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# The Phoretic Copulation of Thynninae in an Ecological and Evolutionary Perspective (Hymenoptera, Tiphiidae)*

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A b s t r a c t : The phoretic copulation and parasitism in thynnine is discussed in an ecological and evolutionary perspective with special regards to the ecosystems of Monte and Puna of Northwest Argentine. The network of some ecological interactions between thynnine, plants, scarabaeids, lamas, condors, and iguanas is documented.

I am interested in problems of functional morphology and its evolutionary and phylogenetic aspects. Some years ago my friends and colleagues the late Manfredo Fritz and Bram Willink from Northwest Argentine invited me to stay with them, and to make excursions together. Twice I had the chance to travel in these regions at different times of the year. I stayed there altogether for more than 5 months. One of my research plans was the study of thynnine.

Within the aculeate Hymenoptera we find some groups (Bethylidae, Mutillidae, Tiphiidae) where males of some species carry their wingless females for different reasons by an almost permanent genital locking on the ground and in the air. This behaviour we call phoretic copulation (Figs.1-3).

Thynnine belong to the large group of tiphiids of the aculeate Hymenoptera (KIMSEY 1992; GENISE & KIMSEY 1993) Their range comprises the Malaysian-Australasian region and South America. Their larvae live as ectoparasites on beetle-larvae, mainly on scarabaeid-larvae (GIVEN 1954; RIDSDILL SMITH 1970). Phoretic copulation is obligatory in thynnine.

In the following I will outline the network of ecological interactions, as it exists in the biotopes of the Monte- and Puna-regions in Argentine, and how the group of thynnine observed, is integrated in them (Fig.7).

At first sight it seems that Puna and Monte are two very different biotopes. But when you get to know them in detail, they resemble each other in many respects: both are a mixture of desert and steppe. The vegetation is rich but seasonal; most of it is visible only for a short time in the year. With regard to Puna (Fig.5), mainly tuft-grasses (Poaceae, *Festuca*) are visible all the year, and that means also available. In the same region the cushion plant Lareta (Umbellifera, *Azorella*) is of special importance for thynnine. With

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regard to Monte (Fig.6), *Baccaris* (Compositae) is an important resource for thynnine (Fig.4).

In these regions the number (individuals, species) not only of small mammals but also of iguanas (*Liolemus*) are remarkably high. On the other hand only two species of tall herbivorous mammals do (or better, did) occur: the guanaco and the vicuña. Today they do not exist anymore in most of these regions. Its ecological role is taken over by wild donkeys or, in some areas, by lamas.

The large mammals feed all round the year on the grasses mentioned above. Their feces are worked into the ground by different groups of beetles as a resource for their larvae, with scarabaeids dominating. The result is an improvement of the soils quality. This in turn promotes the vegetation again. The remarkable variety of seasonal flowering plants is one result.

But the development and distribution of flowering plants itself depends also on pollination. Hymenoptera have the priority in this business. Not only Hymenoptera but also many adult beetles feed on parts of the inflorescence. Scarabaeids dominate again. Other beetle groups feed on plant leaves (curculionids) while others prefer rotting parts of the vegetation (tenebrionids). On the other hand larvae of many beetle-groups feed on the roots of the plants. Furthermore many beetle larvae develop in the feces of the herbivoreous animals mentioned above. In short: beetles work as recycling agents of plants.

Another key connection in the net of ecological and evolutionary relations in the Puna is of course the bodies, the cadavers, of the guanacos and donkeys. First of all condors and foxes are the primary recyclers of these carcasses. In the Monte also pumas and wild dogs play this part. They open the cadaver and tear it to pieces thereby, making it more quickly and easily available to smaller recycling agents: these are again mainly beetles but also ants feeding directly on the carrion and on feces of the carrion-eaters, condor or puma. Beetles and also thynnine themselves are eaten by iguanas and thus recycled themselves. The final phase of these recycling processes, however, is left to the fungi and bacteria, which played a role before all the new recycling agents came into being, and continue to exercise it.

These integrated actions of primary, secondary and ultimate recycling agents provide the constant supply of nutrients, which the plants as producers need. For COLINVAUX (1978) the situation appears to be that "predators ... are to be looked upon as scavengers without the patience to wait for their meat to die". Both, carnivores and herbivores tap the chain of production and are recycling as predators, foragers and parasites (parasitoids). Among them are a great number of parasitic Hymenoptera.

In the "Ecosystem Puna" a great number of parasitic bees (*Nomada*, *Doeringiella*, *Coelioxis* and others) and mutillids belong to this group. They rush at the supply or the larvae of other hymenopterous pollinators. On the other hand thynnine interfere with the succession by attacking the subterraneously living beetle-larvae.

