He published 149 papers. Of these, 128 pertain to the Hymenoptera Aculeata, in which his expertise is recognized worldwide. He also transmitted to his students his enthusiasm and passion for insects, combined with scientific "rigueur" and critical objectivity. He served as the major professor (= promotor) for three Ph. D.'s: Jacques Aubert (expert in Plecoptera and insect migration), his successor at the Musée Zoologique de Lausanne; Fernand Schmidt (specialist in Trichoptera and also birdwing butterflies), now in Ottawa, Ontario; and Claude Besuchet (specialist in beetle families Pselaphidae, Scydmaenidae, and Ptiliidae), Curator of Entomology at the Natural History Museum of Geneva, Switzerland.

De Beaumont had vast and varied field experience in Switzerland as well as abroad. He spent nine months at the Laboratoire de Zoologie marine at Banyuls, France, studying marine organisms, and also collected insects in general, Hymenoptera in particular. He was an untiring and efficient collector. In Switzerland, he visited all the Swiss romande (or French-speaking cantons) and collected not only the Aculeata, the group he liked best, but also innumerable parasitic Hymenoptera and

other insects. These trips became the basis for the faunal inventories of Psocoptera and Odonata in French-speaking Switzerland. On 25 May 1955, he discovered an extraordinary tenthredinid in the region of Pléiades, a creature belonging to a new genus and species, now known as Eopsis beaumonti Benson. Due to this unusual capture, many trips to the Pléiades were organized; the director, curator, assistant and students enthusiastically swept their nets and ended up with three more specimens. J. de Beaumont also collected extensively in the Swiss National Park. In 1947, he headed an important Swiss expedition to Morocco between April and July 1947, accompanied by his friends R. Matthey and R. M. Naef. In 1948, he undertook a collecting trip to Biskra, Algeria. Both African trips yielded representatives of many unknown species and this material was the basis for many taxonomic revisions.

De Beaumont was an active member of many Swiss scientific societies. Most importantly, he was the central president of the Helvetian Society of Natural Sciences, an equivalent of the U. S. National Academy of Science (1953-1958). He was president of the Swiss Entomological Society from 1945 to 1947, editor of the *Mitteilungen* (or *Bulletin*) of that society from 1946 to 1952, and also a founding member of the Entomological Society of Vaud in 1945. He actively participated in activities of the Swiss Society for Nature Conservation (*Ligue Suisse pour la Protection de la Nature*), both in the Suisse romande and in the Swiss National Park.

He retired in 1967, left Lausanne for Auvernier, abandoned entomology and dedicated himself to his collection of Swiss postage stamps and to gardening. He was especially fond of his roses. He remained a taxonomist at heart, studying individual variation between stamps of the same series, and between series printed at different times. The company of his young grandson Davide was a source of great pleasure. The last years of his life, however, were not free of sorrow: the isolation from his friends and students, the death of his son François, his own declining health and subsequent fifteen month hospitalization.

Except for the early part of his career, de Beaumont studied aculeate wasps, mainly Sphecidae. In this field, he was a successor of the two great Viennese researchers of the previous generation, Anton Handlirsch and Franz Friedrich Kohl. His own contribution to wasp systematics is certainly as significant as that of these Austrian authors, although he mainly studied species of the western Palearctic Region rather than the world fauna, and he published no revisions which could compete in size with the monographs by Handlirsch and Kohl. He was an unusually sharp observer, discovering many characters not used by his predecessors (many are now a standard part of morphological descriptions, e.g. the shape of the basitarsus in Astata females. He was aided by an excellent memory and a very good knowledge of the literature, including original sources and rare or little known papers. He methodically and critically reexamined original specimens used by earlier authors for their descriptions (Spinola, Dahlbom, Costa, Marquet, Kohl, Handlirsch, Schletterer, Mercet, Giner Marí), a rare practice among European hymenopterists of his generation. Thus he largely clarified existing nominal species, redescribed those which could not be recognized from their original descriptions, and established numerous new synonymies. From the very beginning he published revisions of genera, either at the local level (e. g. Oxybelus of Switzerland, Tachysphex of Egypt), or for the western Palearctic Region. He laid the basis for the classification of several genera by recognizing species groups (e.g. in Cerceris, Palarus, Philanthus, Tachysphex) which are applicable worldwide. The list of the genera he revised is impressive: Astata, Bembecinus, Cerceris, Ceropales, Chlorion, Crocisa, Dinetus, Gorytes, Hoplisoides, Laphyragogus, Lindenius, Liris, Mimesa, Mimusesa (the latter two as subgenera of Psen), Olgia, Oxybelus, Palarus, Philanthus, Pison, Psammaecius, Psen, Psenulus, Pseudoscolia, Solierella, and Tachysphex. In some instances, he produced several local revisions of the same genus, e.g. Cerceris of France, of North Africa, and of Cyprus. At the generic level, he mainly

