17. 26. ONTOGENY IN THE TYDEOIDEA (EREYNETIDAE, TYDEIDAE AND IOLINIDAE)

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INTRODUCTION

The number of stases in the Tydeidae is fixed at six: a calyptostasic prelarva (first described by Kuznetzov 1980) followed by five "normal" stases: the larva, the proto-, deutero- and tritonymphs and the adult. The ontogeny is similar in Iolinidae (André 1984) and in the ereynetid subfamily Ereynetinae (Fain 1972).

Like the Ereynetinae, the Lawrencarinae are a subfamily of Ereynetidae, the members of which live in the nasal cavities of frogs and toads. The subfamily includes only three genera: *Lawrencarus, Batracarus* and *Xenopacarus*. Currently, only four active stases are recognized: a six-legged larva, two immature eight-legged nymphs usually called proto- and deuteronymph, and the adult (Fain 1962, 1963, 1972).

The third ereynetin subfamily, the Speleognathinae, is specialized in the colonization of nasal cavities in birds and mammals. Apart from adaptive morphological characters related to parasitism, the subfamily is remarkable for the presence of only two active stases: the larva and the adult. This peculiar ontogeny has been commented upon by Matsuda (1979) who writes that "no clearly defined nymphal stages intervene" and states that "in some parasitic ereynetids acceleration of development occurs by *omission* of some developmental stages" (italics are ours). Such a statement is a rough misinterpretation of the observations made by Fain (1963, 1972), to whom Matsuda refers. Actually, the three nymphs are present but reduced to calyptostases hidden within the molting larva. Indeed, Fain (1963, 1972) was able to distinguish in the forepart of the larval exuviae three small "tubes" which he interpreted as the pharynxes of the three nymphs.

ONTOGENY IN LAWRENCARINAE

The study of one of the slides from the type-series of *Batracarus hylaranae* has resulted in an unexpected find. The slide mount of the deuteronymph (correctly labelled "deuto-

nymphe en mue") not only contained a pupating deuteronymph but also, inside, a fully developed tritonymph. The chaetotaxy of the deuteronymph is quite different from that of the tritonymph it contains, and also from that of the protonymph mounted on another slide. The leg chaetotactic formulae of *Batracarus hylaranae* are:

Adult	I(12-3-2-2-0)	II(9-2-3-1-0)	III(8-1-3-1-0)	IV(8-1-2-0-0)
Tritonymph	I(12-3-2-2-0)	II(8-2-3-1-0)	III(7-1-3-1-0)	IV(7-1-1-0-0)
Deuteronymph	I(10-3-2-2-0)	II(8-1-3-1-0)	III(7-1-3-1-0)	IV(7-1-1-0-0)
Protonymph	I(10-3-2-2-0)	II(6-1-3-1-0)	III(5-1-3-1-0)	IV(5-0-0-0-0)
Larva	I(10-3-2-2-0)	II(6-1-3-1-0)	III(5-1-3-1-0)	

while the genital chaetotaxy is: Ad(0-0-3), TN (0-2), DN(0-1) and PN(0-0). The number of genital discs is one pair in the protonymph and two pairs in the following nymphs. Genital discs are double as in other Ereynetidae (André 1991).

ONTOGENETIC TRAJECTORIES

From the study of chaetotaxy, ontogenetic trajectories (sensu André 1988, 1989) of free-living species may be outlined and compared to those of parasitic species. Fig. 1 shows the ontogenetic trajectories of two groups of Tydeoidea: (1) the Triophtydeinae and Meyerellinae which are free-living Tydeidae, and (2) the species belonging to the subgenus *Boydaia* (Speleognathinae) which are parasites living in the nasal cavities of birds. To each group corresponds a bundle of trajectories with a particular shape.

It must be emphasized that, within each bundle, the distance between successive stases of the same species is often greater that the distance between the same stase of two species. In other words, the interspecific similarity within each bundle is higher than the similarity between stases of the same species.

Two evolutionary mechanisms are involved in the evolution of ontogeny in Tydeoidea. First, the evolution within each bundle of trajectories implies small changes, such as a seta which appears earlier or later in the ontogeny. This corresponds to heterochrony. Second, the evolution from one bundle to the other. This implies drastic changes of shape and is related to the occurrence of multiple calyptostases. This evolutionary mechanism corresponds to heterostasy.