In this view we no longer ask: "of what advantage is the phoretic copulation in thynnine to the species?", but: " what kind of contribution does the phoretic copulation make to the maintenance of their ecosystem?".

First of all the great number of subterranean beetle-larvae are an attractive food, which can be used before the larve develop into adults. The requirement for this use is the capacity to locate the subterranean resource, to find it, and to conquer it. Thynnine solve these problems brilliantly.

Their females are highly specialised for the subterranean life and have no problem in locating their host and paralysing it by specific injections. Parallel to this huntingmethod, a number of morphological transformations have evolved, such as the total reduction of the wings and a partial reduction of the eyes and mouthparts.

From the evolutionary point of view it is absolutely necessary to say that phoretic copulation in thynnine evolved before the reductions and specialisations mentioned above could take place. Scoliids and other tiphiids have a comparable parasitic mode of life and do not show these extreme reductions. In the group of mutillids, also with wingless females, only in a very few examples (*Timulla*) a phoretic copulation evolved, but considerable less extreme than in thynnine. Especially the striking specialisations in thynnine of the mouthparts, the mesosoma and the locking mechanism of the genitalia (EVANS 1969; TORO, MAGUANACELAYA & De La HOZ 1979; TORO & CARVAJAL 1989; TORO & ELORTEGUI 1994) and furthermore the direct transport of the female by its male to food and host, is unique.

To give an explanation for the integration of host (beetle) and parasite or better parsitoide (thynnine) in the ecosystem, one has to consider this: The flowering-season of plants in the observed biotopes, lasts 3 months at most, determined by the time of rain and temperature. Adult thynnine live about 4 weeks. The development of their larvae takes about 11 months. In contrast the beetle-larva needs about 2 years for its development.

Beetles indirectly promote the growth of plants by improving the soil, but also recycle these plants in different ways. On the other hand thynnine increase the number of plants by pollination but recycle the beetles in their larval phase.

The differences in the duration, and mode of life in beetles and thynnine, permit the adult thynnine always to maintain the successful grip on their host in spite of their relatively short life. The lifecycle of thynnine is regulated and correlated by the resources, offered by the flowers and of course by the beetle-larvae. The subterranean phase of the lifecycle, both of thynnine and of beetles, is less dependent on seasons.

The care of the male for his female in the case of extreme phoresy makes it possible for thynnine even within a short adult phase to get a sufficient radius of action for providing food combined with host-search and oviposition. Beyond this the transport serves for a wide geographical distribution.

The biological efficiency and with that also the effectiveness of phoretic copulation in thynnine for the ecosystem must be seen at first in the support of parental care. But this support helps already the mother and not only the brood. In the animal kingdom parental care is usually combined with a reduction of the number of eggs (for example fish and amphibians). Fewer eggs means less resource-consumption to produce eggs. The egg-number in the thynnine observed was 8 at maximum! In contrast there are many parasitic insects without phoretic copulation, producing thousands of eggs to enable their species to survive. The special form of reproduction in thynnine, phoresy and parasitism, is obviously so efficient, that this minute egg-number ensures the survival of the group. With regard to the ecosystem we can say the recycling of the beetle-larvae in an early stage very quickly provides new energy to the system and the low rate of egg-production takes less energy from the system, than hundreds of eggs would require.

On the other hand permanence of phoretic copulation saves further energy. A repeated, complicated search for the partner generally does not take place.

With regard to the special genetics in Hymenoptera and the kinship selection (W.D. HAMILTON 1964, E.O. WILSON 1971, R. DAWKINS 1976) one can interprete the phoretic copulation as a possibility for the male to pass on his genetic material, and only his, without competition. Mating with different partners seems to be rare.

As a resume of my studies I can say, that the biological and ecological success of phoretic copulation in thynnine combined with its effect on the ecosystem, in this case Puna and Monte, is documented by the low rate of egg-production.

### Species observed

*Anodontyra andina* (BRÉTHES), *Brethynnus stygius* (TURNER), *Telephoromya rufipes* (GUÉRIN), *(Eucyrtothynnus catamarcensis* (BRÉTHES), *Eucyrtothynnus avidus* (TURNER), and some species more with uncertain taxonomical range.

