

Niels Peder Kristensen - Neues Ehrenmitglied der GfBS

Laudatio

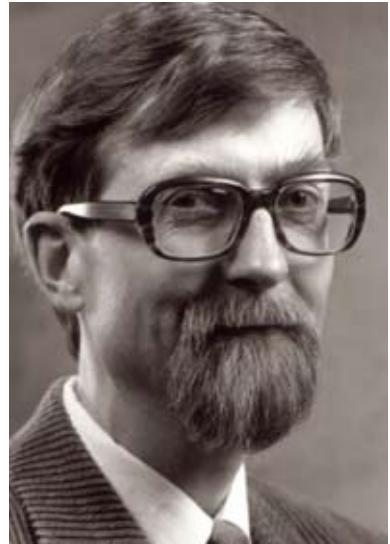
Dear Professor Kristensen, Dear Niels, Dear Members of the Festive Assembly,

Remember Vienna, the Museum of Natural History? On the twenty-first of February, during the symposium of the Gesellschaft für Biologische Systematik 2007, Professor Niels Peder Kristensen was awarded Honorary Membership to the Gesellschaft für Biologische Systematik. It is now a great honour and privilege for me to present a laudation for Niels Kristensen.

As of today, the Gesellschaft für Biologische Systematik now celebrates five Honorary Members: Erich Thenius, Ernst Mayr, Peter Ax, Friedrich Ehrendorfer and Niels Peder Kristensen.

Niels is the youngest in this illustrious company to be bestowed the honour. It's in the nature of things that a laudation for an outstanding scientist normally runs like a condensed carousel of facts, figures and achievements, but nowadays this information can be mostly found in the internet. I will not assume that task today: I would like to portray to you a picture of Niels Peder Kristensen as a human being, a scientist, a teacher, a catalyst.

Niels is a happy scientist, indeed – in the broadest sense of the meaning, he radiates happiness – and this is a gift to all of us. Look at him in the royal portrait – and you will agree. It was, in fact, taken by a Royal photographer on the occasion of his election to membership in the Royal Danish Academy of Sciences and Letters in 1988.



"The Royal Photograph", following Niels' election to the Royal Danish Academy of Sciences and Letters, 1988 | Foto: Rigmor Mydtskov

Niels was very fortunate to be born into a special family and certainly had a protective and supportive childhood. His birth evidently was a magic moment ("Sternstunde") for entomology and systematics. His academic pathway was accompanied by the background of a wonderful family. The photograph showing Niels in New Zealand together with his elder daughter, Mette, assisting him in removing grass seeds from his net is touching and revealing of the tender network keeping the family together.

His academic career rose like a meteorite and was the reward for long and extreme engagement in research and teaching, at home and abroad. This was no reason for Niels to become presumptuous and arrogant. On the contrary – he has always gratefully acknowledged the influences of outstanding personalities, e.g. Søren Ludvig Tuxen, well-known to entomologists, and from abroad Howard Everest Hinton from Bristol should be mentioned. Niels also profited from the

teachings of Professor J. Chaudonneret at the founding site of that unsurpassed 'Dijon school' of insect morphology. In no time at all, Niels had digested Hermann Weber's famous "Insect morphology" and acquainted himself with the philosophy of Willi Hennig in German – a courageous endeavor, indeed. Niels also spent a successful and profitable time at the Victoria University of Wellington and at the Division of Entomology in Canberra. He is grateful for the collaboration with colleagues at home, in the Museum, especially with Nils Møller Andersen, who passed away far too soon, and the enthusiastic Henrik Enghoff. With these and others he made Copenhagen a citadel of entomology. He is proud of his student, Ebbe Schmidt Nielson, who transported the Copenhagen school of entomology to the Australian continent, when he became director of the "Australian National Insect Collection". His unexpected death was a great loss for Niels and a setback for entomology.