CONCLUSIONS

The occurrence of two evolutionary mechanisms leads to the distinction of two bundles of ontogenetic trajectories. One bundle describes the ontogeny of Speleognathinae, the other outlines the ontogeny of all other tydeoid subfamilies. Based on such a sharp distinction, the family Speleognathidae Womersley, 1936, which was lowered in hierarchic rank and considered a part of Ereynetidae by Fain (1957), might be restored. However, the subfamilial status of Speleognathinae is maintained, at least provisionally, pending a revision of the superfamily.
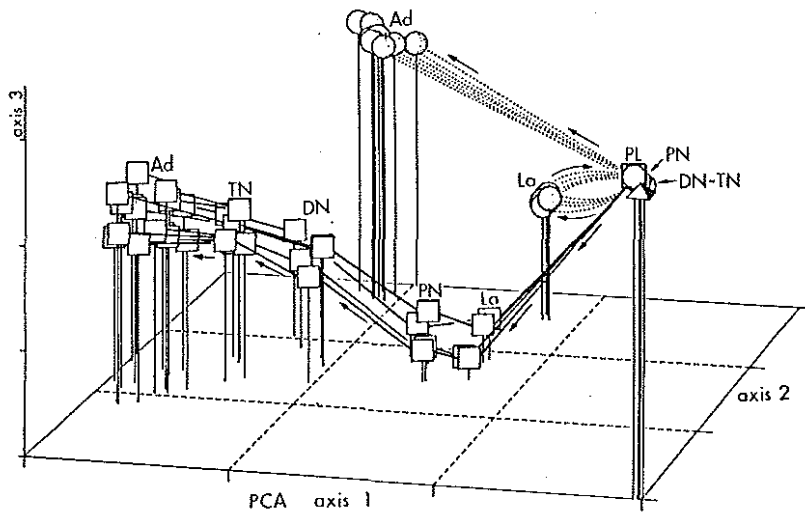
Figure 1. Three-dimensional diagram of the ontogenetic trajectories of free-living (Triophtydeinae and Meyerellinae, 8 species, squares) vs parasitic (subgenus *Boydaia*, 9 species, circles) mites. The diagram results from a Principal Coordinate Analysis using the Euclidian distance and applied onto the original 68-dimensional character space. Characters involved in the analysis are the chaetotaxy (122 setae, total, on each side), the solenidiotaxy (5 solenidia), the poroidotaxy (4 lyrifissures), the eyes (lens or pigments) and the genital acetabula and urstigma (4 elements). All characters are coded as binary data (presence/absence). The pyramid represents the starting point (zero value in all dimensions) of the trajectories, the successive stases of the postembryonic development are the prelarva (PL), larva (La), proto- (PN), deutero- (DN), tritonymph (TN) and adult (Ad).

From a coevolutionary point of view, the most complex ontogenies are observed in the most advanced hosts. In Tydeoidea, heterostasy is obviously related to the colonization of warm-blooded animals. In contrast, free-living forms and species parasitic on cold-blooded animals have kept the fundamental ontogeny.

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REFERENCES

André H.M., 1984. In: Griffiths D.A., Bowman C.E. (Eds.), *Acarology VI*. E. Horwood Ltd., Chichester, Vol. 1, pp. 180-185.

André H.M., 1988. In: Humphries C.J. (Ed.), *Ontogeny and Systematics.* Columbia University Press, New-York, pp. 137-187.

André H.M., 1989. In: André H.M., Lions J.-Cl. (Eds.), *L'ontogenèse et le Concept de Stase chez les Arthropodes/Ontogeny and the Concept of Stase in Arthropods.* AGAR Publishers, Wavre, pp. 83-90.

André H.M., 1991. In: Dusbábek F., Bukva V. (Eds.), *Modern Acarology.* SPB Academic Publishing bv, The Hague and Academia, Prague, Vol. 2, pp. 293-296.

Fain A., 1957. *Revue Bot. Zool. afr.* 55: 249-252.

Fain A., 1962. *Bull. Inst. r. Sci. nat. Belg.* 38 (25): 1-69.

Fain A., 1963. *Bull. Inst. r. Sci. nat. Belg.* 39 (9): 1-80.

Fain A., 1972. *Acarologia* 13: 607-614.

Kuznetzov N.N., 1980. *Zool. Zh.* 59: 1018-1024 (in Russian).

Matsuda R., 1979. In: Gupta A.P. (Ed.), *Arthropod Phylogeny.* Van Nostrand, New York, pp. 137-256.