used the classifications adopted by others, either by his predecessors (e. g. Kohl's system of broad genera for the Sphecinae and Pemphredoninae) or by his contemporaries (e.g. Pate's and Leclercq's system of small genera for the Crabroninae), but he proposed his own classification system for the Nyssoninae. In general, he was reluctant to describe new taxa at the genus level and greatly preferred the use of informal species groups rather than subgenera, thus avoiding an unnecessary proliferation of names. In the Sphecidae, he only described three new subgenera, Holotachysphex, Hoplammophila and Philanthinus, all of which have been raised to full generic status by subsequent workers. Another characteristic of his taxonomic work is a consistent use of trinomial nomenclature based on the concept of geographic speciation. By analyzing the geographic distribution of species and their morphological differences, he reduced a number of them to subspecies (e.g. many species of Kohl and Mercet). He described many new subspecies himself, perhaps too many in some instances. Gradually, de Beaumont became inundated with material from museums and individuals sent to him for identification. He published the results in the form of annotated lists of species (including material he collected in Morocco). These annotated lists cover most of the Mediterranean basin and contain descriptions of new species, comments on diagnostic characters and geographic variation, newly established synonyms, etc. As an unfortunate consequence, many of de Beaumont's original discoveries are buried among endless faunal data. The fact that he did not consider the species described by British authors from Pakistan and India is another drawback; many of these species also occur in the western Palearctic and have nomenclatorial priority. His writing is clear, always to the point, and the information is presented in a concise, synthetic way. I remember O. W. Richards' opinion of de Beaumont's Key to the identification of Swiss Sphecidae: "it contains all the necessary, and nothing but the necessary". Certainly, the years 1940-1970 will be regarded by students of Palearctic sphecsids as de Beaumont's era.

Although mainly interested in morphology and taxonomy, de Beaumont also studied, together with R. Matthey, the life history of the subgenus Sulcopolistes, social parasites of Polistes. They confirmed previously known facts and added new details. He also studied the effects of allometric growth, and morphological changes induced by strepsiteran parasites.

For amateur entomologists and beginners, de Beaumont was always a source of help, advise and encouragement, whether in his office, during a field trip, or at a meeting of the Entomological Society of Vaud. He defended the role of amateurs in a speech delivered at the centennial meeting of the Swiss Entomological Society (he was at this time the central president of the Helvetian Society of Natural Sciences) and defined them in a dichotomy which deserves to be cited here:

1. Individuals who spend money on entomology. .... Amateurs.
- . Individuals who earn money in entomology. .... Professionals.

I first became aware of de Beaumont's existence when I was a second-year student at Wroclaw University, Poland. His revision of the Egyptian Tachysphex fell into my hands casually. I read it and became greatly impressed by the clarity and precision of the language, the number of newly discovered diagnostic characters, excellent key to species, fine illustrations, overall organization, progress achieved, open presentation of difficulties and unsolved problems and, last but not least, by his tact. The paper was titled "A new study of Egyptian Tachysphex," because an earlier version that he regarded as imperfect was published during World War II without his permission or knowledge (he learned of its publication from Zoological Record and he had to wait until the end of hostilities to even see it). Nevertheless, he credited the editor with having the best intentions, rather than expressing justified wrath. After having published my first paper in 1954, I sent him a reprint and a letter and was