The illustration of the "evolution of a director" looks like a constructed scenario of a career, in reality it entails the burden of responsibility, which Niels took upon

his shoulders, sometimes suffering a lot. From Niels' numerous publications I want to emphasize some of special relevance for entomology: The "Eriocraniid Anatomy" of 1968 is a magnum opus, though it is an early work and certainly one of his most significant studies. The short systematic entomology textbook of 1970, also an early work, made a concrete contribution to instilling Hennigian thought to Danish and other Nordic biology students. The "review of hexapod phylogeny" of 1975 – is like a pocket bible for entomologists, a small booklet, but a strong rope to keep one's hold, and then people started to simply say: "... after Kristensen '75." "Studies on the morphology and systematics of primitive Lepidoptera" from 1984, his habilitation thesis, is another magnum opus with a delicious aesthetic component. The 1996 joint paper with the late Ebbe Schmidt Nielsen ...is one of Niels' most significant empirical contributions and a book of friendship. In the "Handbook of Zoology" Niels Kristensen erected a golden monument to Lepidoptera in two tremendous volumes. And finally – and just recently – there is the "Lepidoptera phylogeny and systematics..." – another milestone in entomology.

Niels Kristensen has accumulated numerous honours within his lifetime, the collection is impressive.

Evidently he has managed his personal career quite well. He has ever right to feel a sense of pride for his achievements.



Niels P. Kristensen in the field with daughter Mette. Waitakere Range close to Auckland, 1983 | Foto: Hanne Kristensen

We might ask: Besides all these achievements, what else has he left for entomology and what are his contributions to systematics?

- Although he is a scientific cosmopolitan, he remained loyal to his museum and contributed to make it a center of scientific education. Whoever claimed to come from Copenhagen, was greeted with open arms.
- Younger generations studied in his orbit. He always had faith in and encouragement for his younger colleagues. And the effort has been fruitful.
- For many scientists, he is THE outstanding lepidopterologist of present times – in reality, he is THE personalized phylogeny of the Hexapoda with profundity and vision, bridging classical aspects and modern spirits.
- Niels holds the keys to morphology in his hands – to all of its facets, classical and modern, and he intercommunicates with the molecular scene.
- With scientists like Niels Kristensen the crisis of morphology will be overcome; with scientists like Niels Kristensen the exhibitionism of the biodiversity cult will be clothed with dignity.

Niels Kristensen is deeply rooted in Copenhagen, yet he is omnipresent, he is an extremely serious scientist, yet he finds time to play with his grandchildren – a paradox? No, Niels Kristensen is a cybernetic catalyst ever expanding in knowledge and wisdom by giving and giving and giving...

Thank you, Niels!

Ulrike Aspöck, Wien ■

Unser neues Ehrenmitglied Niels Peder Kristensen:

Early Lepidoptera evolution

As we all know, close to one-fourth of all described organisms are Coleoptera, hence Haldane told us that the Creator must have had „an inordinate fondness for beetles“. With about 160.000 currently described species the Lepidoptera likely come next in the Animal Kingdom. Both counts may actually be taxonomic artefacts, primarily reflecting taxonomists' fondness: the Diptera may soon be overtaking the Lepidoptera in terms of described species, and as I have stated elsewhere, extrapolating from the situation in the best investigated part of the world (namely NW Europe) one may well expect that the Hymenoptera (indeed just the Apocrita) will turn out to be a group for which the Creator had an even greater fondness than for Haldane's beetles. In any case, however, the Lepidoptera are one of the most species-rich groups of extant organisms, and given this species richness they may appear remarkably uniform: About 98-99% of the currently described extant Lepidoptera species (and probably >> 90% of those actually present ,out there') belong to the unquestionably monophyletic Ditrysia whose members are overall homogeneous in structure and life-style. Surely

ditrysiian Lepidoptera superficially look very diverse: they may be large and small, narrow-winged and broad-winged, conspicuously or cryptically coloured, slender-bodied or bulky; similarly their larvae may be smooth, or hairy (even coverage or in tussocks), or set with prominent humps or warts. However, structurally they are basically very similar, sharing a substantial apomorphy complex corresponding to widespread notions of ,the typical lepidopteran'. Also in life-style the Lepidoptera are homogeneous to a degree unmatched by the other mega-diverse insect lineages: in the vast majority the larvae are herbivorous, many fewer are detritivores/fungivores (the distinction between these life-styles and herbivory is obviously sometimes blurred), while predatory/parasitoid caterpillars are few and far between; adults mostly feed on nectar, plant sap, honey dew,

