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# THE NEST MATERIAL OF STENOGASTRINAE (Hymenoptera Vespidae) AND ITS EFFECT ON THE EVOLUTION OF SOCIAL BEHAVIOUR AND NEST DESIGN

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Titre: Les matériaux employés dans la construction des guêpiers de Stenogastrinae (Vespidae) et les effets de ces matériaux sur l'évolution du comportement social et sur la structure des nids.

**Resumé**: L'organisation sociale des Stenogastrinae démontre une certaine uniformité, cependant, la structure des nids dans la sous-famille est tres variée. Le niveaux modeste de l'organisation sociale démontrée par ces guêpes peut etre du au manque des matériaux necessaires pour la construction de grands nids. Polistinae et Vespinae construisent des rayons suspendus d'une tige fine faite de papier dur et fibreux. Cette structure de rayons suspendus a evolué apparamment à cause de la prédation par les fourmis, mais la où les circomstances ont, par la suite, favorisé une evolution sociale plus développée, les matériaux convenaient deja à la construction de nids plus grands. Dans la construction des nids de Stenogastrinae les cellules sont attachées directement au substrat, ce qui provient probablement de la mauvaise qualite du papier où de la lourdeur de la boue dont il s'agit dans leur construction. De tels matériaux ne conveniennent pas non plus à la construction de nids plus grands, tels qu'il faudrait pour abriter des colonies sociales plus évoluées.

**Mots-cles**: Stenogastrinae, matériaux des nids, évolution social

**Summary**: The social organisation of the Stenogastrinae is rather uniform while the design of their nests is very varied. The modest level of social organisation shown by them may be the result of a failure to evolve a building material suitable for constructing large nests. Polistinae and Vespinae build combs suspended from a fine stalk of tough, fibrous paper. This design apparently evolved as a response to ant predation but, where circumstances then favoured further social evolution, the nest material was already suitable for building large structures. The nests of Stenogastrinae are built with the cells attached directly to the substrate, probably the result of the poor quality paper or heavy mud from which they are built; such materials are also unsuitable for the construction of larger nests to house advanced social colonies.

**Key-words**: Stenogastrinae, nest material, social evolution.

## INTRODUCTION

The lives of many species of Hymenoptera is dependent upon the construction of a prepared nest, initially to protect the brood but, in the more social species, the whole colony. It follows from this that living in large colonies must depend upon an ability to build large nests.

Among the Hymenoptera, only the bees and vespoid wasps provide both solitary and highly social species, plus a full range of intermediates. These also provide at least circumstantial support for the notion that either evolutionary changes in the choice of building material or in nest architecture have significantly contributed towards social evolution (Hansell, 1984 a, b). Among the vespoid wasps it seems that the evolution of chewed up vegetation (paper) nests rather than mud nests or burrows has facilitated the construction of large nests and so contributed to the evolution of advanced social behaviour.

This argument is based upon two assumptions. Firstly that construction with paper is energetically more efficient than burrowing or mud building thereby allowing a greater direction of energy towards reproduction in females. This would enhance the probability of overlap of generations, which is an important step towards social living . Secondly that paper is structurally more suitable for the building of large nests, thereby facilitating evolution towards advanced eusociality. These assumptions, though plausible, lack detailed evidence to support them. There is an additional complication. Stenogastrinae in spite of having many species which build nests of mascerated vegetation fragments, never the less have a very modest level of social development when compared with the Polistinae and Vespinae, rarely exceeding seven adult females per nest. The Stenogastrinae therefore appear at first glance to contradict the theory that paper has had a significant influence upon vespine social evolution; however, a superficial glance at stenogastrine paper suggests that it is very fragile compared with that of the Polistinae and Vespinae. So the economic advantages of paper nests may have aided in the evolution of social life of this vespoid subfamily but that unsuitability of stenogastrine paper for building large nests may have inhibited further social evolution (Hansell 1984 a, b). The research reported here is a first step in trying to confirm features of the nest building of the Stenogastrinae which support this theory.

## METHODS AND RESULTS

### Tensile strength of materials

Pieces of cell wall 6 - 8mm long by 4 - 5mm wide were cut from a nest with microscissors. The cells chosen were larval cells with no evidence of previously having contained pupae; this was to ensure that their inner walls were free from any larval silk or secretion produced by larvae prior to pupation. The long axis of the piece was parallel to the long axis of the cell. One of the short ends of the piece was then pressed gently into a drop of rapid drying Araldite placed on a rectangle of 35mm camera film which was slightly wider than the piece of nest. The other end of the piece of nest was attached in the same way to another piece of film. The test piece of nest material was inspected microscopically to ensure that it was not cracked nor had any threads of Araldite lying across it. If accepted, the piece was then suspended vertically from a hook passed through a hole in one of the pieces of film. Another hook was then passed through a hole in the lower piece of film. The upper hook hung by a fine wire from a transducer linked to a pen recorder whose deflection measured the tension on the test piece. The lower hook was was connected by a fine wire to a vertically positioned micro-manipulator by means of which increasing tension could be applied until the piece of nest material failed (Fig.1).