very, very proud when I received an answer starting with "Monsieur et cher collègue". Soon after, I found a museum specimen from Turkey of what I thought was a new, unusual species of Astata. I wrote to de Beaumont, asking him to confirm my opinion. His answer was that he already knew the species, that he had another specimen in his collection and, since I would save him time by describing it, he was sending me the specimen for study. This lesson in generosity I will never forget. From then on our letters became routine, we exchanged specimens, I often asked his advice, and eagerly read each of his papers. Very soon he became my scientific hero, and my respect for him only grew with time. After having collected in Egypt myself, I discovered that much could be added to de Beaumont's revision of Tachysphex, and I have been working on this genus ever since. I met him in Lausanne in 1958, on my way back from Egypt to Poland. I entered the University building, asked an unknown (who turned out to be Matthey!) to show me the way to de Beaumont's office, he lead the way and then shouted: "de Beaumont, il y a quelqu'un pour toi!" (= there is somebody for you). I was almost shocked by such unceremonious behavior toward my hero. Years later, in 1968, he arranged for me to spend a whole month with him by obtaining a Swiss grant to finance my stay. Since his collection (now at the Musée Zoologique de Lausanne) was at his home, I spent entire days with him, also with Madame de Beaumont during lunch, but mostly studying Tachysphex. After lunch, we went for a walk, often along the shore of Lemman Lake, and many times we checked to see if the magnolia tree had already started blooming (the only magnolia with drooping flowers that I know of). I saw him for the last time in 1971, on my way back from Italy, after he moved to the Auvernier mansion. He told me that he had done enough research in his lifetime, that his memory was no longer as good as it used to be, and that he was happy the way he was, with his roses and his grandson. And I felt that he was going away, my hero, a classic. A year later, I received a big box full of rare books on Hymenoptera, and his sphecidological archive (his manuscripts and unpublished notes). They have followed me to the Western Hemisphere.

## SPECIES DEDICATED TO J. DE BEAUMONT

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Anospis beaumontinus Wolf, 1966 (Hym., Pompilidae),  
Anthidium beaumonti Benoist, 1951 (Hym., Megachilidae)  
Cerceris beaumonti Bajari, July 1956 (Hym., Sphecidae; a junior synonym of  
Cerceris parkanensis Balthasar, May 1956),  
Chrysochroa beaumonti Pochon, 1948 (Col., Buprestidae),  
Claveliocnemis beaumonti Wolf, 1981 (Hym., Pompilidae),  
Biblioplectus beaumonti Besuchet, 1955 (Col., Pselaphidae),  
Dryudella beaumonti (Pulawski, 1959) (Hym., Sphecidae), originally in Astata,  
Eopsis beaumonti Benson, 1959 (Hym., Tenthredinidae),  
Glossosoma beaumonti Schmid, 1947 (Trich., Glossosomatidae),  
Hylaeus beaumonti (Benoist, 1958) (Hym., Colletidae), originally in Prosopis,  
Katamenes debeaumonti Giordani Soika, 1952 (Hym., Eumenidae),  
Krombeinella beaumonti (Invrea, 1953) (Hym., Mutillidae), originally in Myrmosa,  
Listriophorus beaumonti Comellini, 1981 (Col., Pselaphidae),  
Leptochilus beaumonti Giordani Soika, 1953 (Hym., Eumenidae),  
Leuctra beaumonti Aubert, 1946 ((Plec., Leuctridae),  
Megachile beaumonti Benoist, 1951 (Hym., Megachilidae)  
Meria beaumonti Guiglia, 1960 (Hym., Scoliidae),  
Mimusesa beaumonti (van Lith, 1949) (Hym., Sphecidae),  
Miscophus beaumonti Balthasar, 1953 (Hym., Sphecidae; a junior synonym of  
Miscophus insolitus de Andrade, 1953),  
Nemoura beaumonti Aubert, 1956 (Plecoptera, Nemouridae),  
Nomada beaumonti Schwarz, 1967 (Hym., Anthophoridae)