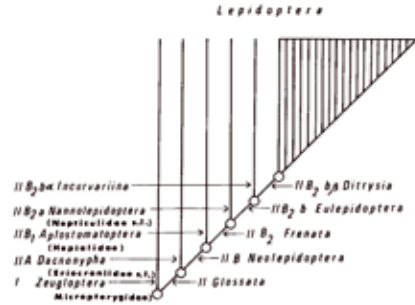


Fig. 1 W. Hennig's Lepidoptera cladogram | From Phylogenetic Systematics, Illinois University Press 1966

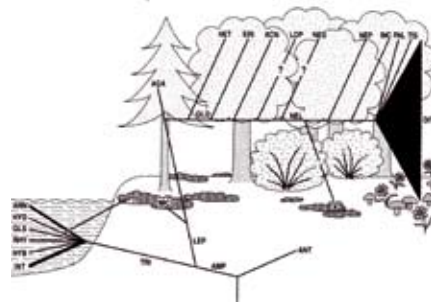


Fig. 2 Outline scenario of basal Amphiesmenopterian evolution | More details in Kristensen 1997. Mémoires du Muséum national d' Histoire naturelle 173, 253-271

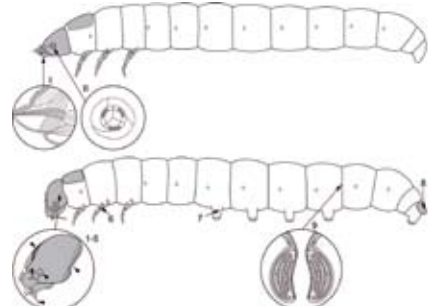


Fig. 3 Diagrams of hypothesized larval ground plan of the Lepidoptera (above) and Ditrysia (below). Numbers refers to selected apomorphies that have evolved within the lepidopteran crown-group | More information in Kristensen et al., Zootaxa 1668, 2007

decomposing organic matter - or do not feed at all. In contrast, the remaining tiny fraction of the order comprises several species-poor lineages which bridge the considerable structural gap between the lepidopteran ground plan - ancestral moths were really overall very generalized endopterygote insects - and the ditrysian ground plan. It appears possible to arrange several of these lineages into a sequence according to their acquisition of successively more elements of the above-mentioned apomorphy complex, i.e., it is possible to make inferences about the sequence in which the individual apomorphies were acquired during early lepidopteran evolution. In Hennig's 1966 milestone *Phylogenetic Systematics* (as in his - evidently less widely read - 1953 German-language benchmark article on insect phylogenetic systematics) he used exactly the basal diversification mode of the Lepidoptera (Fig. 1) to illustrate what had earlier been called 'additive typogenesis'. Hennig predicted that similar modes would prove to be widespread in phylogenetically well researched groups of organisms - hence the colloquial expression 'Henningian comb' for the pectinate topology obvious in many published cladograms.