Twelve pieces of Eustenogaster calyptodoma nest material from six separate nests and 12 pieces of Polistes exclamans nest material taken from four nests were tested to destruction. The break was always sudden and clean across the material. After destruction of the piece, one of the broken surfaces was examined under a dissecting microscope and its lenth and thickness measured to the nearest $0.01^{-mm}$. From these measurements, the cross sectional area of the piece was calculated. The median breaking stress for E. calyptodoma was 13.05 $gm/mm^2$, and for Polistes exclamans 69.24 $gm/mm^2$, $p = 0.0006$ for two tails in a Mann Whitney U test.

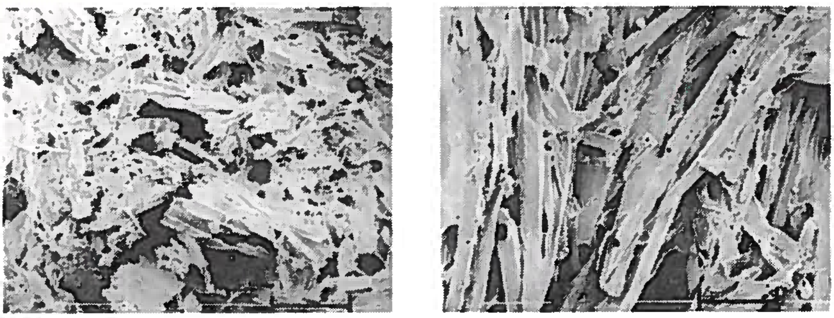
**SEM of nest materials**

Scanning electron micrographs taken from E. calyptodoma and P. exclamans nest material (Fig.1) show that the material of the stenogastrine species is composed of shattered plant cell fragments, possibly from rotted wood, while that of the polistine species is typically composed of largely intact elongate woody stem cells.

**Cell weight plotted against internal cell volume**

The volumes of larval cells of six wasp species was calculated by filling fully developed larval cells with mercury and then calculating the cell volume by dividing by the SG of mercury. The weights of the material required to build a single cell were obtained by cutting out of the nest the same cells as those the volumes of which had been measured. Each cell was then carefully trimmed to ensure that it did not contain any projecting parts that were not wholly its own or shared with a cell neighbour. This material was dried in a desiccator for 24 hours and then weighed. Using larval cells which did not previously contain pupae ensured that no pieces of meconium or cocoon material were present.

Cells from the nests of each of the six following species were removed, dried and weighed: The stenogastrine species, Parischnogaster mellyi (five cells from four nests), Holischnogaster gracilipes (five cells from four nests), Eustenogaster calyptodoma (five cells from four nests) and Liostenogaster flavolineata (six cells from four nests); the polistine wasp Polistes excalmans (five cells from two nests), and the vespine species Dolichovespula sylvestris (five cells from one nest). Fig. 2 shows the weights of these cells plotted against their internal volume.



a b

Figure 1: SEM of the nest material of a) E. calyptodoma and b) P. exclamans at the same magnification. (Each black bar = 100 μm)

Figure 1: Micrographe de matériaux utilisés dans une cellule de nid de a) E.calyptodoma and b) P. exclamans au même grossissement. (chaquee trait noir = 100 μm)

Treating the paper building stenogastrinae (P. mellyi, H. gracilipes and E. calyptodoma) as one group, and the Polistinae and Vespinae as another, an analysis of covariance showed a highly significant difference in the slopes of the lines of the two groups ($F = 20.84$, $P < 0.001$). The points for L. flavolineata cells are not shown in Fig.2 because, being of mud, they are not appropriate to either of the two groups shown, but the mean volume of the six L. flavolineata mud cells was 0.3014 ml (i.e. comparable in size to those of E. calyptodoma) but their mean cell weight was a massive 522.2 mg.

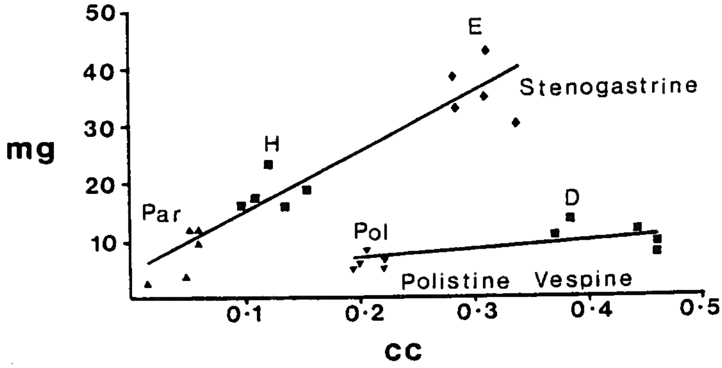



Figure 2: The regression line of the weight of nest cells against their volume for three stenogastrine species, Parischnogaster mellyi (Par), Holischnogaster gracilipes (H) and E. calyptodoma (E), and for two species, one polistine and one vespine, Polistes exclamans (Pol), and Dolichovespula sylvestris (D)