Oxybelus argentatus debeaumonti Verhoeff, 1948 (Hym., Sphecidae),  
Palarus beaumonti Bytinski-Salz, 1957 (Hym., Sphecidae),  
Pemphredon beaumonti Hellén, 1955 (Hym., Sphecidae),  
Pirrhidius beaumonti Besuchet, 1957 (Col., Rhizophoridae),  
Plenoculus beaumonti de Andrade, 1957 (Hym., Sphecidae),  
Pristiphora beaumonti Zirngiebl, 1957 (Hym., Tenthredinidae),  
Rhopalum beaumonti Móczár, 1957 (Hym., Sphecidae),  
Stelis beaumonti Noskiewicz, 1962 (Hym., Megachilidae),  
Symplecis beaumonti Aubert, 1968 (Hym., Ichneumonidae),  
Tachysphex beaumonti Pulawski, 1971 (Hym., Sphecidae),  
Tenthredo beaumonti Benson, 1950 (Hym., Tenthredinidae),  
Tremissus beaumonti Besuchet, 1981 (Col., Pselaphidae).

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## Tributes To O. W. Richards

IN MEMORY OF O. W. RICHARDS

by

G. van Rossem (Ichneumonidae)

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O. W. Richards came to Holland in 1946 to attend a congress of British biologists at Utrecht. I met him through my friend P. M. F. Verhoeff (Sphecologist) and we went on a collecting trip together. We visited "Witte Bergen" near Hillversum, a historic place for Miscophus of Verhoeff.

OW (as we called him) came to see me at Wageningen. I remember him standing in a goods van (Dutch railways were badly upset by the war), arriving at Ede-Wageningen Station with a face saying "this is the ordinary way of railway traveling, I like it".

I was quite taken back when the famous entomologist invited me to stay at his home in Baling (a suburb of London). I was an unknown chap and in that time English people didn't invite strangers into their home.

Richards took a lot of time to introduce me to the body of British entomology. To give a couple of examples: Massee (fruit entomologist); the Pest Infestation Laboratory at Slough; Rothamsted Experimental Station, Barnes (gall midges) and C. G. Johnson (insect flight); the BM(NH), van Emden (Coleoptera, larvae) and R. B. Benson (saw flies) and the Locust Institute where Mrs. Richards worked.

OW made several collecting excursions with me around London and amazed me by his fabulous knowledge of Hymenoptera in the field, e.g. he was a first class connoisseur of Bombus. In the evening he gave me private lectures on Hymenoptera taxonomy and evolution. About the last mentioned subject he was quite reserved, saying "we don't know much about it".

In conclusion I like to express my deep admiration for O. W. Richards and my shame that at the time I scarcely realized who was my tutor.

The following tributes to OWR were sent to Sphecos by Mick Day. I'd like to thank their authors, Richard Southwood and Paul Richards, for allowing me to use this interesting material here. See also M. C. Day's report (1980) of OWR's 80th birthday in *Antenna* 6:224-226 and an obituary by R. G. Davies in *Ent. Mon. Mag.* 122:93-96 (1986) and Mary Jane West-Eberhard in *Ins. Soc.* 32:221-223 (1985) - edit.

PROFESSOR O. W. RICHARDS

Address by Professor Sir Richard Southwood, FRS,  
at the Memorial Service held on February 6th 1985

Owain Westmacott Richards was born on 31st December 1901, the second of the four talented sons of Dr. H. M. Richards who was Medical Officer in Croydon. His youngest brother, Professor Paul Richards will pay a fraternal tribute, calling on memories of times together, so I will pass to 1920 when Owain Richards entered Brasenose College, Oxford as an Exhibitioner and read Mathematics for Moderations; he then switched to Zoology gaining a 1st class degree.