It has been my privilege to participate in the re-examination and expanding of the factual basis for inferences about the phylogenetic systematics and historical ecology of non-ditrysian Lepidoptera in an era when exciting discoveries of previously unknown lineages were made, and ample material was procured of key taxa previously known only from few specimens unsuited for in-depth examination. Overall Hennig's interpretations have stood the test of time, but it will be noted that while in his cladogram the Ditrysia arose in the sixth splitting event recognizable among extant high-rank lepidopteran taxa, now at the very least ten splitting events are recognizable 'below' the one in which ditrysians originated. Evidently the newly discovered/re-examined taxa have enhanced 'resolution' of the apomorphy-acquisition sequence - but, unsurprisingly, have also disclosed previously unknown character conflicts which necessitate ad hoc postulates

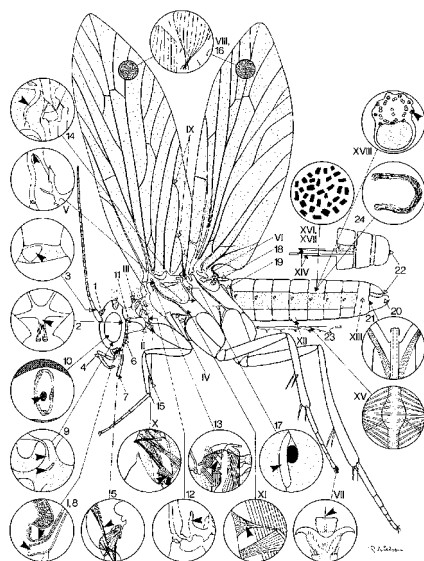


Fig. 4 Diagram of hypothesized adult ground plan of the Lepidoptera. Roman numerals refer to putative synapomorphies of Trichoptera and Lepidoptera, hence autapomorphies of superorder Amphiesmenoptera. Arabic numerals refer to putative lepidopteran groundplan autapomorphies | More information in Kristensen et al., *Zootaxa* 1668, 2007

of parallelism or character reversal. It may also be noted that relationships within the Ditrysia remain largely unresolved, and it must even be emphasized that all indications of ditrysian relationships above the superfamily-level must still be considered very tentative. It is expected, that much more - and better supported - resolution will be forthcoming from the ongoing LepTree project (one of the NSF-supported ATOL projects).



Representatives of the two non-glossatan moth lineages that were described in the second half of the 20th century. top: an agathiphagid: *Agathiphaga vitiensis* Dumbleton, 1952; wing span 27 mm. bottom: a heterobathmiid: *Heterobathmia pseuderocrania* Kristensen & Nielsen, 1979; wing span 10 mm. Paintings by Roland Johansson | From Kristensen et al., *Zootaxa* 1668, 2007

Findings from the last decades have also added evidence for the now robustly supported sister-group relationship between Lepidoptera and Trichoptera (collectively: superorder Amphiesmenoptera) - a relationship which now stands as the best supported sister-group relationship between any insect orders (or, on a more pessimistic note: the only order-level sister-group relationship

the closed tracheal system, and this character state is found also in the few amphibious or truly terrestrial caddisfly larvae, indicating that these represent reversals from a genuinely aquatic life-style.

Altogether about twenty structural synapomorphies of adult Trichoptera and Lepidoptera are now recognized; many of these are indicated in Fig. 4, which shows a hypothetical ancestral lepidopteran. Of special note is a long-recognized trait, viz., the 'double-Y-configuration' of the forewing anal veins (seemingly anastomoses of the third with the second vein, and the second with the first) because this is one of the very few characters that potentially permits identification of stem-lineage

within the Insecta that may be considered established beyond doubt). According to the now emerging ecological scenario (Fig. 2) of early evolution of mecopterid Endopterygota, the larvae of the amphiesmenopteran stem-lineage were what can be broadly described as 'soil' animals, thriving in overall moist habitats; a similar larval life-style can be ascribed to the putative amphiesmenopteran sister-taxon Antliophora comprising the Diptera, Nannomecoptera, Neomecoptera, Mecoptera s.str. (=Pistillifera) and Siphonaptera. From this habitat type transition to the fresh water inhabited by caddisfly larvae was but a small step. One of the most striking larval groundplan autapomorphies of the Trichoptera is