Figure 2: La ligne régressive transcant le poids des cellules de nids comparé à leur volume dans le cas de trois espèces de Stenogastrinae Parischnogaster mellyi (Par), Holischnogaster gracilipes (H) and E. calyptodoma (E), et de deux espèces, l'une Polistinae l'autre Vespinae, Polistes excalmans (Pol) and Dolichovespula sylvestris (D)

## DISCUSSION

The results shown here demonstrate that the nest material of a paper-building stenogastrine wasp species is significantly weaker than that of a polistine species. The basis of this difference in strength can be appreciated from the electron microscope examination of the cells. The material of P. exclamans was intact woody fibres while that of E. calyptodoma was of smaller crumblike fragments of vegetation. Under the light microscope it can be seen that in the cells of P. exclamans, the orientation of the plant fibres is predominantly around the circumference of the cell. This suggests that, had the stress been applied in the direction of difference in breaking stress between material of the two species would have been even greater.

The ability of a polistine species to rasp plant cells from apparently sound woody stems suggests that the mandibles of Polistinae are well developed relative to their overall size when compared with those of Stenogastrinae. Some Stenogastrinae do certainly take very tiny prey items. Metischnogaster (Stenogaster) cilipennis are known to take minute flying insects from the webs of spiders (Pagden, 1962) but generally it is rather difficult to determine the nature of stenogastrine prey, since prey capture is only rarely observed and the arthropod prey are brought to the nest in a finely fragmented form.

Differences in the strength of materials between stenogastrinae and polistinae may also be affected by the amount and quality of the salivary matrix contributed by the wasps as they masticate the material. The nest material of P.exclamans certainly appears to have more matrix in it than that of E.calyptodoma. In some polistinae, the salivary secretion undoubtedly performs the major structural role in parts of the nest. Vecht (1972) describes the nest of Ropalidia opifex as having an envelope which is translucent and "polythene-like", apparently composed entirely or almost entirely of salivary secretion. A very similar type of nest envelope is reported for Pseudochartergus fuscatus (Jeanne, 1976). In Mischocyttarus drewseni the initial comb hangs on a long petiole made of vegetation pulp but, as the comb grows, the petiole is strengthened by the addition of concentric layers of oral secretion alone. Vegetation nests in the stenogastrine genera Eustenogaster, Holischnogaster, Metischnogaster and Parischnogaster on the other hand all seem to have nest material with little matrix in it (personal observations), nor is there a single stenogastrine species capable of building a nest on a petiole constructed of nest material. Many of them are attached to fine supports, but these are always of plant stems, rootlets or, as sometimes in Metischnogaster, a strand of horse hair fungus (Marasmius) (Pagden, 1962).

The advantage to polistine wasps in being able to build their own nest petiole must be in having a greater choice of nest sites while maintaining their protection against predation from ants. The results presented here tend to confirm the theory that the absence of constructed petioles in the nests of Stenogastrinae is a consequence of their inability to produce a strong enough nest material. It is also consistant with the more speculative argument that the Polistinae and Vespinae, having evolved a tough nest material to enable them to construct a petiole, were then in posession of a material suitable for the construction of large nests. They were consequently enabled to progress towards larger colonies with greater social differentiation where selection pressures favoured it. The Stenogastrinae, by contrast, were prevented from further social evolution by the mechanical limitations of their nest material.

The proposal that paper building was an incentive to the evolution of sociality compared with mud building, appears to be contradicted by Liostenogaster flavolineata, which is at least as social as any other known stenogastrine while building a massive comb of mud. A possible explanation for this lies in the type and level of predation to which it is exposed. The chief of Stenogastrinae predators appear to be hornets (Vespula spp.) (Hansell, 1982). One effect of this onslaught by a visually hunting predator has been the evolution of less dectable nest forms. This is seen in the elongate stick designs of Parischnogaster striatula, P. alternata and of the two Metischnogaster species (Pagden, 1962). The nests of Liostenogaster flavolineata are combs with maximal cell wall sharing, apparenty making no concessions to concealment from Vespula, but a three year study on them shows that Vespula leave them completely alone (Samuel unpublished). It seems that the massive nature of the mud structure makes them an uneconomic target for hornet predators. The mud comb is therefore an alternative response to hornet predation; however, the cost is an expensive nest material which is still unsuited to the building of large nests, so progress towards greater sociality is still not possible.

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