With his excellent academic track-record he was elected Christopher Welch Scholar of the University and Senior Hulme Scholar of BNC in 1924 and worked for three years mainly in the Hope Department. Unlike present day Christopher Welch Scholars, Richards was not constrained to prepare a Ph.D. thesis: he spent the three years collecting widely - many specimens in the Hope Collections bear his data labels - and observing insects in the field. With A. H. Hamm, an outstanding field entomologist, he commenced assembling a collection of the prey of insect predators, especially solitary Hymenoptera. But perhaps the greatest achievement of this very productive period was his review of the courtship behaviour of insects - a work published in the second volume of Biological Reviews and destined to become a classic that has never been superseded. It was an exciting time at Oxford: Sir Edward Poulton was at the height of his powers in the Hope Chair and amassing insect material, particularly that showing mimicry, from all over the world; Julian Huxley was a young don and Richard's tutor, Charles Elton, was a demonstrator and Edmund Ford a fellow research student. Like them, Richards was destined to make important contributions to ecology and evolution, at least though he was always first and foremost an entomologist. In the Author's Preface of his classic Animal Ecology Charles Elton wrote (in October 1927) "I am indebted to Mr. O. W. Richards for a great deal of help and criticism. Many of the ideas in this book have been discussed with him and gained correspondingly in value and in particular his extensive knowledge of insects has been invaluable in suggesting examples to illustrate various points." Indeed he had an extraordinary knowledge and with this great wealth of detailed information and his highly critical mind, Richards was often sceptical of generalisations and theories. He and G. C. Robson (of the British Museum) wrote 'The Variations of Animals in Nature' in the early 1930's (although publication was delayed until 1936) - this critical assessment of adaptionist arguments was submerged, virtually at birth, by the Neo-Darwinian wave, but many present-day iconoclasts would find much to their liking in its pages. Whilst Richards readily accepted that plant communities could be an ecological reality, he was much more doubtful about animal communities, stressing how little insects that co-exist might influence each other. Today's proponents of the New Ecology, who question the role of competition in structuring insect communities would delight in reading his Presidential address to the British Ecological Society in 1945. Unfortunately they cannot, because so unpopular were these views at the time, that uniquely for a Presidential address it was not published. It is characteristic of Richards' modesty that he accepted this Editorial decision and spoke lightly of it years later.

Perhaps his greatest contribution to the conceptual corpus of Zoology was his part in the development of quantitative life-budgets, from his pioneering study of the small white Butterfly just before the War, to his major work with Dr. Nadia Waloff on grasshopper and broom insect populations. It was characteristic of him that he sought to understand what happened and, as a true scientist, to measure it - before jumping to general conclusions. At the height of the arguments over density-dependence in animal populations he made a powerful plea for more fundamental field studies where all the relevant factors were measured simultaneously "then we may be able to discuss our theories with more light and less heat." A statement that shows both his powerful insight and his pithy wit.

Great though his contributions were to ecology and evolution I think he always yearned to stick simply to the facts about insects and I felt it was almost with a sense of relief that he told me when he retired that henceforth he would be a straightforward entomologist.

On leaving Oxford in 1927 Richards was appointed a research assistant at Imperial College, London and then to a lectureship in 1930 (when Balfour-Browne retired and J. W. Munro was promoted to the Professorship). In 1937 Richards was appointed Reader in Entomology; he succeeded Munro in the chair in 1954, retiring in 1967. He remained associated with the Department, as Senior Research Fellow until 1979, although he worked mostly at the British Museum (Natural History). At Imperial College, in contrast to Oxford, the emphasis was on the applied aspects of entomology. Richards' first post there was as research assistant on a grant to J. W. Munro, undertaking a survey of insect pests in stored products; later, though in a University post, he still followed a practical problem - the ecology of the insect pests of cabbage; though the advent of the War dictated a return to stored products work.

Richards was the first to recognize and applaud J. W. Munro's drive and ability to obtain grants for the department; he wrote "Munro with his characteristic flair for doing the right thing at the right moment." Nevertheless some aspects of Munro's style of operation must have been anathema to Richards, whilst his entomological knowledge and reputation far outshone those of his nominal chief. This was particularly so in the postwar years when Silwood Park was being established; those of us who were students then noted how Richards just kept out of the administrative and personal controversies that so often raged, he simply concentrated on entomology.