amphiesmenopterans in the fossil record; it may here be noted, that no wing characters are yet known which permit reliable distinguishing between crown-group Trichoptera and Lepidoptera. Also indicated in the figure are the ca 25 currently recognized autapomorphies of the (adult) lepidopteran ground plan. One known to all biologists is, of course, the dense wing-scale vestiture, which not only confers upon the Lepidoptera the multitude of colour patterns, but also, because of its near-non-wettability is the likely principal reason why the fossil record of the Lepidoptera is so much poorer than that of the other mega-diverse insect orders. In contrast to the situation with the adults only very few autapomorphies have so far been ascribed to the larval ground plans (Fig. 3) of, respectively, the Amphiesmenoptera and Lepidoptera; none are known for the pupae. Comparing the hypothesized ground plan of the order Lepidoptera with that of the major subordinal lineage Ditrysia (shown for the larva in Fig. 3) immediately discloses the magnitude of the above-mentioned structural gap between the two.

There are two current competing theories about the primary split recognizable among extant Lepidoptera: either it is between the family Micropterigidae and the rest, or it is between the family Agathiphagidae and the rest. It is the former model which is most generally accepted and which is shown in Figure 2. This is because specializations shared between micropterigids and all other non-agathiphagid Lepidoptera are arguably consistently simple regressive features, while specializations shared between agathiphagids and all other non-micropterigid Lepidoptera include some noteworthy neoformations; also, the so far limited available molecular evidence bearing on the issue does support the Micropterigidae/other-Lepidoptera-dichotomy. The number of known micropterigid species now exceeds 200 (many are still unnamed in collections) and the family occurs in all zoogeographical regions; most are recorded from temperate and subtropical regions (on both Northern and Southern Hemispheres), but the still remarkably sparse representation from the

tropics may at least to some extent reflect inadequate collecting. Micropterigids have long been known to be characterized by a many plesiomorphies, but their monophyly does seem strongly supported by autapomorphic details in their adult anatomy and particularly by the highly specialized larval cuticular structure (with chambered fluid-filled exocuticle, each chamber apparently produced by one epidermal cell) which seems without counterparts among other arthropods. Some members of the family, including our familiar *W. Palaeartic Micropterox* feed as adults on angiosperm pollen (which are ground up by the toothed mandibles, working in a spinose cavity - the 'tritulating basket' of classic authors - on the anterior surface of the hypopharynx) while their larvae feed on a various organic matters including fungus hyphae and decomposing angiosperms. In contrast, most known larvae of other micropterigid genera feed on foliose liverworts, and while many adults are pollen feeders like *Micropterox* some are known to feed on fern spores. This micropterigid non-dependence on flowering plants throughout the life cycle may indeed represent a direct heritage

from the ancestral lepidopteran life-style. According to the phylogenetic model here preferred, then, the two next known splitting events of the main lepidopteran stem lineage gave rise to the families Agathiphagidae followed by Heterobathmiidae. Both were unknown to Hennig by the time of his early writings on lepidopteran evolution. Agathiphagids were described (in the Micropterigidae) in 1952 on the basis of very inadequate material and remained very little known until well preserved material was procured through a breeding programme in the Natural History Museum (London). The family comprises but two known, overall very similar, species occurring in the SW Pacific (Queensland, New Caledonia, Fiji, Solomon Islands, New Hebrides) and their larvae are gymnosperm-feeders, mining in seeds of kauri pines (*Agathis*).

It is uncertain, whether their nocturnal adults feed at all; while their mouthparts are overall generalized, the mandibles are devoid of teeth, and the guts of the few examined specimens caught in nature is empty. It is in the sister-lineage of the Agathiphagidae that lepidopteran dependence on angiosperms likely first evolved. The initial