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## Zusammenfassung

Die phoretische Kopula der Thynniden aus ökologischer und evolutionsbiologischer Sicht (Hymenoptera, Tiphiidae). - Innerhalb der Aculeata gibt es Gruppen (Bethylidae, Mutillidae, Tiphiidae) bei denen die Männchen einiger Arten ihre flügellosen Weibchen mit Hilfe einer komplizieren Genitalverzahnung über längere Zeit mit sich herumtragen, sowohl am Boden als in der Luft. Dieses Verhalten nennt man phoretische Kopula. Die Thynniden gehören zu den Tiphiidae (Anthoboscinae, Brachycistidinae, Tiphiinae, Methochinae, Myzininae, Diamminae, Thynninae). Das Vorkommen ihrer etwa 300 Arten beschränkt sich auf die malaisch-australische Region und Südamerika. Ihre Larven entwickeln sich ektoparasitisch an Scarabaeiden-Larven. Bei ihnen ist die phoretische Kopula obligatorisch. Das Untersuchungsgebiet befand sich in den argentinischen Wüsten (Monte)- und Hochlagen (Puna)- Regionen. Dort leben die Thynniden mit ihrem extremen Parasitismus + Phoresie in einem Netz ökologischer Verbindungen und gegenseitiger Verknüpfungen. Produzenten (Pflanzen) und Konsumenten (Tiere, Pilze, Bakterien) bilden eine Abfolge unterschiedlicher Recycling-Prozesse. Aus ökologischer Sicht heißt die Frage nicht länger: Was nützt die phoretische Kopula den Thynniden? sondern: Was trägt diese außergewöhnliche Paarbindung zur Aufrechterhaltung und Unterstützung ihres eigenen Ökosystems bei? Der biologische, energetische und ökologische Erfolg der phoretischen Kopula bei den Thynniden im Hinblick auf die Effizienz für ihr Ökosystem liegt offensichtlich in ihrer enorm geringen Eiproduktion von maximal nur acht.

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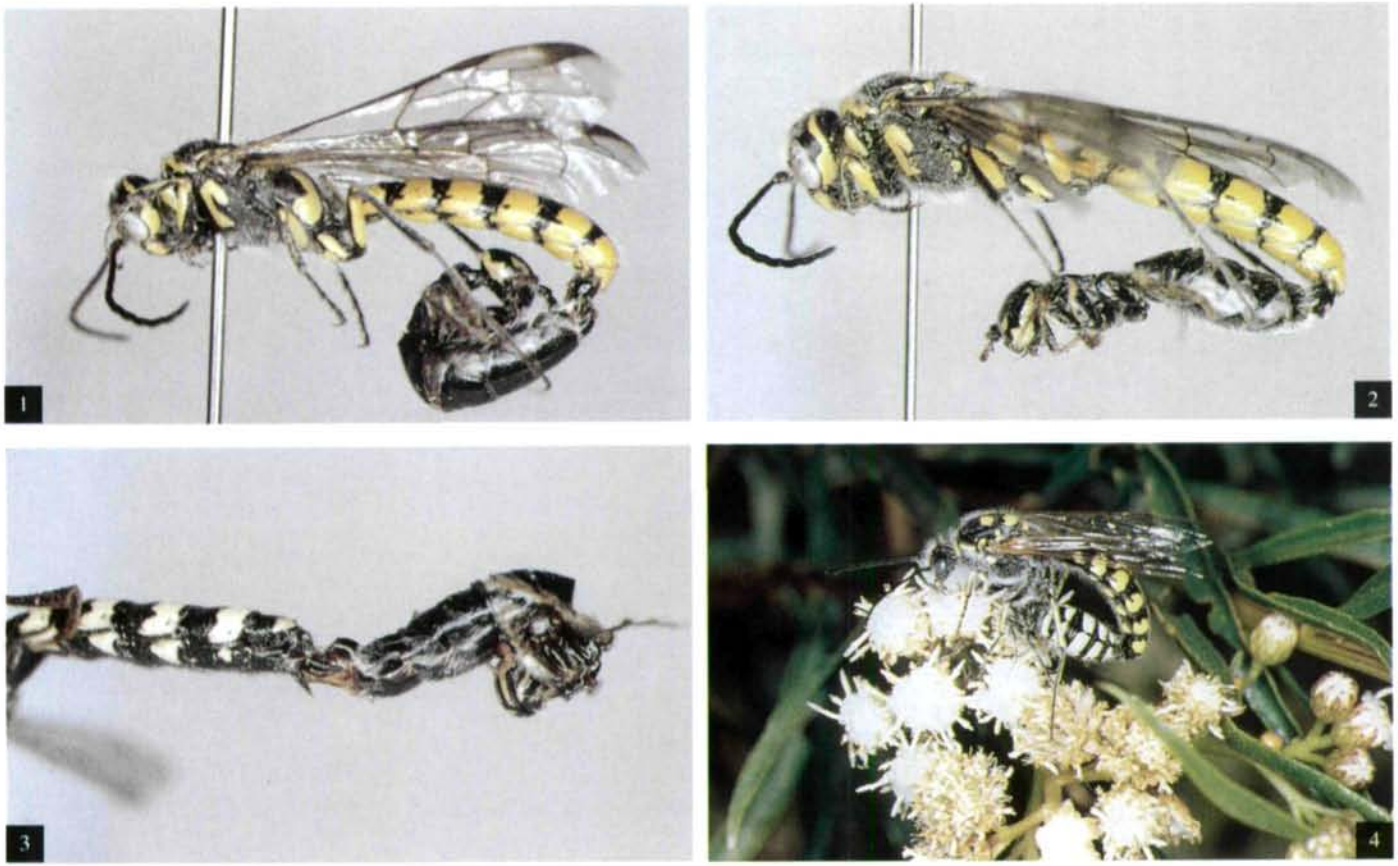