Notwithstanding that there was nothing precipitous about Munro's retirement, when this occurred in September 1953 the College had not appointed a successor and after a short hiatus the then rector suggested to Richards that, still with his rank of Reader, he might be acting head for a year. Richards, by his own account, pointed out that he had been in the College for 25 years and if they did not know him then, they would not know him much better a year later. So the chair was advertised, there were four candidates, but not surprisingly Richards was appointed. He found himself a Head of Department in a college that was embarking on a major expansion, but uncertainties about the future of the biological departments had meant that these had been virtually missed out of the initial plans; there was scant provision of space for them in S. Kensington. A solution might be provided by a significant expansion at Silwood Park and elaborate plans were drawn up in 1953. Richards was enthusiastic about these and I well recollect him outlining them to me early in 1955. However the University Grant Committee visit that winter was a disaster, the plans were rejected and Silwood Park was specifically excluded from the 'Jubilee expansion scheme'. Richards himself wrote "There were probably many reasons for this, amongst them I think I was too inexperienced to handle such an occasion so far as it was my responsibility to do so and that both Zoology and Botany departments were at a low ebb." Undoubtedly the senior officers of the College badly misjudged the situation and failed to offer Richards the support and guidance he needed.

Having kept right out of College and University politics throughout Munro's Headship and not having been formally appointed as Director of Silwood, Richards was on very unfamiliar ground. Over the years he became a very efficient administrator, spending the minimum of time in his office and the maximum in the laboratory or field. Everything that needed to be done was done, punctiliously and very fairly, but, after that initial experience, grandiose plans had no place in his administration. He emphasized research and sound teaching and when he retired he left a department with high scientific standards and a sound basis for future growth. He had trained most of the leading entomologists, not only in Britain, but in the Commonwealth; at the International Congress of Entomology in Canberra in 1972, one tenth of the participants were present or past members of the department.

Richards was an inspiring teacher. His lectures were not orderly presentations of facts, but thoughtful analyses that pointed out uncertainties and inconsistencies, they were laced with exciting suggestions for research. His knowledge of entomology was prodigious, represented on one hand by the successive revisions (with R. G. Davies) of Imm's General Textbook of Entomology and on the other hand by his incredible ability to identify almost every insect one might collect in the field. He always carried a small specimen tube in his pocket and wherever he was, if he saw an insect of interest, into the tube it would go - later to be mounted, labelled and identified! He always stressed the need for an entomologist to be able to identify plants too and he was not only expert on the European flora, but soon became competent in Africa, California and Australia; local biologists in these areas still recollect with shame how 'OWR' knew their own flora and fauna better than they did.

The interest Richards developed in Aculeate Hymenoptera at Oxford remained his principle love in entomology throughout his life. He followed it on two expeditions to British Guiana, on the Royal Society Expedition to Brazil in 1968 and during other extensive travel in Africa, North and South America and Australasia, principally during his retirement. Besides his book 'Social Insects' (1953), he published many papers and two large taxonomic monographs.

Richards was not a keen committee man, though if called upon he would do his duty. An early President of the British Ecological Society, he later undertook the laborious task of Editorship of the Journal of Animal Ecology particularly encouraging the trend towards quantitative papers. Undoubtedly his favourite Society was the Royal Entomological Society where he was both Hon. Secretary (1937-1940) and President (1957-58), but above all an unfailing attender at meetings. In the days when exhibits were common, Richards would often illuminate the discussion knowing more about the species or its biology than the exhibitor.

Few of us will ever have met anyone as conscientious as Professor Richards; even in his retirement he would come to Silwood on a certain day every week and generally spend the other five (that is including Saturday) in the Entomology Department at the British Museum (Natural History). When he was in his late seventies he remarked to me how difficult it was going to be to get to the Museum if the tube train drivers went on strike: it never seemed to occur to him to neglect his voluntary duties. With his powerful intellect and impish humor he could be devastating in his correction on the incorrect or imprecise statement; his colleagues and students gained greatly by learning to seek to minimize such strictures. There was never anything malicious or personal in these comments, though they could be brutally brief - as when called on by the President, at a meeting of the Royal Entomological Society for his views on the paper that had just been given, he replied "Absolute rubbish."