splitting event identifiable in this lineage gave rise to the temperate S. American Heterobathmiidae on one hand, and the stem-lineage of the 'tongue' moths, the Glossata, on the other. Heterobathmiids were described as late as in 1979, and like agathiphagids they were initially (by the late Ebbe Nielsen and myself) placed in the Micropterigidae, particularly because of striking similarities in the biting mouth apparatus of the adult moths. They were only assigned to their current position after their overall very Glossata-like larvae became known in 1981, and the said specializations have since then been ascribed to the lepidopteran ground plan (and hence are symplesiomorphies of the two taxa in question). Heterobathmiid larvae are leaf miners in deciduous *Nothofagus*, while the adults are believed to feed on the pollen of the same trees. In part, the life-style of these moths is strikingly similar to that of the most basal glossatan family, viz., the Eriocraniidae, which are exclusively N. Hemisphere and mainly temperate-zone insects. Like in heterobathmiids the adult moths in eriocraniids are active in early spring, the larvae are leaf miners in trees belonging to Fagales (mostly birches and oaks) and spin cocoons in the soil for pupation. Even the forewing patterns of most of the adult moths in the two families are remarkably similar: iridescent purplish ground colour with + extensive suffusion of silvery scales and a distinctive silvery tornal spot. Did members of the stem lineage of Heterobathmiidae + Glossata share most or all of these characteristics?

The monophyly of the 'tongue-moths', Glossata, appears very strongly supported by morphology, and conflicting molecular evidence has been considered spurious (due to rate heterogeneity of basal glossatan lineages). Principal among the glossatan autapomorphies are, of course, the remarkable 'apomorphy syndrome' associated with the development of the coilable tongue in the adult; it is formed by the elongated galeae, which are medially concave and linked to each other, enclosing a food canal between them. The mandibles have lost well-formed articulations with the

head-capsule and are non-functional (with muscles becoming histolysed) in the post-pharate stage, i.e., after they have served to move the mandibles of the pupal skin during emergence from the cocoon and the pupal skin has been shed. Hence, with respect to adult feeding biology the origin of the Glossata is a point-of-no-returns in lepidopteran evolution: all descendants of these early glossatans can feed on fluid substances exclusively (including solids that are dissolvable in saliva). The tongue is extended by haemolymph pressure, and in the most basal glossatan lineages recoiling is entirely due to its elasticity. An intrinsic musculature which aids tongue recoiling is evolved only in a later splitting event within the Glossata, and the complex arrangement of numerous short intrinsic muscle fibres evolved later still. It is commonplace to associate the coilable lepidopteran tongue with the insects' feeding on nectar in concealed nectaries, but it must be emphasized that none of the extant members of the glossatan families that arose in the first several splitting events are known to be flower visitors. Eriocraniid moths will suck from water droplets (also on sap seeping from injured leaf tissue), and it is possible that water uptake from concealed crevices was indeed a principal function of the tongues of early glossatans. It should be emphasized that glossatan monophyly is supported also by structural traits unrelated to the adult's moth apparatus. One is the development, on the apex of the larval prelabio-hypopharyngeal lobe, of a passively movable appendage which bears the silk gland orifice (it is to this formation the term 'spinneret' is applied in lepidopterists' writings). As with the adult's tongue it might be a priori expected that the origin of a neof ormation of this kind would be accompanied by remarkable behavioural changes, but this does not seem to be the case: basal glossatan larvae like those of non-glossatans apparently only use the silk for cocoon-construction before pupation. Use of silken fabrics in larval pre-pupation behaviour seems to have originated only in the stem-lineage of the Neolepidoptera (Fig. 2). In one of the basal neolepidopteran sister-lineages, the Exoporia, many larvae

have a 'soil-animal' life-style reminiscent of that of microp terigids. This is most likely a secondary trait, like all other cases of non-angiosperm-dependence of descendants of the common ancestor of Heterobathmiidae+Glossata.

Time has allowed me only to outline some of the earliest events in lepidopteran evolution as they can be currently reconstructed, but I hope I have managed to get the message across that Hennig's favourite case story of 'additive typogenesis' continues to be a case story of broad general interest in evolutionary biology. Thank you for your attention - and my sincerest thanks to the Gesellschaft für Biologische Systematik for the immense honour that has been conferred upon me.

Niels P. Kristensen,
Copenhagen ■