**Figs. 1-3**: Couple of *Telephoromya rhombica* (BRÉTHES) showing different positions in phoretic copulation. **Fig.4:** Couple of *Anodontyra andina* (BRÉTHES) feeding on *Baccharis*.

**Fig. 5:** Puna with *Festuca*, *Azorella* and lamas. **Fig. 6:** *Monte region with flowering Amaryllis.*

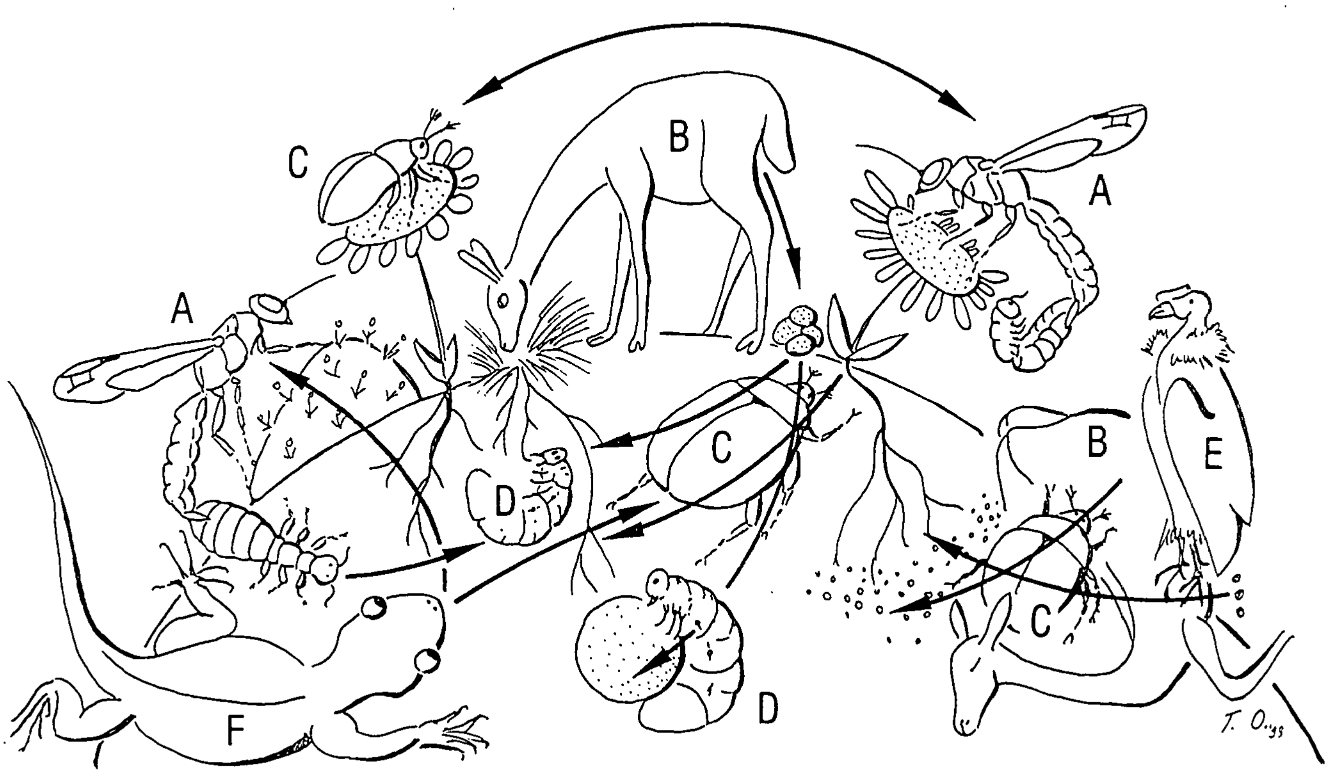


**Fig. 7**: Network of some ecological interactions in the Puna and how thynnine are integrated in it: A. Thynnine as pollinator and searching for hosts, B. Lamas as recycler of plants and producer of feces and cadaver, C. Scarabaeids as pollinator and recycler of feces and cadaver, D. Scarabaeid larvas as recycler of plants and feces. E. Condors as recycler of cadaver and procucer of feces, F. Iguanas as recycler of scarabaeids and thynnine.