Harsh as he could be on bad science, he would always encourage the good entomologist, whether young, old or eccentric and he was really extremely concerned for the personal well being of his friends, colleagues and

students. How many Professors after a full day in the department would travel halfway across London to visit a second year student in hospital? Owain Richards would and did. He was extremely kind and generous, but these actions that so many of us have experienced, were always unobtrusive and he would abhor any fuss or public thanks.

Richards was a man of extremely wide knowledge, not only of the natural world, but of history, music and literature. He wore this erudition lightly and always stressed that he was 'an entomologist', indeed he cited it as his recreation in 'Who's Who'. It was fitting therefore that the initial links for both his marriages were through entomology. With Maud he worked on the biology and reproduction of wasps, publishing a major joint paper (1951) on their expedition to British Guinea in 1937 and undertaking much field work together in Brazil and California and elsewhere. With Joyce, the widow of his close friend and fellow Hymenopterist Bernard Benson, he travelled widely in New Guinea and Australia.

Owain Richards judged people by their personal and scientific integrity, he was not impressed by rank or deference nor prejudiced against them by unorthodoxy of garment or manner. He taught and led by example; his great contribution lives on through his writings, through tens of thousands of specimens in the British Museum (Natural History), in the Hope Collections and at Silwood, and through the hundred of colleagues and students whom he helped and who will have passed, at least some part of his attitudes and ideas, on to their own students.

#### PROFESSOR O. W. RICHARDS

Tribute by Professor Paul Richards

(14 Wooten Way, Cambridge CB3 9LX, England)

at the Memorial Service, Holy Trinity Church, Prince Consort Road,  
South Kensington, London, February 6th 1985

Dick Southwood has spoken very well about Owain as a scientist, teacher and colleague. I would like to add a few words as one for whom he was a beloved and much admired elder brother. He was seven years older and my first memory of him is when he was carried into our house in Surrey after breaking his arm playing leap-frog at his prep school. This must have been in 1911 or 1912, when I was 3 or 4. But it was some years later, when our family was living in South Wales, that a close partnership of common interests between us began which lasted until the end of his life.

In the spring of 1916 my father rented a house at Porthcawl, on the edge of the sand dunes which stretch away to Merthyl Mawr - a splendid place for small boys to run about. Owain was 14 and I was seven. Owain's consuming interest was then in butterflies and moths. I was interested in them too, but also in plants and I was beginning to look at the fascinating wild flowers in the hollows between the dunes. I did not have a butterfly net and the other equipment Owain had and the family tradition is that Owain pushed me in the direction of botany because he needed somebody to identify the plants on which his caterpillars fed.

Owain was already at boarding school but our sharing of interests continued in holiday times and went on year after year even after we were both married: it is still continued by his children and mine. My enthusiasm for butterfly hunting soon faded, but for two or three years in South Wales Owain and I spent much time together on land and freshwater snails. We both made quite large collections which are now in the National Museum of Wales. In those years, as can be imagined, I learned an enormous amount from him.

In 1920 my father moved to London and Owain went to Oxford. There his entomological interests widened to include bees, wasps, beetles and Diptera. I was by now a committed botanist, but something of his new knowledge spilled

over on to me. When I was a year or two older I began to acquire at second-hand a little of what he was learning from great men like Julian Huxley and Charles Elton.

At several points in my life Owain had a decisive effect on my developing interests, notably when the Oxford Expedition to British Guiana was being organized. He suggested that his young brother might fill the bill for a second botanist on the expedition and this started my career as a tropical ecologist.

Owain did not deliberately teach or guide me, but his influence was very great and it was not confined to natural history. I remember that once, when he was an Oxford undergraduate, we rested in a wood during a long walk in Hertfordshire and Owain took out of his pocket a book of Rupert Brooke's poems and read some aloud to me.

I know that many others of his juniors have profited as I did from Owain's great knowledge and understanding. To the end of his life he liked young people and they liked him. The full attendance of his nieces and nephews at his funeral showed how much they appreciated him. This was partly because he was never pompous and because of his very characteristic sense of humor. This was sometimes rough and could be very deflating, but it was never cruel or unkind; it was very much part of his personality.

I think the world will long remember Owain as a great entomologist and as a pioneer in some fields of ecology. We who had the luck to know him well will think of him as a very lovable human being.

